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Endangered and Threatened Wildlife and Plants; Removing the Greater Yellowstone Ecosystem Population of Grizzly Bears From the Federal List of Endangered and Threatened Wildlife

Comment On: FWS-R6-ES-2016-0042-0001

Endangered and Threatened Wildlife and Plants: Removing the Greater Yellowstone Ecosystem Population of Grizzly Bears from the Federal List of Endangered and Threatened Wildlife

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General Comment

On behalf of The Humane Society of the United States ("The HSUS"), please find attached herewith:

1. The HSUS' Comment on the Proposed Rule (HSUS GYE Grizzly Delisting Comment FINAL.pdf);
2. Attachment A to the Comment (Attachment A.pdf);
3. Attachment B to the Comment (Attachment B.pdf);
4. Copies of all works cited or referenced in the Comment (81 files total).

Attachments

HSUS GYE Grizzly Bear Delisting Comment FINAL

Attachment A

Attachment B

Barber-Meyer et al 2007

Balme2013-Leopard-F-Reproduction
Balme-2012-Leopard-AgeBasedHunting
BeckmannBerger2003
BCMinistry2010-FAQ-GB-Hunting
McLellan-1999GB-Mortality
Mattson_1993_Background Standards Security Areas
Hansen2016-savingWBP
Monteith et al. 2014-MD life history
Weaver1996
Packer - 2009 sport hunting paper
Roberts2014-GB&GW
Paillard2015-BrnBears-Ticks-GW
Dunkley-Cattetbaiting2003
Mattson1997-GB-WBP-RedSquirrel-Roads
Swenson2001-InterspecificCubPred
Packer-SportHunt-Conserv
Ripple2014Carnivores
Estesetal2011-trophic
Swenson2001FactorsSSI
Wielgus & Bunnell - 1995- hypotheses of sexual segregation
Mills1996-OneMigrantPerGeneration
Doak-1995-source-sink-GB-lagtime
Wielgus & Bunnell1994- sexual segregation gbears
Moore, V- Tri-State Grizzly Hunting Agreement
Swenson2003-hunting&SSI
Schwartz-Grizzly03
Packer-2011-TH-Lions&Leopards
Packer - 2011 hunting leopards in Tanzania
Wallach-2015-ApexPred

Vaughan&Inman-Houndingbears2002

Wielgus & Bunnell-1994-dynamics of hunted gbears

Bryan-WolfHuntingFacilitatesStressReproduction2014

Inslerman2006

Creel-2015-HuntingWolvesQuestionable

KeehnerWielgus2015pumapreyswitch

Saether-2010-lynx-poaching

Swenson1997-Infanticide-SSI

WYGRIZBEAR_MANAGEMENTPLAN

Doak-GrizzlyBears2013

Keehner-2015-puma-SSI

Schwartz-1987BlackBearDen

Deeke2012-GB-tooluse-cognition

Allendorf and Hard 2009 human selection from hunting

Bojarska2012-GB-globalwarming

Ordiz_etal_2012 Do bears know they are being hunted

Cattet2008-CaptureEffectsUrsids

McLellan-2015-GB-huckleberry-density

Gosselin-2015-HuntingEffectsBears

Allendorf 2008 genetics+hunting

Costello et al_2014_Use of whitebark pine

Hristienko-McDonald-Bears2007

Zedrosser-2013-GB-HuntingEffectsOn

McDonough-2012-GB-size-variation-conservation

Inman-Costello-BearChronHunt2007

Van Manen et al_2016_Grizzlies WBP and density

Obbard et al_Relationships among food, harvest and HBC in ON_Ursus_2014

Darimont2015-HumanSuperPred

Bump-2013BearBaitingIncreasesWolf-DogConflicts

Wielgus-2013-PumaHuntEffectFemales

Andren 2006 lynx poaching

Koehler-mortalitybearsWA2005

Vucetich Influence of harvest climate and wolf

Darimont 2009 - Human Predators Outpace Other Agents of Trait

Wielgus2001-GBpopgrowth

Wright et al 2006. Selection of Northern Yellowstone Elk by Gray Wolves

Cooley.etal.2009.Does hunting regulate cougar populations.A test of the compensatory mortality hypothesis

Cooleypumacompensatory2009

Lambert et al 2006

Vucetich et al 2005 YNP wolf-elk predation

Robinson 2008 - SINK POPULATIONS IN CARNIVORE MANAGEMENT

Craighead-Roads-Wildlife

VanDaele2012-GB-EcoFlexibility-Kodiak

Elfstrom-UrbanBears2014

Wielgus & Bunnell Possible negative effects

Haroldson et al _2002_ Denning chronology

Wielgus2002-GBpop&ReserveSize

Sidor-2015chocolatetoxicityreport

Treves2009Hunting_to_conserve_carnivores

Baldwin-Bears2010

Beck-SocialConsider-BBearHunting-1995



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Re: FWS-R6-ES-2016-0042: Removing the Greater Yellowstone Ecosystem Population of Grizzly Bears from the Federal List of Endangered and Threatened Wildlife; Proposed Rule

Dear Dr. Servheen:

On behalf of The Humane Society of the United States (“The HSUS”), the nation’s largest animal protection organization, and our supporters, we write to express our strong opposition to the U.S. Fish and Wildlife Service’s (“FWS” or “the Service”) proposed rule to remove grizzly bears (*Ursus arctos horribilis*) in the Greater Yellowstone Ecosystem (“GYE”) from federal protection as a threatened species under the Endangered Species Act (“ESA”). *See* 81 Fed. Reg. 13173 (March 11, 2016) (hereinafter the “Proposed Rule”). This comment also addresses elements of FWS’ Draft 2016 Conservation Strategy for the Grizzly Bear in the Yellowstone Ecosystem to the extent that they are referenced and relied upon in the Proposed Rule.

As described herein, the best available science – much of which was not adequately considered in the Proposed Rule – demonstrates that the GYE grizzly bears remain under dire threat such that continued listing is required under the ESA (16 U.S.C. § 1533). Furthermore, recently proposed state management schemes – including provisions allowing trophy hunting of grizzly bears – are both legally and practically inadequate to ensure the preservation of grizzly bears in the GYE absent federal protection. Moreover, the Service has improperly designated GYE grizzly bears as a distinct population segment (“DPS”) solely for the purpose of delisting, inconsistent with the conservation mandate of the ESA.

Because this proposed rule violates both the procedural and substantive requirements of the ESA, FWS must withdraw the Proposed Rule, and may not legally take further action to delist GYE grizzly bears until such time as the best available science supports (a) designation of multiple grizzly bear DPSs that encompass the entire range of the subspecies; and (b) subsequent delisting of a grizzly bear DPS after state authorities have developed and implemented comprehensive and enforceable regulatory schemes to protect grizzly bears from extinction.

I. The Proposed Rule Misapplies the Distinct Population Segment Tool in Violation of the ESA

As an initial matter, the Service cannot lawfully remove GYE grizzly bears from the threatened species list, as this population is currently listed at the subspecies level and the Service cannot lawfully designate the specific GYE population as an independent listable entity without first determining – based on the best available science – that the entire subspecies is no longer threatened across all or a significant portion of its range.

The Proposed Rule functionally consists of two actions under the ESA: (a) the designation of the GYE grizzly bear population as a DPS carved out of the presently listed lower-48 grizzly bear subspecies; and (b) the simultaneous removal of that newly designated DPS from the threatened species list. As discussed below, the best available science indicates that the entire grizzly bear subspecies should remain listed as threatened and the GYE population does not meet the ESA’s five factors for delisting. 16 U.S.C. § 1533(a)(1). Further, as explained below, FWS cannot lawfully propose to delist a DPS without first listing the DPS and establishing recovery goals for that population. *See* 61 FR 4722 (February 7, 1996); 16 U.S.C. § 1532(16).

FWS proposes to designate the GYE grizzly bear population as a DPS at the same time as, and for the purpose of, *removing* – rather than increasing – its protections under the ESA. This directly contravenes the intent of Congress when it amended the ESA to add the DPS tool in 1978. 16 U.S.C. § 1532(16).¹ And it is particularly brazen given the recent opinion of a federal court chastising the Service for doing the exact same thing less than eighteen months ago. *Humane Soc’y of the United States v. Jewell*, 76 F. Supp. 3d 69 (D.D.C. 2014) (most recent in a series of federal cases vacating FWS attempts to designate gray wolf DPS’ for the purpose of delisting or downlisting) (hereinafter “*HSUS v. Jewell*”); *see also Humane Soc’y of U.S. v.*

¹ The legislative history of this amendment strongly suggests that Congress contemplated the DPS tool as being used exclusively to provide ESA protections to discrete and particularly imperiled populations, and never discussed the tool in terms of *removing* protections. *See, e.g.* S. Rep. No. 96-151, at 6-7 (1979). This abundance of legislative history is cited thoroughly in recent federal court decisions on this issue, particularly *Humane Soc’y of U.S. v. Kempthorne*, 579 F. Supp. 2d 7, 9 (D.D.C. 2008).

Kemphorne, 579 F. Supp. 2d 7 (D.D.C. 2008); *Defenders of Wildlife v. Sec’y, U.S. Dep’t of Interior*, 354 F. Supp. 2d 1156 (D. Or. 2005); *Nat’l Wildlife Fed’n v. Norton*, 386 F. Supp. 2d 553 (D. Vt. 2005). As the ESA’s legislative history and more than a decade of litigation on the issue have made abundantly clear, the ESA does not allow FWS to designate a DPS for the purpose of removing ESA protections. *See HSUS v. Jewell*, 76 F. Supp. 3d at 112 (“[A]fter more than a decade of rulemaking, delisting, litigation, vacatur by District Courts, and relisting . . . , the time has come to resolve this long-running dispute [T]he creation or initial designation of a DPS operates as a one-way ratchet to provide ESA protections to the covered vertebrates.”).

The Proposed Rule represents another attempt to designate a DPS solely for the purpose of removing ESA protections – the same action that was found to be “predicated on . . . an untenable reading of the ESA” in *HSUS v. Jewell*, and like that action, “no more valid than the agency’s . . . prior attempts to remove federal protections” for a newly designated DPS carved out of an otherwise listed species. 76 F. Supp. 3d at 75-76. Recognizing the facial illegality of this designation in light of the last decade of ESA case law, the FWS admits in the Proposed Rule that “we recognize that our interpretation and use of the DPS policy to revise and delist distinct population segments has been challenged in [*HSUS v. Jewell*] Our rule was vacated by the district court’s decision. We respectfully disagree with the district court’s interpretation of the DPS policy, and the United States has appealed that decision.” Proposed Rule at 13190. But the ESA’s DPS provisions, which have been tested in court four times since 2005, bar FWS from taking the actions proposed here.

Notably, courts have held that it would be possible to lawfully separate a subspecies-level listing (like lower-48 grizzly bears) into multiple DPSs for more targeted management, but only following a status review of the *entire* listed entity that demonstrates a sound scientific basis that the subspecies as a whole is no longer imperiled and subsequently identifying any DPSs for protection pursuant to FWS’ DPS policy. *See Friends of the Wild Swan v. U.S. Fish & Wildlife Serv.*, 12 F. Supp. 2d 1221, 1133-34 (D. Or. 1997) (vacating FWS decision to split nationwide listing of bull trout into five DPSs but allowing that if FWS “legitimately concludes, after proper and sustainable analysis, that listing of the entire species” is not warranted, then the agency may “proceed[] on a population segment basis” to assign targeted protection). Crucially, FWS may *not* carve a DPS out of an otherwise fully listed species or subspecies-level listing – like FWS proposes to do here – thereby leaving a listed “remainder” population. Such remainder (in this case, all lower-48 grizzly bears minus the proposed GYE DPS) is not a lawfully listed entity under the ESA since it is itself neither a species, subspecies, nor a DPS. 16 U.S.C. § 1532(16).

Here, FWS could have elected to initiate a status review of all *Ursus arctos horribilis*. Then, if the evidence so warranted, FWS could have initiated rulemaking

to designate multiple DPSs that account for the entirety of the listed subspecies (thus avoiding leaving a “remainder” entity), developed DPS-specific recovery plans, and then separately initiated rulemaking to delist a particular DPS if warranted. But that is not the course that the Service has taken here, and therefore, the Service must withdraw the Proposed Rule.

Because the Proposed Rule unlawfully designates the GYE DPS in violation of the ESA, this Comment will not focus on the hypothetical question of whether, if such a designation *were* possible at this time, it would meet the substantive criteria for defining a new GPS. However, the Proposed Rule’s failure to consider the best available science as to ongoing threats warranting continued listing of GYE grizzly bears – described in section II below – casts doubt on the validity of its DPS analysis.

II. The Best Available Science Demonstrates that GYE Grizzly Bears Must Remain Listed as Threatened

a. Legal Standard for Delisting

Even if FWS had properly designated GYE grizzly bears as a DPS, the best available science does not support removing ESA protection for this population.

“A species may be delisted on the basis of recovery *only if* the best scientific and commercial data available indicate that it is no longer endangered or threatened.” 50 C.F.R. § 424.11(d)(2) (emphasis added). *See also* 16 U.S.C. § 1553(b)(1)(A); *N.M. Cattle Growers v. U.S. Fish & Wildlife Service*, 248 F.3d 1277, 1284-85 (10th Cir. 2001) (*quoting* H.R. Rep. No. 97-567, pt. 1 at 29 (1982), the best available science standard is “intended to remove from the process of listing or delisting of species any factor not related to the biological status of the species.”); H.R. Conf. Rep. No. 835, 97th Cong. 2d Sess. 19-20 (1982) (the limitations on the factors the Service may consider in making listing decisions were intended to “ensure that decisions . . . pertaining to listing . . . are based solely upon biological criteria and to prevent nonbiological considerations from affecting such decisions.”).

A delisting determination must be made by considering the five categories of threats to a species set forth in Section 4(a)(1) of the ESA: (A) the present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; and (E) other natural or manmade factors affecting its continued existence. 16 U.S.C. § 1533(a)(1). “Section 4(a)(1) of the Act provides the Secretary ‘shall’ consider the five statutory factors when determining whether a species is endangered, and § 4(c) makes clear that a decision to delist ‘shall be made in accordance’ with the same five factors.” *Friends of Blackwater v. Salazar*, 691 F.3d 428, 432 (D.C. Cir. 2012) (*quoting* 16

U.S.C. § 1533(a), (c)); *see also* 50 C.F.R. § 424.11(d)(2) (FWS regulation governing delisting).

As detailed below, application of the best available science to these five factors – any one of which is sufficient to mandate continued ESA protection – requires that GYE grizzly bears retain their ESA protections. *See Sw. Ctr. for Biological Diversity v. Babbitt*, 215 F.3d 58, 60 (D.C. Cir. 2000) (listing required if “*any* of § 1533(a)(1)’s five factors are sufficiently implicated”) (emphasis added). Specifically, GYE grizzly bears continue to be severely threatened by loss of key food sources, destruction and modification of their habitat, predation on cubs, disease, and poaching. Additionally, the proposed regulatory mechanisms in the GYE states of Wyoming, Idaho, and Montana (the “States”) will lead to overutilization of grizzly bears for recreational trophy hunting and commercial purposes in the event of delisting, and are legally insufficient to support removal of federal protection.

**b. Declining Food Sources, Climate Change, Habitat
Fragmentation, and Human Use Present Current and Ongoing
Destruction, Modification, and Curtailment of GYE Grizzly
Bear Habitat**

**1. GYE Grizzlies are Threatened by an Ongoing Crisis in
Staple Food Sources**

While the Proposed Rule claims that grizzly bears are “extremely omnivorous,” “display great diet plasticity,” and can consume “over 260 species of foods” (Proposed Rule at 13177-8), this conclusion is overly optimistic. GYE grizzly bears, scientists concur, are facing a catastrophic food crisis that threatens their continued existence. FWS claims that GYE grizzly bears “commonly consume” bison, elk, moose, deer, cutthroat trout, roots, tubers, army cutworm moths, and whitebark pine seeds and, when these high calorie food are unavailable, they rely upon lower quality but more abundant foods such as huckleberries, grasses, sedges, and ground squirrels. Proposed Rule at 13178.

But the Proposed Rule misinterprets a shift toward non-staple food sources as evidence of grizzly bears’ capacity to adapt when, in fact, reliance on these unreliable new food sources puts GYE grizzly bears at greater risk than ever. As Dr. David Mattson – a former U.S. Geological Survey Research Wildlife Biologist and leading GYE grizzly bear expert with more than thirty years of professional experience focusing on grizzly bear ecology and management, and whose critique of the scientific underpinnings of the Proposed Rule is attached herewith as Attachment A – explains, GYE grizzly bears have traditionally thrived on just a handful of staple foods and supplemented only opportunistically on other food sources. Attachment A, discussion 7.0, 11.1; Figs. 7.1, 7.2, 11.1.1 (hereinafter “Mattson Critique”). While bears have frequently relied on whitebark pine and

cutthroat trout, these two staple food sources have virtually disappeared from the GYE. Middleton et al. 2013, Roberts et al. 2014, Hansen et al. 2016.

Currently, whitebark pine seeds, native cutthroat trout, army cutworm moths, elk and bison are either expected to decline or are in decline for the foreseeable future as a result of habitat loss, climate change, drought, invasive species and other anthropogenic and natural causes. *See generally* Mattson Critique. When bears spend less time moving to obtain foods, it improves their fitness. Van Daele et al. 2012. But because grizzly bears' most important staples are in decline, GYE bears are on the move, reducing their fitness and putting them in increased danger from intra- and interspecific conflict and human- caused mortality.

A recent study by Roberts et al. (2014) examined food shifts for grizzly bears in the Canadian Rocky Mountains and found that bears' foods are migrating to higher elevations. This exposes low-elevation grizzly bears to greater human-bear conflicts, and these alterations from climate change "may reduce [grizzly bear] survival rates." Roberts et al. 2014. This forecast is also taking place in the GYE. Since 1994, grizzly bear-human conflicts have escalated and dramatically so since 1985, with a record number of conflicts in 2015. Mattson Critique, Fig. 18.1. Yet, the Proposed Rule failed to consider how anthropogenic "ecological traps" – that is, the places where high-quality foods lure grizzly bears into environments where they will have conflicts with humans – have already resulted in greater mortalities. Mattson Critique, discussion 2.1, 11.2; Figs. 9.2, 9.3, 18.1.

FWS takes the position that grizzly bears have reached their carrying capacity in the primary conservation area ("PCA") and are therefore expanding their territory. But there is ample support for an alternative theory: that bears have lost their historic food sources and are now relying more on native and domestic ungulates that necessitate the bears' movement across a larger range. This expanded movement, which is necessary for grizzly bears' survival in light of the declining availability of other food sources, puts them into closer proximity to humans, wolves, and other territorial male bears, resulting in greater conflicts and higher mortality. Doak and Cutler 2013, Elfstrom et al. 2014, Mattson 2016, Wyoming Game and Fish Department 2016. Thus, the direct and indirect effects of the loss of food resources pose novel threats to the persistence of GYE grizzly bears and the Proposed Rule, because it fails to consider these effects, is not based on the best available science. And to the extent that there is any uncertainty about the effects of the loss of these food sources on GYE grizzly bear persistence, the ESA requires that protections be maintained – not removed. *See, e.g., Natural Resources Defense Council v. Pritzker*, 62 F. Supp.3d 969, 1021 (N.D. Cal. 2014) ("To the extent that there is any uncertainty as to what constitutes the best available scientific information, Congress intended 'to give the benefit of the doubt to the species.'" (*quoting* H.R. Conf. Rep. No. 96–697, 1st Sess. 12, reprinted in 1979 U.S.C.C.A.N. 2572, 2576).

i. Whitebark Pine

Whitebark pine lives in montane and subalpine forest areas in the West and is a keystone species. Hansen et al. 2016. It helps to increase cover, protect the snowpack, and prevent runoff, while supplying seeds to multiple wildlife species including grizzly bears. Hansen et al. 2016. This keystone tree species is experiencing “a steep decline because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion management policies, and the introduced disease white pine blister rust (causal agent *Cronartium ribicola*).” Hansen et al. 2016: 2. Of particular historical importance to the decline of the whitebark pine were major fires in 1998 in the GYE, and the bark beetle infestation beginning in 2006 that wiped out crops with higher cone yields (the most important trees for grizzly bear survival, as they produce the most seeds), beginning the terminal decline of the species. Mattson Critique, Figs. 8.2.2, 10.1.

Indeed, FWS has itself acknowledged that the whitebark pine is sufficiently threatened to warrant federal protection: “[t]hreats to the whitebark pine include habitat loss and mortality from white pine blister rust, mountain pine beetle, catastrophic fire and fire suppression, environmental effects resulting from climate change, and the inadequacy of existing regulatory mechanisms.”²

Another significant ongoing threat to whitebark pines is climate change. Whitebark pines are the most vulnerable to climate change of all the conifer species in the Northern Rockies. Hansen et al. 2016. In fact, because of the warming climate, *over 95%* of cone-bearing trees have already disappeared. Hansen et al. 2016. And this trend will inevitably continue, as “[b]ased on the most recent climate projections, mean annual temperatures across the GYE are projected to rise 3–7 °C above the 100-year historical mean by the end of the century and snowpack in the subalpine zone is projected to decrease by 20%–30%.” Hansen et al. 2016: 4.

Whitebark pine trees and their high fat content seeds once provided a core staple for grizzly bears (who raided squirrel middens to obtain them) during the critical period of hyperphagia—the months before grizzly bears enter the den; now, whitebark pine trees have nearly vanished. Mattson Critique, Fig. 8.2.2. The Proposed Rule notes that whitebark pine seeds are a core staple to bears who have these trees in their home range, if whitebark pine seeds “exceed 20 cones per tree” Proposed Rule at 13178.

The Proposed Rule misguidedly attempts to downplay the devastating harms that the catastrophic loss of whitebark pine have on grizzly bear survival:

There has been no correlation between long-term survival of

² <http://www.fws.gov/mountain-prairie/species/plants/whitebarkpine/>.

independent bears with a decline in whitebark pine availability (van Manen *et al.* 2015, p. 11). Nearly one third of grizzly bear home ranges in the GYE do not contain any whitebark pine (Costello *et al.* 2014, p. 2013). Bears in these areas consume other foods even during years of good whitebark pine production

Proposed Rule at 13178. But this conclusion relies entirely on studies (Bjornlie *et al.* (2014), van Manen *et al.* (2016) and Costello *et al.* (2014)) whose methodologies have been discredited. Mattson Critique, discussions 8.2; 10.0; 13.2.

Bjornlie *et al.* (2014) and van Manen *et al.* (2016) were fundamentally incorrect in their assumptions regarding whitebark pine seed availability: during the period that authors said pine seeds were abundant, they were in decline; and when pine seeds were abundant, the authors claimed they were in decline. This is likely because the authors relied on aerial tree counts – which do not account for the variable cone production per tree, but instead extrapolates numbers of cones based on often inaccurate assumptions – instead of using the more work-intensive but reliable method of counting seed cones on trees. Cone-count studies are fundamentally more suited to the analysis of whitebark pine seeds as a food source for GYE grizzly bears, because they more precisely account for the number of seeds available – which can, as described below, sometimes increase even as the total number of trees decreases. Mattson Critique, discussion 8.2; Fig. 8.2.1.

Furthermore, van Manen *et al.* (2016) failed to account for trees lost to Yellowstone’s catastrophic fires of 1988; this study showed a constant abundance of trees for the period 1983 to 2000, but whitebark pines had declined by at least 17% (or 3% to 50%, depending on the area). For the period 1983-1989, van Manen *et al.* (2016) overestimated pine seed abundance, and in 2005-2010 underestimated pine seed abundance. Likewise Bjornlie *et al.* (2014) described pine seed abundance between 1988 and 1989 and showed pine seed decline for the period 2007-2012, but this contradicts the Interagency Grizzly Bear Study Team’s (“IGBST”) cone-count surveys. Mattson Critique, discussion 8, 10; Figs. 8.2.1, 8.2.2, 10.1, 10.2.

Biologists on the IGBST conducted aerial surveys to count whitebark pines in grizzly bear habitats, but this methodology failed to count all the trees in bears’ habitats, especially in lower elevations – this further compounds the authors’ erroneous conclusions upon which the FWS relied. Mattson Critique, discussion 8.0, 10; Fig. 8.1.1.

Using the IGBST’s cone-count data, Mattson found an average of 8 cones per tree in the period 1982 to 2005; and an average of 20 cones per tree in the period 2006-2014: a 150% increase in cone production per tree from the earlier period. At the same time that the *numbers* of whitebark pines were on the decline, *cone production per tree* increased 2.5 fold. Mattson Critique, Fig. 8.2.1. During the time period when pine seed abundance per tree had increased, the overall number of trees were in

terminal decline because of fire, disease, parasites, and drought. But the time period that Bjornlie et al. (2014), Costello et al. (2014), and van Manen et al. (2016) suggested that pine seeds were abundant was incorrect because authors used trees as a proxy for cones. Mattson corrects their error using the IGBST's own pine seed data Mattson Critique, Fig. 8.2.1.

In short, the Proposed Rule relies on discredited studies to downplay the vital connection between whitebark pine seeds and grizzly bear survival. Not coincidentally, this is the same error that led two federal courts to vacate FWS' last attempt to delist GYE grizzly bears in 2007.³ Now, even more than then, the best available science shows that the whitebark pine crisis remains a critical threat to grizzly bear survival that requires continued ESA protections.

ii. Cutthroat Trout

Another historic key source of sustenance for grizzly bears, the cutthroat trout (*Oncorhynchus clarki*), is nearly extinct because of (1) the introduction of an invasive species, lake trout (*Salvelinus namaycush*), who prey on spawning cutthroat trout but prefer deep waters inaccessible to bears; (2) a parasite that causes whirling disease (*Myxobolus cerebralis*); and (3) multiple years of drought. Proposed Rule at 13212. Cutthroat trout have stopped spawning in all of the tributaries of Yellowstone Lake between the 1980s and late 1990s. Mattson Critique at 41. FWS incorrectly suggests that cutthroat trout were never an important grizzly bear staple, writing that bears who shared habitats with cutthroat trout only consumed a few fish each year. Proposed Rule at 13213.

Other biologists have reached a far different – and more accurate – conclusion about the importance cutthroat trout as a food source for the GYE grizzly bears. Middleton et al. (2013) infer the importance of Yellowstone cutthroat trout based on evidence that, following drastic declines in their populations, grizzly bears substantially increased predation on summering, migratory ungulates inside Yellowstone National Park – particularly calves. They observe that: “the magnitude of this diet shift has been sufficient to reduce elk calf recruitment (4-16%) and population growth (2-11%).” Because cutthroat trout have disappeared, grizzly bears have switched to elk calves in order to survive. Unfortunately, this compensatory predation on wild ungulates has caused bears to become a poaching target for elk hunters and state wildlife management agencies that are incentivized to maximize ungulate populations for reasons unrelated to sound ecology. Mattson Critique, discussion 11.4.

Moreover, the loss of this key staple – as with whitebark pine – harms grizzly bear persistence by forcing them to switch to eating meat, exposing them to conflict with

³ *Greater Yellowstone Coal. v. Servheen*, 672 F. Supp.2d 1105 (D. Mont. 2009); *aff'd in relevant part by Greater Yellowstone Coal. v. Servheen*, 665 F.3d 1015 (9th Cir. 2011).

other predators (wolves and other bears) and humans (livestock growers, elk hunters, and people living and recreating in the grizzly bear habitat). This exposure has led to an increase in grizzly bear mortalities over the past decade, with a record 61 bears dying in 2015.

FWS has failed to adequately consider best available science regarding the importance of cutthroat trout to the persistence of the GYE grizzly bear population.

iii. Army Cutworm Moths

Army cutworm moths, a staple for grizzly bears since the late 1990's because of the loss of whitebark pine seeds and trout, are in danger of disappearing from the GYE due to climate change. Army cutworm moths nectar on tundra flowers that exist in alpine habitats extremely vulnerable to global warming (Mattson Critique, discussion 7, 9, 10, 11, 13.3). Yet, the Proposed Rule claims, based only on a single source, that alpine tundra and alpine communities will not be adversely affected by global warming and that moths – based on no evidence – will learn to adapt. But that argument is belied by the best available science. Mattson Critique, discussion 13.3.

iv. Huckleberries

Since 1996, the GYE has experienced decline in huckleberries – another key grizzly bear food source – due to drought, in particular a severe period of drought from 1998 to 2008. McLellan (2015) showed that following a decline in huckleberries in Canada and northern Montana, the grizzly bear population declined substantially – but not until 11 years later. This demonstrated lag, which the Proposed Rule failed to consider, suggests that the full impact of the decline of this food source and on grizzly bear populations may not have been seen yet, counseling strongly against delisting at this time. Mattson Critique, discussion 3.0; 5.0-5.5.

v. Elk and Bison

The food failures facing grizzly bears – most notably, the loss of whitebark pine, cutthroat trout, and huckleberries – have caused grizzly bears to switch to a more meat-based diet, including domestic livestock and hunter-killed elk, with several adverse consequences. First, it brings bears into greater proximity, competition, and conflict with other predators and with humans. This has led to record numbers of lethal actions taken against them by humans, harming their persistence.⁴ As

⁴ Figure 8 of Wyoming's proposed post-delisting management plan shows an increasing trajectory since 1990 in both self-defense and management removals of grizzly bears. (Wyoming Game and Fish Department, 2016) (*available at* <https://wgfd.wyo.gov/WGFD/media/content/Wildlife/Hot%20Topics/FINAL-DRAFT-GB-Mgmt-Plan-3-15-16.pdf>) (hereinafter "Wyoming Plan"). And because of human-bear conflicts

Wyoming states in its proposed post-delisting management plan, “. . . the Department has documented an increase in aggressive encounters, self-defense mortalities, and management removals.” Wyoming Plan at 7. The Wyoming Plan also shows an increasing trajectory in both self-defense and management removals of grizzly bears since 1990, suggesting that these bruins are on the move from their core areas and attempting to find alternative food sources to replace whitebark pine and cutthroat trout. Wyoming Plan, Figure 8.

Furthermore, biologists have noted that grizzly bear cub production has declined (van Manen et al. 2016) – perhaps because of more predation on cubs and small bears by the wolves and other, larger bears with whom they must now compete.

Increasing dependence on meat also means that GYE grizzly bears are adversely affected by declines in ungulate populations caused by other factors – even as the bears themselves are wrongly blamed for those declines. Yellowstone’s Jackson and Northern Range elk herds and its Central Range bison herd are all in decline. Mattson Critique, discussion 11.2, 11.3; Fig. 10.1, 11.2.1, 11.2.2.

Elk, deer, pronghorn, and moose populations in the Northern Rocky Mountains are affected by a suite of factors, including a guild of native carnivores, extreme weather events (e.g., prolonged drought or too much snow), disease, and, especially, overhunting by humans. Vucetich et al. 2005, Wright et al. 2006, Mallonee 2011. In several studies of elk populations conducted in and near Yellowstone National Park, biologists consistently found that human hunters and weather conditions represented the greatest negative effects on elk numbers. In fact, hunters actually constitute the most disruptive mortality factor on ungulate herds by removing prime-age breeding females.

In fact, the number of Yellowstone elk killed by human hunters is considered by biologists to be “super-additive” – meaning that heavy hunting pressures far exceed what would otherwise occur in nature. Vucetich et al. 2005, p. 267, Wright et al. 2006. Humans killed prime-age breeding animals (females with an average age of 6.5), whereas wolves, for example, select for vulnerable age classes of elk (on average 13.9 years). Vucetich et al. 2005, Wright et al. 2006.

In the 1970s and 1980s, the elk population north of Yellowstone was too large to be sustainable. Montana sponsored culling efforts to cut the population. Then several harsh weather events occurred, including droughts. Vucetich et al. 2005, Wright et al. 2006. Two decades later, another extreme drought struck from 1998 to 2005, reducing the amount of forage available to elk (Barber-Meyer et al. 2008), just after wolves had been reintroduced into the ecosystem in 1995.

over domestic livestock and hunter-killed ungulates, significantly more bears have been killed since 2005 compared to the period 1990-2004. See IGBST’s grizzly bear mortality database, available at <http://www.nrmc.usgs.gov/science/igbst/mort>.

While many have blamed wolves and grizzly bears for the elk population decline in and around Yellowstone National Park, a closer analysis shows that human hunting pressure and climate change are far more significant drivers of population declines. Vucetich et al. 2005. Other biologists have implicated bears for “additive” mortality on ungulate herds in the GYE because of bears’ predation on neonate ungulates in the springtime. But new research suggests this mortality is simply “compensatory.” Monteith et al. write:

The influence of bear predation on survival of neonatal ungulates has been emphasized in a number of recent studies (Linnell et al. 1995, Bowyer et al. 1998a, Zager and Beecham 2006, Barber-Meyer et al. 2008, Griffin et al. 2011, Middleton et al. 2013c). Bears specialize on neonates during the period of greatest vulnerability within the first few weeks of life Consequently, among large carnivores, bears have been proposed to have the greatest potential to affect dynamics of ungulate populations, because vulnerability of neonates may not strongly reflect nutrition at that age (Barber-Meyer et al. 2008, White et al. 2010). Although greater nutritional limitation within a population will inherently result in an increase in the proportion of prey predisposed to mortality, *viewing compensatory versus additive mortality as a function of the vulnerability of individual prey—especially neonates—is misleading because the true consequences of mortality are based on the nutritional capacity of the habitat.* Documenting that predation by a particular predator seems to be unaffected by the condition of prey indicates the potential for that predator to have an additive effect, but does not imply that all deaths because of predation were additive. Mortality of neonates on one side of the Sierra crest was partially additive (Fig. 29b), whereas mortality of neonates on the other side was largely compensatory”

Monteith et al. 2014 at 40 (emphasis added).

The decline of the GYE elk and bison herds also means that female grizzly bears will have less carrion to rely upon in the springtime when they emerge from their dens with cubs, which can reduce the survivability of the cubs. Mattson Critique, discussion 11.2; 11.3.

2. The GYE Grizzly Bear Population is in Decline Despite Its Habitat-area Expansion.

Despite bears’ inhabiting a greater land area (as necessitated by the loss of staple food sources described above), their population is in decline because of a variety of new risks that have resulted in greater mortality. Mattson Critique, Figs. 9.2; 9.3, 18.1, 19.4.1. Furthermore, while the FWS claims that densities of grizzly bears have increased since at least 2000, the data do not support this supposition. In fact, data from Mark-Resight – more reliable than Chao2—show that bear numbers have declined in the GYE as individuals are spread out over a larger area. Mattson

Critique, discussion 2.1; Fig. 9.2. Studies upon which the Proposed Rule relies not only used unreliable methods to count bears – particularly females with cubs of the year – they also failed to account for changes in food abundance, rendering their index of population models invalid. Mattson Critique discussion 4.0; 19.0-21.0. Researchers van Manen et al. (2016) and Bjornlie et al. (2014) used their trapping-effort data in lieu of a reliable capture-recapture population count method. While this methodology is unreliable, it nevertheless informs the FWS' index of the GYE grizzly bear population. Mattson Critique, discussion 4.0; 19.0-21.0.

The Proposed Rule also fails to consider that following the decline of major food resources, the best available science indicates there will be a lag time – possibly more than a decade – before the commensurate grizzly bear population decline fully manifests. Doak 1995, McLellan 2015. While a grizzly bear population decline is already occurring, the full force of lagging effects from recent food source losses – whitebark pine in particular – may not yet be over. Mattson Critique, discussion 3.0; 5.0-5.5. Delisting GYE grizzly bears at this time would be premature and contrary to the best available science, which counsels caution until the full effects of staple food losses can be studied.

3. Climate Change is Adversely Altering GYE Grizzly Bear Habitat

Human-caused climate change is predicted to cause catastrophic events across the planet, and indeed has already begun doing so. Despite this well-documented fact, the Proposed Rule gives consideration of climate change on grizzly bears short shrift. FWS writes: “most grizzly bear biologists in the United States or Canada do not expect habitat changes predicted under climate change scenarios to directly threaten grizzly bears (Servheen and Cross 2010, p. 4).” Proposed Rule at 13197. But contrary to the single study relied on in the Proposed Rule, many grizzly bear researchers have extensively studied climate change scenarios and concluded that climate change *will* have detrimental effects on grizzly bears by further altering the availability of food sources in their habitat.

First, the Proposed Rule's conclusion belies the devastating impact, discussed in section (II)(b)(1)(i) above, that climate change is already and will continue to have on whitebark pine availability due to warming winters in the Northern Rockies fostering the spread of bark beetles and blister rust. Hansen et al. 2016.

Additionally, a recent study by Roberts et al. (2014), examined food shifts for grizzly bears in the Canadian Rocky Mountains and found that, as a result of climate change, bears' foods are migrating to higher elevations, exposing low-elevation grizzly bears to greater human-bear conflicts in a manner that “may reduce [grizzly bear] survival rates.” This very scenario is already taking place in the GYE. As discussed above, since 1994, grizzly bear-human conflicts have escalated

dramatically, with a record number of conflicts in 2015, largely on account of movement necessitated by the loss of staple food sources – a trend that will only continue with climate change.

Bojarska and Silva (2012) conducted a seminal worldwide review of grizzly bear food selection relative to their geography (latitude, longitude, altitude) and a multitude of environmental variables such as snow depth and duration. They found that “temperature and snow conditions” constituted some of the “most important factors affecting the feeding ecology of the brown bear.” Bojarska and Selva 2012. Their conclusions demonstrate that FWS must treat climate change impacts on grizzly bears with the utmost gravity:

. . . [I]t may be expected that climate change will greatly affect brown bear food habits through changes in food availability, hibernation patterns, nutritional and energetic demands, and foraging behaviour. Globally increasing temperatures are yielding shorter winters with less snow, especially in northern latitudes and higher elevation areas (Sagarin & Micheli 2001, Wilmers & Post 2006). Early snow melt substantially reduces the amount of late-winter and early-spring carrion, which is vital for bears after hibernation and until other food resources become available (Wilmers & Post 2006). Climate change may affect brown bear feeding habits also through changes in plant distribution and phenology. As a response to warmer temperatures, Rodríguez et al. (2007) documented a long-term decrease in the contribution of boreal and temperate food items in brown bear diet during the hyperphagic season, when brown bears typically consume high amounts of fruit to accumulate fat for winter dormancy and for successful reproduction. Changes in the timing and intensity of fruiting and ripening of fruit and mast, and declines in the availability of high-quality fruits . . . may have important consequences for brown bear population dynamics (Rodríguez et al. 2007). If key brown bear food resources disappear without the corresponding change in the timing of alternative food resources, a serious food bottleneck could develop.

Bojarska and Silva 2012 at 133-4. The best available science is clear: climate change has and will continue to threaten GYE grizzly bears by detrimentally altering their habitat. This will result in further loss of staple foods and an increase in human-bear and inter- and intra-specific conflict as bears attempt to adapt to new food sources.

4. GYE Grizzly Bears are Threatened by Habitat Fragmentation

i. Habitat Fragmentation is Already Occurring

To survive, large carnivores must have secure habitats and avoid human persecution. Weaver et al. 1996, Estes et al. 2011, Ripple et al. 2014, Darimont et al. 2015. A grizzly bear needs large habitat devoid of human conflict in order to search for food, mates, cover and den sites. Proposed Rule at 13178. An ideal grizzly bear habitat must have adequate “food distribution and abundance” in order for bears to thrive. Proposed Rule at 13178. One of the greatest threats to grizzly bear vitality is the incursion of motorized activity in their habitats. Craighead 2002. FWS has defined “secure habitat” as “more than 500 m (1,650 ft) from a motorized access route and greater than or equal to 4 hectares (ha) (10 acres (ac) in size.” Proposed Rule at 13178.

In contrast to FWS’ assertion that 4 hectares is sufficient, Mattson (1993) recommends, after conducting a thorough review of the literature, that a secure grizzly bear area contain a core of approximately 290 hectares and be situated roughly 2-4 kilometers from the nearest road or other human facility. Based upon Mattson’s review – which is the most thorough and well-reasoned consideration of this question in the literature – a secure recommended core habitat is *seventy-two times* larger than the four hectares used by FWS’ analysis and *four to eight times* farther from the nearest significant human facility. Consequently, the Primary Conservation Area (“PCA”) designated in the Proposed Rule and Conservation Strategy (Proposed Rule at 13184 (Figure 2)), is inadequately secure from human-bear or bear-livestock conflicts, and will not suffice as a core habitat for GYE grizzly bears.

**ii. GYE Grizzly Bear Habitat Will be Further
Fragmented by DMA/PCA Boundaries and Exposure
to Lethal Management**

FWS also failed to consider the ways in which the state management boundaries delineated in the Proposed Rule will further fragment GYE grizzly bear habitat. The Demographic Monitoring Area (“DMA”) – the lands within the perimeter located outside of the PCA – is the geographic area where state wildlife agencies in the States will monitor the grizzly bear population. Proposed Rule at 13184 (Figure 2), 13186-88. Outside of the DMA, bears will not be counted toward population objectives or discretionary mortality limits and will, as a result, be subjected to potentially unmitigated persecution. Yet, these outwardly dispersing individuals are vital for providing connections between the GYE population and other populations, maintaining genetic diversity, and preventing genetic drift and inbreeding depression.⁵

⁵ *Genetic diversity* increases a species’ chances of long-term survival because negative traits (such as inbreeding) become widespread within a population when that population is left to reproduce only with its own members. *Genetic drift* refers to a populations’ loss of genes,

In effect, the Proposed Rule draws two concentric circles around the PCA – the DMA, where bears will be subject to unacceptably high, even if theoretically limited, lethal management; and the zone outside the DMA, where no such limits apply. These twin lethal perimeters will function to lock grizzly bears inside the National Parks – the only area where they will be protected from human persecution (although still subject to its effects, as described in the next subsection) – and will foreclose the possibility of further dispersal.

Within the DMA, three criteria will inform grizzly bear management:

- a) 500 bears are maintained within the boundaries of the DMA with 48 breeding females with cubs.
- b) 16 of 18 bear management units (BMUs) will contain breeding females with cubs and no two BMUs will remain devoid of breeding females with cubs for a period of 6 years.
- c) Using a model, Chao2, limits on mortalities will be monitored for independent females, independent males, and dependent young.

As described above, the myriad food failures in prime grizzly bear habitat have forced grizzly bears to switch to a more meat-based diet – causing them to spread out on the landscape in order to find food and survive. The loss of flora and fauna upon which grizzly bears depend in Yellowstone and Grand Teton national parks, in part, explains why grizzly bears are dispersing in greater numbers from park lands to national forests lands, which are grazed by public lands permittees, to search for food. Because of ubiquitous livestock outside of park lands, record numbers of grizzly bears have had lethal encounters with humans, wolves, and other bears.⁶

The DMA’s artificial boundary is insufficient for two reasons: first, it fails to include all currently occupied grizzly bear habitat. Indeed, the IGBST suggests some *currently occupied* habitat is unsuitable for grizzly bears. Wyoming Plan at 10. This is illogical on its face and subjects the individuals living or immigrating outside the bounds of the DMA to unlimited persecution.

Second, bears are more likely than ever to disperse to areas outside of the PCA because their food sources are in decline. Ironically, the Proposed Rule notes that grizzly bears “are the most widely distributed bear species in the world” and capable of living in a variety of habitats, “from deserts to alpine mountains and everything in between” (Proposed Rule at 13178), yet it arbitrarily precludes grizzly bears from living beyond Yellowstone and Grand Teton national parks – even on national forest lands that surround the parks.

making a population less vital, more disease prone, and unable to overcome natural disasters. Mills and Allendorf 1996.

⁶ See *supra*, note 4.

c. Post-delisting Trophy Hunting Will Expose GYE Grizzly Bears to Overutilization for Commercial and Recreational Purposes

The States have already indicated their intent to commence a trophy hunting⁷ season if grizzly bears lose their federal protections, even though the best available science shows that this population cannot sustain recreational hunting (or associated increases in poaching). Pursuant to a tri-state Memorandum of Agreement (“MOA”), the States have provisionally allocated bears for the purposes of “discretionary mortality available for regulated harvest” within the DMA as follows: Wyoming may authorize hunting for 58% of the quota, Montana 34% and Idaho 8%. Moore et al. 2016. State-sanctioned trophy hunting will not only harm individuals; it is also unsustainable for the GYE population and the subspecies as a whole.

Several traits peculiar to the social structure and life cycle of grizzly bears make them particularly sensitive to hunting mortality. They are a large-bodied carnivore only sparsely populated across vast areas; they invest in few offspring; they provide extended parental care to their young; they have a tendency towards infanticide; their females limit reproduction and social stability promotes their resiliency. *See, e.g.,* Weaver et al. 1996, Wielgus et al. 2013, Creel et al. 2015, Wallach et al. 2015. Human persecution affects their social structure (Darimont et al. 2009, Wielgus et al. 2013, Bryan et al. 2014, Wallach et al. 2015) and harms their persistence (Wielgus et al. 2013, Zedrosser et al. 2013, Darimont et al. 2015). The consequence of these characteristics is that the effect of human persecution on grizzly bears is “super additive,” meaning that hunting kills result in mortality exceeding the simple 1:1 ratio contemplated in the Proposed Rule and state harvest plans, and generates pressures on the population that far exceed what would occur in nature (Wielgus et al. 2013, Darimont et al. 2015, Gosselin et al. 2015).

Hunting mortality has direct effects on population growth rates because of increased mortality, but also has devastating indirect effects such as disrupting the sex and age structure of a population (Wielgus et al. 2013, Gosselin et al. 2015). Gosselin et al. state: “In species with sexually selected infanticide (“SSI”), hunting may decrease juvenile survival by increasing male turnover.” These studies show that hunting mortality can harm social organization of species, because it promotes male turnover and thus increases sexually selected infanticide upon cubs of deceased males. This is especially true when – as here – carnivores are hunted as trophies, because trophy hunters tend to select for, and hunting quotas skew toward, males. Gosselin et al. 2015, at 1. “In species with SSI, harvesting males can have an indirect negative effect on the population by reducing juvenile survival.” Gosselin et al. 2015.

⁷ *Trophy hunting* is the practice of killing or pursuing with the intent to kill a grizzly bear (or other wild animal) where the primary motivation is to obtain the animal for display, in whole or in part, or for bragging rights.

Compounding this harm, females with cubs generally avoid males as a strategy of avoiding sexually-selected infanticide, often leading them to choose suboptimal habitats, including habitats in closer proximity to humans, leading to increased human-bear conflict. This also affects their diet quality and reduces their reproductive potential. McDonough and Christ 2012, Gosselin et al. 2015. Avoidance of males as a mechanism to avoid sexually-selected infanticide also ultimately leads to lower fecundity. Gosselin et al. 2015.

In addition to these social structure and infanticide impacts, trophy hunting will also harm the genetic constitution of the vulnerable GYE grizzly bear population. Because hunters tend to target the biggest and strongest males, trophy hunting removes these animals from the breeding pool and unnaturally selects for smaller or weaker animals. In this way, trophy hunting can decrease the genetic resilience necessary for GYE grizzly bears to be able to adapt and survive challenges such as climate change, and cause unnatural evolutionary impairments. These consequences have been studied and confirmed in a range of trophy-hunting contexts in the United States and abroad. Logan and Sweanor 2001, Allendorf and Hard 2009, Packer et al. 2009, Packer et al. 2011, Allendorf et al. 2008.

Native carnivore expert Dr. Robert Wielgus explains that trophy hunting grizzly bears will threaten the entire GYE population – including bears within Yellowstone and Grand Teton national parks that will not be directly exposed to hunting – because of the mortality “multiplier effect” resulting from the take of dominant males. He writes:

The Rule failed to consider the negative effects of grizzly bear hunting seasons on un-hunted bears within the national parks’ boundaries. Because park bears may be killed via hunting outside the parks, causing population disruption or decline within the parks, the bears should not be delisted.

Trophy hunting of older, male breeding carnivores is now widely accepted to result in increased sexually selected infanticide (SSI) of cubs by non-fathers, sexually segregated habitat use by females (females avoid new non-fathers), and reduced forging and reproductive success of females - by causing turnover of breeding males. This phenomenon has been studied for a variety of carnivores: for North American grizzly bears (Wielgus and Bunnell 1994b, a, Wielgus et al. 2001); for European brown bears (Swenson et al. 1997, Swenson et al. 2001a, Swenson et al. 2001b, Swenson 2003); for cougars (*Puma concolor*) (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a, Cooley et al. 2009b, Wielgus et al. 2013, Keehner et al. 2015a, Keehner et al. 2015b); for African lions (*Panthera leo*) (Packer et al. 2009, Packer et al. 2011); for African leopards (*Panthera pardus*) (Balme and AR 2012, Balme et al. 2013).

For *Ursus arctos*, Wielgus et al. (2001), Wielgus (2002), Swenson et al. (1997, 2001a, b) and Swenson (2003) demonstrated that trophy hunting of resident male North American grizzly bears and European brown bears (*Ursus arctos arctos*) corresponds with increased male turnover (compensatory immigration), increased sexually selected infanticide, and reduced female population growth. For protected park grizzly bears, Wielgus (2002) showed that trophy hunting of park fathers outside of protected parks resulted in increased infanticide, sexually segregated habitat use, and reduced female reproductive success within parks - because of increased turnover of fathers in the parks.

Because of these effects (infanticide, sexual segregation), hunting mortality of grizzly bears is not compensatory like in traditional game animals such as deer and elk (increased hunting = decreased natural mortality + increased reproduction = increased population growth = population stability). Rather, hunting mortality of grizzlies is *super-additive* or *multiplicative* (Wielgus et al. 2013, Gosselin et al. 2015) whereby increased hunting = increased natural mortality (infanticide) + decreased reproduction (sexual segregation) = decreased population growth = population decline. Since the current population growth rate in YNP [Yellowstone National Park] and GTNP [Grand Teton National Park] is unity (1.0), any additional hunting mortalities in the boundary zone will cause the park populations to decline.

Trophy hunting around YNP and GTNP will result in hunting-caused deaths of park fathers outside the parks, infanticide of cubs within the parks, sexual segregation into food-poor habitats by females within the parks, reduced reproductive success of females within the parks, and population declines. Because the states of ID, MT, and WY have not committed to plans that will prevent these impacts, the de-listing should not be allowed to proceed.⁸

Trophy hunting that will follow delisting will also cause a host of reproductive harms to female grizzlies. Hunting bears during their period of *hyperphagia* – which is contemplated under present state management proposals – is energetically costly to them as they shift their sleeping patterns and become more nocturnal to avoid being hunted. Ordiz et al. 2012. This can negatively influence a lifetime of reproductive success. Zedrosser et al. 2013. Grizzly bear biologists have made three findings relative to fecundity: 1) body mass of a female grizzly bear in early life is important in all measures of fitness; 2) yearlings that remain with their mothers have greater survival than those that did not; 3) longevity is important factor in lifetime reproductive success. Zedrosser et al. 2013. To compare, before the industrial era, women who had low birth weights and stunted early growth tended

⁸ Analysis of Proposed Rule by Professor Robert Wielgus, Washington State University (Apr. 29, 2016) (on file with The HSUS).

to produce small babies that had a higher incidence of mortality. Zedrosser et al. 2013 (citing Lummaa and Clutton-Brock 2002).

The Proposed Rule allows that States could permit hunting female bears two years of age or older. This is insufficient to protect females of breeding age and will generate additional super-additive mortality – especially if a hunted female has dependent cubs. The Proposed Rule suggests that states should consider that timing and location of hunting seasons to “minimize” the mortality of independent age females. But this suggestion is ineffective because (a) it is not a legally binding requirement; and in any case (b) cannot be achieved, since the timing and location of hunts cannot reliably be manipulated to avoid the take of mature females. The Proposed Rule itself suggests that grizzly bears are not territorial, but rather bears maintain home ranges that overlap. Proposed Rule at 13176-77. Females’ home ranges overlap with multiple other females, whereas a dominant male will typically have a larger home range that will encompass the home ranges of several females. And it will be nearly impossible for state managers to predict when females with cubs will either go into the den for hibernation or emerge from the den in the springtime – as denning times are highly variable depending on food availability and weather conditions. This variability will only increase as the GYE climate continues to change.

The currently proposed Wyoming management plan falsely asserts that spring hunting can be done so as to spare mothers with cubs because nursing mothers are the last segment of the population to emerge from dens. However, Tom Beck, a prominent bear researcher formerly employed by Colorado Division of Wildlife – along with a cohort of five other Western state wildlife managers – warns that despite studies indicating that males emerge from dens earlier than females, the time differential is merely two or three weeks. Beck et al. 1995. These findings have been replicated in numerous other black bear denning studies, which are applicable to grizzly bears.⁹ It is well-established that the chronology of den emergence overlaps between sex and age classes of bears.

The Proposed Rule even admits that the time mothers spend in the den with their newly born cubs is highly variable – from three to four months. Proposed Rule at 13177. The best available science shows that spring hunting – which will be

⁹ In an Alaskan study, Schwartz et al. (1987) found that “no significant difference” between the average den-emergence dates for their study bears. Beckmann and Berger (2003) found that while adult males exited dens before other sex and age classes in March to early April, adult females with cubs exited last, also starting in early April. Black bears in northern New Mexico entered and left their dens at different times depending on their sex, but not so for bears in the southern part of the state, whose denning chronology was the same for both sexes. Inman et al. 2007. Den emergence and hunting is well-studied in black bears, and the conclusions from those studies are applicable as grizzly bear den emergence is also highly variable depending on the year. Haroldson et al. 2002.

allowable after delisting, and has already been proposed in Montana – simply cannot be calibrated to avoid the take of mother grizzly bears.

The consequences of taking a mother with cubs are dire. Grizzly bear mothers spend considerable time raising her cubs, from 2 to 4 years. Deecke 2012. Thus, complex behaviors, including foraging strategies, are transferred from mother to offspring. Deecke 2012. Without the care of their mothers for up to 4 years, cubs are exposed to a greater likelihood of mortality. ESA protections are necessary to avoid the likely orphaning of newly born grizzly bear cubs.

The *manner* of take authorized by the States may also have deleterious impacts on individual grizzly bears and the GYE population at large. FWS asserts that state wildlife agencies will not permit the trapping of grizzly bears. Proposed Rule at 13201. But no legally binding regulation exists in any of the States that would prevent this; rather, States will be granted broad discretion to manage grizzly bears through their own rulemaking processes – and *total* discretion in areas outside the DMA. None of the state mechanisms contemplated in the Proposed Rule would prevent states from allowing trapping. And even if trapping of grizzly bears were not permitted by any of the states, removal of ESA protections would insulate trappers from ESA Section 9 liability for injury and death caused to grizzly bears by traps set for other animals – a key incentive for taking precautions to prevent incidental take.

Trapping is extraordinarily harmful to the welfare of individual bears and can also have population-wide effects by damaging reproductive capacity. Trapping bears can result in capture myopathy, that is, damage to muscles – both skeletal and cardiac – as a result of extreme exertion by the trapped bear that can result in injuries and even death. Cattet et al. 2008, at 984 (“. . . we found evidence that: capture caused significant muscle injury in some bears, especially when captured by leghold snare; movement rates of many bears were affected for weeks after capture; and body condition of bears was negatively affected by capture, an effect directly proportional to the number of times a bear was captured and more evident with age.”) Authors found that snared grizzly and black bears suffered “significant, if not severe” muscle injuries while straining to get out of traps. One grizzly bear they captured died 10 days after release. Cattet et al. (2008: 985) note: “With minor injury, skeletal muscles can repair and regenerate within 4-8 weeks With more severe or extensive injury, pathological changes to muscle structure (necrosis, mineralization, and atrophy) can affect strength and range of motion for a much longer duration” After capture, both black and grizzly bears in that study reduced their movements for 3-6 weeks, which can affect survivability if bears are unable to forage, particularly during the time of hyperphagia. Worse, handling and capturing bears can “affect reproduction and lean body growth negatively, especially in bears captured multiple times.” Cattet et al. 2008: 986.

Baiting and hounding of bears, both of which may also occur in post-delisting state regulations, also carry a host of individual- and population-level harms. Baiting has been proven to increase human habituation, intraspecific strife on small bears, disease transmission (especially rabies), and bait toxicity to bears and non-target wildlife. Beck et al. 1995, Dunkley and Cattet 2003, Inslerman et al. 2006, Sidor 2015. Hounding bears causes orphaning of dependent cubs, strife between bears and dogs, trespass issues on private or national park lands, sex identification problems, mortalities to bears or dogs from overheating during pursuit, and conflicts between hounds and wolves. Beck et al. 1995, Inman and Vaughan 2002, Hristienko and McDonald 2007, Bump et al. 2013.

In sum, the best available science proves that trophy hunting will have deleterious direct and indirect effects on the population size, dynamics, and genetic health of the GYE grizzly bears. These impacts were not adequately accounted for in the Proposed Rule, which oversimplifies the complex and likely devastating impacts of trophy hunting on GYE grizzly bears.

d. GYE Grizzly Bears Are Increasingly Threatened by Predation and Disease

1. Intra- and Inter-specific Predation on Cubs and Small Bears is Increasing

The Proposed Rule notes that adult grizzly bears kill cubs, subadults and even other adult bears and, since 1995, wolves have even killed cubs and at least one female grizzly bear (Proposed Rule at 13205). The extent of wolf predation on grizzly bear cubs is unknown because it is difficult, if not impossible, to count.

Biologists have noted that grizzly bear cub production has declined (van Manen et al. 2016)—perhaps because of more predation on cubs by wolves and other bears as a result of their new and increasing dependence upon a meat-based diet, which (as described in more detail in section (II)(a)(1) above) puts them into closer proximity with other predators (Mattson Critique, discussion 17; Fig. 17.1).

This already worrying trend can be expected to continue if post-delisting trophy hunting is allowed. As discussed in section (II)(c) above, studies on a number of large carnivores, including grizzly bears, have demonstrated that removal of adult males by trophy hunting disrupts social dynamics, leading to increased intraspecific strife on females and their cubs (including infanticide), reduced female population growth, and decline in population-wide genetic fitness.

2. Climate Change Will Generate Increased Risk of Disease Outbreaks

While the Proposed Rule observes that widespread disease has historically not been documented in GYE grizzly bears, this may radically change because of climate change. A recent study in Europe observed that tick-borne pathogens may pose a novel risk to grizzly bears as carrier species migrate (Paillard et al. 2015). This 18-year study of Scandinavian brown bears (*Ursus arctos*) showed that ticks and tick-borne diseases are moving northward as a result of a warming climate (Paillard et al. 2015). This trend is likely already occurring with many parasites in the United States. Indeed, ticks readily feed on bears, including on black bears (*Ursus americanus*), a well-studied phenomenon in the U.S. (Paillard et al. 2015 citing Leydet and Liang (2013) and others). According to the U.S Center for Disease Control and Prevention, the Rocky Mountain region is now a common area for infected ticks.¹⁰

The Proposed Rule failed to consider this science and instead arbitrarily dismissed the likelihood of parasite-borne diseases posing a growing threat to GYE grizzly bears. ESA protections must remain until this risk can be adequately accounted for.

e. Current and Anticipated State Regulatory Mechanisms are Woefully Inadequate to Protect the GYE Grizzly Bears Post-Delisting

Under the Proposed Rule, the States will be the sole authorities responsible for managing grizzly bear populations on approximately eighty percent of the lands within the GYE grizzly bear range – essentially the entire land area outside of Yellowstone and Grand Teton national parks. It is therefore no exaggeration to observe that the health and stability of GYE grizzly bears post-delisting will rest on the judgment of these States’ legislatures and regulatory agencies. The Proposed Rule correctly emphasizes the importance of protections enshrined by State “law and regulation” that are “legally binding” and “enforceable” in its discussion of the adequacy of state regulatory mechanisms. Proposed Rule at 13210-11.

Where the Proposed Rule falters, however, is in its reliance on the mere promise of future state regulatory mechanisms that are not yet in place – mechanisms that, in many cases, have yet to even *begin* making their way through mandatory state administrative processes. And even if each and every state law and regulation were securely in place prior to delisting, these mechanisms will fail to protect GYE grizzly bears because they lack adequate enforcement mechanisms and will allow for unsustainable trophy hunting. In short, the proposed state regulatory mechanisms fail to satisfy both the ESA’s standard for the “adequacy of existing regulatory mechanisms,” 16 U.S.C §1533(a)(1)(D), and FWS’ own stated commitment to meaningful state protections in this particular case. Proposed Rule at 13211. FWS must withdraw the Proposed Rule until such time as it can evaluate – and the public

¹⁰ <http://www.cdc.gov/niosh/topics/tick-borne/>.

can comment on – the adequacy of actually “*existing* regulatory mechanisms,” 16 U.S.C. § 1533(a)(D) (emphasis added).

1. Delisting is Inappropriate Because No Legally Binding State Protections Currently Exist

Delisting is premature because the baseline state regulatory mechanisms that FWS claims would be “adequate to protect the GYE grizzly bear population” (Proposed Rule at 13211) do not yet exist, and in some cases have not even been proposed. Indeed, it is telling that most of the discussion of state regulatory mechanisms in the Proposed Rule takes place in the future tense: e.g., “grizzly bears within the GYE DPS *will be* incorporated into existing game species management plans,” “The regulatory mechanism *proposed* by States . . . *would* govern potential hunting seasons We expect that these State statutory and regulatory changes *will be* made within the next several months.” Proposed Rule at 13210. Yet at the time of the closing of this comment period (two months after the publication of the Proposed Rule) *none* of the three States have made the necessary statutory and regulatory changes that FWS intends to rely on: implementation of specific population goals, plans for census-taking, population estimation methodologies, and allowable total mortality and mortality rate limits; finalization and ratification of an interstate MOA to enforce these limits among the States; and promulgation of state regulations regarding, in relevant part, hunting seasons, hunting zones, handling of nuisance bears, and habitat management on non-Federal lands. Proposed Rule at 13188 (Table 1), 13200-04, 13210-11.

- **Idaho.** Idaho has yet to implement any of the regulatory requirements described above. Its current state management plan, last revised in 2002, does not contain these mechanisms – and in any case, does not itself carry the binding force of law or regulation. A revision of this management plan may therefore be necessary. More importantly, Idaho has also yet to ratify the MOA that has provisionally been negotiated by the States or promulgate *any* regulations implementing the state requirements of the federal Conservation Strategy, including regulations related to commercial and recreational hunting (seasons, quotas, zones, allowable means and manner of take), habitat management, or updated nuisance bear guidelines. The Idaho Fish and Game Commission would need to proceed through administrative rulemaking processes – including, for some of the required regulations, statutorily mandated notice and public comment¹¹ – prior to such regulations going into effect. At this time, no such regulation has even been *proposed*, let alone finalized and published. Furthermore, additional formal rulemaking

¹¹ See I.C. § 67-5222.

may be required in order to classify grizzly bears as a game species, as its status under state regulation is presently unclear.¹²

- **Montana.** Montana, like Idaho, has also not implemented any of the regulatory requirements described above. On May 4, 2016 Montana’s Fish, Wildlife, and Parks Department published a *preliminary* proposal to open rulemaking on the MOA and a set of regulations allowing for trophy hunting seasons (including, notably, a spring hunt) on delisted grizzly bears. These proposals do not include a revision of the state’s management plan, which was last updated in 2013. This pre-proposal will be voted on at the Montana Fish & Game Commission’s May 12, 2016 meeting (two days after the comment period closes on the Proposed Rule) and, if it is approved, will only then be subject to a formal state rulemaking process, including notice and public comment, culminating in possible finalization.
- **Wyoming.** Of the three States, Wyoming has to date taken the most steps toward implementing necessary state regulatory mechanisms. But Wyoming still has not formally implemented any of the requirements detailed in the Proposed Rule. Following a truncated notice period,¹³ the Wyoming Fish and Game Commission is scheduled to vote on finalizing two proposals at its May 11, 2016 meeting (one day after the comment period closes on the Proposed Rule): the MOA and a set of revisions to its state management plan. No regulations related to commercial and recreational hunting (seasons, quotas, zones, allowable means and manner of take), habitat management, or updated nuisance bear guidelines have been proposed, and any such proposals would necessarily proceed through formal state administrative rulemaking processes.

In sum, FWS appears to have been overly optimistic in its March 11, 2016 prediction that all necessary “[s]tate statutory and regulatory changes will be made within the next several months.” Proposed Rule at 13210. In fact, at this time, *none* of those statutory and regulatory changes have been made. Since each state will need to

¹² For instance, one section of the Idaho Administrative Code lists grizzly bears as a game species – a pre-requisite to the opening of hunting seasons and certain protections afforded game species by state law – but another does not. *Compare* Idaho Admin. Code § 13.01.06.100 (Including grizzly bear on list of “big game animals”) *with* Idaho Admin. Code § 13.01.08.010.01 (Omitting grizzly bear on list of “big game animals”).

¹³ This process, which provided only a 30-day comment period was provided and scheduled the first public hearing 15 days from the announcement and publication of the proposals, may have violated the Wyoming Administrative Procedure Act’s minimum notice period requirements, which require a minimum of 45 days for public comment on rulemaking, and further requires that any public hearings on proposed rules be scheduled not less than 45 days from the initial notice of the proposal. W.S. § 16-3-103(a)(i),(ii).

engage formal rulemaking processes in order to implement these changes, some of which have yet to begin, it is presently impossible to predict if and when they will be finalized. And because these regulations remain at the proposal or pre-proposal stage, it is uncertain what the form and content of the regulations will be if and when they are eventually finalized. Expecting meaningful public comment on the Proposed Rule when the post-delisting state regulatory regime is still in such an embryonic stage is thus an exercise in speculation at best, and futility at worst. Therefore, FWS must, to comply with the ESA and Administrative Procedure Act, withdraw the Proposed Rule until stakeholders, experts, and the general public can provide meaningful input on actually “existing regulatory mechanisms,” 16 U.S.C. § 1533(a)(D) (emphasis added), rather than guessing at what such mechanisms *might* eventually be.

More importantly, to delist GYE grizzly bears in reliance on the mere promise of these future management plans and regulations would violate the ESA as it has been routinely interpreted by federal courts. The plain language of the ESA mandates consideration of “existing,” (cf. anticipated) “regulatory mechanisms” (cf. non-binding plans and agreements). 16 U.S.C. § 1533(a)(D). Federal courts – and FWS itself – have interpreted this language as requiring a state protection to have the binding force of law before it may be considered under § 1533(a)(D). *See Defenders of Wildlife v. Jewell*, 68 F. Supp.3d 193, 207 (D.D.C. 2014) (“The Service cannot rely solely on an unenforceable promise as a basis to delist a species”); *see also Colo. River Cutthroat Trout v. Salazar*, 898 F. Supp. 2d 191, 208 (D.D.C. 2012) (“FWS cannot rely on promised and unenforceable conservation agreements in evaluating existing regulatory mechanisms”) (internal citation omitted); *In re Polar Bear ESA Listing & 4(d) Rule Litig.*, 794 F. Supp. 2d 65, 103 (D.D.C. 2011) (“voluntary agreements” are not “regulatory mechanisms”); *Or. Nat. Res. Council v. Daley*, 6 F.Supp 2d 1139, 1155 (D. Or. 1998) (“regulatory mechanism” must be legally binding and include “some method of enforcing compliance”); FWS & NAT’L MARINE FISHERIES SERV., Final Policy for Evaluation of Conservation Efforts When Making Listing Decisions, 68 Fed. Reg. 15100, 15115 (Mar. 28, 2003) (“regulatory mechanisms” must be “laws, regulations, [or] ordinances”) (hereinafter “Conservation Effort Policy”).

The state protections described and relied upon in the Proposed Rule thus do not meet the legal standard of an “existing regulatory mechanism” for two reasons. First, even as to those proposals that may eventually obtain the force of law by being formally promulgated by state commissions, they are not yet “existing” mechanisms and remain merely “promised” protections. *See, e.g., Defenders of Wildlife*, 68 F. Supp.3d at 207; *Colo. River Cutthroat Trout*, 898 F. Supp. 2d at 208. Second, those protections that are contained in current or anticipated future state management plans, rather than in statutes or regulations, may not legally be considered “regulatory mechanisms.” *See, e.g., Conservation Effort Policy* at 15115; *In re Polar*

Bear ESA Listing, 794 F. Supp. 2d at 103. In short, at this time, legally binding mechanisms to protect grizzly bears at the state level – covering 80% of the PCA – are functionally nil. The Proposed Rule instead relies on a package of “mechanisms” none of which are currently “existing” and most of which are not “regulatory” under federal case law. 16 U.S.C. § 1533(a)(D). ESA listing for GYE grizzly bears therefore remains necessary.

Finally, it is arbitrary and capricious for FWS to rely on non-binding or not-yet-implemented state regulatory mechanisms. First, the Proposed Rule clearly commits to only finalizing the delisting “if the appropriate regulatory mechanisms are adopted and maintained by the States in enforceable regulations before this proposed rule becomes final.” Proposed Rule at 13211. We expect that FWS will follow through on this stated commitment – to do otherwise would be an abrupt change in position for which the public was not given an opportunity to comment. Second, Wyoming – the state that controls the largest share of the proposed DPS, and to which most of the GYE hunting quota will likely be allocated – has empirically done a poor job of following through on non-binding commitments to wildlife protection in the wake of federal delisting. *See Defenders of Wildlife*, 68 F. Supp.3d at 203-210 (overturning delisting rule on the basis of Wyoming’s failure to manage gray wolf population in accordance with non-binding commitments made to FWS prior to delisting). In light of this history of inconsistent adherence to post-delisting management commitments, the APA requires that *adequate* and *binding* state protections exist *before* FWS may take any final action.

2. The State Regulatory Mechanisms Contemplated by the Proposed Rule Would be Inadequate Even If Implemented

Even if all of the state regulatory mechanisms contemplated by the Proposed Rule were enacted by the States exactly as FWS hypothesizes, they would not constitute adequate regulatory mechanisms within the meaning of the ESA. The state schemes as articulated in the Proposed Rule are inadequate because they lack meaningful enforcement mechanisms and allow for trophy hunting that will have deleterious consequences on the health of the GYE grizzly bear population.

First, fundamental components of the state regulatory scheme relied on by FWS are – by design – entirely unenforceable. The interstate MOA – the most recent draft of which, dated December 4, 2015, is attached herewith as Attachment B – is meant to “to provide clarity and transparency as to how the states will coordinate with each other and federal land managers to ensure maintenance of the recovered bear population,” including provisions regarding interstate “allocation of discretionary mortality.” Attachment B, at 1 (States’ cover letter to FWS Director Dan Ashe) (hereinafter “Draft MOA”). The Draft MOA describes the process by which the States will coordinate with the IGBST to monitor and annually estimate the GYE

bear population, establishes the algorithm by which allowable “discretionary mortality” (bears that may be commercially or recreationally hunted) is derived from that population number, and allocates that quota among the States proportionally based on the percent of the non-NPS DMA lands each controls. In sum, the MOA is the primary mechanism by which the States intend to implement and coordinate the technical population management requirements set out in the Proposed Rule. Proposed Rule at 13188 (Table 1), 13200-04 (Tables 2, 3), 13210-11.

Yet despite its surface-level formality, the MOA is, in legal effect, little more than an IOU. It should not – and legally *cannot* – be relied upon by FWS for several reasons. First, as with the individual state mechanisms discussed above, the MOA has yet to be formally ratified by any of the three States, and has yet to even be formally proposed by Montana and Idaho.¹⁴ Because the MOA must proceed through individual state rulemaking processes, it is far from certain if – let alone when – it will be ratified in its present form by all signatory parties. Second, even assuming the MOA is ratified by all three States in its current iteration, it contains baked-in provisions that render it ineffective as a legal document:

- It contains no financial or other penalties for breach, meaning there is no incentive for States to comply with the agreement and no recourse if they do not.
- It allows for any State signatory to unilaterally withdraw from the MOA on a mere thirty days written notice, with no penalty for doing so. Draft MOA at 8-9 (Section VII).
- It expressly provides no right of action for private citizens or the federal government to enforce the provisions of the agreement, such that the only parties with standing to vindicate its terms are the signatory States themselves. Draft MOA at 9 (Section IX).
- It includes a provision expressly reserving each State’s sovereign immunity, likely rendering the parties immune from suit in the event of a breach. Draft MOA at 9 (Section XI).
- It expressly provides that it does not obligate any funds on behalf of any signatory, leaving the financing of the many state monitoring and management obligations it imposes unclear and at the discretion of individual state legislatures. Draft MOA at 8 (Section VI).

¹⁴ At the time of submission of this Comment, the Wyoming Fish and Game Commission has solicited public comment on the MOA (though arguably in violation of its state Administrative Procedure Act) and is scheduled to approve it at its May 11 meeting. The Montana Department of Fish, Wildlife, and Parks has issued a pre-proposal notice that will be voted on at the Montana Fish and Wildlife Commission’s May 12 meeting – only after which, if it is approved, it will be opened to public comment and a formal state rulemaking process culminating in possible final approval.

- It allows States complete discretion as to the management of grizzly bears *outside* the DMA portion of the GYE, allowing for unlimited trophy hunting above and beyond the discretionary mortality quotas set by the MOA. Draft MOA at 8 (Section IV(7)).

In light of these manifold enforcement and accountability loopholes, the MOA (assuming it is adopted) could not in good faith be read as a guarantee sufficiently binding to justify tying it to the fate of America’s most iconic predator. *See Or. Nat. Res. Council*, 6 F. Supp 2d at 1155 (D. Or. 1998) (“regulatory mechanism” must be legally binding and include “some method of enforcing compliance”). And recent experience with another delisted bear population – the Florida black bear, where more than *ten percent* of the fragile population was killed in a single hunting season following an abrupt removal of state protections¹⁵ – counsels caution.

Finally, as discussed above in subsection (II)(c), the recreational trophy hunting allowed for by the present iteration of the MOA would prove devastating to the GYE grizzly populations. The Proposed Rule does not adequately consider the best available science as to the super-additive and multiplicative effects of sport hunting on this fragile population, including the increase in intraspecific mortality, disruption in social dynamics, increase in human-bear conflicts, and decline in genetic fitness of described above. Because the ESA requires the FWS to consider the adequacy of state regulatory mechanisms – which in this case, will provided for trophy hunting – prior to delisting, FWS cannot simply ignore these impacts, or shift responsibility to state managers at this time.

In sum, the state management framework described in the Proposed Rule cannot legally or factually be relied upon to protect this fragile population were it to be delisted. Unless and until a substantially more robust and enforceable scheme to protect GYE grizzly bears is devised and implemented by the States, Section 4(a)(1)(D) of the ESA requires that they remain listed as threatened.

f. GYE Grizzly Bears Remain Threatened by Other Forms of Human-caused Mortality

Since 1994, the known number of grizzly bears killed each year by probable human causes has increased dramatically. The IGBST counted a record 61 individuals in 2015 – most were a result of human-bear conflicts because of grizzly bears’ natural resources have been depleted – because of anthropogenic causes.

1. Poaching

¹⁵ *See* Center for Biological Diversity *et al.*, Petition to List the Florida Black Bear Under the Endangered Species Act (submitted to FWS March 17, 2016).

The Proposed Rule does not adequately account for poaching in a matrix that would hand trophy hunting over to the States after FWS takes federal protections away. While the Proposed Rule suggests that: “we do not expect poaching to significantly increase if this proposed action is finalized” because states and tribal entities will enforce poaching laws (Proposed Rule at 13205), the supposition is contrary to the best available science.

Poaching is not diminished when an animal becomes a designated game species. Treves 2009. Poaching is a major mortality factor in large carnivore populations which prevents species recovery particularly if the species occurs at low densities. Andren et al. 2006. Poaching, even in small numbers, can harm populations if the species occurs in low densities. Saether et al. 2010. Approximately half to two-thirds of grizzly bears killed by humans go unreported. Schwartz et al. 2003. Without radio collars, grizzly bear management agencies would be unaware of one-half (46 to 51 percent) of the killings that occur therefore managers need to incorporate unreported killings into their matrix if they hold hunting seasons. McLellan et al. 1999. Researchers in Washington discovered that approximately 20% of hunters in Washington failed to report the black bear they killed. Koehler and Pierce 2005. Additionally almost 25% of bears killed by hunters were lost in vegetation. Koehler and Pierce 2005. Park boundaries are the places where grizzly bears experience high rates of mortality compared to the areas where they are fully protected. McLellan et al. 1999. Furthermore, The HSUS has tracked poaching numbers of gray wolves by state during the periods when wolves were delisted. Minnesota wildlife managers tracked zero poachers during the period when the Western Great Lakes population of gray wolves lost their federal protections and were subject to hunting.¹⁶ In short, studies indicate that if states are permitted to hold a trophy hunting season on grizzly bears, far more bears will be killed by poachers than if they retain their federal ESA protections.

2. Other Human-Caused Mortality

Additionally, the Proposed Rule fails to account for the dramatic increase in other forms of human-caused mortality from 1990-2015. In 2015, the IGBST counted a record 61 total grizzly bear mortalities – only three of whom died from natural causes – even as grizzly bears retain their federal protections.¹⁷ The majority of grizzly bear mortalities come from “management” removals. Wyoming Game and Fish Department 2016. These stem from human-caused problems such as poor domestic animal husbandry practices, unguarded apiaries, or exposed human food

¹⁶ Personal communication between DNR Steve Merchant and Wendy Keefover of The HSUS (Jan. 15, 2015) (on file with The HSUS).

¹⁷ <http://nrmssc.usgs.gov/science/igbst/2015mort>. See also Wyoming Plan.

sources including bird seed, ripening fruits, unsecured garbage, and barbeque grills.¹⁸

III. Conclusion

The best available science as described in this Comment, the critique attached as Attachment A, and the studies included herewith demonstrate the GYE grizzly bears remain under dire threat such that delisting them would be premature and in violation of the ESA. Because the Proposed Rule violates both the procedural and substantive requirements of the ESA, FWS must withdraw it. Only if, and when, the best available science supports designation of a GYE DPS and subsequent delisting of this DPS, and state authorities have developed comprehensive and enforceable regulatory schemes to protect grizzly bears from extinction, may FWS legally propose to delist GYE grizzly bears.

Thank you for this opportunity to comment.

Sincerely,



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¹⁸ Researchers have found that hunting black bears does not lesson human-bear conflicts, because hunters target the wrong animals (Obbard et al. 2014).

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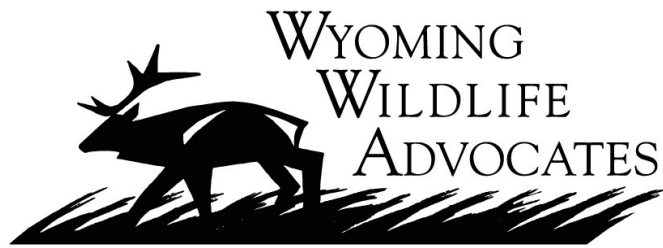
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Attachment A

Dr. David Mattson, Comments on the Proposed Rule (“Mattson Critique”)



David J. Mattson, Ph.D.

Wyoming Wildlife Advocates

Comments on the

US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227

And Related Materials

May 5, 2016

Introduction

On behalf of Wyoming Wildlife Advocates, this package of materials constitutes my review of the Rule and related materials (hereafter the Rule) issued by the US Fish & Wildlife Service (the Service) covering a proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA). The Rule itself was published in the Federal Register 81(48): 13174-13227; I obtained additional related materials from the Service's web site under Docket no. FWS-R6-ES-2016-0042: FXES111309000000C6-156-FF09E42000. These additional materials include the draft 2016 Conservation Strategy plus appendices (hereafter the CS) and the draft Grizzly Bear Recovery Plan Supplement: Revised Demographic Criteria (hereafter the RP).

Together, these materials comprise an astounding 675 plus pages (not counting cover pages), of which 54 pages are triple column, 9-point font, with a provision in the Rule for a mere 60 days within which to submit any comments. Up front, this allocation of such limited time to come to terms with such a large amount of highly complicated materials defies any explanation that invokes a genuine interest on the part of the Service in revision and improvement. That being said, my intent here is provide comments and critiques in hopes that the Service will genuinely engage with the substance of what I offer.

The package of materials assembled by the Service in support of its proposed Rule clearly represents a huge effort on the part of what I am sure are well-intentioned people. However, I see room for major improvement ranging from revision of framing concepts, to inclusion of major bodies of currently neglected research, to improved interpretation of the science that is referenced, to remedy of the many points of internal illogic. My comments cover this entire spectrum.

My Credentials

I am currently Lecturer and Visiting Senior Scientist at the Yale School of Forestry and Environmental Studies, Adjunct Faculty at Northern Arizona University, Science Advisor for Wyoming Wildlife Advocates, and Research

My review adheres to two sets of standards invoked by the Service on pages 13175 and 13176 of the Rule; first, the conventional standard of the ESA requiring use of "the best scientific and commercial information available," and, second, a purported desire on the part of the Service to insure that the Rule is "based on scientifically sound data, assumptions, and analysis." Tacit to this second set of standards is a laudable recognition on the part of the Service that the scientific information most recently published in a scientific journal can, in fact, be junk; hence a need to consider the very merits of this corpus of science, including the nature of the data used, the veracity of analyses employed, and the validity of interpretations, not only in the science products themselves, but also by the Service in application of the science to this Rule.

I also assume in my review that the best available science includes all publicly available data or information of direct relevance to the soundness of this Rule, subject to the same kinds of summaries and interpretations employed by the Service, and regardless of whether it is included in a peer-reviewed journal. For example, I draw heavily on graphic representation and simple statistical analyses of summary data published by the Interagency Grizzly Bear Study Team (IGBST). I also draw at times on other publicly available databases. This approach is based, in turn, on the assumption that there is good faith on the part of the Service—along with a genuine interest in improvement—rather than a focus on dismissing inconvenient input on the basis of some legalistic or less-than-logical technicalities.

My review that follows is organized by numbered main topics with subtopics within, each highlighted in green. The references cited in my comments are in **Attachment 1**.

Associate with the Northern Rockies Conservation Cooperative. My former positions, prior to retirement from the U.S. Geological Survey, included Research Wildlife Biologist, Leader of the Colorado Plateau

Research Station, and Western Field Director of the MIT-USGS Science Impact Collaborative, all with the USGS. I hold degrees in Forest Resource Management and Forest Ecology. My doctorate is in Wildlife Resource Management from the University of Idaho.

I have studied large carnivores for over 30 years. This research has included the incorporation of ecological information from mountain lions and grizzly bears into demographic, habitat, and risk management models as well as investigations of foraging, predation, and relations with humans. My human-dimensions research spans nearly 23 years and has focused on social, political, and organizational dynamics that shape policies and practices of carnivore and other conservation programs. As part of this focus I routinely teach classes on relations between science and policy. My research has been reported in over 120 peer-reviewed publications, including work featured in *Science* and *Ecology* and as

part of invited talks at the Smithsonian, American Museum of Natural History, the American Institute of Biological Sciences, and International Conferences on Bear Research and Management.

Of more direct relevance to these comments, I have studied grizzly bears in the Yellowstone ecosystem since 1979. I was part of the Interagency Grizzly Bear Study Team 1979-1993 and held primary responsibility for field investigations of the IGBST between 1984 and 1993. During this 16- year period I spent most of March-October documenting grizzly bear foraging behavior and involved in other related field projects. My grizzly bear-focused research resulted in over 60 publications, including several that are considered classics in the field of bear research. I continue to closely follow grizzly bear research in the Yellowstone ecosystem with an interest in improving not only the science, but also the use of scientific results in authoritative decision-making.

1. Given current monopolistic scientific arrangements, the Service should use a much more cautious tone when invoking IGBST science in the Rule and remove what is currently a pattern of systematically inflated claims based on this body of science. They also need to give serious consideration to patterns of evidence that call into question IGBST science, many of which are described in this review.

1.1. Virtually none of the most recent science published in peer-reviewed journals by the IGBST and used by the Service in this Rule is reliable.

This problem follows from the simple fact that the IGBST, in concert with the Service, has maintained a monopoly on virtually all of the data of direct relevance to the Rule. There is only one Yellowstone grizzly bear population and only one set of data that has been collected from this population; and none of these data, but a pittance, have been available to any researchers or research teams other than the IGBST and those scientists whom the Team has invited to collaborate. A monopoly such as this debars replication, disallows alternative models and hypotheses, provides ample scope for bias, and cannot be corrected by peer review (see my following point).

Transparency and open access to data and/or to relevant systems is at the core of scientific advancement (e.g., Popper 1959, Merton 1973, Pickering 1992, Maxwell 1998, Losee 2004, and many more). There is no substitute or sufficient remedy when such conditions are lacking. In the absence of ample opportunity for others to independently check, test, replicate, contest, and advance a body of research, those who enjoy a monopoly predictably fall prey to well-documented phenomena, including confirmation bias and groupthink, especially when they are part of a closed or mostly closed research team. They can also more easily fall prey to political influence and the sway of money, especially when there are those involved in crafting or internally reviewing the research who have an outside vested interest, and doubly so when such people provide substantial funds. All of this holds for the IGSBT and the science it has produced during the last decade, which is the purported foundation for this Rule.

These intrinsic problems are further amplified by the fact that most of the science produced by the IGBST and invoked by the Service entails complex models and

complex assumption-ridden statistical methods. Such is the case for all of the results germane to judging the demographic and genetic plight of Yellowstone's grizzly bears. Yet it is well known to even half-way thoughtful scientists that there is no one correct model, and that model-building is perhaps the most vagarious and bias prone of scientific undertakings (see Point 4.2 below). The best we can collectively hope for is that a range of relevant models are produced by as many truly independent researchers as possible for collective deliberations. Unfortunately, what we have is the opposite of this: a closed enterprise under IGBST and Service auspices, privileged with fielding a few chosen models produced under predictably biasing circumstances. Again, as I describe in my next key point, no amount of peer review can correct for this.

I anticipate that the Service's response to this critique will be to list all of the scientists who have been invited by the Service and the IGBST to collaborate on scientific undertakings. Such a list would be largely irrelevant to the basic point I make here, which is that scientific progress and reliability require free and unhindered access to systems and/or data for use by independent investigators as part of independent inquiry.

There are potentially several ways to interpret what appear to be patterns of systematic bias in public statements made by IGBST scientist—and patterns there are. But there is little doubt about the highly problematic structural configurations of the environment within which IGBST scientists have produced the science relied upon disproportionately by the Service in this rule, and which virtually guarantee the production of unreliable science. Put another way, the burden should be on the Service to articulate a compelling argument for how and why a veritable monopoly on the relevant scientific enterprise guaranteed or even increased the odds of reliable scientific outcomes.

1.2. Peer review is unlikely to detect much less correct for bias in IGBST science introduced by monopolistic arrangements.

The IGBST operates under the auspices and authority of the US Geological Survey (USGS). In its various policy documents, the USGS makes many claims regarding the efficacies of peer review, including the assertion that “peer review...insures the scientific quality of USGS information (USGS Manual, 502.4, Fundamental Science Practices) and “peer review, as cornerstone of scientific practice, validates and ensures the quality of published USGS science” (USGS Manual, 502.3, Fundamental Science Practices). It is these claims that apparently undergird the Service’s and the IGBST’s defense of a monopolistic scientific enterprise. In keeping with these policy statements by USGS, the Service and IGBST commonly claim in public that peer review will detect error and ensure, if not guarantee, the quality and reliability of the IGBST’s science. In fact, these assumptions appear to be behind the Service’s elicitation of peer review by three select reviewers as a presumed corrective for error during further development of the Rule.

Put bluntly, the claims made on behalf of peer review by the Service, USGS, and IGBST are not empirically substantiated. The corpus of scientific inquiry into the efficacies and problems of peer review (e.g., Burnham 1990, Armstrong 1997, Campanario 1998, Bacchetti 2002, Biagioli 2002, Benos et al. 2007, and many more) has shown that error is detected at about a rate one would expect by chance, and that, if anything, peer review is about adhering to dominant paradigms and drawing support from the predictably commonplace

reviewers who adhere to them as well. (Not coincidentally, the IGBST has published over 75% of its research since 2004 in *The Journal of Wildlife Management* and *Ursus*, both of which could be considered bastions of dominant paradigms.)

Because of empirically-based concerns about peer review, there has been a corresponding groundswell of criticism of peer review in the scientific community. About the best that thoughtful defenders of peer review can say for this practice is something akin to what Winston Churchill said about democracy: “Democracy is the worst form of government, except for all the others.” Although defenses—and critiques—such as this still allow a constructive place for peer review, they are hardly a basis for putting faith in this process as some sort of guarantor of scientific quality.

Peer review clearly functions as a mechanism for censorship, improvement, maintenance of identity amongst a community of self-styled elites, and a device to be used for political advantage. Unfortunately, claims on behalf of peer review by the Service, the USGS, and the IGBST bespeak a political enterprise more than they reflect any objective and empirically-based assessment of what peer review has to offer (see Appendix 2 for an elaboration of this argument). As above, the burden should be on the Service to provide an empirically-based and compelling argument for how, in fact, peer review corrects for the potential bias-inducing effects at play in this situation. This burden weighs all the heavier because of the monopolistic arrangements I describe immediately above.

2. The frames currently used by the Service and the IGBST to organize information about the interrelations of food quality and quantity, hazards, and birth and death rates are deficient and do not reflect the best available science.

2.1. The Service fails to coherently address the joint dimensions of diet that include food quality and the characteristic hazards associated with consumption of a given food. Because of this failure, the Service's representation and analysis of the interaction of hazards with quality/quantity is haphazard and prone to selective manipulation in service of the immediate argument. This translates into patently deficient logic and analysis throughout the Rule and CS.

The demographic implications of consuming a given food will be defined at a population level by effects on both birth and death rates. Effects on fecundity will be predictably mediated by effects on the condition of reproductive females and the extent to which those effects translate into reproductive rate. Effects on death rate will be dictated by the characteristic hazards associated with using a particular food. A high quality food with positive effects on birth rates can either be associated with foraging opportunities concentrated in highly secure habitat or the opposite. This latter set of circumstances, where a high-quality food lures an animal into a highly lethal environment, has become the focus of scientific inquiry organized under the rubric of "ecological traps" (e.g., Delibes et al, 2001, Schlaepfer et al. 2002, Hale & Swearer 2016), which is interrelated with but distinct from source-sink dynamics (Kristan 2003).

The concept of ecological traps is not new to bear researchers. Most notably, Joe Northrup and Scott Nielson deployed this concept (with Nielson using slightly different terminology) in geospatial conservation assessments for grizzly bears in Alberta (Nielson et al 2006, 2009; Northrup et al. 2012). Moreover, there have been several highly congruent landscape-level assessments of hazards for Yellowstone grizzly bears (Carroll et al 2001, 2003; Merrill & Mattson 2003; Johnson et al 2004; Schwartz et al. 2010) which have been directly relevant to judging the hazards of using different foods with different geographic distributions

(e.g., livestock, whitebark pine, and cutthroat trout), albeit without explicit integration of hazards and productivity under rubrics such as ecological trap.

Yet the Service does not deploy the concept of ecological traps; nor do they, in fact, deploy any explicit framework by which the nutritional benefits and entailed hazards of any given diet or dietary shift are simultaneously considered. Throughout the Rule and CS, nutritional aspects are examined in isolation from effects on survival. This is a major failing given that the Rule and CS devote much text to presumably assessing the consequences of the dietary changes afoot with Yellowstone's grizzly bears, related to the loss of most whitebark pine and cutthroat trout, and the apparent shift of surviving bears to eating more army cutworm moths and meat from terrestrial mammals—among other things. The integration of hazards with nutrition needs to occur if for no other reason than the overwhelming evidence for variation of the hazards incurred by adults when using foods of otherwise similar nutritional quality: e.g., much lower for bears eating whitebark pine seeds and trout compared to bears consuming a diet of meat from ungulates, or any other food that brings bears near and into conflict with people.

At a minimum, the Service needs to differentiate major grizzly bear foods according to some sort of matrix that distinguishes high-quality foods entailing characteristically high hazards from high-quality foods entailing characteristically low hazards, and furthermore differentiate whether the hazards are born primarily by dependent young, independent bears (adults and adolescents), or both. This latter distinction is important to any assessment because 80-90% of all independent-aged grizzlies die from human-related causes (e.g., Schwartz et al. 2006) whereas many dependent young bears die for "natural" reasons, including predation by other bears. Hazards associated with humans are thus thrown into sharper relief in any assessment of dietary shifts among adult bears, whereas hazards associated with potential "natural" predators are a more prominent

consideration in assessing changes for cubs and yearlings. Parenthetically, the Service also needs to assess the hazard-related consequences of shifts in

2.2. The Service fails to adequately frame and address the many environmental changes that have occurred in Yellowstone's grizzly bear range during the last 15 years. As a result, the Service has no basis for judging the effects of any single change, including loss of whitebark pine. This problem partly derives from the fact that the Service relies almost exclusively on science produced by the IGBST, which is similarly deficient in its conceptualizations.

All of Yellowstone's grizzly bear data have been collected as part of an observational study, which translates into serious demands on analysts if they are to arrive at even half-way defensible conclusions regarding cause and effect. Observational studies are almost invariably beset by a host of causal dynamics, many of which interact or are correlated in time and space. As a result, isolating the effect of one factor on an outcome of interest—say, the effect of whitebark pine seed consumption on grizzly bear birth rates—requires somehow accounting for and controlling the effects of all other casual factors of any probable significance.

In practical terms, this requires building replete conceptual models of the system of interest that incorporate as much knowledge about prospective ecological drivers as possible; identifying valid measurable surrogates for each of these drivers; and then incorporating them into some kind of model as covariates or causal variables. Sir Ronald Fisher, the father of modern statistics, was amongst the first to recognize this imperative when he stated “make your theories elaborate” as a precondition for taking the step from association to causation in observational studies. William Cochran, who elaborated on the use of covariates in analyzing data collected from observational studies of complex systems, laid the foundation for following seminal work (e.g., Dawid 1979, Rosenbaum 1984, Hilborn & Mangel 1997) on the importance of having considered enough factors to ensure that the resulting models were sufficient; that is, not likely to substantially change with the introduction of additional covariates. And so on.

consumption of lower-quality foods (e.g., any roots or foliage).

Given the extent to which the Service depends upon science produced by the IGBST, this issue of sufficiency raises the question of whether the conceptual and statistical models produced by the IGBST were defensible—or not; whether they adequately attended to all of the factors that prior knowledge would suggest were drivers of variation in, say, birth and death rates of Yellowstone's grizzly bears. If the conceptual underpinnings of the analyses undertaken by the IGBST were *prima facie* inadequate, there is all the more reason for skepticism of their results, especially in the face of contradictory evidence.

In short, the conceptual models and resulting statistical results produced by the IGBST have been patently inadequate. The Study Team has failed to address a number of potential drivers of birth and death rates, and has not adequately dealt with the high degree of spatial and temporal correlation that besets many of these factors. To date, the IGBST has only considered routine effects (bear sex and age class), plus whether a bear was trapped for research or management purposes (as a surrogate for whether the bear was food-conditioned, habituated, or not); management jurisdiction and nearness to roads (as a surrogate for human lethality and exposure to humans); bear density (through suspect indices; see my later comment on this); and, in earlier analyses, size of whitebark pine cone crops (Schwartz et al. 2006). Spatial representations of whitebark pine forests and density were added recently by Van Manen et al. (2015).

At a minimum, by slavishly relying on the IGBST's science, the Service has failed to address in any sort of integrated way the effects of on-going increases in use of army cutworms and the sites where these insects aggregate; the effects of losing virtually all of the cutthroat trout spawning in streams tributary to Yellowstone Lake since the mid-1990s; the effects of major declines in most elk and some bison herds, also since the mid-1990s; the effects of a severe drought between 1998 and 2008; the effects of a short-term masking trend towards increased

per tree cone crops on whitebark pine since roughly 1997; increasing exploitation of livestock and the remains of hunter-killed elk since roughly 2006; and the extent to which trout losses, ungulate herd declines, losses of whitebark pine, increases in cone crops, increases in availability of moths, and putative increases in bear density were highly correlated in time, sometimes in space, and sometimes as an interaction of both. This multitude of tangled effects probably constitutes as severe an analytic challenge as any analysts have faced trying to divine cause and effect in an ecological system. This complexity also increases the odds that bias can and will be introduced in the necessary simplifications made by the IGBST, its collaborators, and the Service—by the choices of what effects to consider, and how.

In fact, bias is amply evident in the extent to which the IGBST structured its post-2009 inquiry into grizzly bear vital rates as an artificially simplified contest between the extent of whitebark pine forests, on the one hand, and bear density (e.g., density dependence), on the other (see also my comment below on use of the density-dependence concept by the Service and the IGBST). It hardly seems a coincidence that the 2009 and 2011 Court rulings over-turning the Service's 2007 delisting rule were based on the extent to which the Service was perceived to neglect and misrepresent the body of science showing a major effect of whitebark pine seed availability on grizzly bear vital rates. And even during the period of litigation, the Service was contending that bear density alone was driving changes in vital rates, and that losses of whitebark pine were minor. It is hard to avoid concluding that the post-2009 science produced by the IGBST was (and is) merely the fulfillment of a politically-driven agenda.

2.3. The Service fails to use the best available science in its conceptualization of factors driving levels of human-caused grizzly bear mortality. As a result, the Service conflates static spatial delineations of so-called secure habitat with what is, in fact, a highly dynamic set of factors driving current increases in human-caused mortality.

The Service repeatedly states in both the Rule and the CS that maintenance of a select number of GIS-delineated

At this point I need to clarify my critique with reference to the standard practice reported by the IGBST in virtually all of its publications, which is to generate *pro forma* lists of rote models containing permutations of variables that they considered, along with AIC values for each. Such lists do not address the IGBST's and Service's failure to consider certain effects altogether and the Study Team's consistent under-use of useful measures of model goodness-of-fit and predictive value. As I noted above, these are all critically important considerations in the production of models designed to address the complexities of open ecological systems, which, if neglected, can result in nothing more than misleading if not useless results (see Pilkey & Pilkey-Jarvis 2009).

As a bottom line, this problem of deficient conceptualization of the ecological system debars any confidence in how the Service represents or otherwise uses science produced by the IGBST. One option would be to put the Rule on hold and allow for additional investigations of alternative models by independent researchers. Another option would be, at a minimum, for the Service to acknowledge the limitations of the science they rely on, clarify the resulting uncertainties and ambiguities, and adopt a suitably precautionary approach.

But regardless of deficiencies in the research produced by the IGBST, this does not excuse the Service from deploying a conceptual framework sufficient to the complex and demanding task of assessing the effects on Yellowstone grizzly bears of all the environmental changes that have occurred since the time of Listing. In fact, nowhere is there any evidence of the Service deploying such a frame.

spatial habitat attributes at 1998 levels within the PCA will insure that rates of human-caused mortality will be no higher in the future than those that occurred during roughly 1988-1998. These spatial attributes include road densities, the extent of areas >500m away from human infrastructure (so-called "secure" habitat), and numbers of livestock allotments.

These arguments are substantively deficient in several regards. First, the Service fails to recognize that human-

caused mortality is driven by two distinct phenomenon, one with a major geospatial dimension, the other largely without: the simple distinction between how often bears encounter people (frequency of contact) and the likelihood that the encounter will end up lethal for the involved bear (lethality of encounter). Second, and related to the first, the equivalence of static landscape features with main drivers of human-caused mortality is simple-minded and thereby misses several other key factors that render a static geospatial analysis patently deficient.

Taking each of these failings in turn, first, Mattson et al. (1996a, 1996b) provide a clear articulation of the logic behind and implications of distinguishing between frequency and lethality of human-bear encounters as determinants of total human-caused bear mortality. Numbers of deaths can be high under conditions of low-frequency contact, as typified by encounters between grizzly bears and big game hunters or grizzly bears and wildlife managers operating at the behest of livestock producers; and numbers of deaths can be low under conditions of high-frequency contact, as typified by encounters between habituated bears and masses of tourists along National Park roads. It is human lethality, not frequency of encounter as such, that differentiates these kinds of scenarios.

Interestingly, the Service awkwardly and tacitly implies these distinctions in its references to research that has purported to explain variation in grizzly bear mortality rates on the basis of management jurisdictions or delineations (NPS lands versus the PCA versus outside the PCA; Schwartz et al. 2006, 2010). Without explicitly saying so, these effects derive almost wholly from variation in human lethality, which varies, in turn, as a function of whether people tend to be well-armed (e.g., big game hunters), associated with features that generate conflict (e.g., livestock allotments), and tolerant (or not) of grizzly bears (e.g., most amenity migrants versus most livestock producers). And, importantly, human lethality can vary by orders of magnitude over time, as between the 1800s-early 1900s and the period after which grizzly bears were protected under the ESA (Mattson & Merrill 2002). Likewise, the Service tacitly argues in its many claims for the efficacies of its ESA-mandated management that declines in human lethality

were a result of better garbage management, food storage, and education.

The main point here is that human lethality can vary widely in time and space as a function of human attitudes and behaviors. It is a highly dynamic phenomenon that contributes every bit as much as frequency of human-bear contact to total grizzly bear mortality. The Service does not recognize this, which results in other deficiencies in its argument that I refer to elsewhere.

Second, and related, a static spatial representation of absolute lethality of the Yellowstone landscape (which the Service tacitly does through its invocation of a static spatial baseline) fails to recognize that grizzly bears may spend more or less time near people—both inside and outside of so-called secure areas—as a function of social interactions amongst bears and changes in the abundance and distribution of key foods. As important, these redistributions of bears can expose them to people of varying lethality. Grizzly bears can encounter highly lethal people in so-called secure areas at varying rates depending on factors that motivate the bears. The main example of this is grizzly bears encountering elk hunters in the backcountry at frequencies that vary depending upon how strongly the bears orient to the offal left behind from elk kills by hunters (Haroldson et al. 2004). All of this plays out in so-called “secure” areas. And, as I point out elsewhere, bear mortalities resulting from conflicts with elk hunters have skyrocketed since roughly 2007, again, mostly located in what the Service is calling “secure” habitat.

The main point here is that grizzly bears are free agents motivated by a search for preferred food (e.g., Mattson et al. 1992, Haroldson et al. 2004) as well as avoidance of other bears (Mattson et al. 1987, McLellan & Shackleton 1988). These movements and resulting redistributions with respect to humans can systematically change over time (as claimed by Costello et al. 2014), at various scales, with resulting changes in exposure of even the same numbers of bears to varying hazards and levels of risk associated with humans—resulting in varying levels of human-caused mortality even with the same amount of so-called “secure” habitat. The Service essentially ignores all of this in its unqualified claims that maintaining a static spatial baseline dating back to 1998

will somehow insure the security of grizzly bears (e.g., pages 13182 & 13184).

For this and other reasons articulated in my critique, the Service needs to account in its habitat management

prescriptions for all of the social and dietary changes since 1998 that have resulted in increased exposure of grizzly bears to human hazards synchronous with no net change (or increase) in livestock allotments and human infrastructure.

3. The Service employs a simple-minded and unsubstantiated conception of carrying capacity as a basis for in turn making unsubstantiated claims regarding the number of bears able to be sustained in the PCA and DMA, and past and likely future effects of food quality and quantity on Yellowstone's grizzly bear population.

The Service's representation of carrying capacity (K) throughout the Rule and CS is almost wantonly simple-minded and seemly constructed to serve the sole purpose of supporting assertions that (1) there is no more room for grizzly bears in the PCA (and DMA), (2) that no deleterious habitat trends are afoot that might compromise current conditions, and, because of that, (3) the population is secure, recovered, and ready to be delisted.

The gratuitous figure on page of the Rule is emblematic of the Service's problematic use of the carrying-capacity concept. Here, they show K as being static and unchangeable, with population size fluctuating around it—presumably as a representation of what has happened and will continue to happen with Yellowstone's grizzly bear habitat and population. In fact, this representation is utterly at variance with both reality and the several references that the Service cites as if for substantiation.

In fact, carrying capacity not only changes from year to year, but also exhibits long-term trends as a function of long-term changes in availability of critical resources—most importantly, food. As I have pointed out throughout my critique (and as the Service tacitly admits in many places), carrying capacity has changed for grizzly bears in the Yellowstone ecosystem as a function of changes in food availability. Since the mid-1990s positive changes can readily be attributed to increasing consumption of moths in the Absaroka Mountains and increases in the Northern Range bison herd. The more numerous negative changes can be attributed to functional extirpation of cutthroat trout in Yellowstone Lake; 50-70%+ loss of mature cone-producing whitebark

pine throughout the ecosystem; major declines in virtually all of the ecosystem's elk herds; and major recent declines in the Central Yellowstone Park bison herd. A major decade-long decline is also plausibly attributable to the epic drought that lasted 1998-2008 (see the graphs I present under point 10). In the net, K almost certainly declined during the last 20 years. Put another way, it defies reason and all available evidence to credibly argue otherwise—which is what the Service tries to do in the Rule.

Another key point is that, when reckoned against total size of a population that is expanding in distribution, K must be assessed not only for a given area, but also for the cumulative area occupied by the expanding population. This is relevant for Yellowstone's grizzly bear population given that its distribution has apparently expanded by 30-40% (Bjornlie et al. 2013) at the same time that the population was "stable"; i.e., not increasing in numbers. In other words, approximately the same number of grizzly bears was sustaining themselves by occupying an ever-larger area, which presumably cumulatively encompassed an equal or greater amount of food; increasingly including livestock on the periphery of the ecosystem (see my point 9).

Figure 3.1 encapsulates all of these points in graphic form and is presented as a corrective for the egregiously misleading figure offered by the Service in the Rule. Here carrying capacity for the core of the ecosystem is shown by a dark gray line as an annually highly variable value, but with a long-term decline over the long run. The effect of bears expanding into new areas is shown by the light-gray-shaded area above, constituting a mitigating offset for losses in the core. Population size is shown by the red

arrow, and actually exhibits less variation than occurs in K itself. This arises from the fact that grizzly bears can buffer themselves somatically and behaviorally from inter-annual variation in habitat productivity (e.g., Herrero 1973), and because grizzly bear populations are subject to potentially long lags between when habitat change occurs and when this change is manifest in population size (Doak [1995], McLellan [2015]; see my point 5 about lag effects).

As a bottom line, K for Yellowstone's grizzly bear habitat has certainly varied widely and has probably declined substantially. To the extent that the bear population has reached "carrying capacity," this probably has more to do with declines in K than to increases in population size, as such. Understood this way, being at carrying capacity is not an argument for current or long-term security, but rather an argument for current and long-term vulnerability. By itself, a population at K is not an argument one way or another for judging recovery.

The Service needs to correct its misleading and simple-minded representations of carrying capacity along with

relations of K to population size in its risk assessment. In service of this end, the Service has my permission to use the graphic above in the Rule and related materials.

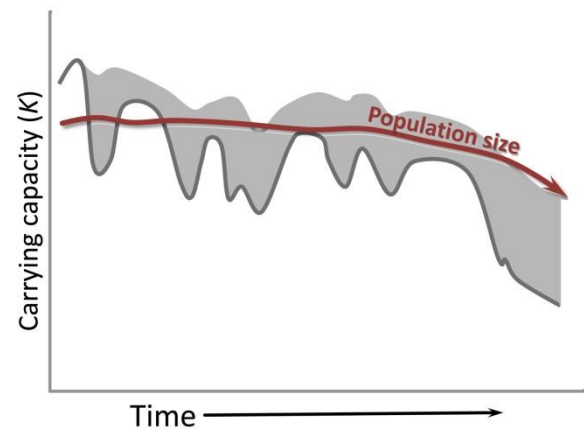


Figure 3.1. A more realistic conceptual portrayal of how size of the Yellowstone grizzly bear population (in red) has reflected—or related to—carrying capacity, in the core (dark gray), and accounting for the mitigating effects of population expansion into new areas (light gray).

4. The Service employs "density-dependent effects" in this Rule with little apparent understanding of the concept and with no reference to, and in contravention of, the most reliable and straight-forward scientific reckoning of trends in grizzly bear density in the Yellowstone ecosystem.

The Service claims throughout the Rule that changes in the demography of Yellowstone's grizzly bear population since the mid-1980s have been driven largely (if not solely) by changes in population density, entraining "density-dependent effects." On this basis the Service then goes on to dismiss effects attributable to changes in abundance of whitebark pine—or any other food. The primary basis for this oft-repeated claim is Van Manen et al. (2015), although with parenthetical reference to Schwartz et al. (2006), who also purport to have detected "density-dependent effects." The Service, citing Van Manen et al. (2015), attributes declines in survival rates of cubs and yearlings to increasing bear densities, but otherwise flags few other effects of density on either birth or death rates.

The Service's claims suffer from an invocation of naïve if not downright misleading conceptions of density-dependence and from critical—even fatal—failings of the cited research. Its claims that density has increased since around (or even before) 2000 are also contradicted by straight-forward and unambiguous scientific data, and otherwise have little scientific credibility. In short, the Service's invocation of density is one of many slender broken reeds upon which its arguments are based.

Starting with the most straight-forward point first: grizzly bear densities almost certainly did not increase in the Yellowstone ecosystem during the 2000s and after. As the Service frequently asserts, the population "stabilized" during this period, meaning few if any increases in numbers of bears. A trend line fit to Mark-

Resight-based estimates of population size (a less bias-prone method compared to the Chao2-based approach) substantiate this assertion, with the added possibility of population declines since around 2006-2007 (see the bottom graph in figure 5.3.1). At the same time, the distribution of the population increased by roughly 40% (Bjornlie et al. 2013). Simple math shows that if you have the same number of individuals spread out over a substantially larger area (n/area), density axiomatically decreases. To the extent that demographic rates of the Yellowstone grizzly bear population have changed at all during the last 15 years, it is almost certainly not because of increased bear densities—at least by our most straight-forward and unambiguous reckonings of density.

Turning more specifically to the methods employed by Schwartz et al. (2006) and Van Manen et al. (2015): In the case of Schwartz et al. (2006), they used a time-specific population-wide index of “density” based explicitly on annual counts of females with COY. As I point out elsewhere (my point 19), this index of population size almost perfectly mirrors changes in efforts by researchers and managers to find bears, along with changes in the intrinsic sightability of the bears they were seeking. By contrast, the correlation between annual counts of females with COY and actual population size is unknown and almost certainly meaningless if not deceptive. Moreover, the index used by Schwartz et al. does not account for steady increases in the distributional extent of the population (e.g., Schwartz et al. 2006b, Bjornlie et al. 2013), which introduces further unaccounted-for bias. Compounding these intrinsic problems is the fact that Schwartz et al. (2006), like Van Manen et al. (2015), did not control for a number of major temporal changes in abundance of key foods that were correlated with their purported index of bear density (e.g., cutthroat trout, elk, bison, and army cutworm moths), which debars any isolation of a density effect—even assuming a valid index—and introduces major statistical problems related to covariance of explanatory variables.

In contrast to Schwartz et al. (2006a), Van Manen et al. (2015; and Bjornlie et al. 2014) used a purported index of population density that varies not only by year, but also with respect to a grid of cells sized to approximate the extent of female home ranges. Because of this spatial and temporal resolution, the Bjornlie/Van Manen index

gives the reassuring impression of high-resolution precision to those looking at their results with an uncritical eye—which seems to be the case for the Service.

In fact, this index is yet another instance of a metric with no known relationship to the parameter it purports to indicate (i.e., bear density), and almost certainly substantially contaminated by, in this case, efforts of researchers and managers to capture and collar grizzly bears. Briefly, the density index is directly based on the number of bears trapped and radio-marked in a given area during a given year, weighted by rote survival rates to “extrude” [sic] these bears forward and backward through time, after which the “extruded” bears are stacked and added to come up with a purported index of density. Van Manen and Bjornlie attempt to “validate” this index, *prima facie* biased by trapping effort, by correlating it with two other metrics that have no known relationship to density—other than what Van Manen and Bjornlie assert through argumentation. More tellingly, the population-level results of the arcane and unsubstantiated Van Manen/Bjornlie density index contradict the straight-forward calculation I describe immediately based on estimates of total population size and distribution.

And, again, because both Bjornlie et al. (2014) and Van Manen et al. (2015) fail to account for numerous other major changes in Yellowstone’s grizzly bear habitat—also correlated in both time and space with their purported density index (see my point 10)—they have no basis for isolating any density effect, even assuming the index they use is valid. Given all of these problems with the Van Manen/Bjornlie density index, the burden is clearly on the Service to reconcile the contradictions between, on the one hand, the best available science regarding population size and distribution and, on the other, grossly deficient science that uses a *prima facie* problematic unproven index of density in context of patently inadequate analyses that fail to account for most of what is likely to affect grizzly bear birth and death rates (as per most of my review here). More to the point, the Service does not, in fact, use the best available science regarding density effects and, instead, relies almost solely on science of comparatively little merit.

Finally, the Service and the IGBST research that it invokes employ a simple-minded and often misleading conception of “density-dependence” that offers little insight of relevance to the deliberations of this Rule. As one insightful and well-respected population ecologist put it: “Density is not a mechanism” (this from Charles Krebs [1995, 2002]). What he meant by this is that birth and death rates of animals are driven by levels of predation, disease, and intra- and interspecific competition, along with the quality and abundance of foods, especially those eaten by females. If population density has any effect at all, it is through somehow modifying these critical factors. There is no direct effect of density, even in New York on a subway. Invoking density as an explanation for anything is equivalent to assuming that animals are ping-pong balls moving at random, with each ball equal in all of its effects.

To the extent that density has any effect, it necessarily interacts with carrying capacity and changes in the microscale and mesoscale distributions of individual bears in reflection of dietary changes driven by changes in availability of foods. In other words, at the same exact density, the frequency and lethality of interactions among bears can vary substantially depending on total abundance of food and the extent to which these foods are concentrated in time and space—as with differences in British Columbia between coastal areas with salmon spawning runs and interior areas with abundant by

widely-distributed berries. The upshot of this is that a simple shift in diet among Yellowstone’s female grizzly bears from pine seeds to terrestrial meat (see my comments under point 9) could substantially modify levels of interactions with other bears, especially males, and without any change in bear densities.

Parenthetically, as I point out elsewhere (point 17), changes in cub and yearling survival rates can be plausibly explained simply by changes in foraging behaviors of female bears, and without needing to resort to poorly conceptualized and unsubstantiated claims regarding density. Survival rates of cubs and yearlings have probably declined simply because adult female grizzlies are eating more meat and incurring substantially more hazards for their dependent offspring; hazards primarily, but not solely, related to increasing odds of predation by other adult bears and wolves.

The Service needs to upgrade its conceptualization of density effects; recognize deficiencies in the science it currently invokes to justify its density-related arguments; adopt, instead, the best available science; and, finally, realize that changes in demography and trend of Yellowstone’s grizzly bear population are almost certainly a result of changes in food availability, diet, carrying capacity, and distributions—not increasing densities and presumed “density-dependent” effects.

5. The Service fails to adequately address the issue of lag effects in the Rule. There are no habitat-based standards proffered by the Service that would trigger reviews by the IGBST or Service; nor is there any history of the IGBST seriously engaging in its research with the existing suite of monitored habitat indicators; nor is there any history of managers or researchers in the Yellowstone ecosystem seriously considering any habitat trends except in response to litigation or threat posed by research published by other researchers.

On page 13224 of the Rule the Service addresses the issue of lags between changes in habitat and manifestation of these changes in population size and trend by asserting: “...the IGBST will monitor a suite of indices simultaneously to provide a highly sensitive system to monitor the health of the population and its habitat and to provide a sound scientific basis to respond to any changes or needs with adaptive mgmt. actions. This “lag effect” is only a concern if the sole method to

detect a change in habitat is monitoring changes in population size. ... [W]e feel confident that we will be able to detect the consequences of significant changes in habitat.”

This treatment of an important even critical issue by the Service is deficient in several regards. First, the only standards proffered by the Service that would trigger an authoritative review by the IGBST or Service are linked

solely to population size—or mortality rates as a partial function of population size. Second, the history of how habitat trends have historically been treated by the IGBST and the Service provides no basis for trust. Third, there is no indication that the IGBST or the Service are responding to current evidence of unfolding lag effects with anything other than dismissal. And, fourth, the current suite of habitat indicators is lacking. Parenthetically, “feeling” confident seems a poor substitute for concrete authoritative measures and a history of competence and attention. Taking each issue in turn:

5.1. The Service does not describe any habitat-based standards in the Rule that would trigger authoritative reviews by the IGBST or Service.

According to the Rule, the only standards that would trigger an authoritative review by the IGBST or Service are linked to population size—or mortality rate as a partial function of population size. There are no triggers that link to trends in foods or other important features of habitat; all such effects are presumably filtered through population responses before warranting some sort of significant response by either state or federal managers.

In other words—and contrary to the Service’s current innuendo—the provisions of the Rule that fundamentally matter ignore lags effects and solely invoke lagged population responses as a basis for triggering any meaningful management response.

5.2. The IGBST and Service have responded historically to lag-inducing trends in food and habitat with inattention or dismissal, and almost solely in reaction to litigation or threats posed by independently-published research. This is not a basis for trust.

The Service deploys what is essentially a “trust us” argument in its description of how the IGBST and managers will respond to trends in the “suite of indicators”—and this in the absence of any authoritative provisions for triggering a response (as per 5.1). Put bluntly, history provides no basis for trust.

In fact, history shows that the IGBST and Service and have responded to changes in foods and habitat (e.g.,

whitebark pine) either with inattention, dismissal, and, if attentive, only in response to litigation or research that threatens current hegemony. For example, nowhere in any of the IGBST research published during the last 10 years is there evidence that this research group has explicitly considered trends in the existing suite of habitat indicators that it monitors—with the exception of cone counts on whitebark pine transects (more on this later). Trends related to cutthroat trout, moths, spring carrion, and numbers of hunters and park visitors are reported each year in IGBST Annual Reports, and then essentially ignored in any analyses of grizzly bear movements or demography.

On a more positive note, the IGBST and Service have seriously engaged with the effects of changes in whitebark pine abundance on grizzly bear movements and demography. However, as I describe elsewhere in these comments, these efforts are fatally flawed and seemingly politically motivated. As evidence, the science on whitebark pine effects undertaken by the IGBST—at the behest of the Service—has almost solely been in response to either litigation or a challenge by independent researchers. The Service describes on pages 13175-1376 how rulings by the Montana federal District Court and 9th Circuit Court of Appeals motivated the current crop of whitebark pine-focused science. Prior to that, the treatise by Schwartz et al. (2006) covering whitebark pine effects did so primarily in response to a publication (Pease & Mattson 1999) that authoritatively flagged the issue as something to be considered.

Likewise, improvements in methods for monitoring population and mortality occurred in response to outside research that flagged short-comings in current approaches: Keating et al. (2002) and Cherry et al. (2007) in response to Mattson (1997c); and Cherry et al. (2002) in response to Mattson (1998). Spatially-explicit appraisals of habitat suitability and hazards by Schwartz et al. (2010, 2012) occurred in response to Merrill & Mattson (2003) and Johnson et al. (2004). The point here is that, during the last 15 years, the IGBST and Service have not demonstrated an interest in proactively addressing potentially lag-inducing habitat trends—or other science issues of import for that matter.

5.3. The IGBST and Service have shown no response to current evidence of lagged environmentally-driven changes in population size and trend; if anything, the response has been dismissal and denial.

Over 20 years ago Doak (1995) explicitly related the concept of lag effects to dynamics of the Yellowstone grizzly bear population. More recently, McLellan (2015) demonstrated lag effects of this nature for a grizzly bear population in the North Fork of the Flathead River drainage of British Columbia and Montana. A sustained crash in huckleberry production began in 1996 followed by the beginning of a correspondingly sustained decline in population growth rate the year after. However, tellingly, a definitive and dramatic decline in population size did not manifest until 11 years later—beginning in 2007—after which the population declined substantially.

Lag effects are highly relevant to judging the current status of Yellowstone's grizzly bear population given the major declines in major food sources that have occurred during the last 15 years, most notably, the terminal decline in whitebark pine seed availability beginning in 2007. Yet, if anything, the Service portrays a static world for Yellowstone's grizzly bears in its portrayal of carrying capacity (see my comment 3), while at the same time claiming that all changes will be subsumed by the bears' remarkable—even magical—absorptive omnivory and resilience.

Figure 5.3.1 is illustrative of unfolding lag effects for Yellowstone's grizzly bear population, referenced to data from the Flathead study taken from McLellan (2015). At top I've presented trend data for population size and growth rate for the Flathead grizzly bear population; my representation of growth rate is based on a 6-year moving average of proportional change in population size from one year to the next (i.e., λ = lambda). Green dots represent population density and gray squares represent growth rate. The take-away from the Flathead data is that population growth rate began to decline almost as soon as berry production tanked around 1996, but didn't turn negative until roughly 5-years later. More importantly, population size, as such, didn't begin a substantial long-term decline until 10-11 years after the berry drought started.

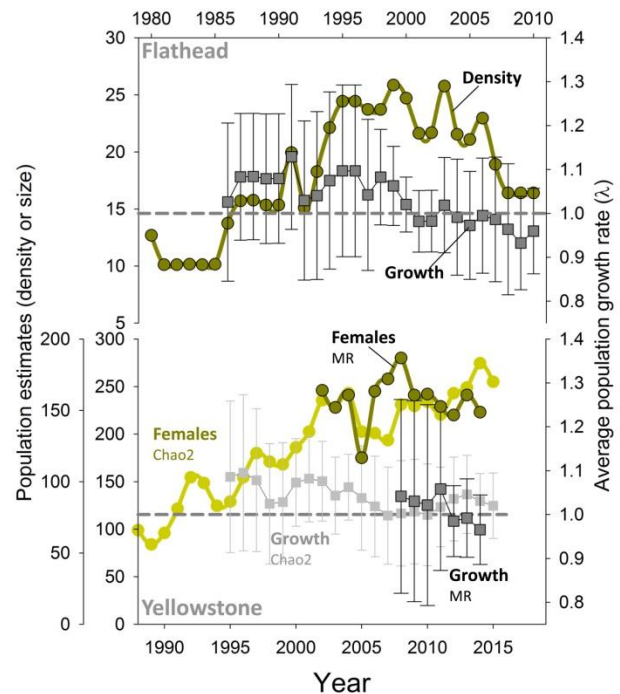


Figure 5.3.1. Trend data for the grizzly bear population in the North Fork of the Flathead, top (McLellan 2015), and for the Yellowstone grizzly bear population, bottom. Dark green dots represent best estimates of density or total population size, and the dark gray squares, derivative estimates of population growth rate (λ ; as a 6-yr running average). Uncertainty bars around estimates of growth rate represent standard deviations. Yellowstone estimates based on the highly-biased Chao2 estimator are shown as yellowish-green dots and as light gray squares.

I show Yellowstone data in the bottom graph of figure 5.1. The darker green dots represent estimates of population size using the Mark-Resight (MR) method, which is less biased than the flawed Chao2 method adopted by the Service (see my point 19). The dark gray squares represent a running average of population growth rate based on MR population estimates. I also show population estimates using the Chao2 method (in light yellowish-green) and derivative estimates of growth rate (in light gray). The take-away point here is that average population growth began to decline around 2008, shortly after the onset of terminal declines in whitebark pine seed availability, and became negative (i.e, showing decline) only in 2012. Meanwhile, total population size has appeared more-or-less-static, with the slight suggestion of a down-turn during recent years.

Trends unfolding for Yellowstone's grizzly bear population bear an uncanny resemblance to trends that unfolded in the North Fork of the Flathead between 1996 and 2006, which substantiates concerns about on-going lag effects in Yellowstone, with worse yet to come. More to the point, the IGBST and Service show no evidence of, first, acknowledging these dynamics or, second, responding to them.

5.4. The foods and habitat features currently monitored by the IGBST, and presumably comprising the suite referenced by the Rule, are inadequate.

The IGBST currently monitors and reports on availability and grizzly bear use of moth sites, cutthroat trout streams, and spring carrion on ungulate winter ranges, along with numbers of cones on whitebark pine at fixed transects.

These monitoring efforts are inadequate because they fail to include foods or aspects of foods that are of unambiguous importance to detecting early signals of change in Yellowstone's grizzly bear habitat. More specifically, the IGBST needs to add numbers of elk and bison in various ecosystem herds as well as aerial extent of whitebark pine to its suite of indicators. The IGBST itself shows that meat from ungulates is becoming

increasingly important to Yellowstone's grizzly bears (Schwartz et al. 2014, Ebinger et al. 2016) and that aerial extent of whitebark pine forests is a critical dimension of grizzly bear habitat (Bjornlie et al. 2014, Van Manen et al. 2015).

5.5. The Service needs to make substantial revisions to the Rule to insure that lag effects are adequately dealt with.

The Service needs to make several substantive changes to the Rule designed to remedy the short-comings that I describe here. For one, the Service needs to set meaningful standards linked to monitored foods and habitat features that will authoritatively trigger reviews by the IGBST and Service. These standards and associated triggers should be designed to anticipate and help mitigate for unfolding changes that will likely drive lagged responses in population size and trend. For another, the Service needs to add numbers of elk and bison in the ecosystem as well as aerial extent of mature whitebark pine to the suite of habitat features to be monitored by the IGBST. Finally, The Service needs to demonstrate that it takes the issue of lag effects seriously by acknowledging and accounting for unfolding trends—in contrast to its current pattern of denial and dismissal.

6. The Service fails to use the best available science when describing the taxonomy and evolutionary biogeography of Yellowstone's grizzly bears. Instead, the Service uses outdated science to categorize Yellowstone's grizzly bears as part of a purported continent-spanning subspecies when the best available science clearly shows that the Yellowstone population is part of a clade (Clade 4) with an ancient and unique history, a restricted distribution, and warranting consideration as an evolutionarily unique and threatened genetic lineage.

The Service makes reference in the Rule to an antiquated research paper (Rausch 1963) as a basis for lumping Yellowstone's grizzly bears in with a presumed subspecies that spans the entirety of western North America. The best available science, comprised of a large body of post-1995 research, clearly and emphatically shows that Yellowstone's grizzlies are, instead, part of the Clade 4 lineage. This matters because Clade 4 brown bears have a unique and ancient history and a current distribution that is restricted to central-western North America and an isolate on the island of Hokkaido. In

North America, Clade 4 bears probably extend no farther north than central Alberta and British Columbia, which makes them the most fragmented Clade in North America, and collectively as threatened as the Clade 1 bears of Europe and Clade 5 and 6 bears of southern and southeastern Asia. The details of all this are elaborated in Attachment 2, which I have included both as substantiation for my comments and to assist the authors of the Rule, who are apparently unacquainted with the referenced body of literature on brown bear taxonomy and biogeography.

As brief background, Clade 4 brown bears were probably the first representative of *Ursus arctos* to migrate across Beringia into North America, certainly before 30,000 years before present, and perhaps as early as 70,000+ years ago. By all indications, bears of this clade were then isolated south of the continental ice-sheets for 10s of thousands of years. As the ice sheets melted during the early Holocene, Clade 4 bear migrated north where they encountered more recently arrived Clade 3 brown bears moving south from Beringia. With arrival of Europeans, Clade 4 grizzlies bore the brunt of post-1800 extirpations, and are unique among all North American Clades in being the most diminished of all. Yellowstone's grizzlies currently represent the southernmost relic of Clade 4 brown bears.

The Service does not make reference to this unique evolutionary and biogeographic circumstance of Yellowstone's grizzly bears anywhere in the current delisting package. This is a major omission. Nor does the Service anywhere make mention of the unique and much diminished status of Clade 4 grizzly bears. If duly considered, all of this information would logically support a larger vision for recovery of this Clade, including explicit provision for connectivity of Yellowstone's grizzlies with other Clade 4 populations farther north, which the Rule

does not currently include. Moreover, such a perspective would lead to recognition of the special taxonomic and historical status of Yellowstone's grizzly bears, all of which would argue for a more cautious approach than is currently being taken by the Service.

In short, the Service needs to update its taxonomic reference for Yellowstone's grizzly bears; describe the unique evolutionary and biogeographic status of this population; develop an explicit plan for recovery of at least the US portion of Clade 4 grizzly bears, including an explicit provision for connectivity amongst all representative populations; and put the move to delist Yellowstone's grizzly bear population on hold until such plans and provisions have been developed.

In making this recommendation I realize that I am calling into question the very standards by which the Service has chosen to judge recovery of Yellowstone's grizzly bears, which is a logical consequence of the Service's failure to update the Recovery Plan for this population so as to reflect the massive amount of "best available science" that has been produced since the early 1990s. In other words, this critique is a commentary on the Service's failure to exercise due diligence, including following through with its own 2011 recommendation to update and revise the Yellowstone grizzly bear Recovery Plan.

7. The Service fails to account for the nutritional ecology of grizzly bears in its assessment of recent dietary shifts because it inaccurately, incompletely, and erroneously represents the best available science. This arises from the extent to which the Service engages in tortuous logic and selective even grossly incomplete representations of relevant research. Because of this, the Service reaches patently erroneous conclusions.

The Service's representation of nutritional ecology is a critical aspect of its overall argument that historical and prospective food losses, and resulting dietary shifts, "do not and will never pose a threat" to Yellowstone's grizzly bears. The Service claims that grizzly bears are not just omnivorous, but "*extremely* omnivorous," and, on top of that, "display *great* diet plasticity." As evidence of this claim, the Service then cites Gunther et al. (2014), that Yellowstone's grizzlies are documented to eat over "260 species of foods...representing 4 of the 5 kingdoms of life." Thereafter the Service asserts outright or by innuendo that one food is basically as good as another—this despite giving lip service on page 13178 to the fact

that energy concentration and nutrient content vary among foods—and that Yellowstone's grizzly bears are thereby well able to substitute one food for another. The Service then goes on to presumably substantiate this assertion by offering presumed evidence for how losses of whitebark pine and cutthroat trout have not affected birth and death rates of the population.

Put bluntly, the Service's treatment of nutritional ecology reads more like propaganda than it does like a deliberative consideration of the best available science to arrive at a prudent conclusion. In other words, the Service misconstrues, misrepresents, and altogether

misses a considerable body of relevant science in apparent service of reaching a preordained/pre-decisional outcome. The short-comings of the Services representations are so egregiously deficient that I feel compelled to offer a corrective primer on nutritional ecology (hereafter, the Primer; Attachment 3) as an attachment to these comments. But more specifically:

The nutritional quality of foods available to and eaten by grizzly bears in the Yellowstone ecosystem varies by orders of magnitude. Mattson et al. (2004) as well as the Primer provide a summary of digestibilities and protein content for Yellowstone's bear foods. In other words, all foods are not equal insofar as digestible protein and energy are concerned. Moreover, and perhaps more importantly, bear foods are especially disparate in concentrations of dietary fat. Fat is perhaps the most important of all nutrients to bears (Erlenbach et al. 2014), and is uniquely abundant in army cutworm moths, whitebark pine seeds, and late-season ungulates such as elk and bison (Mattson et al. 2004, Erlenbach et al. 2014).

On top of this, the density, architecture, and comparative nutrient contents of foods have a major effect on foraging efficiencies, efficiencies of weight gain, and accretion of fat versus lean body mass among bears, with subsequent effects on mass dynamics during and after hibernation (The Primer; e.g., Farley & Robbins 1995; Atkinson et al. 1996; Welch et al. 1997; Hilderbrand et al. 1999a, 1999b; Rode & Robbins 2000; Rode et al. 2001; Felicetti et al. 2003; Robbins et al. 2007; McLellan 2011; Robbins et al. 2012; Erlenbach et al. 2014). Generally speaking, smaller bears fare better than larger bears on fleshy fruits and grazed foliage, whereas larger bears disproportionately benefit from eating meat (The Primer). Even so, all bears are beset by a need to balance the energy and protein concentrations of their diet to maintain lean body mass and accrue fat (The Primer). On top of this, the energetic costs of extraction vary among foods substantially, to the extent that extraction costs largely negate the greater digestible energy available in most root foods (Holcroft & Herrero 1984, Mattson 1997a, Mattson et al. 2004). In other words, foods are of varied relative benefit to bears based on body mass, sex, and overall diet composition. Not all foods are equal, nor are all foods equal to different bears.

Parenthetically, and at risk of stating the obvious, bears are not Latin taxonomists. In other words, bears are not wandering around in the woods with a copy of the *Flora of the Pacific Northwest* keying out different foods before they eat them—say, differentiating one *Poa* from another, or *Poa* from wheatgrass. In other words, taxonomic distinctions have little or no relevance for grizzly bears. As per what I outline immediately above, differences among foods arise from characteristic densities and architectures at foraging sites, the energetic expenses of extraction, and per gram densities of energy and nutrients—and how all of this varies seasonally and from one year to the next. In other words, the fact that Yellowstone's grizzly bears eat “260 species of foods...representing 4 of the 5 kingdoms of life” is largely irrelevant, disingenuous, and prey to artificial inflation based on the resolution of taxonomic distinctions employed (e.g., should we be talking about genera, or species, or even subspecies?).

With this as background, it is worth looking critically at where Yellowstone's grizzly bears obtained most of their energy and nutrients—say, between 1977 and 2003—and the comparative importance of vegetal foods that the Service in places features so prominently as potential generic dietary alternatives to whitebark pine seeds and cutthroat trout; and elk, for that matter (see below).

Figure 7.1 immediately below offers a seasonal picture of relative contributions of different foods to digested energy and ingested protein and fat of Yellowstone's grizzly bears for the period 1977-1993, differentiating contributions from large herbivores (elk and bison; Mattson 1997b), cutthroat trout, and whitebark pine seeds. This representation is based on a sample of >6000 bear feces collected over a 16 year period throughout the Yellowstone ecosystem, and corrected for differential detectabilities (Hewitt & Robbins 1996) and digestibilities (Mattson et al. 2004) of each food, and then further adjusted to reflect the proportional numbers of bears out of dens (Haroldson et al. 2002) as well as varied levels of monthly feeding activity (Mattson et al. 1991a). But this comes with a proviso. Consumption of army cutworm moths is underrepresented in this sample of feces because of the remoteness of the sites where this food is eaten by grizzlies.

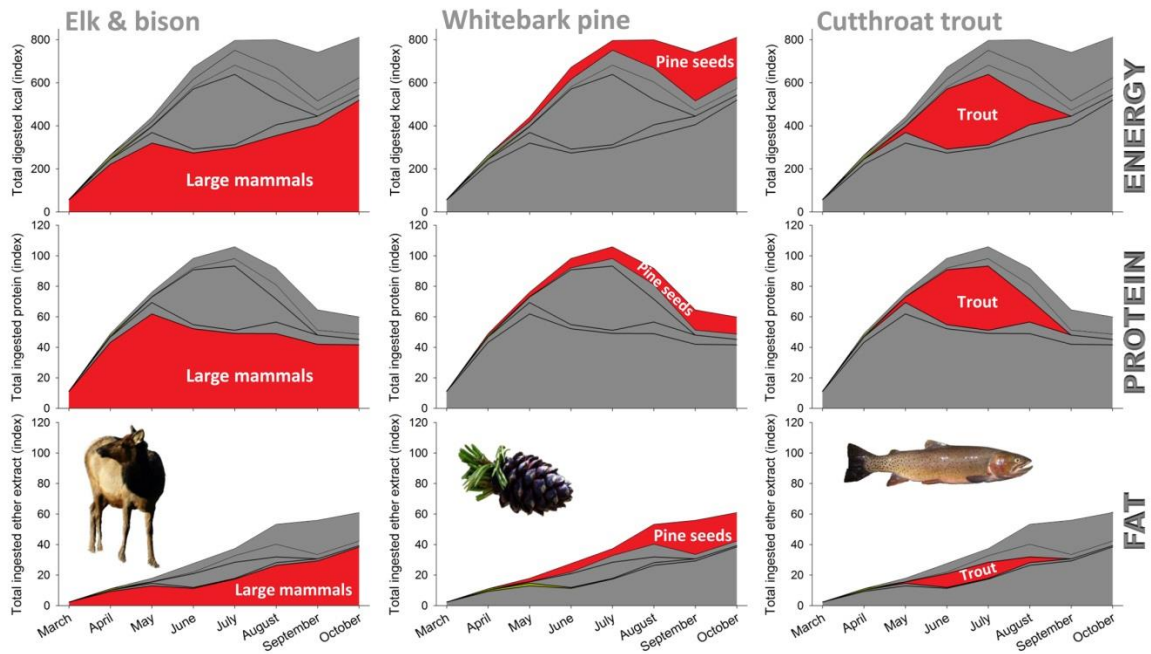


Figure 7.1. Seasonal fractional contributions of ungulates (elk & bison, left), whitebark pine seeds (center), and cutthroat trout (right) to the 1977-1992 diet of Yellowstone's grizzly bears, differentiating digested energy (top row) from ingested protein and fat (middle and bottom rows, respectively). This representation accounts for detectabilities, digestibilities, and monthly population-level differences in overall consumption and is based on a corrected sample of >6000 grizzly bear fecal remains. Army cutworm moths are under-represented because of sampling issues.

The key point of this graph is that ungulate meat, cutthroat trout, and whitebark pine seeds (plus army cutworm moths, more on that later) historically contributed the overwhelming majority of energy and nutrients to Yellowstone's grizzly bear diet. This representation is broadly consistent with similar estimates corrected for detection, digestibility, and prevalence made by Mattson et al. (2004:26-28) and Lopez-Alfaro et al. (2013). Parenthetically, the major contribution of ungulate meat to Yellowstone's grizzly bear diet correlates well with other independent estimates made on the basis of feeding site examinations (Mattson 1997b) and analysis of isotopes in tissues collected from captured or killed bears (Jacoby et al. 1999; Schwartz et al. 2014).

Insofar as army cutworm moths are concerned, the evidence for their dietary importance is more circumstantial, but nonetheless compelling. First, when the composition of feces collected on or near moth sites is corrected for differential passage through the digestive tract, moths comprise 80-90% of the total (Mattson et al. 1991b). Second, the numbers of bears seen on moth sites has climbed steadily since the mid-1980s and currently

accounts for hundreds of sightings (300-400 recently) and, since 1996, roughly 15-45% of all initial sightings of unduplicated females with cubs-of-the-year (IGBST 2015), the range depending on the specific year. Third, high levels of bear activity on moth sites are sustained over a 2-month period, from roughly mid-July through mid-September (see my point 11.5). Taken together, this evidence is consistent with moths being a major food for grizzly bears within range of moth sites.

Put another way, given the overwhelming reliance by Yellowstone's grizzly bears on essentially four foods (lumping elk and bison together as ungulates), major losses of any one are almost certainly to have major impacts. The Service confesses to major losses of cutthroat trout and whitebark pine. Moreover, as I point out below, elk populations have declined substantially since the mid-1990s, with prospects of army cutworm moths being hit hard by climate warming (see my point). This begs the question of whether plausible alternative foods are (and would be) of sufficient quality, simply from a nutritional perspective, to compensate for the losses of the euphemistic "big 4" that we've seen.

Figure 7.2 summarizes information on the net digested energy estimated to be obtained by Yellowstone grizzly bears from five different groups of foods on a per gram basis and from a given feeding bout (or feeding site). These data come from (Mattson et al. 2004) and

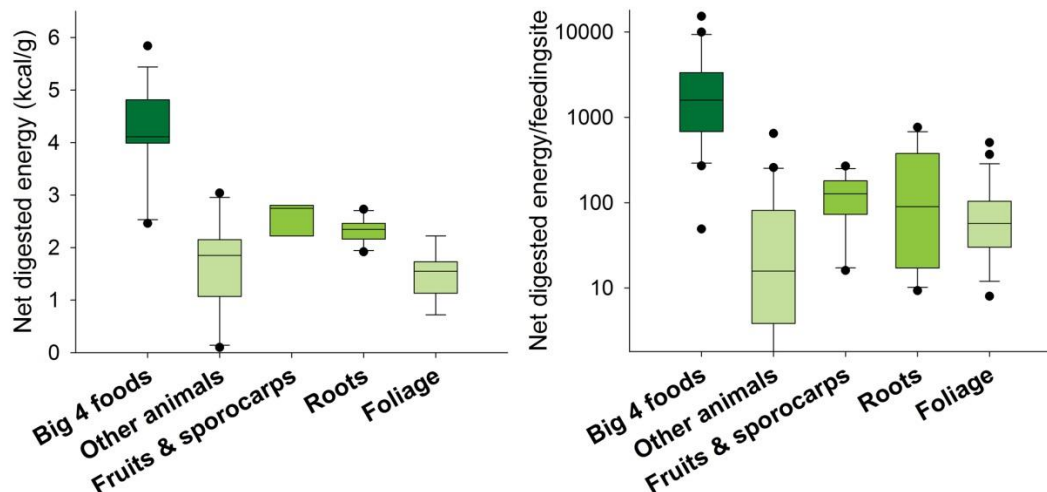


Figure 7.2. Box and whisker diagrams showing the energetic benefits of different categories of foods, including the “big 4” (ungulates, army cutworm moths, whitebark pine seeds, and cutthroat trout) and other categories of foods that include items plausibly turned to in compensation for losses among the “big 4.”

The pattern is pretty obvious. Even accounting for outlier items, the “big 4” are energetically superior to any other foods that might be used by bears in compensation for losses, including other animal foods (e.g., rodents and ants) and fruits and fungi (i.e., sporocarps); and this without taking into account the landscape-level abundance of foods or the extent to which they occur at sites in such a way as to favor efficient use (which relates to the density, architecture, and ease of extraction issues).

There is another important point that further belies any tacit or outright claims by the Service that changes in food abundance can be blithely accommodated by “extremely omnivorous” and “resilient” grizzly bears. This point relates to continent-wide differences in grizzly bear densities and the extent to which these densities reflect differences in habitat productivity. Perhaps the seminal paper putting all of this together is Mowat et al. (2013). These authors show that grizzly bear densities

differentiate the “big 4” (ungulates, cutthroat trout, whitebark pine seeds, and army cutworm moths) from other categories including foods that might be included in dietary shifts in response to losses of current dietary mainstays.

systematically vary by orders of magnitude as a direct function of habitat productivity. The most obvious difference is between coastal areas with spawning salmon and interior areas without. But, even in interior areas, densities can, again, vary by orders of magnitude in reflection of various factors that are surrogates for overall productivity.

The final point of relevance here is that the Service’s argument of potential last resort has no merit. In other words, these comments extensively cover the Service’s numerous fatal errors and failings that debar any dismissal of changes in foods and diet as drivers of historical and prospective future changes in demography of Yellowstone’s grizzly bears. In fact, there is ample evidence for detrimental effects arising from losses of whitebark pine, cutthroat trout, and elk, including major increases in mortality arising from the greater reliance of bears on meat—which has included consumption of livestock.

8. The Service fails to account for the effect of recent widespread losses of whitebark pine by its reliance on fatally flawed science produced by the IGBST. This IGBST research fails to account for temporal and spatial variation in availability of whitebark pine seeds as well as temporal and spatial variation in other critically important bear foods. As a result, no confidence can be placed in conclusions reached by the Service regarding the effects any driver of grizzly bear birth and death rates, including losses of whitebark pine.

8.1. The Service fails to accurately account for the spatial distribution of cone-producing whitebark pine trees when making its many claims regarding the lack of historical importance of pine seeds. This failure follows, in part, from the Service's near exclusive reliance on spatial analyses produced by the IGBST that were based on a map of whitebark pine distribution containing substantial errors of omission.

The IGBST used a map of whitebark pine distribution for its spatial representation of whitebark pine forests that was derived from remote sensing. This map was used for analyses of grizzly bear demography, home ranges, and habitat selection (Costello et al. 2014, Bjornlie et al. 2014, Van Manen et al. 2015), and was the basis for the Service's claims that roughly 23-33% of all recent bear ranges were comprised of <1% whitebark pine forest.

Put succinctly, the map of whitebark pine distribution used by the IGBST is contaminated by large errors of omission. Even more egregiously, this map shows large areas as being without mature whitebark pine which, in fact, contained significant enclaves of mature cone-producing trees. These omissions are the entire basis for claims made by Bjornlie et al. (2014), Costello et al. (2014) and later by the Service in its Rule and CS that a significant percentage of grizzly bear ranges lacked access to cones produced by mature whitebark pine trees. Quite simply, these claims are unfounded and false.

I base this conclusion on comparing the distribution map used by the IGBST with the distribution of sites where grizzly bears were documented by the IGBST to feed on whitebark pine seeds between 1977 and 1996 (Fig. 8.1.1). Feeding on whitebark pine seeds was documented by field crews during the course of investigations that involved humans being standing on the ground, looking at the remains of whitebark pine cones savaged by grizzly bears, and then looking upwards at the canopy, almost invariably to observe mature whitebark pine trees. Or,

put another way, compared to remotely-sensed maps, these ground observations are a more definitive reckoning of, not only the presence of cone-producing whitebark pine, but also the presence of these trees in sufficient numbers to support grizzly bear consumption of pine seeds.

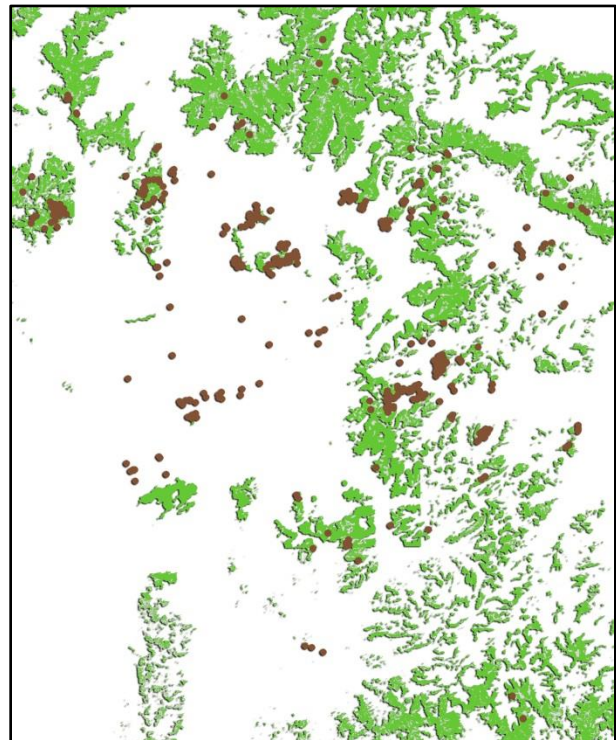


Fig. 8.1.1. This map shows the distribution of known instances where grizzly bears fed on whitebark pine seeds (dark brown dots) relative to the mapped distribution of whitebark pine used by the IGBST in recent analyses relied upon by the Service (in green). The numerous feeding sites far outside the mapped distribution correspond with the central plateaus of Yellowstone National Park.

The map in Figure 8.1.1 shows the distribution of known grizzly bear feeding on pine seeds as dark brown dots superimposed on the map of whitebark pine distribution that the IGBST used in analyses undertaken by Bjornlie et al. (2014), Costello et al. (2014), and Van Manen et al. (2015) shown in green. The mapped distribution contains

only 42% of all known instances of grizzly bear feeding on pine seeds. Being generous and assuming, for inexplicable reasons, that IGBST field crews had a systematic tendency to erroneously locate feeding sites as much as 200 m outside the mapped distribution of whitebark pine, the level of inclusion increases to only 63%. Fully 25% of feeding sites are located >650 m away from the nearest mapped whitebark pine. Importantly, almost all of the pine seed feeding sites missed by the mapped distribution are located at lower elevations, and of those missed by the farthest distance, almost all are on the central plateaus of Yellowstone National Park, which is precisely where Bjornlie et al. (2014), Costello et al. (2014), and the Service (repeatedly) claim that grizzly bear home ranges contained little or no mature whitebark pine.

In short, Bjornlie et al. (2014), Costello et al. (2014), and the Service, in turn, are simply wrong in claiming that 23-

8.2. The Service fails to account for the impacts of recent widespread losses of whitebark pine on Yellowstone's grizzly bears because it relies on science that is fatally flawed. This IGBST science conflates the extent of whitebark pine forests with levels of cone and seed availability, thereby misrepresenting periods of pine seed abundance as periods of pine seed shortage, and periods of pine seed shortage as periods of pine seed abundance.

At the risk of stating the obvious, Yellowstone's grizzly bears do not eat whitebark pine trees, as such. Rather, they eat the seeds contained in whitebark pine cones, most of which they obtain by raiding larders made by red squirrels (e.g., Mattson & Reinhart 1997). As a result, any annual or even multi-annual representation of whitebark pine seed availability to Yellowstone's grizzly bears needs to be in terms of cone or seed production, not the number of cone-producing trees, as such, or even the aerial extent of forests containing mature whitebark pine. Yet the IGBST conflates temporal trends in abundance of mature trees with seed production in its recent analyses of the effects of whitebark pine on grizzly bear demography (e.g., Van Manen et al 2015).

This matters because during and after massive numbers of mature trees had died from an outbreak of mountain

33% of historic grizzly bear ranges contained little or no whitebark pine and, from that, further claiming that whitebark pine was unimportant to a corresponding percentage of bears. In fact, very few grizzly bear home ranges probably contained little or no whitebark pine. The exact percentage is still unknown given that I do not have access to the home range delineations used by IGBST scientists, but this percentage is almost certainly trivial. In addition to the error made by Bjornlie et al. (2014) in their temporal representations of pine seed availability (see below), this additional error makes the Bjornlie research and related Service claims based on it baseless. Furthermore, the major errors of omission in the map of whitebark pine distribution used by Costello et al. (2014) and Van Manen et al. (2015) introduce yet more error and bias into these researchers' analyses, on top of the fatal errors introduced by their treatment of annual variation in availability of whitebark pine seeds (see below).

pine beetles, median annual cone production apparently increased by as much as 2.5-fold on surviving trees. Figure 8.2.1 shows counts of cones on whitebark pine trees monitored on fixed transects by the IGBST, averaged per annum over all monitored trees. The running three-year average of annual values is shown as a yellow-green line, which is relevant because of the somatic and behavioral averaging that goes with the three-year reproductive cycle of Yellowstone's female grizzly bears. In addition, I show medians of annual averages for three time periods corresponding with breaks in long-term trends. Of relevance to my point here, the median for the period 2006-2014 is roughly 2.5-times greater than the median for either 1982-1995 or 1997-2004. In other words, at the same time that we were losing—or had lost—perhaps the majority of cone-producing trees in the ecosystem (Macfarlane et al. 2013), cone production on the remaining trees increased by over 2-fold.

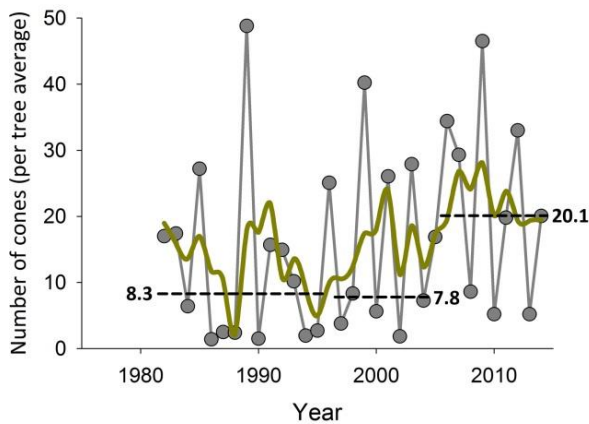


Figure 8.2.1. Average number of cones counted on whitebark pine trees at fixed transects by the IGBST between 1982 and 2014 (gray dots) along with a 3-yr moving average of these values (yellow-green line) and medians calculated for annual values for three different time periods (dashed lines).

As noted before, the IGBST purports to represent availability of pine seeds with remotely-sensed estimates of the aerial extent of mature whitebark pine trees. These estimates are shown in Figure 1 of Van Manen et al. (2015). One way to integrate information about the size of cone crops on surviving trees with an estimate of the numbers of such survivors is to simply multiply the index generated by Van Manen et al. (2015) by the average number of cones on live trees at fixed transects, as per Figure 8.2.1. This logically produces an index of the total landscape-level abundance of seed-containing cones available to Yellowstone's grizzly bears during any given year. This is, in fact, the relevant metric for use in any analysis of bear demography or movements given that, as I noted before, bears eat seeds not trees. The results of this metric, along with an annually averaged representation of the data in figure 1 of Van Manen et al. (2015), are shown in Figure 8.2.2: the index of cone availability as the dark yellow-green line and the index of tree abundance as the gray line.

There is one important error to note even in the way that Van Manen et al. (2015) represent the aerial extent of whitebark pine forests: they neglected to include the considerable losses that occurred during 1988 as a result of massive wildfires. The constant abundance that they show between 1983 and roughly 2000 should actually drop by around 17% (3-50%, depending on the precise area; Mattson 2000) between 1988 and 1989. In addition to blatantly ignoring cone production, this is itself a non-

trivial error even in the metric they do use—an error that I correct in generating the estimate of total seed availability.

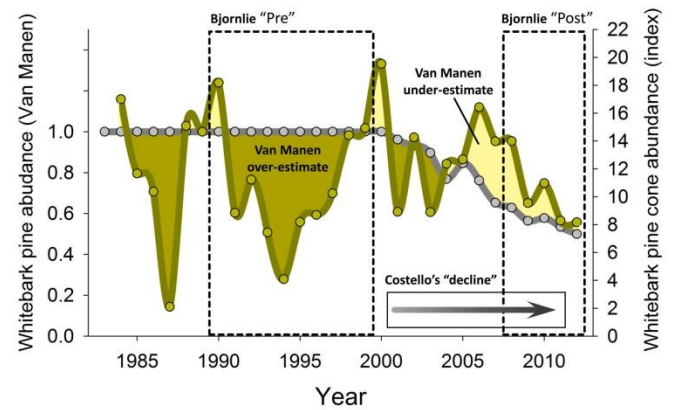


Figure 8.2.2. The IGBST index of mature whitebark pine is shown by the dotted gray line; the index of landscape-level cone availability, accounting for losses of trees to bark beetles and the 1988 wildfires, is shown by the dotted green line; and time periods relevant to errors in three key IGBST research publications are denoted by the first author's name and, in the case of Bjornlie et al. (2014), by dashed boxes, in the case of Costello et al. (2014), by an arrow, and, in the case of Van Manen et al. (2015), by the extent of erroneous over- and under-estimations.

But more importantly, the index of cone availability shows a dramatically different inter-annual pattern compared to the index of tree availability. More specifically, pine seeds were least available during two early periods that the IGBST claimed were typified by the greatest abundance of whitebark pine. By contrast, the large average increase in cone crops on surviving trees largely mitigated losses to bark beetles that occurred during the early 2000s. It was only after 2006 that losses of trees to beetles began to swamp the effects of larger cone crops, resulting in the onset of a terminal decline. More to the point here, the IGBST under-represented availability of pine seeds during the early 2000s by its reliance on an index of tree abundance.

These errors are fatal and, more specifically, render the results of Bjornlie et al. (2014) and Van Manen et al. (2015) meaningless if not downright wrong. Both papers are central to the Service's arguments in the Rule and CS. The IGBST misrepresented early periods of cone shortage as periods of cone abundance and later periods of cone abundance as periods of cone shortage. They and the

Service got things pretty much entirely backward, barring the terminal decline beginning in 2006.

Figure 8.2.2 shows in more detail the implications of this problem for the three referenced papers. The analysis of home ranges by Bjornlie et al. (2014) was based on the premise that the period 1988-1989 was a period of pine seed abundance, and the period 2007-2012 a period of pine seed dearth. In reality there was greater pine seed availability during the later period compared to the earlier periods. They got it entirely backwards. Likewise, the analysis of demography by Van Manen et al. (2015) grossly over-estimated pine seed abundance during 1983-1989 and substantially underestimated pine seed abundance during 2005-2010, which turned their assumptions upside down.

Having made this point in reference to the veracity of recent IGBST analyses and the Service's arguments that derive from them, I need to at the same time make clear that losses of mature whitebark pine trees are real and on-going (e.g., Logan et al. 2014). Looking to the future, even though losses have been largely masked by increases in per tree cone production—especially during the early 2000s—such natural mitigations will eventually run the course. When that happens, consequences will almost certainly unfold that are even more dramatic than any we have so far seen. In fact, the record number of grizzly bears dying during 2015 is a likely preview of more of the same to come.

9. The Service fails to account for—or even acknowledge—convincing evidence of major deleterious consequences arising from losses of whitebark pine in the Yellowstone ecosystem. Most prominently, these consequences include compensatory increases in consumption of meat from ungulates by Yellowstone's bears and, with that, dramatic increases in meat-related bear-human conflicts and resulting human-caused bear deaths.

Throughout the Rule and the CS the Service freely asserts that losses of whitebark pine have had little impact on the Yellowstone grizzly bear population. These assertions are based wholly on fatally-flawed IGBST science and on the Service's own misrepresentations of the nutritional ecology of bears. I critique the Service's deficient representation of what we know about nutritional ecology elsewhere (point 7). Points 8 and 10, immediately before and following, describe fatal flaws in recent IGBST research that renders this science useless at best, but which the Service liberally invokes as a primary basis for its many correspondingly flawed arguments. In short, the Service has no basis for dismissing the potential impacts of losing whitebark pine in the Yellowstone ecosystem.

Perhaps more important, the Service does not acknowledge nor present the compelling body of evidence showing major deleterious changes in grizzly bear behavior and demography coincident with terminal losses of whitebark pine—and cutthroat trout—in the Yellowstone ecosystem. These changes include increasing consumption of meat from terrestrial sources

and, along with this, a dramatic increase in meat-related conflicts with people, leading to increases in numbers of human-caused deaths. Moreover, the decline in cub and yearling survival rates that the Service attributes to "density-dependent effects" (citing IGBST [2012] and Van Manen et al. [2015]) is more plausibly attributable to the consequences of reproductive females eating more meat in the wake of trout and whitebark pine losses. All of these changes have ultimately manifested in a dramatic rise in known and probable grizzly bear deaths that correlates perfectly with terminal losses of whitebark pine, and which amounts to a substantial increase in grizzly bear death rates at a time when the population has reached stasis and even begun to decline (see point 19.4).

Taking each of these points in turn, there is ample evidence of grizzly bears eating more terrestrial meat coincident with losses of whitebark pine and cutthroat trout. Mattson (1997) first noted that grizzlies in Yellowstone tended to eat more meat during years of poor whitebark pine seed crops—this at a time when Jacoby et al. (1999), and Mattson (2000) showed that,

compared to females, male grizzly bears ate up to twice as much terrestrial meat, and all of this prior to widespread losses of whitebark pine that began during the early 2000s.

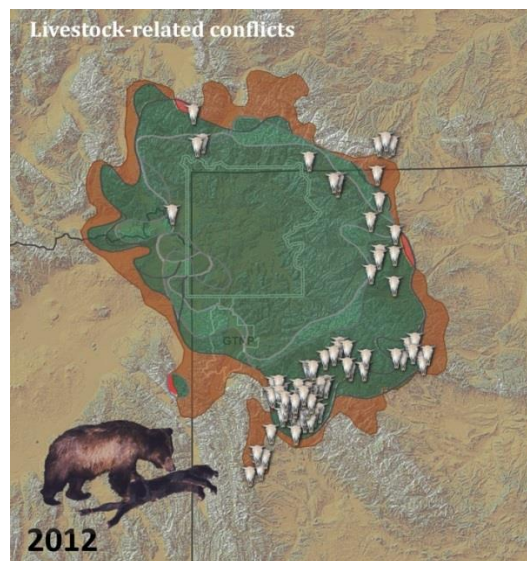


Figure 9.1. This map shows the current distribution of Yellowstone's grizzly bear population in relation to livestock-related conflicts that occurred during 2012 (each represented by a cattle skull) and the distribution of moth sites (encompassed by yellow-green blobs). Grizzly bear distribution is differentiated by the area occupied by bears prior to circa 2000 in green and areas occupied since then in orange.

In the wake of losses of cutthroat trout during the late 1990s and early 2000s and whitebark pine during the mid- to late-2000s, overall consumption of terrestrial meat has trended upward (Schwartz et al. 2014, Ebinger et al. 2016), with much of that increase fueled by increased predation on elk calves (Fortin et al. 2013, Middleton et al. 2013) and scavenging of offal from elk killed by big game hunters (Orozco & Miles 2013). Even more consequentially, grizzly bear exploitation of livestock has increased dramatically, almost all of it concentrated on the periphery of the ecosystem in areas first occupied by bears after the mid-1990s and early 2000s—and much of this figuratively downslope from moth sites also first occupied during this same period (see maps of conflicts presented each year in IGBST Annual Reports; also, see the map in figure 9.1 at left which shows data for an emblematic year together with locations of moth sites). As important for the population, differences between the sexes in consumption of meat have diminished (Fortin et al. 2013, Schwartz et al. 2014)

presumably as females increasingly resort to eating meat in the wake of losing other key foods.

In short, grizzly bears in the Yellowstone ecosystem seem to be eating more meat from elk and livestock, with most livestock consumption concentrated on the ecosystem periphery, and with little current difference in dietary meat between males and females. And meat now potentially accounts for the majority of energy and nutrients for both sexes.

Nutritionally, this dietary shift has probably not been detrimental. Mattson et al. (2004) and the Primer on Nutritional Ecology attached to these comments clearly show that meat is a high-quality bear food, and that during fall ungulates can offer bears a substantial quantity of fat. As a result, there is no reason to expect major changes in female fecundity, which is consistent with recent data on reproduction (e.g., litter sizes as reported in IGBST Annual Reports).

The problem with meat consumption arises from the entailed hazards for any grizzly bears engaging in this activity (see my point related to a frame that jointly accounts for both hazards and nutrition). Figure 9.2 shows, at top, trends in numbers of grizzly bears dying because of conflicts with big game (primarily elk) hunters together with trends in number of hunters afield and, at bottom, trends in numbers of livestock-related human-bear conflicts and numbers of bear dying because of these conflicts. All of these data come from IGBST databases or Annual Reports. Each figure also shows terminal declines in whitebark pine cone/seed availability that I describe more fully under point 8.2.

The temporal correlation between declines in cone availability and stark increases in meat-related conflicts and deaths is quite good. Given that bears seem to be compensating for losses of whitebark pine by eating more meat, these astounding increases in meat-related grizzly bear deaths can hardly be considered a coincidence.

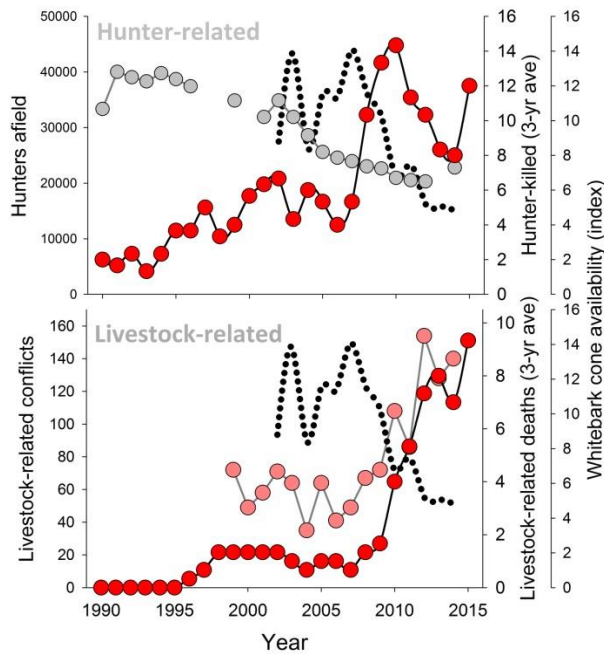


Figure 9.2. Trends in numbers of grizzly bears killed (top) because of conflicts with big game hunters (red dots) and (bottom) conflicts over livestock (red dots as well). Gray dots in the top graph show numbers of hunters afield and pink dots in the bottom graph, total numbers of livestock-related conflicts. The black dotted lines show trends in whitebark pine cone availability since onset of losses to bark beetles.

On top of this, rather than being ascribed to “density-dependent effects,” the increased death rates of cubs and yearling seen recently in Yellowstone are more plausibly ascribed to the increased hazards for these vulnerable young bears arising from their mothers eating more meat. (Parenthetically, see my critique of how the Service uses the concept of density-dependence under point 4). These hazards for young bears derive partly from the human-associated hazards incurred by their mothers, but also from hazards associated with increased predation by wolves and other bears (for more on this, see my point 17).

As a bottom line, dramatic increases in total known and probable grizzly bear deaths in the Yellowstone ecosystem—both natural and human-caused—are clearly correlated with terminal declines in availability of whitebark pine seeds (Figure 9.3). Much of this increase

is equally clearly driven by the consequences of dietary shifts entrained by loss of whitebark pine, as per the shift to eating more meat.

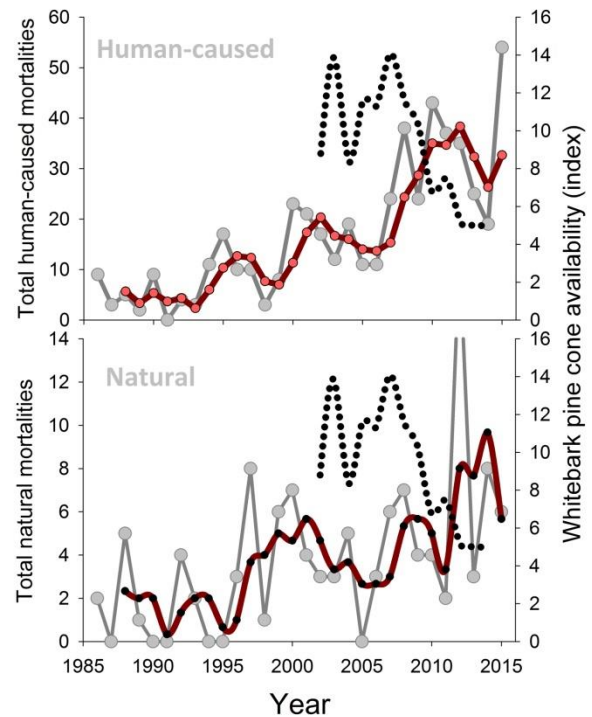


Figure 9.3. Trends in total numbers of known-probable human-caused grizzly bear deaths, top, and probable natural deaths, bottom. The gray lines are annual counts and the red trend lines running 3-year averages. The black dotted lines show trends in whitebark pine cone availability since onset of losses to bark beetles.

Taken together, this constitutes compelling evidence for substantial deleterious population-level effects arising from loss of whitebark pine (and cutthroat trout) in the Yellowstone ecosystem, with more foreseeable negative effects yet to come (see my critique of the Service’s treatment of trout, ungulates, whitebark pine, and moths, especially in relation to climate change). Quite simply, the Service has no credible basis for dismissing losses of whitebark pine as being inconsequential. In fact, the Service’s representation of this issue appears arbitrary and capricious. The Service needs to correct what amounts to an egregious error in its analysis supporting this Rule.

10. The Service fails to account for major changes in abundance of other key bear foods besides whitebark pine because of its reliance on unsubstantiated rhetorical arguments and fatally deficient IGBST research in the Rule. This IGBST research does not include any explicit consideration of an epic decade-long drought or variation in abundance of cutthroat trout, elk, bison, and army cutworm moths in its analyses of movements and demography. The Service consequently has no scientific basis for any claims regarding drivers of change in the demography and movements of Yellowstone's grizzly bears.

The Service relies heavily—almost exclusively—on recent research published by the IGBST. The Service invokes this research as its primary basis for claiming that recent losses of whitebark pine have not resulted in any changes in the demography of Yellowstone's grizzly bears. The three seminal papers cited repeatedly on pages of the Rule are Bjornlie et al. (2014), Costello et al. (2014), and Van Manen et al. (2015), the first dealing with changes in home ranges, the second, changes in movements and habitat selection relative to whitebark pine and secure habitats, and, the third, changes primarily in death rates. The first and last conclude that losses of whitebark pine to bark beetles, 2001-2012, had no effect, and that all changes could be attributed to changes in bear densities. Notably, these papers claim to have looked at both spatial and temporal variation—but limited only to considerations of density and extent of whitebark pine forests.

Elsewhere I address fatal errors in how the IGBST—and Service—addressed availability of whitebark pine seeds to grizzly bears both in space and time (point 8). I also cover problems with both the IGBST's density argument and density index under a different comment (point 4). Here I point out another fatal flaw in the IGBST's and Service's analysis that is rooted in lack of attention to a number of major changes in Yellowstone's grizzly bear habitat—in addition to changes in whitebark pine abundance. All of these ignored dynamics are of *prima facie* importance given that they pertain to availability of patently important grizzly bear foods, including elk, bison, cutthroat trout, army cutworm moths, and foods affected by levels of drought (also see my point 11.1).

Before delving into particulars of the neglected factors, it is worth reiterating my first comment (1.1): most of the science produced by the IGBST and invoked by the Service entails complex models and complex assumption-ridden statistical methods. Such is the case for all of the results germane to judging the demographic plight of

Yellowstone's grizzly bears. Yet it is well known to even half-way thoughtful scientists that there is no one correct model, and that model-building is perhaps the most vagarious and bias prone of scientific undertakings. Moreover, any credible inference based on complex models of open ecological systems depends almost entirely on insuring that all factors likely to have had a significant effect on outcomes of interest (i.e., changes in demography) were accounted for. Isolating the effect of any single factor such as bear density or whitebark pine abundance depends upon controlling for the effects of every other factor of plausible importance.

In other words, by failing to account for a number of plausibly important changes in Yellowstone's grizzly bear habitat, the IGBST—and Service—have no basis for making any claims about effects of density or whitebark pine on grizzly bear birth and death rates, and this aside from the fatal flaws in how they putatively addressed the factors they did consider.

Figures 10.1 and 10.2, below, provides some specifics. I show trends in known important foods over time, encompassing the span of relevance to the various analysis undertaken by the IGBST. These foods, top to bottom, include size of whitebark pine cone crops (not extent of whitebark pine forests), bear use of army cutworm moth sites, numbers of spawning cutthroat trout, numbers of elk in the ecosystem's two largest herds, and, finally, at bottom, numbers of bison in Yellowstone's two herds.

These figures also show how time period was treated in the three seminal IGBST papers, denoted by the vertical bars shaded different colors of orange. Bjornlie et al. (2014) assumed two time periods, one before (pre) and one after (post) major losses of whitebark pine to beetles, assuming that the only changes in the Yellowstone environment between these two periods were extent of whitebark pine forests and bear density.

The vertical shading in the graph farther right shows how Van Manen et al. (2015) approximated the presumed decrease in whitebark pine forests with ever-darker hues of orange—and again, without considering any other

environmental trends. Finally, the center graph shows the time period addressed by Costello et al. (2014) as a shaded vertical box, and, again, this researcher assumed that the only change afoot pertained to whitebark pine.

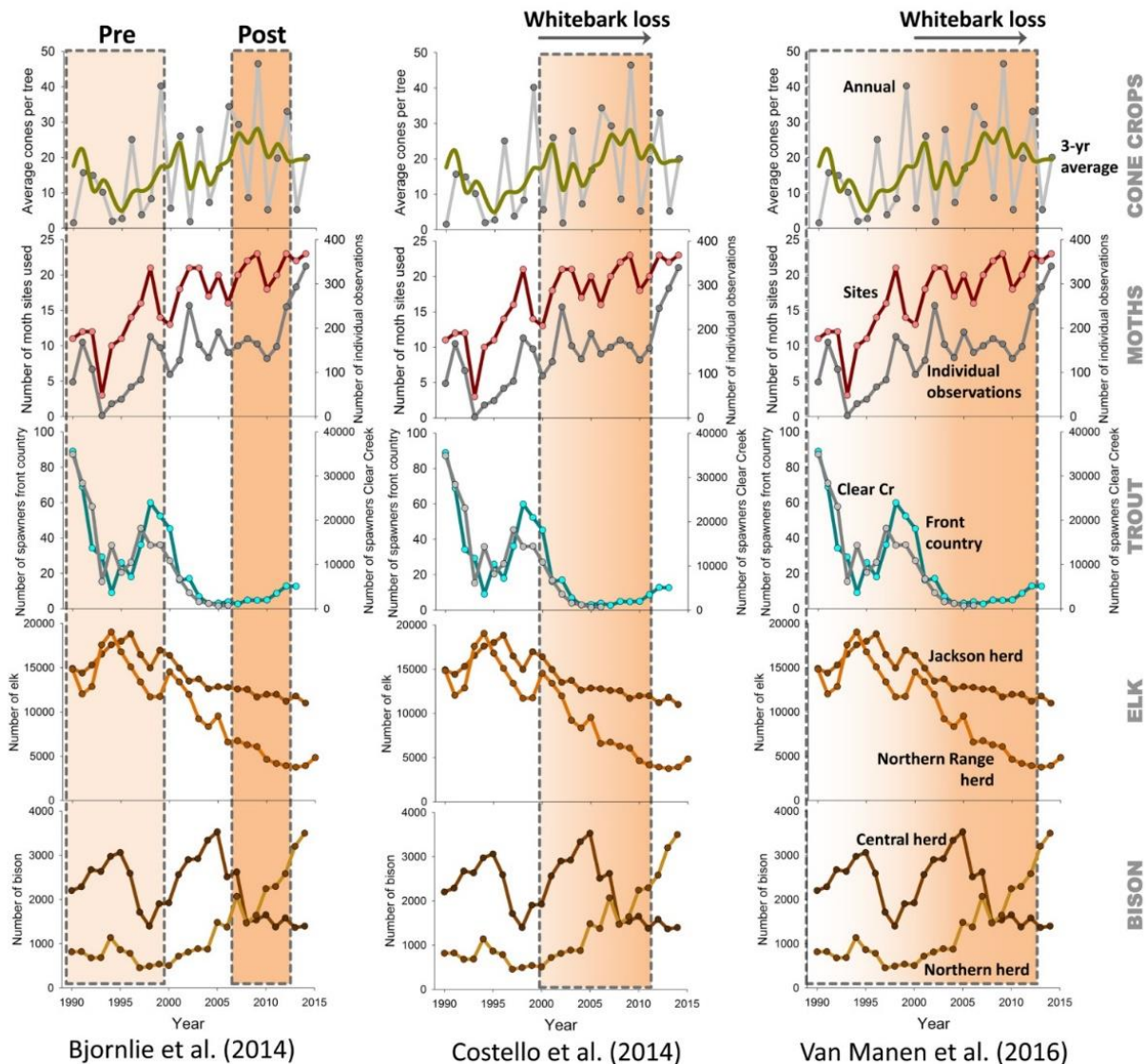


Figure 10.1. Trends in indicators of abundance for key Yellowstone grizzly bear foods are shown by rows, from top to bottom, intersected with rows denoting how three different analyses reported by the IGBST treated time periods, show as vertical boxes shaded various hues of orange. Progressively darker hues of orange denote less versus more whitebark pine, at least as treated in the IGBST analyses.

The takeaway from figure 10.1 is pretty straight-forward. The IGBST failed to account for major unfolding trends in food abundance. Bjornlie et al. (2014) failed to account for the fact that elk and cutthroat trout had declined and moth site use and whitebark pine cone crop sizes had increased between the 'pre' and 'post' periods. Likewise, Van Manen et al. (2015) neglected to account for these

very same trends as continuous temporal (and spatial) phenomena. Costello et al. (2014) failed to account for trends towards increasing sizes of whitebark pine seed crops, increasing levels of moth site use, and decreasing numbers of elk. All of these failures fatally compromise these analyses.

Figure 10.2, below, makes the added point that these three IGBST papers not only failed to account for trends in abundance of important foods, but also neglected to account for some longer-term trends in weather, with near certain effects, in turn, on other vegetal and animal foods. More specifically, Bjornlie et al. (2014) failed to account for a higher average summer temperatures

during their 'post' period; Van Manen et al. (2015) for an epic drought and for a trend towards progressively higher summer temperatures; and Costello et al. (2014) for the gradual recovery from deep drought. All of these patterns plausibly affected grizzly bear movements and diet.

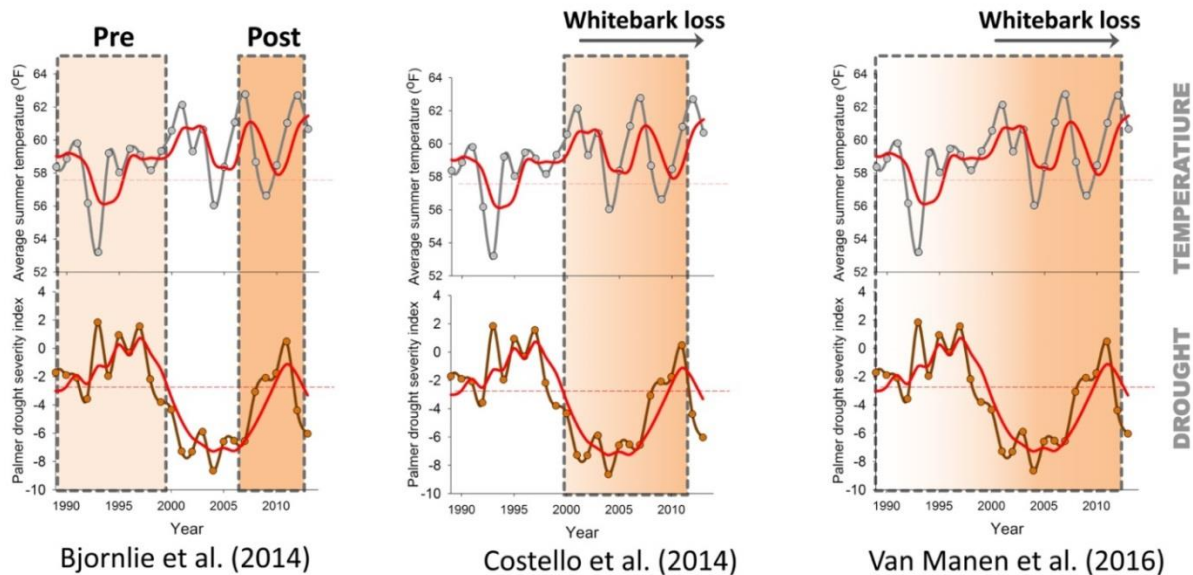


Figure 10.2. The basic configuration here is the same as in figure x.1, but featuring trends in summer temperature (top row) and drought severity (bottom). The red lines are 3-year moving averages and the gray dots, annual values. Drought is indexed by the Palmer Drought Severity Index. All data are publicly available from NOAA.

Finally, in addition to fatal neglect of temporal trends, the IGBST's science—and Service's derivative claims—fail to account for potential interactions between spatial distributions of and temporal trends in key food resources. This specific critique is relevant both because the IGBST pretends to deal with spatial aspects of food availability (albeit limited to whitebark pine) and because interactions among environmental factors in space and time are a very real consideration in any analysis of complex ecological systems. And, in fact, there are many potential interactions that were altogether neglected in analyses by the IGBST and Service.

Figure 10.3 illustrates a subset of potential interactions (the legend for this figure explains the various map features). For one, moth sites (the grayish-green blobs) correspond almost exactly with where we have seen the greatest losses of whitebark pine (in gray). In other words, availability of moths has very likely partially compensated for the severe losses of whitebark pine that

occurred in this area. For another, as per trends for Yellowstone's two bison herds shown in figure 10.3, bison have declined in precisely the same areas (the Central herd) where near extirpation of cutthroat trout also occurred, resulting in an amplification of the effects of trout losses. By contrast, the Northern Range bison herd (in green) has increased, with some likely compensation for losses of whitebark pine and declines in elk numbers in the northern part of the ecosystem.

As a bottom line: by failing to account for both the temporal and spatial aspects of major changes in the environment of Yellowstone's grizzly bears the Service fatally compromises its assessment of past and prospective future changes in demography and behavior of Yellowstone's grizzly bears. A prudent course of action would be for the Service to withdraw this draft Rule and remedy the profound deficiencies in its analysis and the science it has so far relied upon.

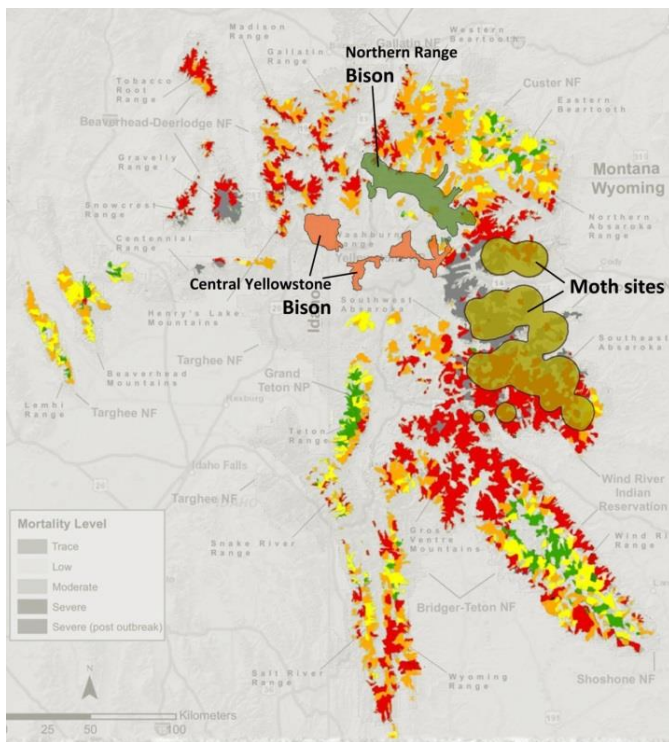


Figure 10.3. Distributions of whitebark pine forests, moth sites, and core bison ranges in the Yellowstone ecosystem. Whitebark pine forests are shown in various colors corresponding to the magnitude of mortality from bark beetles as of 2009; gray indicates near total mortality, red, high levels, green, healthy forests, and yellow and orange somewhere in between (Macfarlane et al. 2013). All known moth sites are encompassed by buffers denoted by yellowish-green shading. The Northern Range bison herd range is shown in green and the Central bison herd in off-orange.

10. The Service’s assumption that maintenance of a simplistic version of the 1998 human footprint will insure sustainable future human impacts is flawed for a number of reasons, including failure to account for changes in bear behavior in response to habitat conditions, changes in human lethality, and changes in edge effects attributable to development on lands adjacent to the PCA.

In multiple places the Service asserts that maintenance of certain GIS-delineated human features within the PCA will insure conservation of the Yellowstone grizzly bears into the indefinite future by maintaining demographic characteristics that ostensibly prevailed during a period of sustained population growth. The spatial attributes that presumably govern grizzly bear demography include road densities, the extent of areas >500m away from human infrastructure (so-called “secure” habitat), and numbers of livestock allotments.

This all-critical assumption that a static few GIS-delineated landscape features will insure anything into the indefinite future fails for numerous reasons, including (1) over-stated population growth during the invoked benchmark period of 1988-1998; (2) failure to account for a critical sources of human-caused mortality that can vary independently of the chosen few landscape

features; (3) failure to account for changes in bear behavior driven by changes in diet and food availability that will affect how often bears encounter the mapped lethal human features—independent of any change in these features; (4) changes in the lethality and behavior of people both in relation to and independent of mapped and monitored features; (5) changes in numbers of people on, off, and nearby to the mapped features, with resulting effects on encounter rates between bears and people; and (6) related edge effects associated with human population growth and residential and recreational developments on private lands near and inside the PCA. Taking each one of these in turn:

1. As I describe in my critique of the currently-adopted Chao2 method for monitoring trend of Yellowstone’s grizzly bear population (point 19.1), this method has almost certainly overstated growth, including for the

period 1988-1998. Which means that, although some growth was very likely happening, it was of a lesser magnitude than being asserted—and relied upon—by the Service in the Rule. As a practical matter, this translates into less of a buffer on this basis alone than the Service would have us believe (but see all my following points).

Perhaps more importantly, the 1998 footprint has, in fact, been associated with a range of demographic conditions, including (according to the Service) a decline in population growth rate to the point where the population has not changed in size for roughly 15 years. In fact, as I argue elsewhere (point 5.3), the population has likely declined during the last decade and has perhaps passed a tipping point. The entire premise of the Service's argument is rendered implausible by the fact that a wide range of human-caused grizzly bear mortality rates has been encompassed by a set of landscape conditions presumably designed to guard against such amplitude (see 19.4).

2. Currently, the primary human-related causes of grizzly bear mortality in the Yellowstone ecosystem are: availability of attractants at residences and recreational developments; conflicts over livestock; and conflicts with big game hunters. Additional minor causes include collisions with vehicles and removals because of more direct human-safety concerns. *As a spatial phenomenon*, most of these causes are covered by the Service's monitored features, but with the important exception of big game hunters. Hunters are particularly lethal to grizzly bears and, more importantly, often distributed in a way that is poorly correlated with roads, "secure" habitat, and livestock allotments. The upshot is that the monitoring spatial features provide a poor basis for monitoring what's happening with numbers and distributions of a certain class of human that is a major cause of grizzly bear mortality.

3. As I describe at length elsewhere in this critique (and as the Service also avers), the diet of Yellowstone's grizzly bears has changed substantially, with prospects of even more change to come. These changes organize around loss of cutthroat trout and whitebark pine seeds in some of the most secure habitats in the ecosystem, along with prospective losses of army cutworm moths, also in remote secure areas. There is little doubt that,

among other things, grizzly bears are turning to eating more meat, including livestock and scavenged offal left by hunters. As a consequence, grizzly bears are spending more time in highly lethal environments typified by grazing allotments and areas used by big game hunters (e.g., my points below; Haroldson et al. 2004). Use of alternate foods also seems to draw bears more often into less secure habitat nearer roads and other human facilities (Haroldson & Gunther 2013, Costello et al. 2014), as has been the case since the 1980s (Mattson et al. 1992). Even farther back in time, closure of garbage dumps in and around Yellowstone National Park during 1959-1962 had profound impacts on how grizzly bears distributed themselves relative to a comparatively static human infrastructure, but with catastrophic consequences for the bear population (Craighead et al. 1994). The main point here is that grizzly bears can end up being exposed much more often to lethal human-associated features as a result of habitat and diet changes and without any spatial change in the extent of human facilities or livestock grazing allotments—as per the 1998 human footprint.

4. Augmenting issue 3, a given number of people can change how they orient to mapped and monitored spatial features and, perhaps more important, can become more or less per capita lethal to bears. This point is historically emphasized by the fact that grizzly bears would have probably come closer to near-total extirpation in the Yellowstone ecosystem during the early to mid-1900s but for the fact that aggregate human lethality changed, and in spite of increasing human numbers (Mattson & Merrill 2002). More recently, as the Rule describes, human lethality has been reduced by instituting measures that reduce availability of human-associated foods around human facilities, thus reducing human lethality—all without any explicit correlation with roads and grazing allotments. We can only hope that humans continue to become ever less lethal, ever more assiduous in managing attractants, and continue to concentrate as much on roads, but simply monitoring roads and livestock grazing allotments will not provide any information on this critical dimension of the human footprint.

5. As the IGBST recognizes through its monitoring of big game hunters afield on national forest lands, and human recreational activity in Yellowstone and Grand Teton

National Parks, numbers of people matter to grizzly bear conservation, even given a fixed human infrastructure. It is thus probably relevant that numbers of visitors to Yellowstone Park increased by roughly 400,000 between the 1990s and 2010s, although remaining nearer the same in Grand Teton (IGBST 2015). But of perhaps even greater relevance is that visitation to these parks has trended ever upward from 2005 to the present (2,868,317 to 4,097,710 in Yellowstone; 2,463,442 to 3,149,921 in Grand Teton), meaning ever more people on roads and at recreational facilities, which no doubt creates mounting challenges for managers attempting to control attractants and risky human behaviors—but with no change in the physical infrastructure. Here, again, numbers alone matter. More directly, the management challenges that sheer numbers pose matter, with prospects of affecting grizzly bears that are exposed to areas near the human infrastructure.

6. It perhaps goes without saying (and as the Rule describes), population growth and associated development on private lands in the Yellowstone ecosystem continues at a rapid but, more recently, accelerating pace, with development disproportionately concentrated near protected areas and in productive riparian habitats (e.g., Gude et al. 2006). Strangely, the Service fails to feature research by Schwartz et al (2012) that explicitly estimates the impacts of projected exurban development on Yellowstone’s grizzly bears, differentiating impacts by whether they will occur in the PCA or outside in occupied grizzly bear habitat. “Boom” or even status quo growth could bring major loss of source habitats, contributing to even more habitat fragmentation than exists now (see my comments under point 14). These results are summarized in figure 10.1 immediately below.

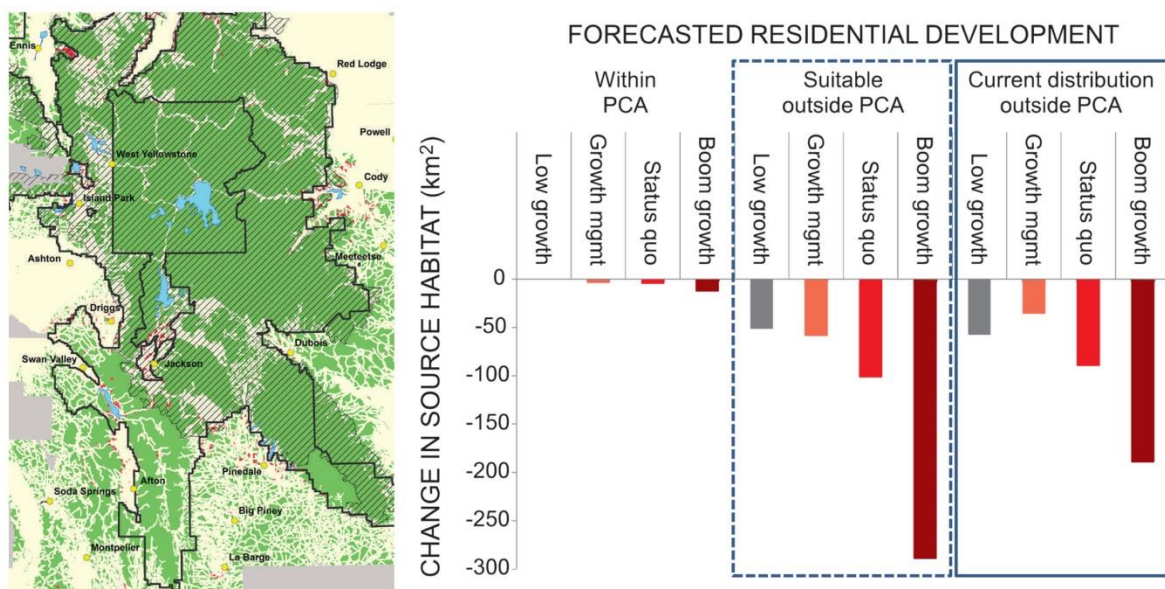


Figure 10.1. Figures extracted from Schwartz et al. (2012) pertaining to projected effects of exurban development on Yellowstone’s grizzly bear habitat. The beige in the map at left corresponds to projected human-impaired habitat. The bar graph to the right shows loss of source grizzly bear habitat in and out of the PCA under four different scenarios for growth of the human footprint.

The Service liberally employs the notion of ‘edge effects’ as a basis for excluding habitat near sheep allotments in the Wind River Range from its classification as “suitable” habitat. The Service’s usage in that circumstance is problematic. However, edge effects are a very real consideration in relation to on-going and foreseeable exurban development adjacent to the PCA, with the possibility of transboundary effects plausibly attributable to the boundary-spanning movements of both bears and

people. The map at left in figure 10.1 shows this potential in graphic form, with projections of lethal habitat shown in beige. The point of this being that effects of mounting human activity on private lands in and near the PCA will engender largely negative effects that will not be accounted for in the 1998 benchmark pegged to federally-managed lands. The Service engages in what largely amounts to a bunch of hand-waving on pages 13199-13200 of the Rule about how extra-

jurisdictional activities on the part of state and federal managers will somehow mitigate for this. Such claims are unsubstantiated. Moreover, there is precedent for federal managers undertaking mitigation on public lands for harm arising from activities on nearby private holdings (e.g., the 1997 Swan Valley Grizzly Bear Conservation Agreement). In other words, the Rule's current arm-waving is not good enough in light of prospective trends in private land development in the Yellowstone ecosystem.

Parenthetically, the Service will probably assert in response to my critique of their 1998 benchmark that, even if valid, there are other safeguards in place in the form of methods for monitoring and managing mortality. As I hope is clear from the remainder of my critique, there are, in fact, critical failings and short-comings affecting all of these safeguards that debar them from providing a reliable backstop.

11. The Service fails to meaningfully account for past changes in major Yellowstone grizzly bears foods; this on top of the problems with its analysis regarding whitebark pine. Among key foods that the Service essentially dismisses out of hand are elk, bison, cutthroat trout, army cutworm moths and all of the vegetal foods that are affected by growing season drought. In short, not only does the Service fail to provide any useful basis for assessing past and prospective future changes in natural foods, but, even more problematic, fails to acknowledge and address clear scientific evidence that the Yellowstone grizzly bear population is in trouble and threatened by further deterioration of habitat conditions.

11.1. The Service fails to use or even acknowledge scientific evidence showing that there is *prima facie* reason to expect that availability of ungulates, army cutworm moths, cutthroat trout, and drought have affected grizzly bear death rates, with prospects of leading to elevated death rates over the next decade to century.

On page 13212 of the Rule the Service references a single research paper of only peripheral relevance (Schwartz et al. 2010) as a basis for asserting that “...only whitebark pine seeds are known to have an influence on grizzly bear mortality risk and reproduction. There is no known relationship between grizzly bear mortality risk or reproduction and any other individual food.” The Service then uses this assertion to dismiss out-of-hand any serious consideration of demographic consequences arising from past and likely future trends in any food source other than whitebark pine. In rushing through these bemusing leaps of logic the Service altogether ignores a trove of scientific information relevant to judging whether other foods might—or even do—have an effect on birth and death rates of Yellowstone’s grizzly bears. When taken seriously, this body of science paints a fundamentally different picture—which is the picture I paint here in my following points as well as throughout the rest of my comments.

It is first worth noting that the Service fails to explain how “...some of the highest calorie food sources available to grizzly bears in the GYE”—and of enough importance to be monitored by the IGBST (page 13212)—can be dismissed essentially out of hand. Or, related, why the ample trend data from foods important enough to be monitored year-after-year by multiple state and federal agencies is not worth the Service’s consideration (as with army cutworm moths, cutthroat trout, and ungulate carrion). Even without pursuing this issue any further, these twists of logic suggest an up-front disinterest by the Service in seriously engaging with the effects of foods

such as elk, bison, army cutworm moths, and cutthroat trout—or all of the other foods that might be affected by drought.

Moreover, it takes convoluted logic to conclude that “there is no known relationship” simply because the Service chooses to rely solely on fatally flawed science that failed to consider the possibility of such relationships in the first place (see my points 2.2 & 10 above). Failure on the part of a few scientists to exercise adequate scientific rigor does not constitute a thorough and sufficient examination of the science relevant to judging why birth and death rates of Yellowstone’s grizzly bears might have changed in the past, and how these rates might be affected in the future.

Beyond these logical problems, one important point to reiterate (see my point 7) is one that the Service itself makes in several places, including on page 13212. There are, in fact, only a handful of foods from which Yellowstone’s grizzly bears historically obtained perhaps as much as 80% of their energy and nutrients: meat from elk and bison; meat from cutthroat trout; seeds from whitebark pine; and army cutworm moths. As the Service notes in its (far from adequate) review of nutritional ecology, other foods the bears ate aplenty, but none came even close to providing the same amount of energy, protein, or fat as the four dominant foods. On this basis alone there is ample reason to expect that all of the four key foods—not just whitebark pine seeds--affected birth and death rates of Yellowstone’s grizzly bears in some measure. Certainly, on the basis of energetics and nutritional considerations alone, such a conclusion is more defensible than any other, including the conclusion hastily reached by the Service.

And, as I point out in numerous other places, it is fundamentally problematic that ALL but one of the analyses relating food abundance to grizzly bear

demography in the Yellowstone ecosystem failed to even consider the effects of moths, trout, elk, or bison—or any other food for that matter (Mattson et al. 1992, Pease & Mattson 1999, Schwartz et al. 2006, Van Manen et al. 2015). The only food effect that was entertained by these researchers was that of whitebark pine seeds. It is no wonder that if you don't look for or otherwise even consider additional effects, you probably won't document any. And, importantly, such a failure of scientific rationality does not equate to the absence of such effects—such as potentially those of trout or moths or elk or bison on grizzly bear birth and death rates. In fact, the single more replete analysis (Mattson 2000), detected effects of meat-eating on cub survival and root consumption on litter size.

More positively, though, there is evidence that death rates of Yellowstone's grizzly bears have varied in reflection of moth, elk, and trout abundance—also perhaps as a function of drought—especially between 1990 and 2005. Elsewhere I present definitive evidence that an increase in consumption of meat by Yellowstone's grizzlies as compensation for losses of whitebark pine seeds led to the sharp increases in natural and human-caused mortality since 2006 (see my points 9, 17, & 18). But here I focus on 1990–2005 using publicly available data from the IGBST, the National Park Service, the states of Wyoming and Montana, and NOAA, realizing that a rigorous analysis of all data currently sequestered by the Service would also entail spatial and temporal interactions.

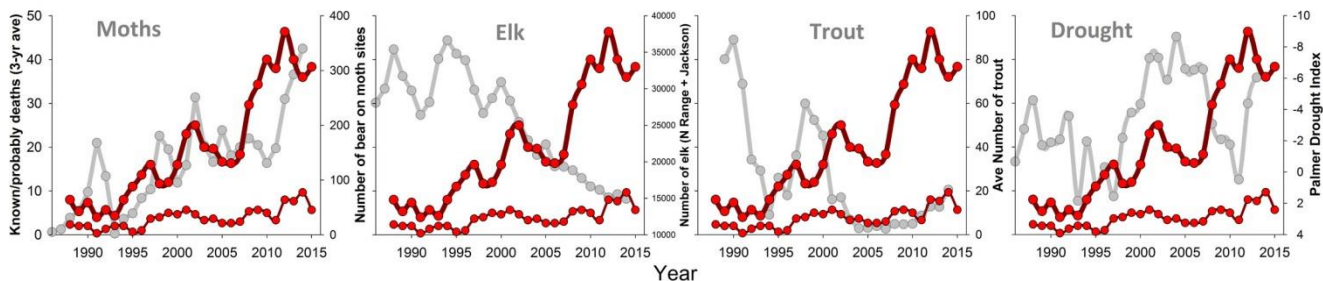


Figure 11.1.1. These four panels superimpose trends in total known-probable grizzly bear mortality on trends in abundance of four foods plus drought for the period 1986–2015. Mortality is shown in red as a 3-year running average, with natural mortality (lower red line) differentiated from total mortality (top red line). The gray lines show trends, left to right, in number of bears seen on moth sites; numbers of elk in the Northern Range and Greater Jackson herds; average per stream numbers of trout counted in spawning streams around Yellowstone Lake; and an inverted representation of the Palmer Drought Index for the highest-elevation drainages of the Yellowstone ecosystem (i.e., peaks in the trend line indicate greater drought severity).

Figure 11.1.1 shows trends in total known and probable grizzly bear deaths in red as a 3-year running average superimposed on trends in foods, or food proxies, all of which are currently neglected by the Service.

Put simply, trends in human-caused and total grizzly bear deaths can be largely explained in terms of trends in availability of key foods. For example, a simple regression model containing trends in elk populations and availability of whitebark pine seeds (see my point 8.2) explains 74% of total and 76% of human-caused mortality (with P-values <0.0001)—with both food effects negative, as one would expect. A similar model including elk, trout (also negative), and drought (positive) explains 70% of human-caused mortality (also with P<0.0001). Another model yet, in which I used latent variables to deal with the high degree of temporal

correlation among covariates (i.e., principal components), explains 70% of total deaths and 72% of human-caused mortality, with elk, trout, and whitebark pine all having negative effects, and moths and drought, positive effects.

Parenthetically, I suspect that the anomalous *positive* relationship between grizzly bear death rates and use of moth sites is related to geography. As shown in Figure 11.1.2., all of the moth sites are on the east side and towards the periphery of the ecosystem, in areas where we have seen expansion of the grizzly bear population, and a burgeoning of livestock-related conflicts and resulting grizzly bears deaths (see my point 9). Emblematic of this, the cow skulls in figure 11.1.2 each represent a grizzly bear-livestock conflict for one representative year, of which a disproportionate number

are figuratively just downslope from a moth site. The point of this being that moth sites are spatially correlated with an emerging major cause of grizzly bear deaths, and thus probably positively correlated with temporal trends in deaths largely as an artifact of this geography.

As a bottom line, there is strong evidence that all of the key grizzly bear foods have had a strong if not dominant effect on death rates, enough so that essentially all of the trends in total and human-caused grizzly bear deaths since roughly 1990 can be explained by availability of elk, cutthroat trout, whitebark pine seeds, army cutworm moths, and drought (as a proxy for other vegetal foods). On the basis of straight-forward nutritional considerations, there is also good cause to expect that these same foods have had, and will continue to have, strong effects on grizzly bear birth rates.

Quite simply, there is no excuse other than perhaps prejudice, laziness, and limited imagination for the Service's failure to consider the effects of all nutritionally important foods on birth and death rates of Yellowstone's grizzly bears. The Service needs to remedy its currently deficient analysis and seriously address past effects and future prospects for army cutworm moths, cutthroat trout, elk, and bison—as I outline in more detail in my following points.

11.2. The Service fails to meaningfully account for declines in elk populations and foreseeable threats to this source of bear food in its assessment of current and prospective threats to Yellowstone's grizzly bear population. This failure further compromises the Service's attempt to disentangle drivers of recent and prospective near-future changes in demography of the bear population.

Meat from terrestrial sources has contributed between 25% and >60% of the energy and nutrients obtained by Yellowstone's grizzly bears from their environment, the range depending on the sex and age cohort and time period (Mattson 1997, Jacoby et al. 1999, Fortin et al. 2013, Schwartz et al. 2014). During the 1970s-early 1990s, elk were the source of the majority (c. 53%) of this meat (Mattson 1997). Moreover, terrestrial meat has been invoked as an important compensatory substitute

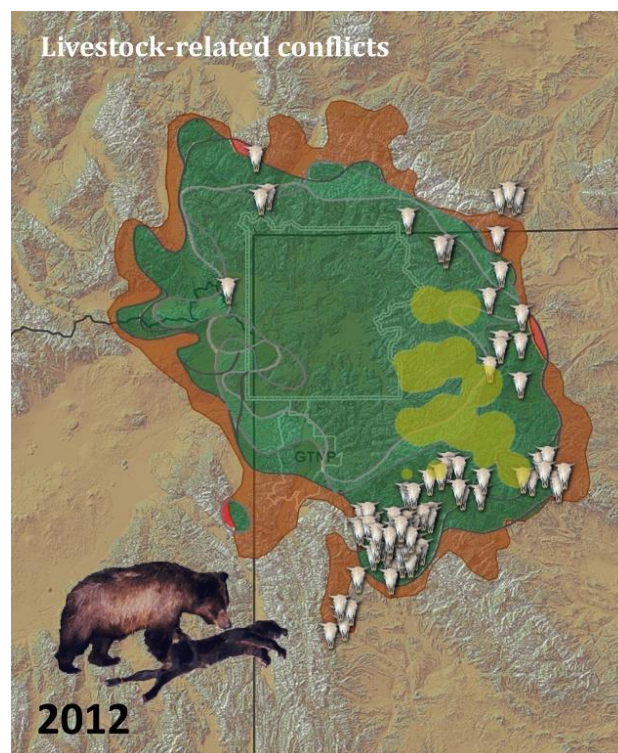


Figure 11.1.2. All of known sites where grizzly bears feed on moths in the Yellowstone ecosystem are shown here encompassed by the yellowish-green blobs. The cattle skulls each represent a location of a grizzly bear-livestock conflict during the emblematic year of 2012. The greenish shaded area represents the distribution of grizzly bears as of circa 2000 and, the orange, areas newly colonized by grizzlies during the last decade or so.

for losses of cutthroat trout and whitebark pine seeds (Fortin et al. 2013, Middleton et al. 2013, Ebinger et al. 2016; the Rule). For all of these reasons—in addition to the *prima facie* evidence I present under 11.1.1 above for strong effects of elk availability on death rates—past and prospective future trends in elk populations necessarily factor into any assessment of current and future prospects for Yellowstone's grizzly bear population. Negative trends would axiomatically constitute a threat.

Despite this, the Service fails to address the past, present, and future prospects for Yellowstone's elk populations in any meaningful way. Its analysis amounts to nothing more than a patently superficial and rushed treatment on page 13212 of the Rule. Moreover, this failing is non-trivial given unfolding trends and foreseeable threats.

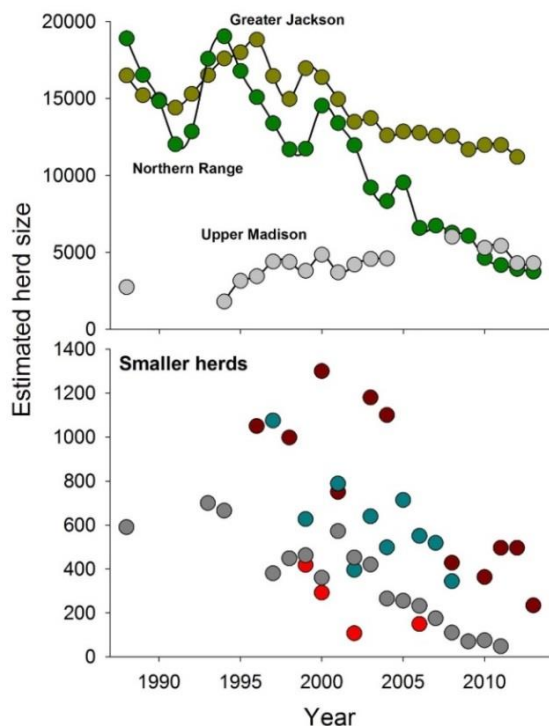


Figure 11.2.1. Trends in size of elk populations in Yellowstone's occupied grizzly bear habitat. Trends for larger herds are shown at top and for smaller herds at bottom. Because estimates are made only irregularly for the smaller herds, annual estimates are shown at dots with each color corresponding to a different herd.

Figure 11.2.1 shows trends in size of all of the elk populations in Yellowstone's occupied grizzly bear habitat (parenthetically, all of these data are publicly available from the National Park Service and the states of Wyoming, Montana, and Idaho). The point is obvious: all of the herds but one (the Upper Madison) have declined, some dramatically—even catastrophically—resulting in probable substantial increases in human-caused grizzly bear mortality (see my point 11.1. above). These herd declines closely track declines in cow:calf ratios, shown in figure 11.2.2. This latter correlation substantiates results presented by Middleton et al. (2013) strongly suggesting that declines in elk numbers are being driven partly by deteriorating summer-range conditions and related diminishment of fat reserves among female elk. Declines have also been linked to a near-tripling of mortality rates among elk calves due largely to increasing levels of bear predation (Middleton et al. 2013). Regardless of the cause, the numeric declines are dramatic and unambiguous, at the same that Yellowstone's grizzly bears have apparently become increasingly dependent

on meat from terrestrial sources, while dying in increasing numbers (see my points 17 & 18 below).

Moreover, declining elk populations have almost certainly driven a decline in availability of spring carrion (figure 11.2.3), which historically has been a disproportionately important food for Yellowstone's female grizzly bears (Mattson 1997, 2000). The Service fails altogether to even recognize its own trend data regarding this phenomenon, and instead merely speculates that a reduction in spring carrion could happen, citing two papers that don't directly address these well-documented trends in carrion availability. All of this in service of rush to its ill-substantiated conclusion that "fluctuations" (euphemistically) in ungulate populations are not a threat to GYE grizzly bears.

Looking to the future, prospects are not good for Yellowstone's elk populations. If declines have indeed been driven partly by lower-quality summer forage and increased bear predation, the future can only hold worse to come. Bears are a classic case of subsidized predators when it comes to predation on ungulates calves, best documented in the case of moose and elk (e.g., Gasaway et al. 1992, Ballenberghe & Ballard 1994, Testa 2004, Zager & Beecham 2006). Which means that bear predation can persist at unsustainably high levels even as elk populations continue to decline. Climate change also promises to bring ever worse summer drought (Chang & Hansen 2015)—with predictably negative effects on the quality of elk summer forage. Moreover, despite being dismissed out of hand by the Service on page 13212, Chronic Wasting Disease looms as a potentially major catastrophe for elk and elk scavengers in Yellowstone's ecosystem (e.g., Jennelle et al. 2009; Wyoming Game & Fish Department 2015, 2016). Future prospects for Yellowstone's elk populations are not bright.

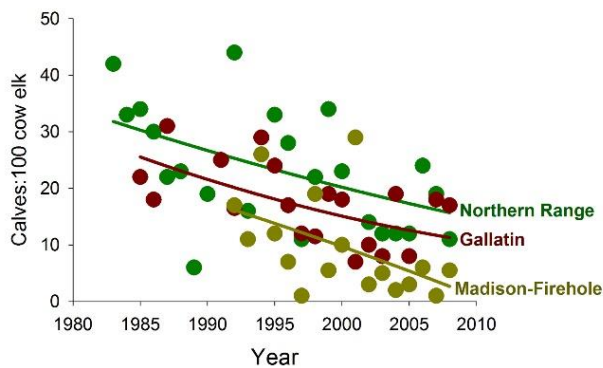


Figure 11.2.2. Cow:calf ratios for three of Yellowstone's elk herds, with each herd denoted by a different color.

That being said, my brief assessment here of status and trends for Yellowstone's elk populations is merely a preview of what is incumbent on the Service in support of this proposed Rule. The Service needs to critically assess past effects of and future prospects for this important grizzly bear food rather than breeze through a

11.3. The Service fails to meaningfully account for changes in bison populations and foreseeable threats to this source of bear food in its assessment of current and prospective threats to Yellowstone's grizzly bear population. This failure further compromises the Service's attempts to disentangle drivers of recent and prospective near-future changes in demography of the bear population.

Mattson (1997) and Green et al. (1997) documented the disproportional importance of bison as a source of meat for Yellowstone's grizzly bears primarily owing to the large mass of and related abundance of meat on bison carcasses. Mattson (1997) estimated that bears obtained nearly a quarter of all ungulate meat from bison. Given the increasing importance of terrestrial meat in the Yellowstone grizzly bear diet (Schwartz et al. 2014, Ebinger et al. 2016), bison have very likely become more rather than less important to this bear population. In fact, even as total number of carcasses from winter-killed elk and bison has decreased on Yellowstone's ungulate winter ranges, bison have comprised an ever-larger percentage of the total (Figure 11.3.1).

superficial analysis apparently on its way to a foregone conclusion.

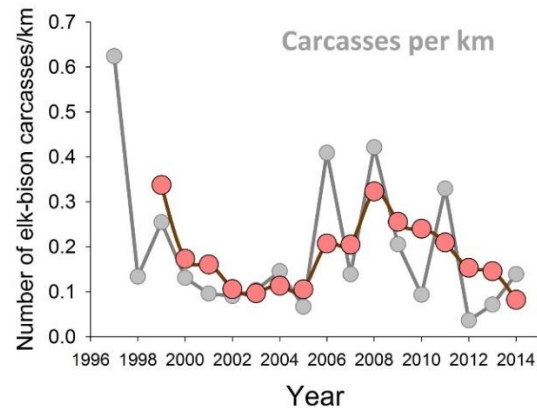


Figure 11.2.3. Ungulates carcasses counted per km of transects surveyed during spring on Yellowstone ungulate winter ranges. Gray dots are annual values and pink dots represent a 3-year running average..

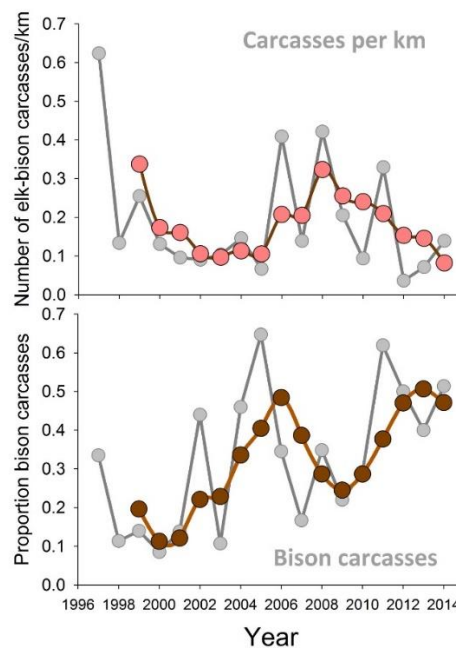


Figure 11.3.1. Results from annual spring surveys of carcasses on Yellowstone National Park winter ranges. The top graph shows number of carcasses detected per km of survey, with annual values in gray and a 3-year running average in pink. The bottom graph shows the proportion of all elk and bison carcasses that were of bison.

As with elk, because bison are such an important bear food, the Service needs to critically assess past, present, and future likely trends for bison as part of its risk assessment for Yellowstone's grizzly bear population. Yet the Service fails to present such an analysis anywhere in the Rule other than its superficial treatment on page 13212, primarily in reference to management of brucellosis in bison.

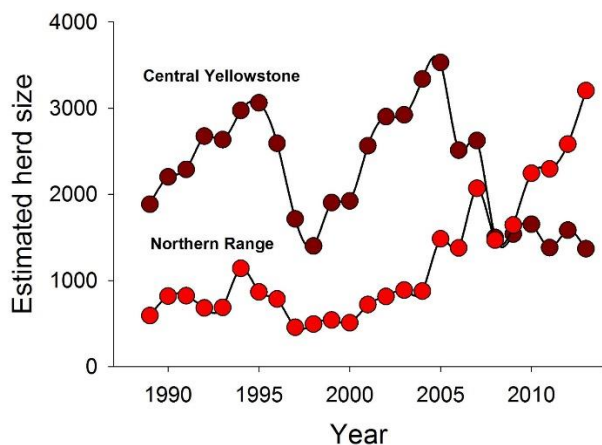


Figure 11.3.2. Trends in size of Yellowstone's two bison herds, the Northern Range herd in red and the Central Yellowstone herd in burgundy.

Elsewhere, the Service offers some offhand claims substantiated only by a distorted reading of the scientific literature, most notably its reference to Fortin et al. (2013) page 13192. Fortin et al. (2013) documented radio-marked bears feeding on bison at 9% of all investigated feeding sites in a study area restricted to the environs of Yellowstone Lake—a figure the Service then

uses to dismiss bison as an important grizzly bear food. The Service's logical fallacies are emblematic of its fallacies throughout the Rule and include, first, conflating a small percentage of sites with what is, in fact, a huge amount of high-quality food, second, extrapolating results from a spatially restricted study area to an entire ecosystem, and, third, failing to note that the results of Fortin et al. (2013) pertain to the Central Yellowstone bison herd, which has declined, while altogether missing areas that coincide with the Northern Range bison herd, which has increased (see Figure 11.3.2).

Given the extent to which state and federal management of Yellowstone's bison has been driven by concerns about brucellosis, any assessment of future prospects for bison necessarily needs to meaningfully consider prospective future management regimes for control of brucellosis. The Service's encapsulation of this issue in a blithe and meaningless reference to the objective of the current brucellosis management plan ("maintain a wild, free-ranging population of bison" [US National Park Service & USDA Animal and Plant Health Inspection Service 2000]), is grossly insufficient to the Service's analytic task. In fact, the dramatically negative recent trend of the Central Yellowstone bison herd no doubt reflects the current brucellosis management regime, more than factors such as decreasing winter severity (Geremia et al. 2011, White et al. 2011). The Service has no basis for its flip dismissal of brucellosis management as a factor in bison abundance and as a potential threat to Yellowstone's grizzly bears.

11.4. The Service fails to meaningfully assess past (and future) threats posed by major declines in populations of Yellowstone Lake cutthroat trout by its use of convoluted logic organized around a distorted and selective representation of the best available science. The Service's distortions and omissions are so strikingly egregious that I devote a considerable amount of space here to rectifying these deficiencies.

present, and prospective future threat posed to Yellowstone's grizzly bears by the functional extirpation of cutthroat trout in Yellowstone Lake. All of this is based on a selective and distorted reading of essentially two scientific references. In fact, an adequately thorough and less distorted review of relevant scientific information reveals a fundamentally different picture in which trout constituted an important bear food; loss of trout resulted in harm to Yellowstone's grizzly bears; with prospects for harm continuing.

On Pages 13212 and 13213 of the Rule the Service devotes 1 paragraph to summarily dismissing the past,

Put succinctly, spawning cutthroat trout were a major source of energy and nutrients for grizzly bears living within range of Yellowstone Lake between the mid-1970s and late 1990s (see below). Roughly 15% of the bear population exploited this resource between mid-May and late July (Reinhart & Mattson 1987, Haroldson et al. 2005), although few grizzlies still consume trout. These percentages are based on estimates from the two referenced studies of 45 and 70 trout-consuming bears, and estimates of roughly 325 and 500 total bears in the population for the two corresponding time periods (Eberhardt & Knight 1995, IGBST 2003). Or put another way, the Service's bald assertion that "only a small portion of the GYE grizzly bear population uses cutthroat trout" is mystifying and unsubstantiated, especially given that the Service references the somewhat dated work by Haroldson et al. (2005) as its authority.

Figure 7.1., under Point 7 above, summarizes the estimated monthly contribution of cutthroat trout to dietary energy and nutrients of the Yellowstone grizzly bears between the late 1970s and early 1990s. These estimates are based on an analysis of fecal material ("scats") deposited by grizzly bears throughout the Yellowstone ecosystem during 1977-1993, weighted by average nutrient and energy contents, adjusted for digestibilities, and corrected for differences between ingested and fecal volumes (as per Mattson et al. 2004, Lopez-Alfaro et al. 2015; see my comments under point 7). Monthly variation in total amounts varies substantially because of seasonal differences in overall levels of feeding activity (low in the spring, high in the fall and late summer; Mattson et al. 1991a), as well as differences in numbers of bears out of their dens early and late in the active season (Haroldson et al. 2002).

Figure 7.1 shows that trout were an especially important source of energy and protein, provided in pulses that peaked during June and July. There is little doubt that the functional extirpation of trout in a number of spawning streams has left a major nutritional hole during these months that bears have needed to fill, apparently by preying more heavily on elk calves (which are particularly vulnerable this time of year) and by more heavily consuming lower-quality vegetal foods (Fortin et al. 2013, Middleton et al. 2013, Ebinger et al. 2016).

Nonetheless, it is not altogether clear to what extent cutthroat trout were an important source of energy and nutrients for female versus male grizzlies. The main contradictions arise from the results of Mattson & Reinhart (1995) and that of Felicetti et al. (2004). Felicetti's results suggest that male grizzlies made roughly five times more use of trout compared to female grizzlies (135g/kg versus 26g/kg), whereas Mattson & Reinhart (1995) suggest otherwise. A critically important contextual distinction pertains to the status of trout populations when the research supporting each result happened. The research reported in Mattson & Reinhart (1995) occurred during the peak of Yellowstone's cutthroat trout population (1985-1987); Felicetti's when the population was at low ebb, albeit during a minor resurgence (1997-2000; see my discussion of trends below).

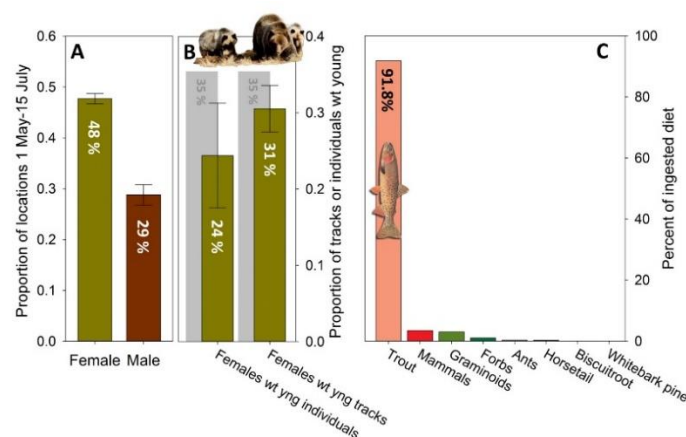


Figure 11.4.1. (A) Proportion of adult female and adult male telemetry locations concentrated within 2-km of Yellowstone during cutthroat trout spawning season, only considering bears with ranges overlapping spawning streams; (B) Proportion of all individuals and tracks documented along spawning streams during spawning season (in green) relative to the proportion of each expected by the total in the population; and (C) percent contribution of various foods to the ingested diet of bears concentrated along spawning streams during spawning season.

Some key results from the mid-1980s are summarized in figure 11.4.1. Of the bears strongly suspected of consuming cutthroat trout, females spent nearly 1.6 as much time near spawning streams as did males (during the spawning season; left above, Panel A), although females with dependent young were present in proportions less than one might expect (indicated by the discrepancy between the gray and green bars in panel B).

Moreover, analysis of scats collected within 500 m of spawning streams suggests that the bears that were present had a diet comprised of 90%+ cutthroat trout (corrected to reflect ingestion; Panel C). Although scats dropped by females couldn't be distinguished from scats dropped by males, the overwhelming conclusion is that any bear near a spawning stream during the spawning season was eating almost wholly cutthroat trout. The logical conclusion is that females were eating more trout than were males, at least during the mid-1980s. The only way this could not be the case is if females were concentrating near spawning streams, but not eating trout, which seems implausible in light of everything we know about what motivates the foraging behavior of animals.

Another interesting paradox arises from the fact that Felcetti et al. (2004) estimated the median consumption of trout by bears during 1997-2000 to be around 0.024-1.09 kg per individual, at the same time that Haroldson et al. (2005; from whom she obtained her samples) estimated that bear activity around spawning streams--including fishing--had not dramatically diminished from highs during the mid-1980s (see my discussion of trends below). But the claims by Felcetti and Haroldson find little support in independent observations. For one, trout populations had declined substantially--if not catastrophically--between the 1980s and late 1990s (see below). Given the strong relationship between trout densities and bear fish activity (Reinhart & Mattson 1987), it seems implausible that such a decline in trout populations would have had a minor effect on bear activity. The claim by Felcetti that trout were roughly 5-times more important a source of energy for males

compared to females is also in stark contradiction of the results described immediately above. Finally, the fact that grizzly bears have been documented to consume roughly 6 kg of trout in a single 41-minute bout of fishing suggests that any bear spending any amount of time fishing streams under favorable circumstances would have consumed many kg of trout during a single season--not something less than 1 kg.

An explanation for contradictions between the results of the mid-1980s and late-1990s studies potentially takes two forms. One is that the differences are simply a result of starkly different numbers of spawning cutthroat trout (see below), with related changes in relative access to streams by females versus males. There is ample evidence that adult male grizzlies can dominate concentrated food resources such as spawning trout, especially to the exclusion of security-conscious animals such as females with dependent young (the case two years out of three for Yellowstone females). Thus, if prime fishing opportunities had become increasingly spatially restricted, males would have become the primary winners, and females the losers. The result would have been a shift from disproportional use of the trout resource by females to disproportional use by males--leaving females bearing most of the harm arising from losses of cutthroat trout.

And, indeed, Yellowstone Lake's cutthroat trout population has exhibited huge ups and downs since the 1940s, when the Park Service first began to track trout numbers. Consumption of trout by bears has correspondingly varied. The composite figure below (figure 11.4.2) summarizes these key trends.

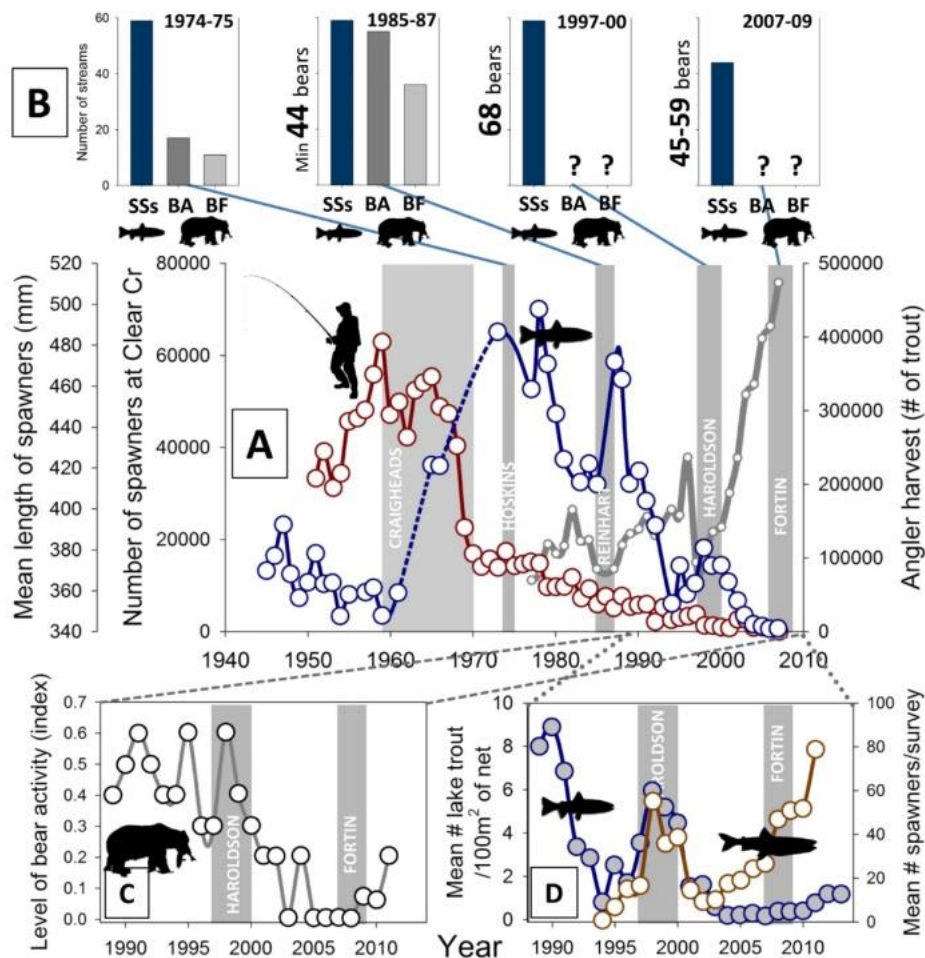


Figure 11.4.2. Trends in numbers of Yellowstone Lake cutthroat trout and related trends in related levels of bear fishing and other activity, with reference to the various studies that I reference here.

Panel A shows trends in numbers of spawning trout censused in Clear Creek, a major spawning stream on the east side of Yellowstone Lake (the blue line); the average length of trout captured in trawl nets (gray line); and numbers of fish killed by human anglers (all of these data can be found in Kaeding 2010 and other public archives). Key trends in numbers of spawning trout have been: a major increase during the 1960s, a substantial dip in the early 1980s, a resurgence in the late 80s, and a subsequent sustained decline to the present. Average size of trout has consistently varied inversely to population trends, indicating lack of recruitment of fish into smaller size classes during periods of decline.

Panel C shows levels of bear activity along spawning streams since 1989 (transects are located on streams concentrated on the west and northwest shores of the Lake; from IGBST Annual Reports). During 1989-1998

bear activity was substantial but varied. However, beginning in 1999, activity declined to the point where, now, bears rarely fish for spawning trout. This decline in bear activity is self-evidently related to the decline in numbers of spawning trout shown in blue in Panel D. Panel D also shows, in brown, numbers of lake trout captured in gill nets, standardized to reflect level of effort. Non-native lake trout were first documented in Yellowstone Lake in 1994, after which their numbers increased, then declined, and then increased again to the present. Lake trout prey on cutthroat trout and are implicated in the decline of cutthroat numbers.

One important feature of Panels A, C, and D is the denotation, as gray vertical bars, of different grizzly bear studies of relevance to documenting consumption of trout around Yellowstone Lake; each study is labeled with the name of the lead investigator(s). The Hoskins,

Reinhart, Haroldson, and Fortin (Fortin et al. 2013) studies surveyed tributary streams specifically to document bear activity along with size and duration of spawning runs. Panel B at the very top summarizes the results of each of these studies in terms of: number of streams with spawning runs (SSs, dark blue bar), with bear activity of any sort (BA, dark gray bars), and with sign of bear fishing (BF, light gray bars). As Fortin et al. (2013) and Middleton et al. (2013) document, although there has been a decline in numbers of bears active around Yellowstone Lake, the decline has not been catastrophic.

But, as I point out above, the brunt of declines in trout has probably been born by female grizzly bears, resulting in a turn to eating more terrestrial meat, especially in the form of predated calves, resulting in a probable increase in cub and yearling death rates (see my point 17) and a related overall increase in total grizzly bear mortality, especially during 1993-1997 and again during 2000-2003 (see my point 11.1 above).

11.5. The Service fails to adequately address the effect of army cutworm moths on birth and death rates of Yellowstone's grizzly bears, and thereby fails to account for the past effects of dramatic increases in consumption of moths by bears and prospective future effects of losses of this food on Yellowstone's grizzly bear population.

Army cutworm moths are amongst the highest-quality of grizzly bear foods in the Yellowstone ecosystem (Erlenbach et al. 2014). By summer's end, over-summering moths can consist of 50-80% fat (Kevan & Kendall 1997, White et al. 1998b). This high concentration of fats predictably accelerates accumulation of body fat amongst female grizzly bears that eat them (Robbins et al. 2007, Robbins et al. 2012, Erlenbach et al. 2014) and, with that, the odds that these females will achieve the substantial body fat—in excess of 20%—needed to produce and sustain cubs (Farley & Robbins 1995, Hilderbrand et al. 2000, Robbins et al. 2012).

Perhaps more importantly, it would stretch the bounds of plausibility to conclude that carrying capacity *has not* declined in areas around Yellowstone Lake occupied by bears that had made heavy use of cutthroat trout—which is what the Service strongly implies. Carrying capacity has almost certainly declined and, more importantly, this decline has occurred in the most protected core of the ecosystem centered on the southern part of Yellowstone National Park. Combined with the effects of increasing moth site use on the eastern periphery of the ecosystem (see below), this geographic redistribution in carrying capacity will predictably draw grizzly bears into more lethal environments outside of the National Parks, in comparatively less protected parts of Wyoming.

Given the picture that I present here based on the preponderance of evidence and associated logical deductions, the Service needs to undertake a more rigorous and less patently biased assessment of the threats posed directly and indirectly by losses of cutthroat trout.

Moreover, the sites where grizzly bears consume moths are located in areas that are amongst the most remote from people of any in the Yellowstone ecosystem (Mattson et al. 1991b, French et al. 1994, Gunther et al. 2014). And remoteness from people has repeatedly been shown by researchers to be one of the most important spatial factors affecting survival of adult grizzly bears in and near the Yellowstone ecosystem (Mattson et al. 1996; Merrill et al. 1999; Carroll et al. 2001, 2003; Merrill & Mattson 2003; Johnson et al. 2004; Schwartz et al. 2010).

Consumption of moths by grizzly bears, which occurs primarily between mid-July and mid-September, has increased dramatically from essentially nil during the mid-1980s to high levels that have been sustained since the late 1990s (Mattson et al. 1991b, IGBST 2015:42-43). Individual sightings of grizzly bears on moth sites have numbered between 240 and 350 during the last three years (IGBST 2015:42-43), which strongly suggests that a substantial number of individual bears use this food resource—perhaps the majority of those living in eastern

portions of the ecosystem. All of the 31 known sites where grizzlies consume moths are located on US Forest Service lands in the Absaroka Mountains east and southeast of Yellowstone National Park (Gunther et al. 2014). Six of these sites are located outside of the Primary Conservation Area (Van Manen, F.; personal communication).

Nowhere in the proposed Rule or CS does the Service address the prospective effects of past increases and future losses of army cutworm moths on grizzly bear demography, other than through patently convoluted logic transparently designed to sidestep this issue. None of the demographic analyses relied upon and referenced by the Service (e.g., Schwartz et al. 2006, Van Manen et al. 2015) have in any way explicitly incorporated the effects of army cutworm moth consumption in their analyses of grizzly bear birth or death rates. Lacking this foundation in analysis of prospective past effects, the Service has no basis for representing or judging what those effects have been or might be in the future. Nor do they have any basis for differentiating effects that they attribute to “density,” as such, from effects of increasing

consumption of cutworm moths given that both are highly correlated in time, as well as correlated in space (Gunther et al. 2014, IGBST 2015:42-43, Van Manen et al. 2015)

Lack of attention to this issue by Schwartz et al. (2006) and Van Manen et al. (2015) does not obviate the burden on the Service to consider the available relevant science, which is summarized here. Using this available science, and in the absence of anything more definitive, the preponderance of evidence supports concluding that increased availability and consumption of moths has very likely led to increased birth rates and decreased late-summer deaths rates amongst bears with access to this food, and that future loss of moths would lead to the opposite. Certainly, this conclusion is better supported than either of the two alternatives: that availability and consumption of moths has resulted in either no effect or negative effects, and that past and future abundance of this food is of little or no consequence to long-term conservation—which is essentially what the Service has claimed.

12. The Service disregards and misrepresents the best available scientific information in its assessment of the impact of wolves on Yellowstone’s grizzly bears on page 13212 of the Rule—in fact, the Service essentially disregards wolves altogether as a factor to be considered in their own right.

On page 13212 of the Rule the Service presents a superficial and otherwise inadequate mini-assessment of the past and prospective future impacts of wolves on Yellowstone’s grizzly bears in an apparent rush to reach its hasty conclusion that “fluctuations” in ungulate populations have not nor will ever threaten grizzly bears in this ecosystem. In fact, a clear-eyed reading of the best available science shows that wolves have very likely harmed Yellowstone’s grizzly bears, albeit to an unknown extent.

Female grizzly bears historically consumed a disproportionate amount of the terrestrial meat that they ate by scavenging carrion during the spring, in contrast to adult male bears that ate disproportionately more meat during summer and fall and, of that, more by outright predation (Mattson 1997, 2000). Since the

reintroduction of wolves, amounts of spring carrion have declined (figure 12.1), primarily as a result of declining elk populations (see my point 11.2 above). These declines in elk have probably been driven by a combination of unsustainable sport harvest, adverse weather, grizzly bear predation on calves, and wolf predation on elk of all sex and age classes (Vucetich et al. 2005, Evans et al. 2006, Eberhardt et al. 2007, Barber-Meyer et al. 2008, Griffin et al. 2011, Brodie et al. 2013, Proffitt et al. 2014). The point being that wolf predation has very likely played a part in very real declines in spring carrion, especially because of selection by wolves for the older and weaker elk that almost certainly would have otherwise died overwinter and been available to female grizzlies as carrion (Evans et al. 2006, Wright et al. 2006).

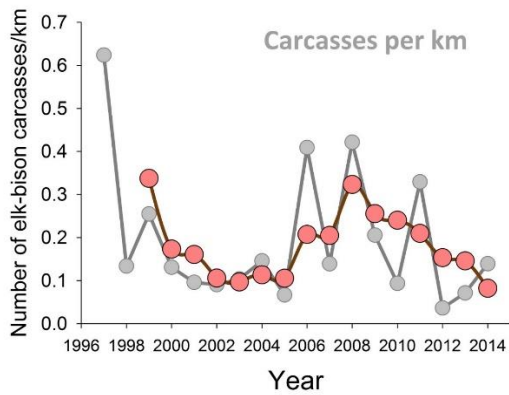


Figure 12.1. Ungulate carcasses counted per km of transects surveyed during spring on Yellowstone ungulate winter ranges. Gray dots are annual values and pink dots represent a 3-year running average.

The Service ignores this probable indirect role of wolf predation on female grizzly bears, along with an effect that is more direct. Specifically, wolves have been known to kill grizzly bear cubs (see page 13205 of the Rule), a phenomenon that is notoriously difficult to detect and thus almost certainly under-documented (see my point 17). There is no way that this predation by wolves on grizzly bear cubs can be construed as a neutral much less positive effect.

The Service concludes its putative mini-assessment of wolves by asserting that grizzly bears have probably benefitted from the extent to which they have been able to appropriate wolf kills for their own consumption, citing research conducted in Alaska (Ballard et al. 2003), while entirely overlooking highly relevant research undertaken in Yellowstone (Gunther & Smith 2004). These Yellowstone researchers found that females very rarely if ever usurped wolf kills. In fact, adult male grizzlies—which are of little relevance to population-level productivity—were essentially the sole beneficiaries of wolf kills. In other words, whatever meat wolves were directly provisioning for bears was going almost entirely into the bellies of adult males.

In short, wolves have been and will probably continue to be a detrimental feature of Yellowstone’s grizzly bear habitat, thereby constituting a threat; and the Service utterly fails, first, to give this issue due regard and, second, to sufficiently and accurately represent the relevant best available science. If considered properly, wolves will probably threaten grizzly bears directly through predation on young bears and indirectly through effects on ungulate populations, now and for the foreseeable future.

13. The Service fails throughout the Rule to account for the effects of climate change on past, present, and prospective future changes in habitat and demography of Yellowstone’s grizzly bears. The Service neglects most of the relevant best available science; distorts what little it does cite; deploys otherwise faulty logic; and relies, instead, largely on a single workshop publication and related assertions regarding the opinions of an amorphous “majority” of bear scientists.

The Service is remarkably obtuse in its assessments of how climate change has, is, and will foreseeably affect Yellowstone’s grizzly bear population. Much of its argument is presented on pages 13197, 13216, 13217 of the Rule, from which I have extracted the following synoptic quotes:

On page 13197, the Service cursorily states its central conclusion: “Most grizzly bear biologists in the United States and Canada do not expect habitat changes predicted under climate change scenarios to directly threaten grizzly bears (Servheen and Cross 2010, p. 4). These effects may even make habitat more suitable and food sources more abundant.”

On page 13216 and 13217 the Service marches through several paragraphs in which it acknowledges the obvious fact that unprecedented climate change is happening; that the western United States will be warmer; and that hydrologic regimes will change. After this pro forma recitation, the Service then leaps to again conclude: “Most grizzly bear biologists in the United States and Canada do not expect habitat changes predicted under climate change scenarios to directly threaten grizzly bears (Servheen and Cross 2010, p. 4). These changes may even make habitat more suitable and food sources more abundant.”

On page 13217 the Service perambulates through another pro forma acknowledgment that climate change will, indeed, affect the abundance and distribution of plant and animal species only to repeat a variant of its emerging mantra: “While the extent and rate to which individual plant species will be impacted is difficult to foresee with any level of confidence (in their entirety: Walther et al. 2002; Fagre et al. 2003), there is general consensus that grizzly bears are flexible enough in their dietary needs that they will not be impacted directly by ecological constraints such as shifts in food distributions and abundance (Servheen and Cross 2010, p. 4; IGBST 2013, p. 35).

Finally, on page 13217 the Service again marches through yet another pro forma discussion of prospective changes in fire regimes to reach its master conclusion regarding prospective effects of climate change on Yellowstone’s grizzly bears: “Because grizzly bears have shown resiliency to changes in vegetation resulting from fires, we do not anticipate altered fire regimes predicted under most climate change scenarios will have significant negative impacts on grizzly bear survival or reproduction, despite its potential effects on vegetation. Therefore, we conclude that the effects of climate change do not constitute a threat to the GYE grizzly bear DPS now, nor are they anticipated to in the future.”

The short-comings of the Service’s treatment of climate change are striking—and consistent with a track record of disregard recently highlighted by the US Montana District Court’s ruling on the Service’s failure to list wolverines under the ESA.

13.1. The Service fails to adequately represent the best available science of direct relevance to projecting environmental change in the Yellowstone ecosystem.

The Service’s at times lengthy recitation of literature that forecasts generic effects of climate change is clearly *pro forma*, as evidenced by the fact that the Service doesn’t even pretend to explicitly link such effects to the particulars of Yellowstone’s bears and bear habitat.

Emblematic of its failure to address Yellowstone’s specific conditions, the Service (barring once) almost totally ignores the large body of research that directly addresses climate change in Yellowstone, including projections for climate, vegetation, and wildfire. In the one instance where the Service does cite regionally-specific research (i.e., Romme & Turner 1991), the results are misrepresented in an apparent attempt to dismiss the threat posed by climate change to army cutworm moths (for more on this, see my comments specific to moths). But perhaps most problematic, the Service fails to address what we do know about grizzly bear behavior, diet, and habitat in the Yellowstone ecosystem and instead substitutes platitudes such as “most grizzly bear biologists” and “general consensus.”

Briefly, climate has warmed and will continue to warm substantially in the Yellowstone ecosystem, with a net projected increase in growing season drought, albeit mitigated by some projected increase in precipitation. Without being exhaustive, Pedersen et al. (2010), Rice et al. (2012), Chang & Hansen (2015), and Tercek et al. (2015) provide what is probably the most relevant and up-to-date information on past and prospective future changes in climate of the Yellowstone ecosystem. Temperatures have already increased substantially, especially since the late 1940s, and will continue to increase at a rapid rate under all plausible forecast scenarios (Figure 13.1.1). Total precipitation has been stable during the last 60 years or so, but is projected to increase modestly with climate change, with offsets by warming resulting in a net projected increase in droughty conditions, especially late in the growing season. For various reasons, snowpack has declined significantly since 1980, but in large measure due to warmer winter and spring conditions—consistent with broad-scale west-wide trends (Clow 2010, Pederson et al. 2013). The resulting hydrologic changes have been detrimental to cold-water fish such as cutthroat trout (Williams et al. 2009; Isaak et al. 2010, 2012, 2015; Wenger et al. 2011). The magnitude of these historical and forecasted changes is non-trivial and potentially even catastrophic—and at variance with implications made by the Service in the Rule that uncertainty is perhaps a defining feature. It is not. The forecasts are thematically unambiguous, convergent, and consistent with recent historical trends.

Numerous researchers have projected climate-driven changes in the distributions of either vegetation formations or individual plants species at a resolution meaningful to regional assessments for the Yellowstone ecosystem (e.g., Romme & Turner 1991; Bartlien et al. 1997; Shafer et al. 2001; Schrag et al. 2007; Crookston et al. 2010; Coops & Waring 2011; Diaz & Eischeid 2007; Westerling et al. 2011; Bell et al. 2013, 2014; Gray & Hamann 2013; Chang et al. 2014; Hansen & Phillips 2015; Rehfeldt et al. 2006, 2012). Again, unlike some of the Service's innuendo in the Rule, the projections are unambiguous and consistent. We can expect massive changes in the distributions and abundance of plant species, including the prospective loss of most (90% plus) alpine and high subalpine environments. Among the species expected to experience major declines are subalpine fir, Engelmann spruce, and whitebark pine,

with invasion of higher elevations by Douglas-fir and lodgepole pine—continuing trends that have been underway for the last 13,000 years (Iglesias et al. 2015).

Fire regimes are expected to change substantially. Westerling et al. (2011), Luo et al. (2013), Stavros et al. (2014), Barbero et al. (2015), and others project an increase in fire frequency and/or extent perhaps sufficient to essentially eliminate forest conditions from most of the Yellowstone ecosystem—albeit with a potentially progressive lessening of fire intensity (Parks et al. 2016). These future fire regimes will likely amplify the rote effects of climate change in driving an increase in the extent of non-forest conditions (Rice et al. 2012, Chang & Hansen 2015), but with an additional likely CO₂-driven trend towards increasing concentration of biomass on shrubs such as *Artemisia* sp. (e.g., Harte & Shaw 1995, Polley et al. 1997, Morgan et al. 2007).

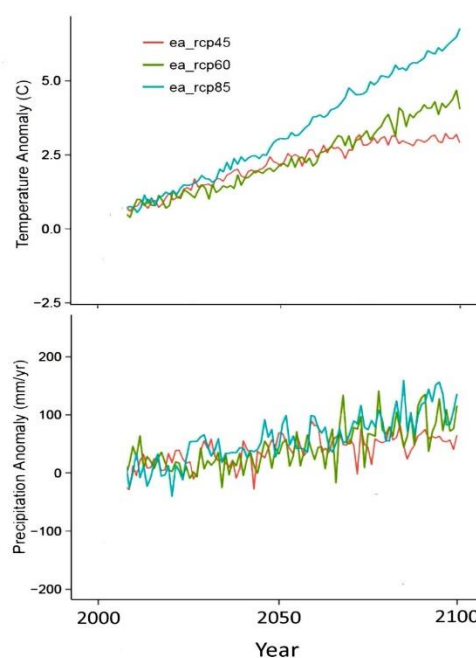


Figure 13.1.1. Projected increases in temperature and precipitation specific to the Yellowstone ecosystem (Chang & Hansen 2014).

This very brief review emphasizes the extent to which the Rule neglects high-relevant regionally-specific research, provides a backdrop of prospective change, and provides an opportunity to actually examine (in brief) what climate change might bring—and has already brought—for Yellowstone's grizzly bears; and with reference to the particulars of grizzly bear research in

this ecosystem instead of resort to platitudes and figurative arm-waving.

13.2. The Service fails to adequately account for the prospective terminal loss of whitebark pine as a functional part of Yellowstone's grizzly bear habitat.

There is little doubt that climate warming has been a major driver of devastating—even catastrophic—losses of mature whitebark pine to bark beetles, especially since the early 2000s (Logan et al. 2010, Macfarlane et al. 2013). In fact, these losses are the very premise of the IGBST research that the Service cites so extensively (e.g., Bjornlie et al. 2014, Van Manen et al. 2015; but see my other comments regarding the fatal flaws of this work). Looking to the future, virtually every study that has been done projects terminal losses of virtually all whitebark pine in the Yellowstone ecoregion from a combination of climate warming, increased fires, insidious spread of white pine blister rust, continued outbreaks of bark beetles, and competition from lower-elevation species such as lodgepole pine and Douglas-fir (e.g., Romme & Turner 1991, Bartlein et al. 1997, Warwell et al. 2006, Schrag et al. 2007, Coops & Waring 2011, Coops et al. 2011, Hatala et al. 2011, Jewett et al. 2011, Simard et al. 2012, Gray & Hamann 2013, Weed et al. 2013, Chang et al. 2014, Miller et al. 2015). The preponderance of evidence unambiguously supports the conclusion that whitebark pine will continue to be lost and will not return as a functional part of Yellowstone's grizzly bear habitat. This conclusion holds, the apologia of Mahalovich (2013) notwithstanding, especially given that this author would have us believe that something never before achieved is possible: i.e., the artificial selection (or engineering) of a new species that is simultaneously highly resistant to blister rust and beetles, a better competitor under warmer drier conditions, with continued production of ample nutritious seeds, and, as a practical matter, able to be propagated in sufficient numbers to make any functional difference. Unlikely at best.

And recent, on-going, and foreseeable losses of whitebark pine have had and will almost certainly continue to have major negative impacts on Yellowstone's grizzly bears. As I point out elsewhere, bear mortality, in general, and in relation to use of human-associated meat, has sky-rocketed coincident

with terminal declines in whitebark pine seed availability beginning 2006-2007. Moreover, whitebark pine seeds were unambiguously an important source of dietary fat—a critical diet nutrient—and, historically, of roughly twice the importance to females as to males (Mattson 2000, Felicetti et al. 2003).

13.3. The Service fails to adequately account for the prospective terminal loss of army cutworm moths as a functional part of Yellowstone's grizzly bear habitat.

On page 13213 of the Rule, the Service invokes a single publication to claim that, because “vegetation types in Yellowstone have a wide elevational range,” alpine tundra and other alpine communities will not be adversely affected by climate warming. They then go on to claim, based on an additional single citation, that army cutworm moths will not be adversely by climate warming, not only because alpine environments will somehow survive intact, but also because moths will somehow otherwise adapt. These claims are not substantiated nor are they logical.

For one, alpine environments are, in fact, defined by a very specific climatic envelope, as is the corresponding domain of the plants that comprise alpine tundra (Lütz 2011, Körner 2013). Moreover, every single scientific projection for alpine environments under different plausible scenarios of climate change predicts (or projects) major if not catastrophic losses (e.g., Grace et al. 2002, Pauli et al. 2003, Walther et al. 2005, Grabherr et al. 2010, Dullinger et al. 2012, Elmendorf et al. 2012, Gottfried et al. 2012). Projections specific to the alpine zone in the western United States are no exception (Romme & Turner 1991, Diaz & Eischeid 2007). These projections are consistent with the climatic and physiological factors that sustain alpine plants in the face of competition from other species better adapted to less harsh lower-elevation environments (for example, see a rich scientific literature dating back to Tranquillini [1964] and Billings & Mooney [1968]).

On top of this, every instance where bears have been documented to feed on aggregations of army cutworm moths in the northern Rocky Mountains has been restricted to alpine fellfields near alpine tundra: the Mission Mountains, Scapegoat Mountains, Glacier

National Park, and the Absaroka Mountains (Chapman et al. 1955, Craighead et al. 1982, Mattson et al. 1991b, French et al. 1994, O'Brien & Lindzey 1998, White et al. 1998a). As a corollary, every study of summer cutworm moth ecology has demonstrated that the moths subsist on the nectar of tundra flowers (French et al. 1994, O'Brien & Lindzey 1994, Kevan & Kendall 1997, White et al. 1998b). It is somewhat mysterious, then, as to how and why grizzly bears would shift to feeding on moths in an environment where feeding on moths has never before been documented and where moths have never before been documented to thrive. The Service not only fails to reference any of the highly relevant literature listed here, but also convolutes and contradicts all available evidence.

Whereas it is true that no one can say for sure how over-summering army cutworm will respond to loss of alpine environments, this does not in any way substantiate the assertions made by the Service that alpine environments will somehow be unaffected by climate warming, that moths will somehow adapt, and that grizzly bear foraging will be minimally affected. Such claims, in fact, defy not only the weight of evidence, but also everything we do know about grizzly bears, cutworm moths, and prospective effects of climate change on the habitats that over-summering moths currently depend on.

13.4. The Service fails to adequately account for the prospective terminal loss of cutthroat trout as a functional part of Yellowstone's grizzly bear habitat.

Yellowstone cutthroat trout are a cold-water-adapted species that is, together with bull trout, amongst the most vulnerable of any fish to prospective warming of aquatic habitats (Bear et al. 2007, Kaeding 2012). Although cutthroat trout will grow more quickly in warmer waters (Bear et al. 2007, Kaeding 2012, Al-Chokhachy et al. 2013), this advantage is offset by elevated competition, incidence of disease, spread of non-native species, and worsening flow regimes that typically accompany warming—which is also often coincident with drying (Koel et al. 2006, Gresswell 2009). In Yellowstone Lake, the primary threats from non-natives species are in the form of whirling disease (at a 20% plus infection rate among native cutthroat trout), New Zealand mud snail (as near as the Madison River), and Lake trout—a highly piscivorous predator on

cutthroat trout first detected in Yellowstone Lake during 1994.

There is no doubt that Yellowstone Lake cutthroat trout populations have declined catastrophically since the late 1970s, to the point where this species has been functionally extirpated as a source of food for Yellowstone's grizzly bears (see my comments under above). There is likewise no doubt that predation by Lake trout played a major role in this decline (Ruzycki et al. 2003, Koel et al. 2005). However the role of worsening hydrologic conditions is under-appreciated. Kaeding (2010) presents convincing evidence that hydrologic conditions (indexed by total annual air degree-days) drove declines in cutthroat trout populations perhaps even more than Lake trout predation, explaining the fact that the beginning of substantial declines in the cutthroat trout population predated detection of Lake trout by roughly 15 years.

Looking to the future, there is also little doubt that climate change will bring worsening rather than improving conditions for Yellowstone Lake cutthroat trout, including elevated water temperatures, early peak flows in spawning streams, worsening late-summer low flows, increasing blockage of spawning stream outlet channels, and less thermal buffering because of more prevalent wildfires (e.g., Williams et al. 2009; Isaak et al. 2010, 2012, 2015; Wenger et al. 2011; Tercek et al. 2015). The basis for this prognosis is consistent and strong. Insofar as threats from non-native species are concerned, even though there is evidence for the efficacies of recent efforts to control Lake trout in Yellowstone Lake (Syslo et al. 2011, Koel et al. 2015), such efforts will likely need to be sustained indefinitely, with virtually no prospect of ever completely eliminating Lake trout (Koel et al. 2006, 2015; Gresswell 2009). Moreover, there is no plan in place with prospects of ever controlling whirling disease or preventing the eventual introduction of New Zealand mud snails. In other words, the long-term prospects for Yellowstone Lake cutthroat trout are bleak, albeit with the possibility of modest positive trends in the next several decades. More certainly, cutthroat trout will not return as a major grizzly bear food in the most protected core of the ecosystem.

13.5. The Service fails to adequately account for the prospective effects of climate change on populations of elk and bison in the Yellowstone ecosystem.

Belying the cursory treatment of elk and bison by the Service on page 13212 of the Rule, an assessment of how climate change might affect these ungulates, along with consequent effects on grizzly bears, is perhaps the most complicated of any for foods of recent importance to bears. Certainly, the Service's hasty conclusion that "fluctuations in the availability of ungulates are not a threat to the GYE grizzly bear population now, or in future" is irresponsible and simple-minded.

Elk populations in the northern Rocky Mountains, including the Yellowstone ecosystem, are limited and regulated by a combination of factors, most notably sport hunting, winter severity, summer forage, and predation. The Service would claim that sport hunting is discretionary and therefore entirely under the control of managers. Without questioning any assertions about control over sport harvest, climate *is not* controllable by wildlife managers.

Not surprisingly, a number of publications have implicated winter severity as a limiter of elk populations, primarily through effects on survival of short-yearling and senescent animals (Garrott et al. 2003, Lubow & Smith 2004, Vucetich et al. 2005, Brodie et al. 2013, Proffitt et al. 2014)—something that the Service acknowledges in the Rule. But an even larger body of research implicates summer forage conditions, primarily through effects on female pregnancy and early calf survival (Merrill & Boyce 1991, Coughenour & Singer 1996, Cook et al. 2004, Lubow & Smith 2004, Vucetich et al. 2005, Parker et al. 2009, Griffin et al. 2011, Middleton et al. 2013, Proffitt et al. 2014) —something the Service does *not* acknowledge. And calf survival is increasingly recognized to be a driver of elk population growth (Raithel et al. 2007).

Compared to elk, much less is known about the limitation or regulation of bison populations, especially in Yellowstone's unique environment. Perhaps the best synopses of this information can be found in the Elsevier Press book "The Ecology of Large Mammals in Central Yellowstone," specifically in Bruggeman et al. (2009),

Fuller et al. (2009), Geremia et al. (2009). All of these researchers found that winter severity reduced bison survival rates, but in a way that entailed complex interactions with anthropogenic factors and bison population densities.

In short, winter severity (e.g., Snow-Water-Content [SWE]) and summer weather (e.g., late-season forage conditions) have strong effects on elk populations, whereas winter severity seems to be the dominant climate/weather effect on bison. With those themes in mind, it is relevant to look at projections for SWE on Yellowstone's elk and bison winter ranges, drought (i.e., summer precipitation and temperature) effects on summer ranges, and the likely extent and nature of non-forest conditions—which, on the face of it, would be tied to the extent of favorable forage conditions for both ungulates.

As it turns out, the amount and extent of severe winter conditions, at least as indexed by SWE, are not projected to change much, if at all, on Yellowstone's winter ranges for the next 75 years or so (Marcus et al. 2012: 126-127)—this because most nearer-term effects of winter warming will be experienced at lower elevations below the rising elevational threshold of the rain-snow transition (Klos et al. 2014). Thus, at least for the foreseeable future, there is not likely to be much mitigation of limiting effects attributable to winter severity—and, thus, no related positive population responses.

The forecast for summer drought and related decreases in forage quality is less certain for the Yellowstone ecoregion (Rice et al. 2012, Chang & Hansen 2015). But, to the extent that drought effects manifest later in the growing season, and are driven by an offset of less certain precipitation forecasts by more certain temperature ones (Marcus et al. 2012: 126-127), odds are better that incidence and severity of drought will increase rather than decrease. In fact, such a prognosis is consistent with West-wide spatially-explicit forecasts of drought (Guzler & Robbins 2011, Gai 2012), especially the incidence of severe episodes (Strzepek et al. 2010).

This weight-of-evidence prognosis needs to be considered in the balance with likely increases in non-forest conditions. As I note earlier, this increase probably

will not be of a simple nature, with the prospect of more biomass being concentrated on woody shrubs compared to forbs and grasses, to the detriment of both elk and bison.

All of this constitutes a basis for reaching some provisional conclusions regarding climate-driven prospects for elk and bison in the Yellowstone ecoregion. Carrying capacity for bison will probably not increase in the foreseeable future simply because winter severity will not likely diminish. By contrast, carrying capacity for elk will likely increase, primarily as a function of an

13.6. The Service fails to adequately account for nature, quality, and potential effects of alternate foods that may be used more heavily by Yellowstone's grizzly bears in response to losses of currently-important foods.

All of this begs the question whether Yellowstone's grizzly bears will find alternative foods to eat that are of sufficient quality and quantity to offset past and prospective future losses of foods that were (and are) known to be important sources of energy and nutrients: whitebark pine seeds, cutthroat trout, army cutworm moths, elk, and bison. Perhaps as important, will bears likely end up eating these alternative foods under circumstances where risk of death is elevated? Answering these questions requires more than what the

increase in non-forest conditions, but to an extent strongly conditioned on the prevalence of growing-season drought. As a bottom line, there is no simple prognosis for elk and bison, especially given that populations of both are strongly affected by anthropogenic forces such as sport hunting (elk) and, increasingly, incidence and management of disease (elk and bison). In other words, there is no basis here for the Service's blithe conclusion.

Service currently offers in the Rule, which amounts to assertions and platitudes based on invocations of "omnivory," "resilience," and the ill-framed opinions of bear researchers who probably know little about climate change and even less about the Yellowstone ecosystem (for more on this see my comments related to nutritional ecology, point 7).

So, what evidence is there to draw on? Perhaps the most comprehensive evidenced-based forecast of climate-driven dietary changes for Yellowstone's grizzly bears was done by Mattson (2000). Because this is the sole example of such an effort, I quote extensively from it as follows, noting that some citations are dated simply because of this dissertation's 2000 publication date:

"There is evidence from this study that grizzly bear foraging is temperature and moisture sensitive. The abundance and related use of ants by grizzly bears clearly seem to be dependent on ambient warmth [see also Mattson 2001] as, to a lesser extent, do growth and use of dandelions and thistles. It is likely that use of these foods by bears will increase with climate warming, assuming that moisture relations remain unchanged. However, use of many vegetal foods was sensitive to amounts of precipitation. The likelihood that bears would excavate a food declined during dry months, as did the likelihood that they would graze many of the forbs and grasses. All else equal, it is likely that grazing and root grubbing would be less common if climate warming caused drier soils during the growing season. In addition, the sensitivities of grubbing for biscuitroots and rodents to total winter precipitation suggest that use of biscuitroots would decline and use of rodents would increase if winters became drier.

Currently, it is strictly a matter of speculation whether total amounts of vegetal foods would change in bear range, aside from whether these foods would be used by bears or not as a function of proximal conditions. Compared to use of biscuitroots, use of yampa is conceivably more sensitive to widespread drying because yampa is restricted to moist sites (Mueggler & Stewart, 1980; Mattson, 1984) and is typically more difficult to extract (Mattson et. al. 1999 [2004]). It also is likely that consumption of clover by Yellowstone's grizzly bears will be more sensitive to changes in ambient conditions than many other bear activities because use of this food is so strongly associated with dense swards on moist soils. Otherwise, use of mushrooms and *Shepherdia* may increase because bear use of these foods is strongly linked to low-elevation lodgepole pine-dominated types (LPICO and LPIEN; Table 3; [see also Mattson 1997]). These types will likely become more extensive under warmer conditions (Romme & Turner, 1991).

Fire had a number of effects on the behavior of Yellowstone's grizzly bears that would likely ramify if climate warming induced more frequent and extensive burns. Grizzly bears were more likely to graze dandelions and early-season graminoids after the 1988 wildfires compared to before. On the other hand, the likelihood that they would excavate osmorrhiza roots or whitebark pine seeds declined substantially along with the intensity of excavations for pine seeds. The former activities were more likely to occur in recent burns, while the latter were not (Blanchard & Knight, 1990; Mattson, 1997a; Table 3). All of these consequences are logically related to fire-caused increases or declines in these foods (Blanchard & Knight, 1990; Singer & Harter, 1996; Mattson, 1997a). The post-1988 decline in bear use of rodents and rodent food caches during Spring and Estrus could have been a consequence either of fire-caused pocket gopher mortality or bears choosing to graze instead. Unfortunately, there is little research on the consequences of fires to pocket gophers that might provide insight into which was a greater effect. Even so, the increase in post-fire use of rodents during Hyperphagia suggests that pocket gopher mortality was not a factor and that the explanation lies in trade-offs with opportunities to graze graminoids, year-round."

As a bottom line, though, any invocation of ants, hornets, foliage, rodents, or roots as substitutes for foods that have been lost—and will prospectively continue to be lost—has no *prima facie* merit simply on the basis of nutritional and energetic considerations (e.g., Mattson et al. 2004). I cover this in more detail under my comments related to nutritional ecology. In other words, contrary to assertions (or innuendo) by both the Service and Gunther et al. (2014), dandelions or roots of various types quite simply will not provide compensation, especially at a population level. Likewise, remarks such as those by Fortin et al. (2012) suggesting that fungi have, and will, compensate for on-going losses of foods such as cutthroat trout and whitebark pine seeds has little merit. Fungi offer little fat (a critical nutrient for bears), and consumption of false truffles (and other mushrooms) has largely been confined to a limited portion of the ecosystem concentrated in lodgepole pine forests on the rhyolite plateaus of Yellowstone National Park (Mattson 1997, 2000; Mattson et al. 2002, 2004; Fortin et al. 2013). And, when fungi in the feces collected by Fortin et al. (2012) are corrected for the differential passage and digestibilities of various foods, the overall dietary contribution of false truffles and other fungi is trivial (Lopez-Alfaro et al. 2015).

There is a chance that high-quality foods from warmer climes could migrate to the Yellowstone ecosystem with time. The most obvious candidate is Gambel's oak—a source of acorns and a high-quality bear food in areas where it does occur, the nearest of which is roughly 130 miles south of Yellowstone's occupied grizzly bear habitat. In fact, several projections suggest that suitable climatic environments will emerge for Gambel's oak in the Yellowstone ecosystem over the next 100 years (e.g., Rehfeldt et al. 2006). That still begs the question of how

long it would take oaks to colonize newly opened environments over a 100 miles distant, especially given that migration rates have emerged as a major prospective consideration amongst those projecting changes in plant distributions (e.g., Pearson 2006). Perhaps more to the point of these deliberations: we can be more certain of what will happen with *in situ* foods compared to speculative foods relocating from a considerable distance.

13.7. The bottom line when it comes to the prospective effects of climate change:

The Service does a grotesquely inadequate job of assessing the prospective effects of climate change on Yellowstone's grizzly bears and, to the extent that it does attend to this task, the Service's intent seems to be out-of-hand dismissal of such effects in service of rushing to a preordained/pre-decisional conclusion. When given due regard, the net assessment is one of continued major losses of known high-quality foods, dietary shifts among surviving bears to greater reliance on lower-quality foods, and a substantial decline in unit area carrying capacity of the Yellowstone ecosystem. Moreover, grizzly bears will likely be spending more time foraging in high-risk environments, especially to the extent that they eat more foods at lower elevations nearer people—or foods such as livestock that bring them into greater conflict with people. It is certainly the case that past, on-going, and prospective future losses of whitebark pine and moth foraging sites will deprive grizzly bears of foods in some of the most remote and secure parts of the Yellowstone ecosystem. By contrast, essentially all prospective replacement foods (including Gambel's oak, should it ever arrive) tend to occur in more hazardous lower-elevation habitats. The preponderance of evidence

clearly supports a different conclusion from that reached by the Service. Climate change has had and will continue

to have devastating impacts on Yellowstone's grizzly bears.

14. The Service's assertion on page 13197 of the Rule that "there are no data to indicate habitat fragmentation within this population is occurring [sic]" is wrong because it contradicts the totality of best available science. There is, in fact, ample evidence of habitat fragmentation within the current distribution of Yellowstone's grizzly bears, which renders the Service's assertion both wrong and arbitrary.

On Page 13197 of the Rule the Service asserts that "The GYE grizzly bear population is currently a contiguous population across its range, and there are no data to indicate habitat fragmentation within this population is occurring [sic]." Realizing that fragmentation and

contiguity often come in degrees rather than as absolutes, this statement by the Service flatly contradicts the best available science as well as its own representations of "secure" habitat. In other words, this assertion is unsubstantiated and wrong.

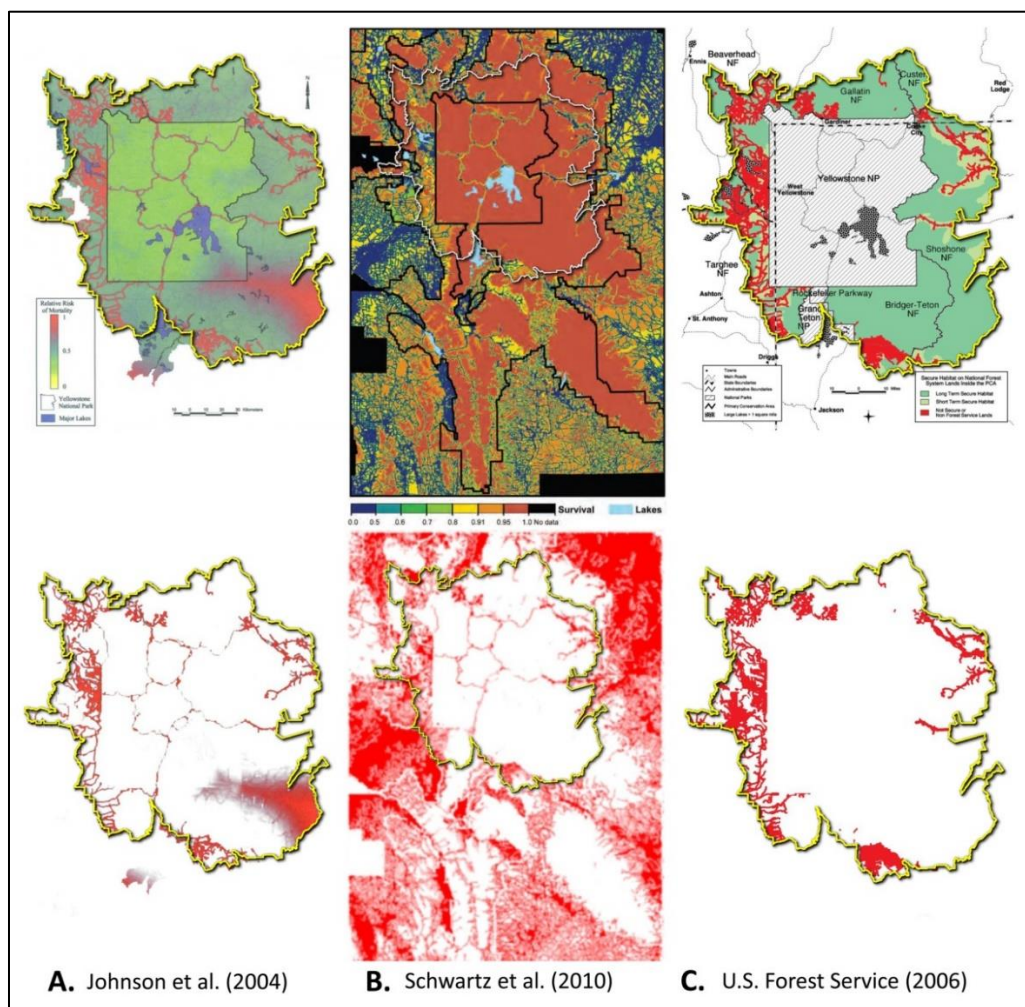


Figure 14.1. This figure presents three maps extracted from the most recent assessments of habitat fragmentation and impairment in the Yellowstone ecosystem (top), with the areas of fragmented and impaired habitat extracted and uniformly shown in red in the bottom array (e.g., Schwartz et al. [2010] invert their color scheme and show the most impaired habitat in blue and the least impaired in red). The PCA boundary is shown in yellow in the three bottom maps.

Figure 14.1, immediately above, shows the mapped results of three out of the total of six studies that have explicitly looked at contiguity and fragmentation of grizzly bear habitat in the Yellowstone ecosystem. The six include Merrill et al. (1999), Carroll et al. (2001), Merrill & Mattson (2003), Johnson et al. (2004), U.S. Forest Service (2006), and Schwartz et al. (2010). The results above are from the three latest studies, with areas of fragmentation or contiguous impaired habitat extracted and shown in red in the three images arrayed left to right at the bottom. Parenthetically, the map produced by Schwartz et al. (2010) purports to represent odds of survival for grizzly bears, with the red denoting all of the areas where modeled survival rates are well below what is considered to be sustainable. The map produced by the U.S. Forest Service is based explicitly on delineations of “secure” habitat as defined by the Service. The PCA is delineated in yellow in the three bottom images.

The results of all of these studies constitute a remarkable consensus, including the three not explicitly represented

in figure 14.1. All show high degrees of fragmentation and substantial areas of impaired or otherwise deficient habitat. Within the PCA, these areas are concentrated in the west on the Targhee and Gallatin National Forests (NFs), in the far south on the Bridger-Teton NF, and in the northeast on the Shoshone and Gallatin NFs. Immediately adjacent to the PCA, there is a substantial zone of fragmented habitat separating the PCA from a sizable chunk of suitable habitat in the Wind River Range. Not coincidentally, a large fraction of conflicts between livestock and grizzly bears are currently concentrated in this fracture.

Even allowing for different and shaded definitions of fragmentation, the Service is egregiously deficient in its representation of this substantial body of convergent scientific results. The Service needs to acknowledge and adequately represent this literature, provide a functional and justified definition of “fragmentation,” and then reconcile that definition with the scientific results referenced here.

15. The Service’s assertion that “we do not expect such development [of mining claims] inside the PCA will constitute a threat to the GYE grizzly bear DPS now, or in the future” is unsubstantiated, counter to the primacy of the 1872 General Mining Law, and thus arbitrary.

The Service asserts on page 13196 of the Rule that the CS ensures that habitat security will not be compromised or “threatened” by the development of mining claims. The rule goes on to state that there are 28 mining claims with operating plans in the PCA. The Rule then asserts that federal land and minerals managers (primarily the U.S. Forest Service) will somehow allow for operation of only one new mine at a time, forestalling the operations of any others—and thus “ensuring” no net loss of habitat security. At the end of the section devoted to Mineral and Energy Development, the Service concludes “we do not expect such development [of mining claims] inside the PCA will constitute a threat to the GYE grizzly bear DPS now, or in the future.”

These claims and assertions are unsubstantiated and belie the history of mining claim development, including the impacts on grizzly bears that were anticipated and

documented by regulatory agencies during previous evaluations of proposed mining operations. For one, the CS will not trump provisions of the 1872 General Mining Law. As the U.S. Forest Service states in its 2006 EIS covering Forest Plan revisions for management of Yellowstone’s grizzly bear habitat: “Projects would be permitted according to the requirements of the 1872 Mining Law” (p. 208) and “Processing of mineral operations under the 1872 General Mining Law is not discretionary” (p. 271). Barring major political intervention, any proposed mining operations will proceed. And there are currently two mining operations in the process of development in and near the PCA (the Crevice Mine and the Emigrant Mine). The New World Mine dating from the early 1990s was deemed to have major potential impacts on grizzly bears (e.g., Mattson 1995) and did not pass regulatory review only because of

Presidential intervention and a special Congressional allocation to purchase the entailed mineral claims.

In short, a long history of legal precedent, together with realities on the ground, cannot be over-turned or otherwise magically transformed simply by the Service's

unsubstantiated assertion. The Service needs to recognize the primacy of the 1982 Mining Law, the implications of this primacy, the fact that mining claims are being and will continue being developed, and that these realities will likely constitute some degree of threat to the Yellowstone grizzly bear population.

16. The definition of "secure" habitat adopted by the Service is unsubstantiated by any referenced scientific research, roughly 72-times smaller than the compilation of best available science would recommend, and thus arbitrary. This gross underestimation of the dimensions of a secure area leads to inflated estimates of total secure habitat in Yellowstone's Bear Management Units. Moreover, the Service argues against its own definition of secure habitat in excluding certain areas from being deemed "suitable."

The Service defines "secure habitat" on page 13194 of the Rule as "those areas with no motorized access that are at least 4 ha (10 ac) in size and more than 500 m (1,650 ft) from a motorized access route or recurring helicopter flight line..." The cited authority for this definition is the U.S. Forest Service's 2006 EIS for revision of Forest Plans in the Greater Yellowstone Ecosystem.

Yet this document contains no justification for the adopted definition of secure habitat other than a reiteration of the dimensions given in the Rule. As a result, the Service does not provide nor reference any justification grounded in the best available science for this key facet of current and prospective habitat management under terms of the CS. Moreover, the asserted definition of secure habitat is ill-conceived and substantially at odds with the best available science, and thus amounts to an arbitrary determination.

By contrast, a compilation of the best available science by Mattson (1993), referenced to a thoroughly articulated justification, recommends that "microscale" security areas contain a core roughly 290 ha (716 ac) in size, roughly 2-4 km from the nearest road or other human facility. The resulting area, including core and buffer, would be 28.3 km² (c. 7000 ac) in size. The recommended core would be roughly 72-times larger than the 4 ha used by the Service and roughly 4-8 times farther from the nearest significant human facility. The secure core recommended by Mattson (1993) corresponds to the size of 24-48 hr foraging areas documented for Yellowstone's grizzly bears, whereas the buffering distance from human facilities attends to not

only to the extent of characteristic habitat alienation, but also the characteristic zone within which human-caused mortality has been documented to concentrate. There has been essentially no science since 1993 that would support a change in the recommendations made by Mattson (1993).

Perhaps as important, the standards developed by Mattson (1993) have been codified through litigation and through a US Fish & Wildlife Service Biological Opinion on the 1997 Revised Forest Plan for the Targhee National Forest. The Service fails to address this discrepancy between its past and present deliberations.

Interestingly, the Service tacitly refutes its own definition of secure habitat in its argument on page 13185 of the Rule for excluding fragments of habitat adjoining sheep allotments in the Wind River Range from "suitable" habitat. The Service's argument rests on an ill-defined invocation of "edge effects"; i.e., that edges of an unspecified dimension are somehow unsecure enough to warrant exclusion from "suitable" habitat. Without being privy to the exact dimensions of these "edges," they are almost certainly larger, each, than the 4 ha (plus 500 m buffer) threshold that the Service argues elsewhere is sufficient to ensure "security." The Service thus presents us with a prospective logical contradiction that needs to be reconciled.

In short, given the importance of habitat security to grizzly bear conservation, the Service needs to provide a readily-accessible and coherent justification for its

definition that is grounded in the best available science rather than bald assertion. If such a justification is not forthcoming, the Service needs to revise its standard for

secure habitat to reflect the best available science and then uniformly apply that definition in its delineations and deliberations.

17. The Service disregards and misrepresents the best available scientific information in its dismissal of natural predation as a threat to Yellowstone’s grizzly bears on page 13205 of the Rule.

The Service claims that natural predation of grizzly bears is rare and then recites the number of bears known to have been killed by other bears (28 between 1986-2012, roughly 1 per year) and by wolves (a total of 8 during an unspecified period of time) in the Yellowstone ecosystem as a basis for then concluding “...this source of mortality does not constitute a threat to the GYE grizzly bear DPS now, or in the future.” These statements constitute a selective and distorted representation of the best available science which would, in fact, support a different conclusion.

Most of the grizzly bears that die because of natural predation are cubs and yearlings (for substantiation, see the Service’s own referenced literature). Most of these deaths are not documented because of the very nature of natural predation, which is very opaque to researchers. In the large majority of cases, young bears are noted to have disappeared between one sighting of the mother and the next, without any clue as to the cause. Only rarely do investigators get on the ground in a timely enough way to “document” the natural cause of death, which is almost invariably predation—rarely senescence or a natural accident. Nonetheless, a large number of cubs and yearlings disappear, almost all likely because of predation.

When all potential natural deaths are considered—again, most likely attributable to predation—a different picture emerges compared to the one painted by the Service. Drawing on IGBST data, the median number of bears that likely or almost certainly died from predation is actually nearer 3 per year rather than 1 per year for the period 1986-2015. Perhaps of more relevance to the Rule, these numbers have increased substantially over time, as shown by figure 17.1. Whereas the per annum median was 1 between 1986 and 1996, the median since 2010 has been 6. Throughout the period 1986-2015, 66% were

cubs and yearlings. The dramatic and non-trivial jump in deaths potentially attributable to predation corresponds with loss of foods such as whitebark pine and cutthroat trout (see my point under 11.1) and a probable shift by many of the affected bears to eating more meat from ungulates—which is likely to be particularly hazardous for the offspring of involved adult females (see my comments elsewhere, including the inadequate conceptual frame used by the Service to assess hazards associated with bear consumption of different foods [X]).

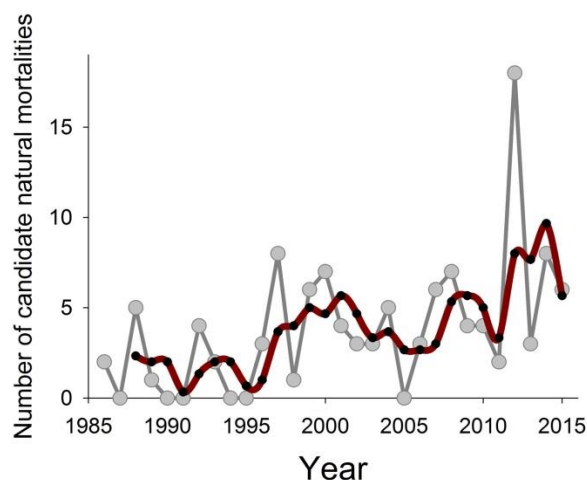


Figure 17.1. Number of known and probable mortalities likely to have been caused by natural predation, 1986-2015. Annual numbers are shown by the gray dots, a running three-average by the thicker red line. Data were provided by the IGBST and the Service.

In fact, this jump in known and probable deaths, likely attributable to predation, coincides almost exactly with the dramatic decline in cub and yearling survival rates documented by Van Manen et al. (2015), which they also attribute to bear predation (but under the rubric of “density-dependence,” a causal claim that is unsubstantiated for reasons that I articulate elsewhere). Regardless of the cause, Van Manen et al. (2015)

attribute the stalling of population growth beginning in the early 2000s in large part to this jump in deaths of young bears. In other words, this increase in deaths has had non-trivial effects on population trajectory.

As a bottom line, weight of evidence supports concluding that natural predation on especially cubs and yearlings has increased at the same time that survival rates of these younger bears has substantially declined, all with

demonstrable effects on population growth rate. As such, weight of evidence would support concluding that natural predation does, in fact, pose a “threat” to the population, especially given that weight of evidence further supports concluding that increases in natural predation are due primarily to a deteriorating environment—shifts in diet driven by losses of key foods such as whitebark pine seeds.

18. The claim by the Service on page 13207 of the Rule that “Because human-caused mortality has been reduced...this source of mortality does not constitute a threat to the GYE grizzly bear DPS now, or in the future” is a completely arbitrary unempirical assertion.

The Service deploys a number of bald assertions together with varying degrees of tortured logic on page 13206 and 13207 of the Rule in an effort to dismiss the threat posed by human-caused mortality to Yellowstone’s grizzly bear population as a basis for then concluding that ““Because human-caused mortality has been reduced...this source of mortality does not constitute a threat to the GYE grizzly bear DPS now, or in the future.” This conclusion and its supporting arguments are not only unsubstantiated by any empirical evidence, but also contradict the best available scientific information.

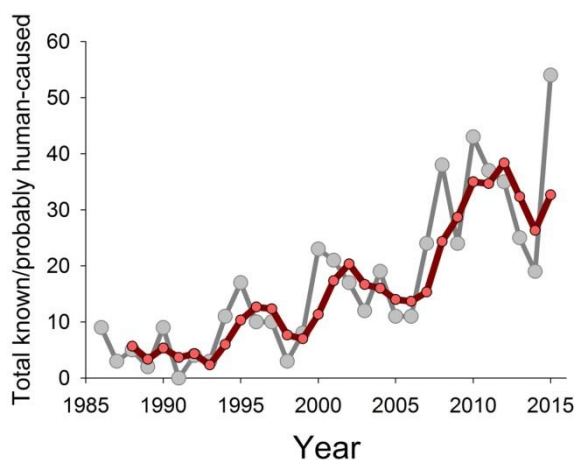


Figure 18.1. Total known and probable human-caused mortalities, by year, for the proposed Yellowstone grizzly bear DPS. The gray line and dots shown annual counts and the red line a 3-year running average. All data were obtained from the IGBST and the Service.

My claim is illustrated by a simple graph and derivative calculation using publicly-available scientific information obtained from the IGBST and the Service. Figure 18.1. shows the number of human-caused grizzly bear deaths in the Yellowstone ecosystem (i.e., the PCA, DMA, and proposed DPS) for each year, 1986-2015. The gray dots represent tallies for each year and the red line a 3-year running average of the same to emphasize trend. The result is unambiguous and in stark contrast to claims made by the Service in the Rule.

Total human-caused mortality has risen steadily since roughly 1994, and risen dramatically since 2007. More succinctly, human-caused mortality rose by 8.9% per year 1986-2015 and, even more remarkably, by 7.0% per year 2002-2015. This most recent period is especially relevant because the Service states in multiple places that “the population stabilized” during this approximate 15-year period. In other words, at the same time that the Service claims that the population did not increase, human-caused mortality was increasing by 7% per annum. If true, then human-caused mortality rates axiomatically substantially increased between 2002 and the present.

Parenthetically, if mortality rates were increasing during this 15-year period, one would expect the beginnings of a population decline. Elsewhere I present evidence that such a decline is, in fact, evident. But my point here takes the Service’s assertions regarding population growth and the data pertaining to human-caused mortality at face value. The inescapable conclusion is that all of the

management actions referenced by the Service on pages 13206 and 13207 of the Rule at best kept increases in human-caused mortality from being worse than they already were, but not enough to prevent the major observed increases.

As a bottom line, the only defensible conclusion to be drawn from the best available scientific information is that past (and prospective future) management actions were not sufficient to curb increases in human-caused mortality and, for that reason, human-caused mortality constitutes a threat to the GYE grizzly bear DPS now and in the future.

19. The Service employs methods for monitoring population trend and mortality rates that are unreliable, optimistically biased, insensitive to unfolding conditions, and prone to producing nonsensical results. These methods do not provide dependable information regarding status and trend of Yellowstone's grizzly bear population now or when prospectively applied after proposed removal of ESA protections. Moreover, the Service's methods are likely to allow for over-killing.

19.1. The Chao2 method adopted by the Service for monitoring population trend does not represent the best available science and is, moreover, beset by biases that have introduced systematically inflated and overly-optimistic estimates of trend for the Yellowstone grizzly bear population.

The Service repeatedly asserts throughout the Rule, CS, and Recovery Plan Appendix that the so-called Chao2 method is "the best available science" for estimating population size and, from that, population trend. These assertions are unsubstantiated and contradicted by what is, in fact, the best available science. Even more mystifying and problematic, the Service fails to acknowledge ample of evidence of bias affecting the Chao2 method, which results in systematically inflated estimates of trend for the Yellowstone grizzly bear population.

The Chao2 method is driven by counts of unduplicated females with cubs-of-the-years (Females with COY). Once these counts are ascertained, the Chao2 calculation presumes to account for all of the females with COY that were not detected (unknown, unrecorded). Once the known and unknown females with COY are added together and summed over a three-year period, this presumed estimate of total numbers of reproductive females in the population (given a 3-year reproductive interval) is multiplied by various factors to account for other sex- and age-classes of grizzly bears, thereby yielding a purported estimate of total population size.

Doak and Cutler (2014a, 2014b) present a compelling critique of the Service's approach to estimating population trend based on counts of females with COY, adjusted by the Chao2 method. Doak and Cutler show that essentially all of the positive population trend presumably exhibited by Yellowstone's grizzly bear population between the early 1990s and the present is likely to have been an artifact of biases introduced by increased search effort and increased intrinsic sightability of bears. Van Manen et al. (2014) attempted to refute Doak and Cutler's original critique, but were refuted, in turn, by Doak and Cutler's more recently published paper (2014b), which constitutes the last word insofar as the best available science is concerned. Interestingly, the IGBST itself admits to the very bias identified by Doak and Cutler in Table 2.1 of the Workshop Report (IGBST 2012) that the Service invokes throughout the Rule.

The figures below are illustrative of the major problems besetting the Service's Chao2 method. For one, the Chao2 calculation introduces an implausibly small adjustment to presumably account for unseen undocumented females with COY—on average, only an additional 6, or 19% more, per year. In other words, the Service is essentially claiming that roughly 81% of all females with COY are seen and documented, which is *prima facie*, unlikely. Similarly, as figure 19.1.1 illustrates, adjusted and underlying counts are 0.92 correlated, which means, not only that underlying counts of females with COY explain 84% of the total variation in resulting

estimates of the cohort total, but also that the Chao2-adjustment introduces essentially no additional information. As a bottom line, it is highly unlikely that the Chao2-adjustment corrects for much of anything, meaning that the resulting estimates of total population size are driven almost entirely by counts of females with COY alone. Importantly, these underlying counts are based on all sightings from all sources, without accounting for any factors that might influence such sightings.

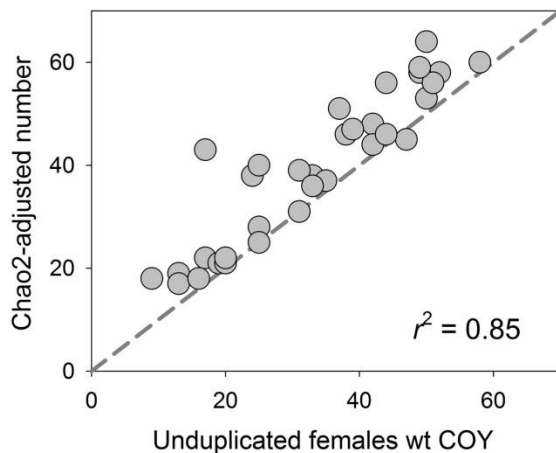


Figure 19.1.1. The relationship between annual numbers of unduplicated females with COY (x-axis) and the total number of females with COY after adjustments introduced by the Chao2 estimator (y-axis). Each gray dot represents one year's data; the dashed line represents a perfect 1:1 relationship.

Figure 19.1.2., to the right, illustrates perhaps the central problem with the Chao2/females with COY method. The top graphic in this figure shows long-term trends in numbers of females with COY (dark gray dots) along with the minor adjustments introduced by the Chao2 calculation (the light gray line above). This trend is the primary (but not sole; see my comments below) basis for the Service's claims regarding increases in Yellowstone's grizzly bear population. Then notice the trend lines in the graphic at bottom. The burgundy dots show the numbers of hours flown by researchers and managers in efforts explicitly designed to sight females with COY, which matters because roughly 66% of all sightings of females with COY are made from the air. The yellowish-green dots show the number of sites known to be used by bears feeding on army cutworm moths, which matters because, unlike any other feeding activity, essentially all of the bears engaged in this activity are seen by aerial

observers (O'Brien & Lindzey 1998). In other words, levels of feeding on moth sites are indicative of intrinsic sightability of the bears being sought out by researchers and managers.

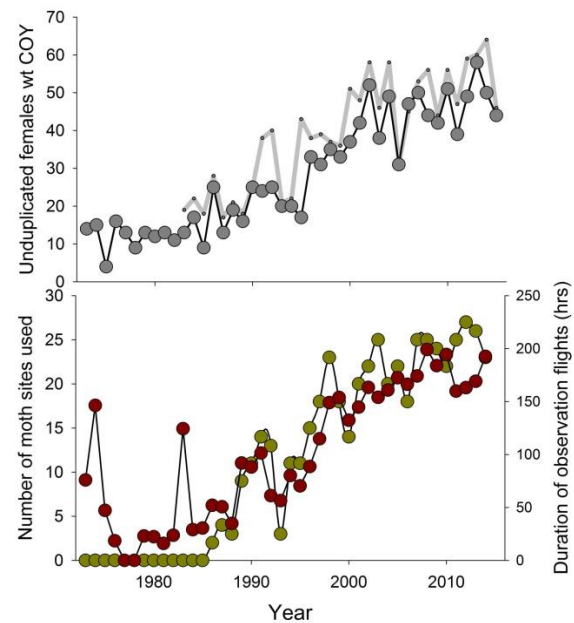


Figure 19.1.2. The top graphic shows annual counts of females with COY (gray dots) and presumed adjustments by the Chao2 method to account for unseen undocumented females. The bottom graphic shows aerial search effort by managers and researchers as part of observation flights (burgundy dots) and number of moth sites used by grizzly bears (yellow-green dots).

The parallels are striking. Presumed trends in counts of females with COY almost perfectly mirror search effort and moth site use, the latter (as I point out immediately above) an indicator of overall sightability. Figure 19.1.3 puts this in more literal terms by relating annual counts of females with COY to aerial effort (top) and number of exploited moth sites (bottom). The take-away here is that, depending on which relationship you want to consider, search effort could explain 70% and moth site use 80% of the total variation in annual counts of females with COY—which leaves little residual variation to reflect much of anything happening with underlying true population trend. These relationships simply reiterate in graphic form the main critique of the Chao2 method made by Doak and Cutler (2014a, 2014b).

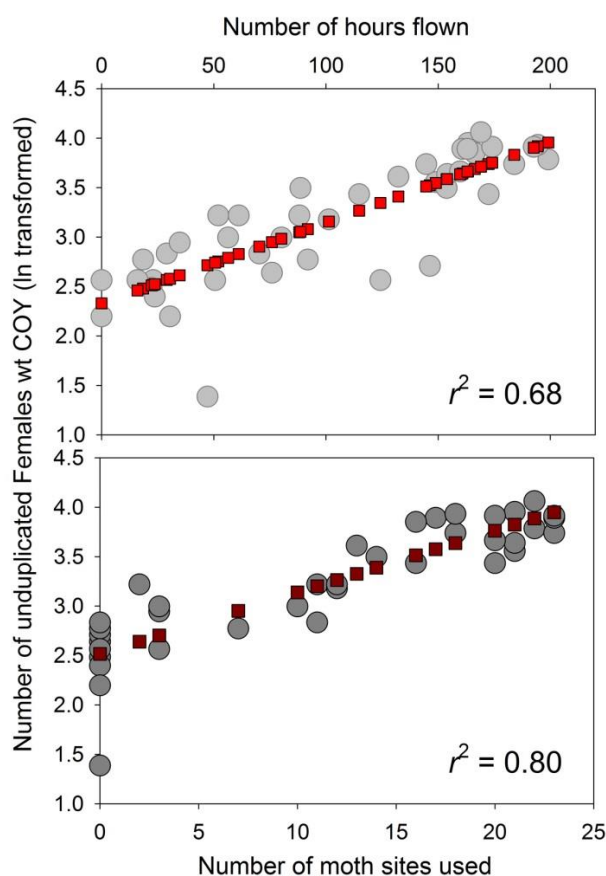


Figure 19.1.3. The figure at left shows relations between annual counts of females with COY (natural-log transformed) and aerial search effort (top) and number of moth sites used by grizzly bears (bottom). The gray dots correspond to data for a given year and the red squares to the predicted value given the modeled relationship.

Unfortunately, Chao2 estimates and underlying counts of females with COY have continued to be contaminated with bias during the last 20 years from increases in search effort and sightability—despite claims by the Service and IGBST that search effort has more-or-less stabilized. Illustrative of my point, figure 19.1.4. shows trends in aerial search effort, moth site use, counts of females with COY, and Chao2 adjustments for this period.

Parenthetically, the IGBST has argued that aerial search effort increased simply as a function of the increased distribution of Yellowstone’s grizzly bear population. As it turns out, even when standardized to distribution of the

population at any given point in time, aerial search effort per unit area doubled between the mid-1990s and late 2000s.

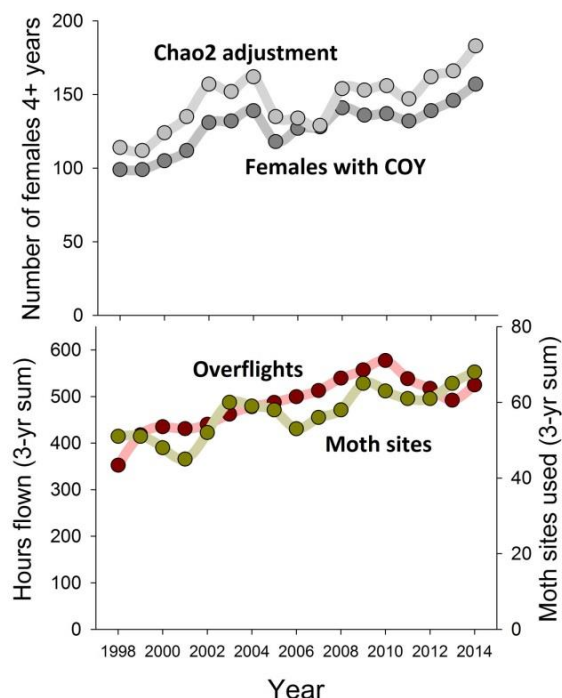


Figure 19.1.4. Three-year sums of females with COY and related Chao2 adjustments (top) and 3-year sums of aerial search effort and moth site use by grizzly bears (bottom) for the period 1995-2014.

In short, if you have a compelling argument showing that most variation in annual estimates produced by the Chao2 method is an artifact of bias—as I have demonstrated here—any assertion that the method produces reliable and useful indicators of trend is essentially arbitrary, if not capricious—as with the Service’s assertions that this method is reliable and “the best available science.”

Having made this point, deficiencies in the Chao2-based approach could be partly remedied by having the Service insure that search effort and search distribution remain constant in the future, while at the same time relinquishing any claims to being able to estimate past trend in population size using this method (see my comments 20.4 and 20.5).

19.2. The so-called “model-averaged” approach adopted by the Service to produce estimates of population size and, from that, estimates of population trend, is insensitive to unfolding problematic conditions. Estimates of trend from this approach are also vulnerable to manipulation depending on the time period adopted for model specification.

Even taking the egregiously deficient Chao2 method at face value, the so-called “model-averaged” approach adopted by the Service contributes to an overall method that is remarkably insensitive to rapidly unfolding conditions in the Yellowstone ecosystem. This matters because, as I document extensively in my comments, environmental conditions are, at best, rapidly changing and, much more likely, substantially deteriorating.

The model-averaged approach basically fits a regression model to Chao2-adjusted annual estimates of total females with COY, and then uses the intercept and slope from the model to, in turn, estimate the current year’s total. This approach presumably “smooths” short-term trends. Moreover, the regression model is fitted to data going back to 1983, presumably to produce a “reliable” estimate of trend with narrower confidence intervals, this as a consequence of employing a larger n .

The logic behind this approach is inane. The Service is basically substituting statistical precision for ecological relevance by inflating sample size through inclusion of annual data that have long since become irrelevant to judging status of the population. Why include annual counts of females with COY from 1983-1995, or even from 1995-2000, given the dramatic changes that have occurred and continue to occur in the Yellowstone ecosystem since the mid-1990s and early 2000s (see my comments elsewhere)? This conflation of precision with ecological importance is an error that most textbooks on biostatistics warn against—but apparently to no avail with the Service. More specifically, for the regression methods employed by the Service (and IGBST) to be valid, the distributional relationship of females with COY to time is assumed to be “stationary”—in essence meaning that underlying system dynamics are not changing. This assumption clearly does not hold here.

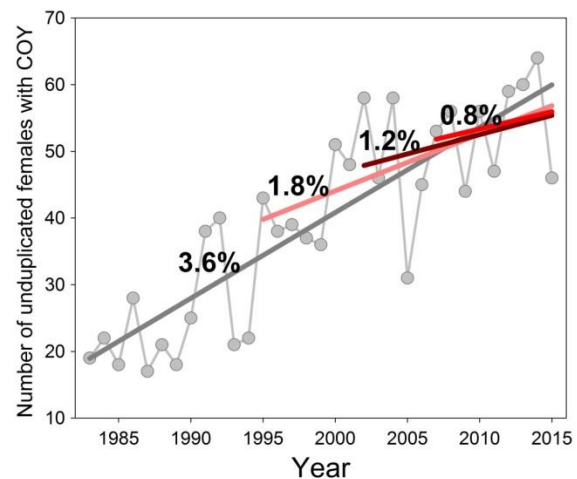


Figure 19.2.1. This graph shows trend lines fit to data for numbers of females with COY in the Yellowstone ecosystem, with each line representing a fit to a different span of years. The percent change per annum is shown for each trend line, emphasizing that estimates of trend change and become progressively approach zero as the time interval is truncated closer to the present.

Moreover, results of the “model-averaged” approach depend substantially on the time period being modeled—not only in generating an estimate of trend, but also in producing an estimate of population size (as a function of the β coefficient indicating trend). This matters because, the farther back you go in time with Yellowstone’s grizzly bear data, the more optimistically you bias your results. So the Service (or whomever) can more-or-less arbitrarily generate different results by basing estimates on different periods of time.

Figure 19.2.1 illustrates this problem. I show annual Chao2-adjusted estimates of females with COY as gray dots in the background. I also show trend lines fit by regression to natural-log transformed values, with each line corresponding to results using different relevant periods of time: 1983-2015 (the Service’s default); 1995-2015 (when we began to see major declines in trout and elk as per my comments elsewhere); 2000-2015 (when we first started to see major beetle-caused whitebark pine mortality); and 2007-2015 (when we saw the terminal decline in availability of whitebark pine seeds, also as per my earlier comments). The numbers above each line are the trends estimated for each period, represented as annual percent change. The point is pretty basic: population trend declines as you

progressively truncate the included years, which, in turn, yields a lower estimate of current total population size.

Finally, the Service's use of a model-averaged approach is flawed because it makes a further nonsensical assumption: that there is some theoretically-justified intrinsic relationship between counts of females with COY and time that can be specified mathematically and statistically in terms of an underlying model. A relationship between numbers and density? Perhaps. A relationship between numbers and food abundance? Yes. But not a relationship between numbers and the mere passage of time.

Even if one were to buy off on this unsupported assumption, one then needs to justify the form of the model adopted for estimating trend as a basis, in turn,

19.3. The mortality rates presented by the Service in Tables 1 and 3 of the Rule as benchmarks for managing mortality are liberal and thereby allow for over-killing of grizzly bears relative to objectives keyed to different population sizes.

The basis for this concern arises from the recent critique of IGBST estimates of population trend by Doak & Cutler (2014a, 2014b). They showed that there was good reason to think that population growth rate had been over-estimated by the IGBST using both the Chao2-based method and more complex calculations using death and birth rates estimated from known fates of radio-marked grizzly bears. More specifically, Doak & Cutler found that Schwartz et al. (2006) and IGBST estimations thereafter had not accounted for senescence in both birth and death rates of female grizzly bears, and that when accounted for, female survival rates and population growth rate (as estimated by Harris et al. 2006) dropped significantly.

Van Manen et al. (2014) claimed to have rebutted the original Doak & Culer (2014a) analysis. Aptly enough, the response of Doak & Cutler (2014b) to this presumed rebuttal was entitled "Doth Protest too Much." More specifically, Doak & Cutler found that the Van Manen et al. response was larger confirmatory of their original critiques. To quote Doak & Cutler: "[the Van Manen et al.] results show that incorporating senescence sharply reduces previously estimated population growth from

for estimating total numbers of females with COY. Linear? Quadratic? Cubic? Asymptotic? Logistic? A different choice will yield a different model-based estimate of current population size. And yet the Service employs linear and quadratic models, without statistical or theoretical justification. In short, this aspect of the method, like choice of time frame, entails arbitrary and capricious decisions on the part of the Service.

The Service needs to abandon its "model-based average" approach given the insensitivity of this method to rapidly changing environmental conditions in Yellowstone and because it does not constitute the best available science. An approach based on a running average of annual growth rate over a sensible number of preceding years—say six—would probably service the purpose instead.

1983 to 2001"; and "[the Van Manen et al.] study shows that there is so much uncertainty in population estimates that inferences about population trends are extremely weak." In other words, the collective results presented, not only by Doak & Cutler (2014a, 2014b), but also by Van Manen et al. (2014) show that population growth rate from 1983-2001 was over-estimated by the IGBST, and that all of the methods used by the IGBST for monitoring the Yellowstone grizzly bear population provide an "extremely weak" basis for inference.

Insofar as the Rule is concerned, the best available science shows that the mortality benchmarks in Tables 1 and 3 are too liberal by virtue of being linked to inflated estimates of population growth—which means that purported management objectives will not be achieved by employing these rates. More specifically, a 7.6% and 15% mortality rate for females and males, respectively, will not maintain a stable population, but rather yield unintended declines. And given all of the other problems with methods for monitoring and responding to mortality rates that I describe in my comments 19 and 20, there is a good chance that such declines will not be detected nor addressed in a timely manner, and certainly not in a way that would allow a meaningful response to prospective lags between environmental degradation and demographic responses (my point 5).

Given these considerations, the Service needs to: (1) acknowledge rather than glibly dismiss the unreliability

of all its current indicators of mortality and population growth rates; (2) revise all of the benchmark mortality rates in Tables 1 and 3 downward by several percentage points to acknowledge and account for the liberal bias of the rates they currently use—for example, from 7.6%

19.4. The Service employs a method for indexing annual mortality rates that has no known or unbiased relationship to the mortality standards/thresholds presented in Tables 1 and 3 of the Rule. As a result, allowable levels of mortality calculated using the Service's proposed methods for post-delisting management entail a non-trivial risk of over-killing Yellowstone's grizzly bears, and thereby pose a threat.

The mortality rates codified in tables 1 and 3 of the Rule are presented by the Service as if they were reliable guidelines for managing grizzly bear mortality to achieve either population stability, increase, or even declines. The rates associated with maintaining a stable population (for example, 7.6% per annum for independent-aged females) are assumed to be sufficient for the purpose because they are associated with presumed population increases. But there are major problems with this approach sufficient to nullify it as a reliable guide for management.

The Service proposes to manage grizzly bear mortality so as to achieve various population goals by comparing the ratio for a given year of estimated total dead to total live bears against a benchmark rate calculated from the known fates of radio-marked bears. In other words, an estimated total number of dead bears (D) is divided by an estimated total population size (N) for a given year to yield a purported estimate of death rate (i.e., a ratio of dead to live bears)—this for each of the monitored sex-age classes of grizzly bears. Total dead bears are estimated using methods described in Cherry et al. (2002) and total live bears using the Chao2-based estimation of total reproductive females, coupled with multipliers to account for dependent young, pre-reproductive females, and independent males. This purported rate is then compared against a benchmark rate billed as being selected so as to achieve the

down to 5.6% for females at a population size of ≤ 674 ; and (3) put its move to delist Yellowstone's grizzly bear population on hold until it has a better basis for managing mortality.

management purposes attached to a given population size: e.g., ≤ 675 , 675-747, or >747 .

The benchmark rate was calculated as (essentially) the probability that a given radio-marked bear would have died during a given year at a given age—in other words, based on known fates of bears that had been captured and ratio-tracked. Any given rate based on known fates is related to a prospective population objective (growth, stasis, or reduction) based on simulations of population growth using a range of birth and death rates. In other words, if the population was estimated to be growing or stable, then the death rates computed from fates of radio-marked bears are estimated to be those compatible with any future population growth or stasis.

One key assumption in the management approach described in the Rule and MOA is that there is equivalence between population growth rate and death rates. This assumption is tenuous at best because it does not deal with variation in birth rates: population growth is, axiomatically, the difference between birth and death rates. In other words, one half of the equation is left out of any explicit consideration. The only presumed corrective is allowances made in both the Rule and MOA for a reevaluation of demographic rates by the IGBST should the grizzly bear population be declining for reasons that don't comport with applied death rate guidelines. And this is to happen only if prescribed death rates are exceeded 3 years in a row (for problems with that provision see my comments under 20.3).

But the other important assumption is that the calculation used to estimate annual death rates (\hat{D} / \hat{N}) correlates perfectly with the benchmarks estimated from known fates of radio-marked bears—and with a 1:1 slope. As it turns out, the exact relationship between the benchmarks and the index being used to monitor death rates is unknown. Certainly—emphatically—there is no equivalence between the methods underlying each. Put another way, even if we calculate a putative death rate

of 7.6% for adult females in the population during a given year, we don't know whether that 7.6% is either "real" or unambiguously equivalent to the rate being proffered as a standard and a guideline.

This is a case where apples are being compared to oranges and where, moreover, the Service is either not identifying this discrepancy or even cognizant of it in the first place. But, again, as with lack of attention to birth rates, the presumed corrective will be some sort of management review if and when a mysterious population decline were to occur—but then almost certainly much delayed because of the current provision for review only if mortality standards are violated three years in a row (and, again, see my point below).

What makes this situation all the more risk-ridden is the *fact that the methods by which total deaths and total live bears are calculated are prone to substantial bias* (\hat{D} and \hat{N} are merely biased estimators)—of a nature that can both amplify or dampen bias in a relationship with benchmarks that is already unknown. Hence, the nature and magnitude of change in bias from one year to the next is, and will continue to be, unknown, with the distinct possibility of unintentionally over-killing bears.

More specifically, as the IGBST (2012) notes in table 2.1 of a recent review of population monitoring, the method for estimating total mortality is "Slightly Low (slightly more deaths may have occurred than estimated because heterogeneity in data greater than accounted for in estimator; effect would lead to underestimating total mortality)" (see my comment immediately below). And, if "Low" is approximately of the same magnitude as "Low" (in the same report) for the Chao2 estimator, then there are major problems. Likewise, the Chao2-based estimator of total population size is likely to vary with search effort (as I document in my point 19.1). In other words, if there is little effort invested by managers in finding bears, then estimates of population size will probably be increasingly biased low, in ways that could partially offset or mitigate for underestimates of total mortality. But—importantly—the Service doesn't know exactly how these biases interplay. And search effort to document females with COY has increased dramatically, so the bias towards a low estimate of population size is lessening at the same time that our estimates of total mortality are varying in unknown ways relative to biases

introduced by "heterogeneity" (Cherry et al. 2002, USGS 2012). In other words, bias is varying all over the place in unknown and undocumented ways, with potentially major effects on a metric central to monitoring the Yellowstone grizzly bear population, now, and in the future.

Finally, estimates of total population size are substantially affected by the multipliers used to account for dependent young, pre-reproductive independent females, and independent males, all with the potential for introducing yet more bias. As I point out below (my point 19.4), the multiplier used to account for independent males was increased substantially during and after 2012, according to the IGBST because death rates for independent males had decreased—substantially. Yet, as I point out below (point 19.4), survival rates of independent males very likely did not increase, but rather decreased—the opposite. Which is to say that a bogus multiplier was applied resulting in an artificial inflation of total population size by around 100 bears, with this biased estimate of total population size then used as the denominator for indexing death rate—with predictably yields a lower "rate." And this on top of the systematic inflation of total population estimates introduced by continuing increases in search effort and sightability of bears (see my point 19.1).

As a bottom line, the method being billed by the Service as insurance against over-"harvest" of grizzly bears is beset by a substantial amount of uncorrectable bias that introduces non-trivial risk of over-killing bears. This arises from multiple causes, including (1) using a method for estimating death rates that has no known relationship to the standards being used to guide management (the apples and oranges problem); (2) substantial biases affecting methods for estimating both total numbers of annual deaths (the death rate numerator) and females with COY during a given year (the root of the death rate denominator); and (3) bias and outright error affecting multipliers used to derive estimates of total population size. The chain of potentially compounding errors debars any confidence in the Service's method for monitoring grizzly bear death rates.

If there is a corrective, it entails, at a minimum: (1) standardizing search effort for females with COY (as per my points 19.1 & 20.5); (2) further developing the

method for estimating total numbers of deaths so as to account for biasing “heterogeneity”; (3) rigorously account for variation in birth rates as part of an on-going (versus discretionary and episodic) analytic process; and (4) employing a precautionary (rather than incautious)

19.5. The Service produces inflated estimates of population size and trend that are largely an artifact of implausibly high estimates of survival rates for male and female bears 2+ years old. Moreover, these survival rates are also insensitive to rapidly changing conditions. Together, these short-comings constitute a methodological threat to the Yellowstone grizzly bear population.

As I preview in my comments above under point 19.3., the Service uses estimates of death rates derived from fates of radio-marked bears at several critical junctures in its proposed and current methods for monitoring and managing mortality of Yellowstone’s grizzly bears. For one, these rates are the basis for the seminal benchmarks presented in Tables 1 and 3 of the Rule for achieving either population increase, stasis, or decline—depending on estimated population size. The mortality rates are also directly used to determine the proportions of different sex-age classes in the population, in turn, the basis for multipliers used to arrive at total population estimates. The estimated proportions of independent males, pre-reproductive independent females, and dependent offspring are essentially inverted and each used to multiply annual Chao2-based estimates of total reproductive females.

These multipliers obviously can have major effects on total population estimates. For example, beginning in 2012 the IGBST began using a larger multiplier to account for number of independent males, this because they claimed that the most recent estimate of death rates for males, using data from 2002-2011, had decreased. Hence there were presumably more males in the population than had been thought. In fact, the difference between population estimates using the old and new multipliers averaged 107 for 2012-2014, which amounted to an instantaneous 17% increase in total population size. Axiomatically, this substantial increase in the denominator for calculating the index of mortality rate translated into decrease in this rate—by roughly 15%. In

approach to developing multipliers to account for sex-age cohorts other than reproductive females. Meanwhile, the Service needs to remove the inflated claims that it makes in the Rule for the efficacies of its current approach to managing mortality.

other words, depending on the multipliers, you can be either substantially over or under a given mortality rate threshold such as those presented in Tables 1 and 3 of the Rule.

For these reasons the estimates of death rates derived from fates of radio-marked bears need to be unimpeachable. But there are two major problems with these rates, one of which is chronic, and the other particularly evident during the last 15 years.

The chronic problem has to do with the inherent extent to which death (and birth) rates calculated from fates of radio-marked bears are insensitive to rapidly changing conditions. This arises from the fact that reliable estimates depend on large sample sizes, and the only way one can come up with a large sample size is to include data that span a number of years—a decade or so. In other words, these death rates (or, inversely, survival rates) are slaved to the past and, in an environment such as Yellowstone’s, 10 years can rapidly become irrelevant to the present and near future. In fact, this problem holds for all estimates obtained from fates of radio-marked bears, including birth rates. As a result, episodic future reviews of demography by the IGBST, through the lens of data from ratio-marked bears, will stand little chance of offering critical insights needed to remedy deteriorating population-level conditions—contrary to assertions in both the Rule and the MOA.

But the more important problem is the extent to which death rates derived from fates of radio-marked bears are not only discrepant from, but also fundamentally at odds with, straight-forward and unambiguous trends in numbers of grizzly bears dying in the Yellowstone ecosystem.

Figure 19.4.1 illustrates this problem. The red lines show three-year running averages for numbers of known-probably deaths of female (top) and male (bottom) grizzly bears >2 years old. The black dashed line towards the top

of each graph shows what is probably our most reliable annual estimates of total population size derived from the Mark-Resight method (a less biased although less precise estimator compared to Chao2). I show the two trends in juxtapose for good reason given that death rate (as above) is essentially the number of bears dying as a fraction of the number of bears alive. In other words, if the number of live bears is static or declining at the same time numbers of dead bears are increasing dramatically, then death rates *must* be increasing. And, in fact, numbers of male and female deaths were increasing at an astounding rate of 9-10% per annum for the period 2002-2011, at the same time that total population size was essentially static. In other words, death rate *must* have been increasing dramatically during this period of time for both sexes.

Yet, as I noted above, the IGBST claims (in its 2012-2014 Annual Reports), not only that death rates of male bears were *decreasing* during 2002-2011, but also that death rates of female bears *remained unchanged*. It is as if the data I present in figure 19.4.1 and the data the IGBST used to calculate revised death rates were drawn from two different universes. Which are to be believed? I would argue that the data I present here (all from IGBST databases and Annual Reports) are straight-forward and virtually impossible to refute, whereas the death rates estimated by the IGBST from fates of radio-collared bears derive from assumption-ridden, complex, and refutable models. There is good reason to believe the unambiguous trend data.

19.6. The method adopted by the Service for estimating total numbers of grizzly bear mortalities during a given year tends to under-estimate this total and is insensitive to unfolding trends that have likely increased rather than decreased the magnitude of this under-estimation.

The Service repeatedly invokes the method developed by Cherry et al. (2002) as its basis for estimating total

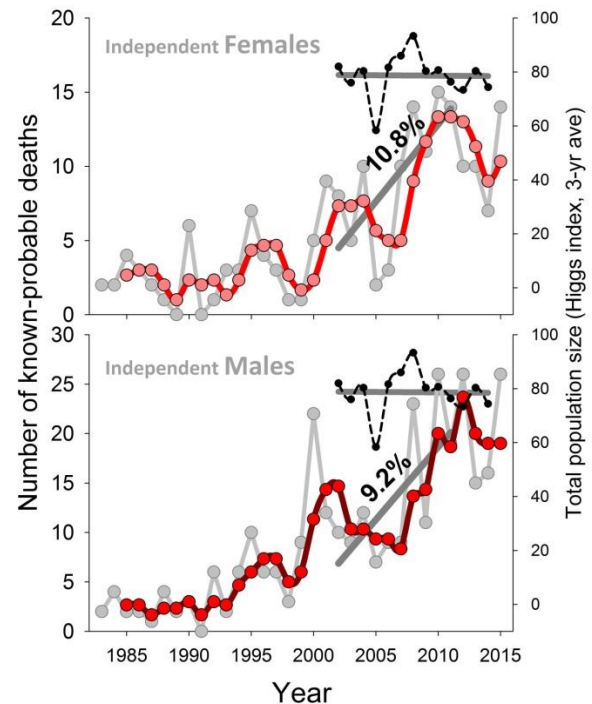


Figure 19.4.1. Trends in annual numbers of known-probable grizzly bear deaths for females (top) and males (bottom) juxtaposed with trends in annual estimates of total population size using the Higgs et al. (2013) Mark-Resight method. The red lines are 3-yr running averages of deaths and the light gray lines behind the annual numbers. Total population size is shown by the dashed black line. I've also included trends lines and associated estimates for deaths, 2002-2011.

In short, the death rates that the Service draws on so heavily in the Rule and that the states employ so centrally in the MOA stand impeached. At the very least the Service needs to adequately explain the contradictions that I high-light here. Moreover, the Service's frequent assertions that current mortality rates do not threaten Yellowstone's grizzly bear population are unsubstantiated and, in fact, contradicted by the best available science.

number of grizzly bear deaths, a value which is then used in the numerator of the calculation used to annually index death rates in the Yellowstone ecosystem. This rate index is compared to the benchmarks in Tables 1 and 3 of the Rule to determine whether numbers of deaths were compatible with different management objectives. I describe other problems with the Service's overall method for monitoring and managing mortality under

other points but focus here on problems with its adopted method for estimating total numbers of dead bears.

There are two basic and relatively well-recognized problems with the Cherry et al. (2002) method. First is a tendency to under-estimate total mortality. Second is a related vulnerability to systematic bias interjected over time as a result of changes in cause of death as well as capture and radio-collaring efforts.

The risk-inflating tendency of this method to under-estimate mortality is noted in Table 2.1 of the seminal 2012 IGBST Workshop Report: “Slightly Low (slightly more deaths may have occurred than estimated because heterogeneity in data greater than accounted for in estimator; effect would lead to underestimating total mortality).” This is a chronic problem that is exacerbated or mitigated by changes in bias affecting estimates of total population size—which is the denominator in calculations of annual indices of death rate.

But there is a second problem, prominently noted by Cherry et al. (2002): “The assumption of a constant reporting rate for radio-collared bears over time was important in our specification of the prior and in application of the method to the count data. This assumption could be violated if, for example, the probability of a death being reported depended on the cause of death and these causes changed over time. Mattson (1998) argued that this has in fact occurred...there is some evidence that reporting rates have declined in recent years.” In other words, if causes of death are trending towards those that are less likely to be reported, then the Cherry et al. (2002) method will be prey to an ever-increasing under-estimation of total deaths.

Moreover, estimates of total deaths will be further biased by level of effort to capture and radio-collar grizzly bears in the Yellowstone ecosystem. This bias arises from the fact that deaths of radio-collared bears are not subject to the multiplier introduced by Cherry et al. (2002) to presumably account for unreported-unknown mortalities. In other words, if ever more effort is being exerted to capture bears, resulting in ever-more radio-marked bears, you are likely to end up with a larger number of deaths each year attributable to marked bears and thus not subject to any adjustment to account for

unknown mortalities—this simply as a function of effort on the part of researchers and managers and without any intrinsic relationship to numbers of bears dying.

Figure 19.5.1. shows that grizzly bear captures have in fact increased at a far more rapid rate than any probable change in total population size, which is consistent with capture effort alone magnifying the extent to which total grizzly bear mortality is being under-estimated. As shown by the yellowish-green dots, numbers of bears captured and then monitored have increased at 5% per annum since 2002, at the same time that estimates of total population size based on the Mark-Resight method have essentially not changed (the gray dots). Ergo, a larger fraction of the population is being marked, predictably yielding a larger number of dead bears that were radio-collared—which is, in fact, the case, at a rate of roughly 4% per year since 2002.

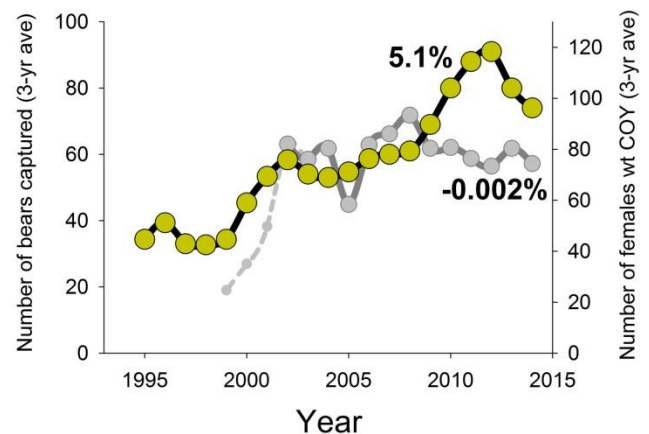


Figure 19.5.1. Trends in numbers of bears captured each year (yellowish-green dots) and estimated total population size (gray dots, based on Mark-Resight). Both values are presented as 3-year running averages, along with estimates of annual change in each time series by the numbers shown for each.

In short, the Service fails to acknowledge the several problematic biases affecting its promoted method for estimating total numbers of dead bears in the Yellowstone grizzly bear population. On top of this, the Service fails to acknowledge that these biases amplify risk and, perhaps more importantly, that these biases have probably increased over time resulting in an ever more pronounced under-estimation of total mortality. As a result, death rate is probably being increasingly under-estimated, leading to increased errors by managers regarding the sustainability of current levels of mortality.

The Service needs to acknowledge these biases affecting estimation of total grizzly bear deaths and the risks that they bring. Related, the Service needs to surrender any of its claims regarding past trends in mortality rates and focus, instead, on efforts to improve methods so as to

reduce bias. At a minimum these include upgrading the current Cherry et al. (2002) method to account for changes in cause of death for unmarked bears, and standardizing capture efforts so as to not introduce bias arising simply from increased exertions on the part of managers and researchers.

20. The Rule and the accompanying Memorandum of Agreement (MOA) developed by the states for managing Yellowstone’s grizzly bears post-delisting are inadequate in provisions for calculating and managing total allowable mortality. Moreover, both the MOA and the Rule are deficient in terminology and provisions for managing grizzly bear distribution.

20.1. The methods described in the Rule to account for ‘background’ mortality are not only discrepant with methods described in the MOA, but also fail to account for unknown-unreported grizzly bear deaths, thus constituting a major methodological threat to the Yellowstone grizzly bear population.

On page 13203 of the Rule the Service walks the reader through an example of how ‘discretionary’ mortality will be calculated—of which presumably all could be provisionally allocated by the states at the beginning of a given year for sport hunting. The example calculations purport to account for ‘background’ mortality, which is defined in the previous paragraph as including various causes, including “unknown/unreported calculations.” Yet the example given by the Service, fails, in fact to account for “unknown/unreported” mortalities, leading to an inflated estimate of the number of bears candidate for ‘discretionary’ mortality. This is a major error given that discretionary mortality for independent females and males ends up being over-estimated by approximately 75% and 200%, respectively. In other words, this is a non-trivial even fatal mistake on the part of the Service.

The Service needs to account for unknown-unreported mortalities in its calculations. Given the current IGBST method used to estimate unknown-unreported deaths, this foreseeable cause needs to be subtracted before other foreseeable ‘non-discretionary’ deaths are deducted. Given that the unknown-unreported fraction during 2010-2014 has averaged 39% of the total known-probable deaths for independent females and 37% of the same for independent males, these fractions need to be the first to be subtracted from the initial calculation of allowable mortality. After that, other ‘non-discretionary’ causes can be deducted.

The other major missing piece in the Service’s proposed method for estimating and allocating ‘discretionary’ mortality is its lack of provision for the National Park Service. This is especially glaring in the MOA, which presumably further codifies methods described in the Rule. In other words, all of the ‘discretionary’ mortality is

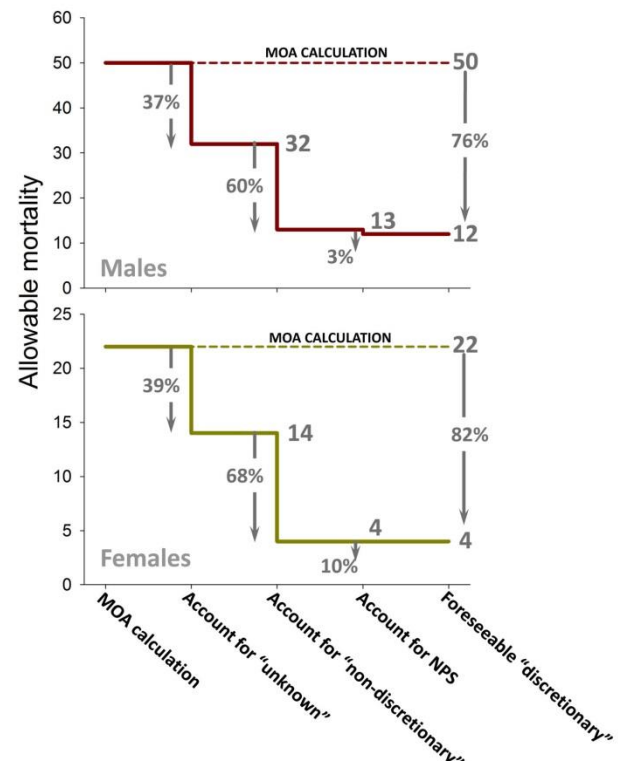


Figure 20.1.1. An illustration of reductions in allowable mortality that need to happen if unknown-unreported and other ‘non-discretionary’ deaths are to accounted for, in addition to ‘discretionary’ deaths foreseeably occurring on NPS jurisdictions—prior to any determinations regarding bears available for ‘discretionary’ management on non-NPS lands.

assumed to go to jurisdictions managed by the states of Wyoming, Montana, and Idaho, and none to National Park Service-managed lands. Recent history would suggest that this NPS fraction is roughly 10% of the ‘discretionary’ total. In other words, explicit provision needs to be made for this foreseeable mortality occurring on NPS jurisdictions, with corresponding

deductions from the states' share of 'discretionary' up for grabs as a prospective sport hunt.

By way of clarification, figure 20.1.1, illustrates the nature of the stepdown that needs to occur in the Service's calculations; first accounting for unknown-unreported, then other 'non-discretionary', then the NPS share—this for a population of roughly 717. The percentages I use are approximations. Exact percentages

20.2. A guideline for total mortality rate, with the intent of producing population growth, is needed in both the Rule and the MOA for an estimated population size of ≤ 600 bears.

The rationale for this recommendation is pretty straightforward. Managers should set a goal, expressed in terms of total mortality rates, that will likely produce growth in the Yellowstone grizzly bear population should it drop below the basement number of 600. Even taken at face value, the mortality guidelines currently set for any population less than or equal to 674 are, by the Service's own admission, rates associated with a stable population at best.

The agencies may argue that they already have a provision for eliminating virtually all 'Discretionary'

20.3. Review of current management approaches should be mandated whenever mortality guidelines are exceeded during any two consecutive years, for any of the three specified cohorts of bears, rather than the standard of three consecutive years specified in the current Rule and MOA.

Both the Rule and the MOA specify that a review of management leading to potential changes in harvest would occur only if recommended mortality rates were exceeded in 3 consecutive years. If the sequencing was right (e.g., 2 years of excess followed by one year within bounds, followed by two more sequences of this nature), this protocol would allow the states to kill bears in excess of recommended guidelines for 7 out of 10 years, which,

(or at least transparent methods for calculating exact percentages) for each stepdown need to be calculated and presented by the Service

Finally, the methods described in the MOA for calculating 'discretionary' mortality are considerably discrepant from those described in the Rule. This discrepancy needs to be corrected, along with other corrections that I have outlined here.

mortality once 600 is reached—tantamount to a drop in total mortality rate. This is not enough. An explicitly named target rate would provide incentive to reduce what the agencies are currently calling 'Non-discretionary' mortality once the population is at or near 600; and this mortality rate should be several percentage points below the 7.6% and 15% caps applied to males and females when the population is < 675 . Given that there are a 1.4% and 5% drops in the benchmark mortality rates for females and males, respectively, once the population drops below 675, it would be logical to apply a commensurate drop in benchmark rates once the population drops below 600, to around 6% for females and 10% for males. (Also, see my 20.6, below, for more on the problems of using 'Discretionary' and 'Non-discretionary').

taking all of the other elements of the MOA at face value, would be a recipe for producing a declining population—and without provision for introducing a timely change in management. Under the current approach, a check would only be introduced if estimated population size dropped below 600, at which point, options for reversing course would be intrinsically limited.

With the change recommended here (review after 2 rather than 3 successive years of violated mortality rate targets), timely review would be triggered much more often and with the prospect of actually reversing course prior to excessive declines in the bear population. Certainly, the current proposed approach is not precautionary nor in any other way conservative.

20.4. Both the Rule and the MOA need to commit to resetting or recalibrating all aspects of the methods used to monitor trend, calculate allowable total mortality, and trigger various outside reviews if and when new methods are adopted for estimating total population size. Without this provision, the existing approach constitutes a methodological threat to the population

The Rule and MOA describe methods for calculating total allowable mortality ('Discretionary' plus 'Non-discretionary') that are highly sensitive to estimates of total population size. Given that different estimators of total population size can yield numbers that vary by as much as 40%—even using the same inputs (e.g., Mark-Resight versus Chao2; Higgs et al. [2013] and IGBST [2015])—the Service needs to include language in the Rule that explicitly guards against state agencies introducing a new method that dramatically increases estimates of total population size without any commensurate adjustments in reckonings of trend, methods for estimating total allowable mortality, or thresholds that trigger outside reviews—all of which is currently allowed in both the Rule and the MOA.

As is, state management agencies could (for example) adopt the existing Mark-Resight method for estimating total population size as soon as Yellowstone's grizzly bears are delisted, and produce a dramatic purported "increase" in the population. This would instantaneously translate into a markedly positive increase in putative population trend along with numbers of bears available for 'discretionary' mortality—without any change whatsoever in the underlying population or on-the-ground conditions.

20.5. The MOA and the Rule need to explicitly specify that population monitoring will continue indefinitely at the same intensity (neither more nor less) and according to the same design as occurred during the 5 years prior to delisting.

Given vulnerabilities of the Chao2 method—or any other foreseeable method—to bias introduced by search effort and intrinsic sightability of bears (see my comments

Allowance for such a scenario not only introduces substantial risk, but also, even more importantly, emasculates and otherwise renders immaterial all of the presumed safeguards against over-exploitation described by the Service in the current Rule. A population that the Service currently represents as numbering around 675 could suddenly be inflated to over 925, thereby allowing for a potential sport harvest of, not 15, but rather nearer 25, a 67% increase. Likewise, a population at a threshold of 600 that would debar all sport harvest could be inflated to over 800, with instantaneous allowance for harvest of 15 or so bears. And, even more problematic, a population at the threshold of 500, that the Rule claims might trigger a status review by the Service, could be suddenly increased to 700, well above such a trigger.

Whether such scenarios came to pass intentionally or unintentionally, they would unambiguously pose a serious threat to the population embedded in methods currently contained in the Rule. The Service needs to remedy this unacceptable risk. There are several options, amongst which the least ambiguous and straight-forward would be to commit to continued use of the Chao2 method for estimating total population size, but with an accompanying commitment to rigorously standardize search effort and distribution (see my comment 20.5 below). This would help control for the bias that besets the Chao2 method. Another option would be to commit in the Rule and MOA to use the lower bound of uncertainty intervals for estimates of total population size generated by the Mark-Resight method, should it be adopted. This would presumably mitigate for the major short-coming of this method identified by IGBST (2015), which is the large uncertainty in annual estimates.

under 19.1), the Rule and MOA both need to contain a commitment to maintaining the current exact intensity and distribution of search effort devoted to documenting the presence of females with COY. Such a commitment would help curb any tendencies on the part of management agencies to temporarily inflate population estimates through increased search effort, especially if such an increase were coupled with greater orientation towards areas where grizzly bears are most easily seen.

20.6. Terminology for referring to bear mortality should be changed in the Rule and MOA from 'Discretionary' versus 'Non-discretionary' to 'Management' versus 'Other'.

The semantics of the current distinction between 'Discretionary' and 'Non-discretionary' mortality in the Rule and the MOA lead to confusion. Moreover, the distinction is disingenuous. By using these terms, the Service and state managers lead both themselves and their readers to assume that they have no control or influence over so-called 'Non-discretionary' mortalities—that this category of mortalities “needs” to happen or is the result of some act of God. This is not the case. History has shown (as the current Rule would claim) that managers do, in fact, have substantial influence over the so-called 'Non-discretionary' mortalities through activities such as law enforcement, education, and sanitation. The Rule even strongly implies that managers have influence over “natural” mortalities to the extent that sport harvest of specific cohorts of bears can amplify or dampen levels of mortality caused by conspecifics—especially infanticide (e.g., Swenson et al. 2001a, 2001b; Bellemain et al. 2006; Bischof et al. 2009; Gardner et al. 2014). In other words, 'Non-discretionary' mortalities can, in fact, be 'Discretionary'.

When you look at the more concrete categories of bear deaths that the Rule and MOA are allocating to 'Discretionary' versus 'Non-discretionary', it turns out that the distinction is fairly straight-forward distinction. 'Discretionary' deaths are simply those that will be directly sanctioned by managers and meted out by either uniformed employees of a state agency, by Wildlife Services, or by those licensed to act on a state agency's behalf (e.g., licensed hunters). 'Non-discretionary' deaths are simply all others resulting from the actions of those (including other animals) who are not explicitly and directly authorized, in any immediate sense, to kill grizzly bears.

In fact, the current category of 'Discretionary' correlates closely with historical deaths of grizzly bears caused by managers responding to conflict situations, including threats to human safety—in other words, 'management' removals. 'Non-discretionary' correlates with all of the other historical categories. For the sake of clarity and in service of reducing ambiguity, I recommend that the Service revise the Rule so as to refer to 'Discretionary' kills as 'Management' kills and 'Non-discretionary kills' as simply 'Other'.

21. Occupancy provisions for adult females need to apply to all portions of the DMA, not just the PCA, stratified on the basis of what are currently called 'Flight areas'.

The current approach outlined in the Rule and the MOA essentially loads all of the 'Discretionary' mortality allotted for independent females on those without dependent young (lone females) outside of National Parks. Under current provisions, no sport harvest of females accompanied by dependent young would be allowed. This amounts to the brunt of 'discretionary' human-caused deaths among females being borne by lone bears on the periphery of the DMA.

On average, only 1 of 3 adult females will be without young during a given year. Moreover, some percentage of these lone females will be inside National Parks where they will not be subject to hunting. As a result, something

less than 33% of the adult females in the population (say, 25%), all concentrated on the ecosystem periphery, will be subject to most of the planned killing each year. And, importantly, the current approach essentially uses females inside National Parks to subsidize calculations of allowable sport harvest outside.

The end result will be patently unsustainable killing of females on the periphery. Source-sink population dynamics would also certainly be amplified which, according to Doak (1995), could lead to increased vulnerability of the population to unintended and long-lagged declines.

Preferentially killing females that would otherwise have given birth to cubs the following year could introduce yet other unpredictable amplifications of population trends. On the face of it, amplified oscillations might be curbed by the fact that, with fewer females giving birth to cubs any following year, estimates of total population size based on observations of females with COY would be smaller, which might then lead to a lower 'Discretionary' kill the year after. But there would then be a pulse of cubs from females that were subsequently subject to a light harvest, which would lead to an inflated estimate of population size and a resulting inflated sport harvest the year after...and so on. In short, the approach described in the Rule and the MOA will lead to fewer females living on

the ecosystem periphery and less predictability regarding the consequences of management actions.

A requirement by the Service for occupancy of all management units by reproductive females, including 'flight areas' outside the DMA (see figure 21.1 below), would introduce a curb on excesses built into the Rule and MOA, which currently have punitive implications for females outside National Parks. Alleviating these current excesses would result in proportionately greater numbers of females on the periphery, which would foster eventual connectivity between Yellowstone and the NCDE.

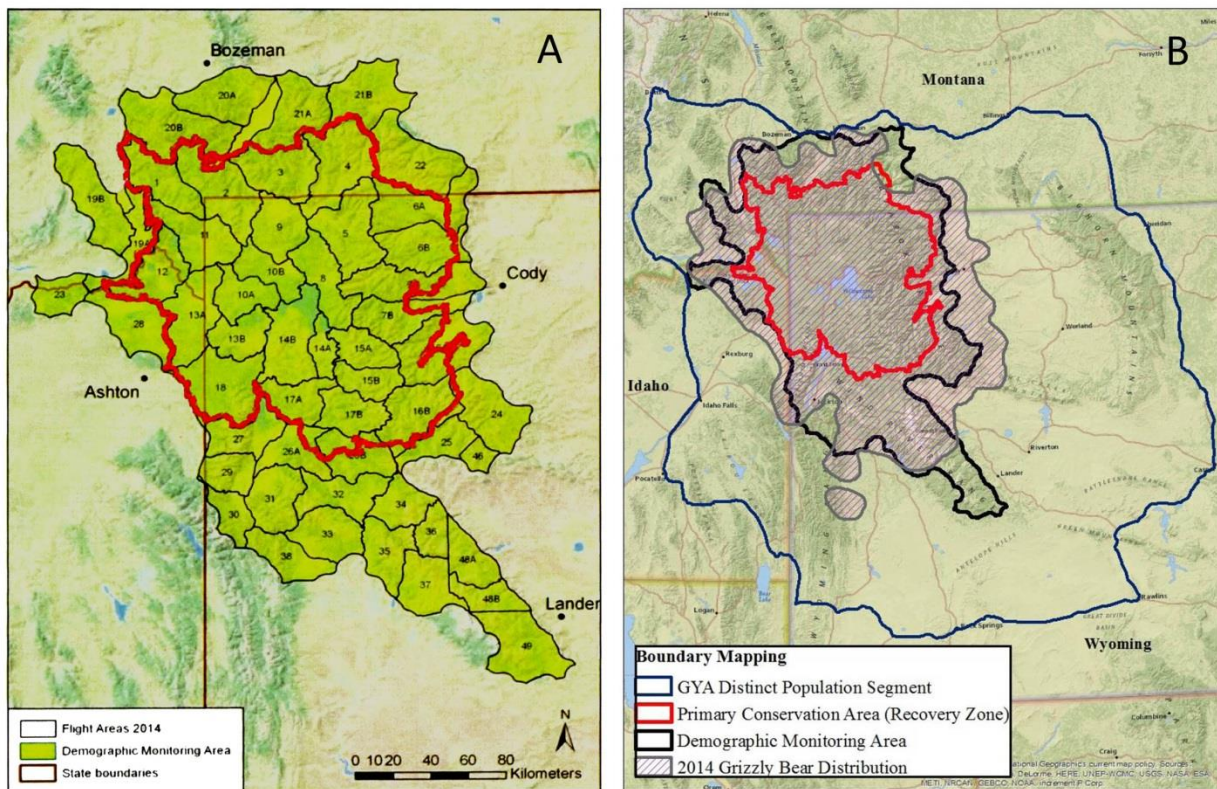


Figure 21.1. Map A, above, shows the PCA (delineated by red, as shown in map B) relative to the full extent and partitioning of the DMA (in yellow). The Rule and current MOA only provide for insurance of occupancy by adult females within the units contained by the PCA and leaves occupancy of all the other units ('Flight Areas') in the DMA up in the air when it comes to presence of reproductive females.



Attachments

David J. Mattson, Ph.D.

Wyoming Wildlife Advocates

Comments on the

US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227

And Related Materials

May 5, 2016

Attachment 1. Literature Cited

to accompany

David J. Mattson, Ph.D., Wyoming Wildlife Advocates, Comments on the US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227; And Related Materials

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Attachment 2. Primer on Nutritional Ecology of Bears

to accompany

David J. Mattson, Ph.D., Wyoming Wildlife Advocates, Comments on the US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227; And Related Materials

Digestion

Bears are omnivores, which simply means that they eat a varied diet potentially comprised of either almost wholly meat or almost wholly vegetation. Yet they have the simple monogastric digestive tract of a carnivore lacking specialized chambers able to sustain anaerobic fermentation by symbiotic microbes. More to the point, they lack a rumen and a cecum, although there is evidence of some microbial fermentation in the bears' simple large intestine. As a result, they obtain little nutritional benefit from the fiber that they ingest. This fiber can comprise 10-30% of the foliage they graze or browse, which means, in turn, that their most digestible foods consist of those rich in either digestible protein or fat or containing high concentrations of simpler carbohydrates such as fructose, sucrose, or starch.

Comparative digestion in bears & herbivores

Figure 1 illustrates the general digestive plight—or strategy—of bears in contrast to fore- and hindgut fermenters (i.e., ruminants and non-ruminants), as well as in comparison to other carnivores. This graph illustrates the relative digestibility of several broad categories of foods by bears and other taxa (with percent digestibility shown as medians and interquartile ranges). For the purposes here, bears are parsed out in different ways, with giant pandas and grizzly bears differentiated for illustrating digestion of foliage and roots, and all bears lumped together as "ursids" for illustrating digestion of meat. These data come from multiple sources.

The basic patterns are pretty obvious. Bears are as well able as any other carnivore to digest most of the meat they eat—around 90% plus. By contrast, grizzly bears digest roughly 20% less of the foliage they consume compared to ruminants and 10% less when compared to non-ruminant herbivores. Starchy roots are digested by grizzly bears with about the same efficiency as foliage is digested by ruminants—which makes roots a comparatively beneficial vegetal food for bears, at least when reckoned simply in terms of digestibility.

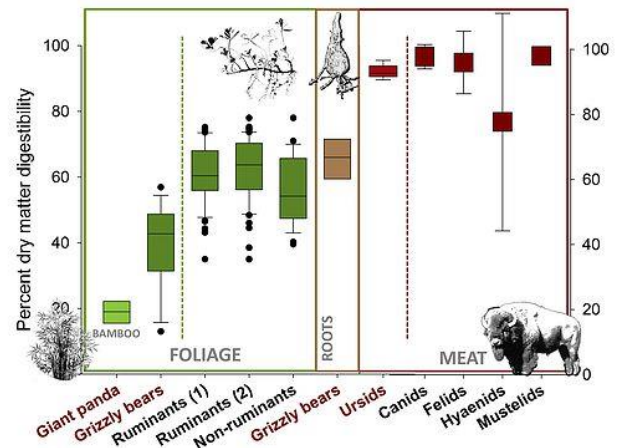


Figure 1. Percent dry matter digestibility of different types of foods by mammals of different higher-order taxa.

But the other key element of a digestive strategy is not just how well an animal can digest a given gram of ingested food, but also how many grams are being ingested in total. In other words, an animal can compensate to some extent for low digestibility by increasing the throughput of ingested food, which seems to be the strategy adopted by bears, especially giant pandas.

Figure 2 illustrates this pattern. Again, broad categories of animals are differentiated with non-ruminant herbivores separated by whether most fermentation of fiber occurs is the cecum versus the colon. Bears (i.e., ursids) are differentiated by whether they are ingesting foliage and fruit versus wholly meat. The top graph shows the rate at which these different types of animals ingest food, standardized to metabolism-corrected body mass, whereas the bottom graph shows the mean time that digesta is retained in the digestive tract (i.e., gut; the inverse of the rapidity of transit).

All of this suggests that, when possible, bears ingest vegetal material at a higher rate and retain it for a far shorter period of time compared to specialized

herbivores, especially in contrast to foregut fermenters (i.e., ruminants). This would partly compensate for the lower efficiency with which bears digest most vegetal food. By contrast, bears ingest meat at a slow rate and retain it for roughly twice as long as they do their vegetal food. For the high digestibility of meat to be realized, bears probably need to retain it longer in the digestive tract, but still not as long as herbivores dependent on fermentation retain foliage or browse. Meat also probably passes through the gut more slowly simply because there is less accompanying fiber to hasten it along compared to when bears eat vegetation.

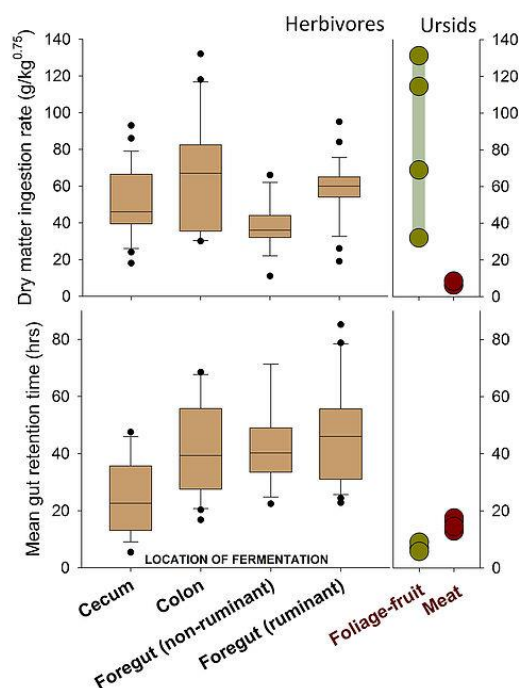


Figure 2. Ingestion rates and transit times for digesta by mammals with different digestive adaptations and by ursids eating meat versus vegetal foods.

The implications of these patterns for bears and bear foraging seem pretty obvious. Bears should prefer meat whenever they can get it, at least until sated, and up until a need to balance nutrient intake comes into play. Beyond that, roots (and berries) should be preferred vegetal foods, but only if the energy required for acquisition does not unfavorably alter the overall energetic equation—which, in the case of roots, is probably often the case because of the potentially considerable costs of excavation. Finally, bears should be able to profit from grazing only when they have access to large amounts of readily acquired and comparatively digestible foliage. And, as shown below, digestibilities of foliage can vary widely, not only among sites, but also among plant species and seasons.

Specific foods

In keeping with the broad patterns described above, the digestibilities of specific bear foods vary widely. Emblematic of this, Figure 3 shows the percent of energy contained in different foods that is digested by grizzly bears (the black, gray, and white dots). The varying shades of gray, from black to white, correspond to digestibilities during different seasons in instances where there is documented seasonal variability: black for spring, dark gray for estrus, light gray for early hyperphagia, and white for late hyperphagia. The reddish dots represent the percent of each food that is comprised of protein, again with seasonal variation denoted by varying shades: bright red for year-round or spring values; burgundy for mid-season; and white for late-season. All of these foods are specific to the Yellowstone ecosystem.

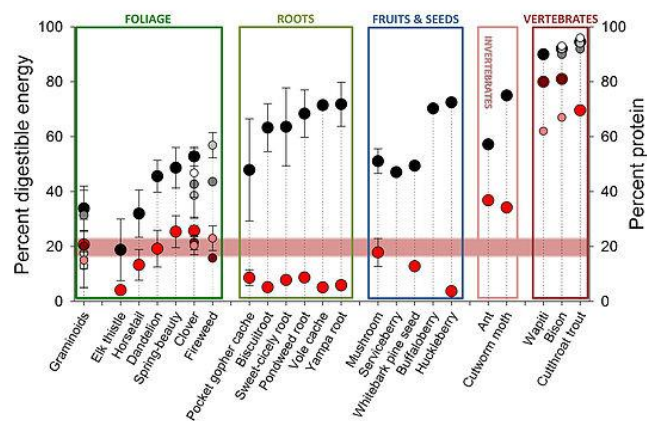


Figure 3. Percent digestible energy and percent protein for different grizzly bear foods common to the Yellowstone ecosystem.

Meat from any source is more digestible than other types of food. Roots, insects, and fruits and seeds are of comparable digestability, but with roots and fruits offering far less protein. Most of the digestible energy in these vegetal foods is contained in sugars and starches, with the proviso that much of the protein in ants, in particular, is bound up in chitin. Finally, the digestible energy in foliage varies widely, with forbs such as clover, fireweed, and dandelion offering the most, and elk thistle, horsetail, and grasses and sedges (i.e., graminoids) the least.

As a final note on Figure 3: The pinkish horizontal band corresponds to the optimal level of protein in bear diets; the point being that grizzlies would be hard-pressed to maintain an optimal level of protein intake if they subsisted solely on vegetal foods, especially roots, fruits, and seeds.

Protein & Energy Effects

Nutrition obviously entails more than just the digestibilities of different foods. The absolute and relative amounts of various macronutrients (e.g., proteins, lipids, and carbohydrates) are critical elements of nutrition, as are the absolute and relative amounts of digestible energy. Even though all of these additional nutrient-related aspects of nutrition are correlated with the digestion of various foods in the gut, there are additional consequences that play out through metabolic processes involved in the creation and use of body protein, fat, and glucose--i.e., protein biosynthesis and proteolysis, lipogenesis and lipolysis, and gluconeogenesis and glycolysis. Moreover, the density of digestible energy in foods matters for reasons that transcend simple nutrient composition. Resting metabolism varies widely in close synchrony with nutrient-specific processes and related energy expenditure--with consequences for levels of heat production in the body (i.e., thermogenesis).

The net result of all of this is not only variation in the efficiencies of energy, protein, lipid, and glucose metabolisms, but also variation in the composition, efficiency, and total level of body mass accretion or loss. Different combinations of relative and absolute amounts of protein, fat, carbohydrates, and digestible energy in the diet can determine whether an animal gains or loses body mass, and whether that mass gain or loss is comprised of lean body mass or fat reserves.

With respect to bears, then, this amounts to a lot of complexity when it comes to understanding the ramifications of different diets.

Efficiencies, protein, & growth

Given that a bear eats a diet containing ample digestible energy (say 800 kcal per kg raised to the 0.75 power per day), it turns out that there can be both too little and too much protein when it comes to efficiencies of gain in body mass. The graphs in figure 4 are relevant to this point, adapted from those in a paper on which Joy Erlenbach was lead author—a paper in which she synthesized a lot of research specific to bear nutrition. Each figure features a bunch of dots of two different colors corresponding to the metabolic and accretional consequences for bears fed diets comprised

of different macronutrients, including diets rich in protein or carbohydrates (salmon colored) as well as diets rich in protein or fat (burgundy).

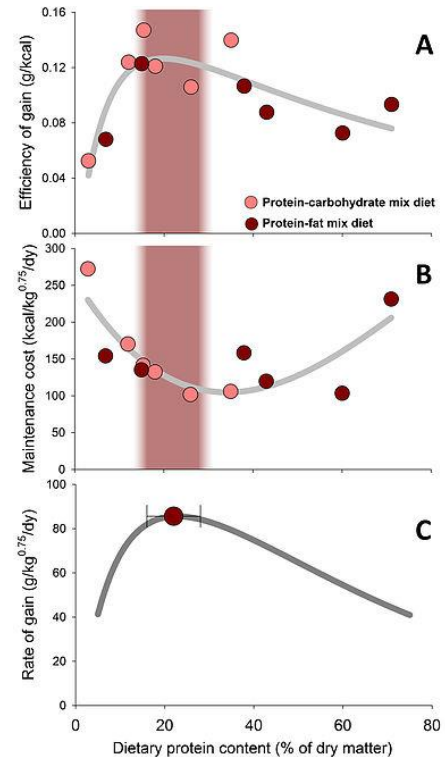


Figure 4. Effects of dietary protein content on (A) efficiency of mass gain, (B) energetic maintenance costs, and (C) rate of mass gain by grizzly bears fed diets of different protein content.

The main points? The top figure (A) shows that the efficiency of weight gain rises rapidly to a peak as diet protein increases from roughly 1% to 15% and then gradually declines, all of this with the density of diet energy remaining roughly the same. Correspondingly, the middle figure (B) illustrates a decline in resting metabolism (i.e., energetic costs of maintaining the body) as diet protein increases from 1% to roughly 30%, after which maintenance costs increase. When you put these two trends together you get the bottom figure (C) which shows the predicted total rate of gain per kg of body mass, standardized to the expected basal metabolic rate for carnivores (i.e., raised to the 0.75 power); a rapid rise as diet protein increases, followed by a steady decline.

It turns out that the predicted level of diet protein at which rates of gain in body mass peaks (roughly 21%) corresponds almost exactly with the mean diet protein content of diets selected by bears when given a free choice of what to eat (22% plus or minus 6%)--shown by the large burgundy dot and horizontal error bars in figure 4C.

From this a person could conclude that the optimal protein content of a bear's aggregate diet is around 22%, at least as far as growth of body mass is concerned--and without considering whether that growth is primarily in terms of lean body mass or fat; but with some important provisos. This rule of thumb for diet protein holds for a given energy concentration in the diet (in this case, around 800 kcal/kg 0.75/day) and for bears of intermediate body size. But bear size does affect nutrition in several ways, as does energy concentration of the diet (see below).

This all begs the question of why a diet protein content of around 20% yields greater growth rates than, say, 60%--all of this, of course, standardized to a given volumetric intake and to the metabolic rate expected at a given body mass. As a start, all else equal, elevated diet protein causes greater heat production in the body compared to elevated carbohydrates or fats. This thermic effect is called diet-induced thermogenesis (DIT). Much of this elevation in metabolic rate (as shown in figure 4B, above) is attributable to the thermic properties of protein synthesis, including increased heat production and reduced energetic efficiency. Depending on total diet composition, some of the increased heat production associated with a high-protein-content diet can be attributable to heightened formation of glucose (gluconeogenesis) above and beyond what would occur with a high-carb diet.

What about the effects of too little protein? Generally speaking, if a bear's diet is deficient in protein, it compensates by increasing the volume of intake, usually of foods rich in carbohydrates (think berries and roots; see Digestion). But the results above pertain to an isocaloric intake, that is, a constant or equal intake of calories. So the results explicitly pertain to differences in diet composition, not amount of energy intake. As figure 4B above shows, the metabolic rate of bears fed a low-protein diet increases substantially, which, because of the resulting increased energy expenditure, leads to decreased absolute and relative rates of gain in body mass. Why? Ultimately, because an increased proportionate consumption of fats or carbohydrates when bears are fed a diet low in protein leads to a chain of energy consumptive phenomena. The sympathetic nervous system is stimulated, which increases production

of the hormone norepinephrine, which stimulates brown adipose tissue metabolism, which results in an elevated metabolic rate; in the end, more energy expenditure and less weight gain.

Intake, protein, and growth

At this point it is worth looking at what happens (unlike above) when the amount of dry matter ingested and digested by bears varies, adding to this variation in diet protein content. And, of course, the complement to variation in diet protein is complementary variation in diet fat or carbohydrates.

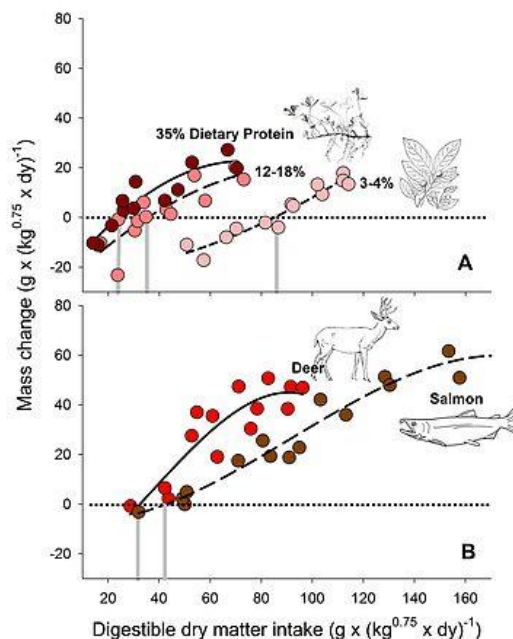


Figure 5. Change in mass of bears feed diets of different protein content as a function of total digestible dry matter intake.

The graphs in figure 5 summarize the results of several studies done in Charlie Robbins' lab, unified by a design that allowed bears to eat different amounts of digestible dry matter (the horizontal or x axis) while measuring responses in terms of change in body mass--i.e., growth (the vertical or y axis). All of this is standardized to the metabolism-corrected mass of the involved bear and considers diets with different amounts of protein, ranging from berries (3-4%) to deer and salmon (nearer 70% or more). In addition to the data points and curves describing the response in mass gain to variation in dry matter intake I've also benchmarked where each curve transitions from mass loss to mass gain (the vertical gray line).

The basic patterns are pretty obvious. In all instances weight gain tends to plateau (i.e., tends towards an asymptote) as intake increases. At some point, increased intake does not yield increased mass gain; the bears reach the limits imposed by internal metabolic processes. But this plateau is considerably higher (45-60 g per kg raised to 0.75 per day) for meat diets (B) compared to vegetal diets (nearer 20 g; A). Even so, the transition from weight loss to weight gain is similar (around 20-40 standardized ingested grams) for meat diets and vegetal diets having at least 12-18% protein content, the latter of which is within the lower range of optimal (see above). The biggest deviant is the low-protein-content diet comprised of berries. Weight gain only occurs when the standardized volumetric intake is high--in excess of 80 g, which is roughly 2-4 times higher than for other diets.

The implications? Even given the standardized metabolic inefficiencies associated with a protein-rich diet shown in figure 4, bears can grow much more rapidly on such a diet, especially if they have access to large volumes. The most notable example of this circumstance would be along salmon spawning streams during the height of spawning runs, which is why we see very large coastal brown bears. By contrast, bears with access primarily to berries have to eat relatively large volumes to gain mass and, even so, the potential for growth is relatively limited. This holds for bears in the interior regions of British Columbia, northeast Washington, northern Idaho, and northwest Montana. One important proviso to all of this is that there is no distinction made regarding the tissues in which weight gain occurs, principally whether in fat or lean body mass, which introduces the next topic.

Intake, protein, energy, & composition of growth

So a key question is whether the location of accreted (or lost) of body mass is as fat or lean tissue. Of relevance to this question, the graphs in figure 6 show differences in allocation of gain (or loss) for diets of two different protein contents: a berry diet comprised of 1.6-3.5% protein in A, and a mixed diet comprised of 15.4% protein in B. The red dots and associated trend line show changes in lean body mass (LBM) for each diet; the orange dots and associated trend line, changes in body fat.

All of the gain in body mass at a very low diet protein is as fat (A), whereas the majority of gain at moderate diet protein is in lean body mass (B). Moreover, bears eating a very-low-protein diet consistently lose lean body mass, which is an untenable situation. An important note: These patterns are as much a reflection of the fact that a

vegetal diet low in protein (as in A) is necessarily rich in carbohydrates, whether glucose, sucrose, or starch (see [Digestion](#)). So the patterns in these figures reflect not only protein metabolism but also metabolic processes associated with varying concentrations of digestible carbohydrates, especially related to lipogenesis and protein biosynthesis.

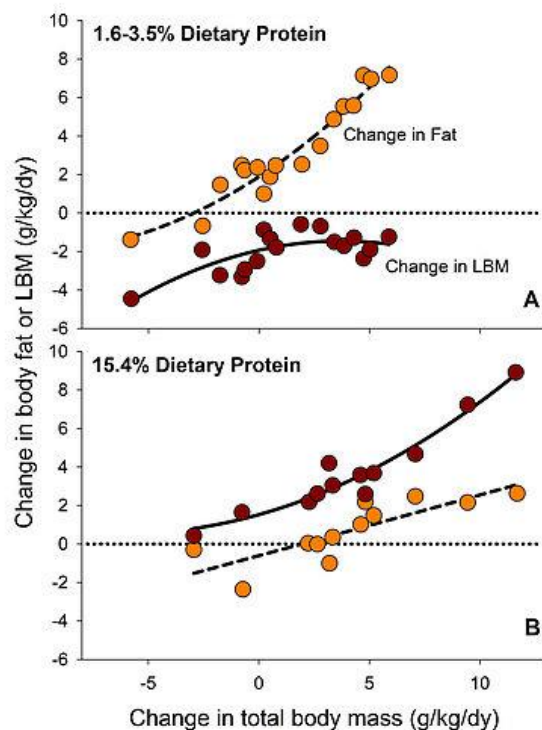


Figure 6. Change in lean body mass and body fat of bears fed diets of different protein content.

The implication? If a bear, eat a diet rich in carbohydrates and get fat while potentially losing lean body mass. Admix some amount of protein in the diet and you will maintain if not gain lean body mass. So a carbohydrate-rich diet with enough protein to maintain LBM makes more sense for a female needing to put on fat to reproduce; protein more sense for a male needing to grow physically large, which fits [patterns of dimorphism](#) among bears.

So now bring *diet energy*, as such, into the picture, and slightly recast the dynamics of total intake per day, at least for protein. Figure 7 shows the relation between standardized accretion of body fat and standardized ingestion of energy--regardless of the contributing macronutrient. And this for various diets comprised of very low (1.6-3.5%, the pink dots) and closer to optimum (15.4%, the red dots) concentrations of protein. In short, as intake of energy increases, so does accumulation of body fat. But more importantly, bears tend to gain more

body fat (as above) on diets low in protein content, which is tantamount to saying on diets rich in either carbohydrates or fats. In fact, high-fat diets contain the highest concentrations of digestible energy, which translates into high rates of body fat gain.

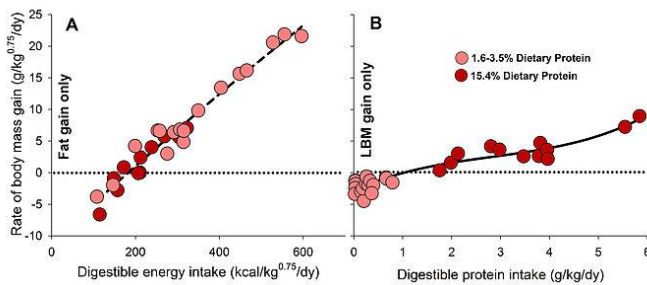


Figure 7. Rate of body mass gain standardized to metabolic rate as a function of total digestible energy and digestible protein intake for diets of two different protein compositions.

Figure 7B complements figure 7A by showing rates of lean body mass gain related to the total intake of digestible protein--with both values standardized. Not surprisingly, the more protein that a bear ingests and digests, the more lean body mass it accretes, with highest rates of both associated with diets containing a higher concentration of protein. And, as in the figure 6, protein intake on diets very low in protein content (1.6-3.5%, e.g., berries) does not allow even for maintenance of LBM. By contrast, the rate of LBM gain is remarkably high (8-9 grams per kg of body mass raised to the 0.75 power) at the highest rates of protein intake (around 6 grams per kg of body mass); in other words, in excess of a 1:1 translation.

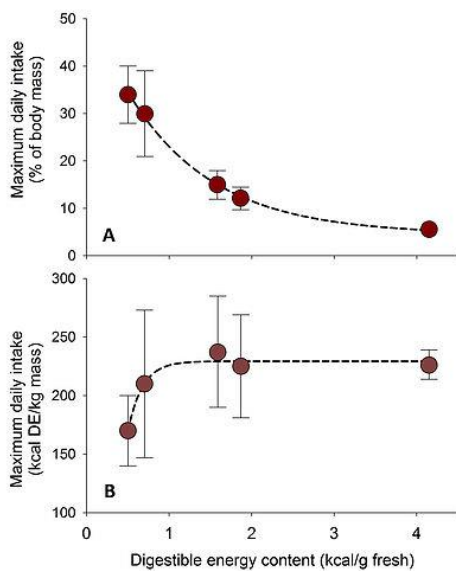


Figure 8. Maximum daily intake of digestible energy as a function of dietary digestible energy concentration.

Figure 8 illustrates an interesting phenomenon. Even when bears eat a diet increasingly rich in calories, overall intake of energy, standardized to body mass, doesn't correspondingly increase, especially once a threshold of 1 kcal of digestible energy per gram of fresh food is reached. This is most clearly illustrated in figure 8B; figure 8A shows the same trend standardized to body mass as percent of total mass.

Just to be clear, larger bears can and do ingest more absolute amounts of digestible energy during a given day, even as the digestible energy in the food they eat increases from 1 to 2 and even 4 kcal per gram. The point is that the energy *per kg of mass* doesn't increase and, as a percentage of total mass, even decreases, which pertains to efficiencies as much as anything.

To put this another way, a diet richer per gram in digestible energy--as would be the case with a diet rich in fat or protein--doesn't necessarily translate into a lot more digested energy for any kg of mass that a bear might be carting around. Related back to [digestion](#), this pattern fits the much lower rates of transit and accompanying higher rates of digestion for ingested food for bears fed a diet of meat.

I conclude this section on the effects of nutrients, per se, with a few points that are either not adequately encompassed by the data presented above or that simply need additional clarification, and then end by quoting an elegant synopsis of nutritional fundamentals for bears that was included by Joy Erlenbach in her 2014 paper.

First, diets comprised solely of fruit are a potential problem for bears, especially if the involved bear is large in size. The low protein content and high glucose or fructose content of fruit diets require bears to eat exceptionally large volumes just to maintain LBM, but with resulting high rates of energy intake. This energy either needs to be dissipated as heat (diet-induced thermogenesis) or converted to body fat through lipogenesis, which is notably elevated on diets rich in fructose--one of the main sugars in blue- and blackberries. Large bears are notably much less efficient than small bears at harvesting any given concentration of fruit, which means that mass standardized consumption of fruit is maximized for large bears at rates far less than what they need to meet protein and even energy requirements. Hence, fruit-eating is more often a strategy of smaller bears or bear species (e.g., juveniles, females, and black bears) than it is of those that are larger (e.g., adult males and grizzly bears; for more on

the implications of size see Foraging efficiency and Body mass effects below).

Second, bears prefer fat-rich foods and diets. In instances where captive bears had free access to diets of different composition they ended up eating diets from which they obtained roughly 68% of metabolisable energy from fats. Fats provide the highest concentrations of digestible energy of all macronutrients and are, in turn, the most efficiently converted of any to body fat. And ample body fat, to the point of obesity, is a center-piece of the bear life strategy. Moreover, unlike diets rich in protein or carbohydrates, diets rich in fat do not trigger auto-regulatory reductions in intake, which also contributes to high rates of body fat accumulation on high-fat diets. Or, put another way, diets comprised mostly of protein or carbohydrates are not optimal for most bears.

Third, related to the points immediately above, bears are energy maximizers. In fact, as noted by Joy Erlenbach,

bears exhibit some of the highest levels of standardized energy intake observed for any mammal. When offered unlimited access to food these rates can be twice what some early researchers such as James Kirkwood considered to be the maximum rate likely or possible, and up to 18 times greater than the expected basal metabolic rate for carnivores, which is a lot of energy.

In conclusion, quoting Joy Erlenbach, bears live by three "rules" when it comes to intake of energy and nutrients:

- (1) Maximize energy intake while optimizing dietary protein intake.
- (2) Select lipids over digestible carbohydrates, which reduces dietary protein while maximizing food energy density.
- (3) If lipids are not available, use digestible carbohydrates to optimize diet protein.

Body Mass Effects

The relationship shown in figure 9 is an interesting and compelling introduction to the effects of body mass on foraging efficiencies and weight gain of bears. Each dot represents the results of a controlled experiment involving one bear allowed free access to different kinds of foods. All of these data, again, are thanks to research by Dr. Charles Robbins and his graduate students at Washington State University.

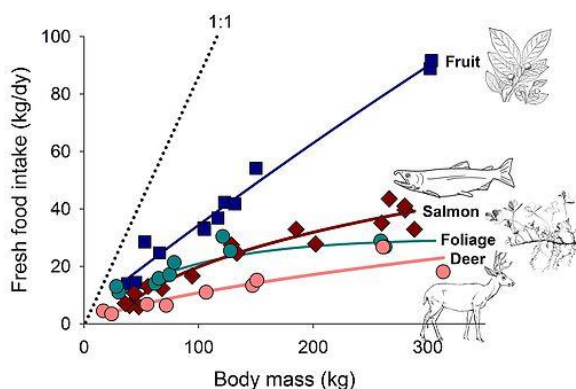


Figure 9. Total ad libitum fresh food intake as a function of mass of the involved bear.

At one level, figure 9 shows something that might be considered self-evident: larger bears tend to ingest greater volumes when given unlimited access to food. But, then, they would need to given their greater

energetic needs, even accounting for the lower rate at which metabolic needs increase relative to each increment of body mass (at roughly the 0.75 power). Energy consumption, even at rest, increases nonetheless.

But the interesting thing is that the rate at which intake increases varies substantially among foods, but especially for berries in contrast to everything else. You might expect intake of protein-rich foods such as deer or salmon to increase at a lesser rate as body mass increases. Each gram of such a food delivers a substantial amount of digested energy entailing a comparatively slow rate of passage through the gut, with gut length and passage rate scaling at less than a 1:1 rate with body size (see [Digestion](#)). And intake of deer is probably less than intake of salmon at any given body mass because of the comparatively greater effort required to process a gram of tissue from a deer compared to a more easily ingested and chewed gram of fish.

It would be reasonable to expect that intake of foliage would increase at roughly the same rate as intake of berries given that both of these are vegetal foods. So, why is the intake of foliage so depressed compared to berries for large bears? For the answer, see the section below on [Foraging Efficiencies](#). But, in short, when bears graze, ingestion is partly limited by the time it takes to chew a mouthful of fibrous foliage, which means that bite rate drops as a function of bite size; which means

that bears need large standing volumes of tall-statured foliage to increase total ingested volumes in defiance of the limits imposed by chewing time--which rarely happens.

Insofar as berries are concerned, figure 9 only pertains to bears offered unlimited access to food. Which begs the question of why such large volumes are ingested as body mass increases? Unlike with foliage, processing time for berries, once ingested, is not of great consequence. Moreover, bears are highly motivated to ingest large volumes of protein-deficient berries (see Digestion) in an effort to meet their protein requirements, but with a resulting glut of digested energy which is either expended as heat or stored as body fat (see the section above on Protein and Energy Effects).

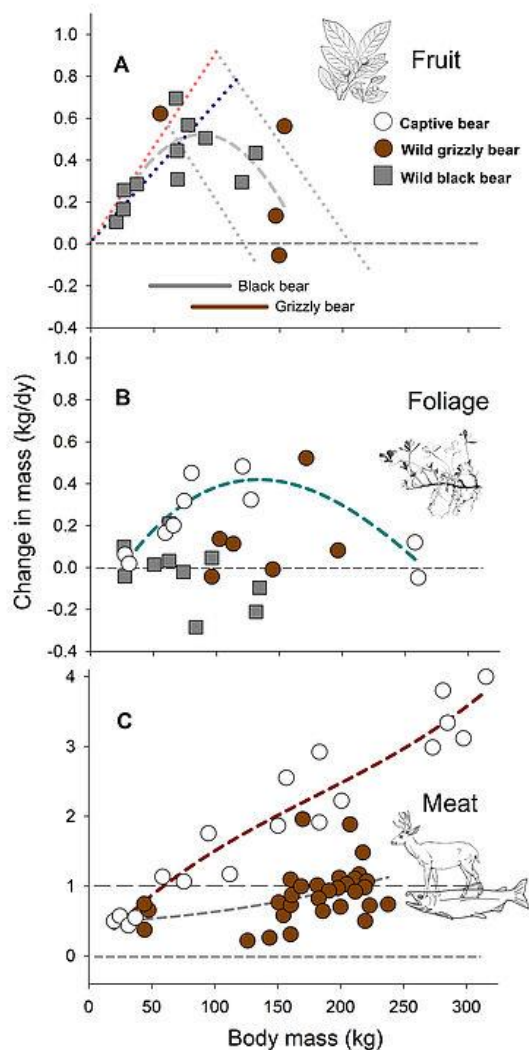


Figure 10. Daily change in body mass as a function of beginning body mass of the involved bear for (A) fruit, (B) foliage, and (C) meat, differentiating salmon (open dots) from deer (solid brown dots).

But where things get really interesting is when you look at per day rates of gain in body mass as a function of bear size--especially under circumstances where the involved bears did or did not have access to unlimited amounts of different kinds of food.

The graphs in figure 10 summarize this relationship for a number of individual bears that ate fruit (A), grazed foliage (B), and consumed meat from either deer or salmon (C). The open circles denote the results for captive bears; the brown dots, results for grizzly bears in the wild; and the gray squares, for black bears in the wild. Importantly, the captive bears had access to unlimited amounts of the various foods, whereas the wild bears typically did not.

Going over these graphs in reverse order, from bottom to top starting with meat: notice that, unlike with foliage and fruit, the trend lines for captive (dotted) and wild (solid) bears increase without reaching a plateau or peak, which means that bears are able to grow increasingly large even as their body mass increases. When fed unlimited amounts of meat, these gains can be phenomenal--upwards of 4 kg per day for a 300 kg bear. Moreover, no bear lost body mass eating a diet comprised mostly of meat. And, it is worth emphasizing that these gains were mostly as lean body mass, and despite the depressed per kg energetic efficiencies of a high protein diet (see Protein and energy effects).

With foliage, it is perhaps not surprising that a number of wild bears seemed to lose body mass when subsisting almost wholly on such a food. Foliage is not very nutritious or digestible (see Digestion). No wild bear but one gained much weight. But, the important trend is the one documented for captive bears with access to unlimited amounts of foliage (the dashed line). These captives were able to gain weight up until around 125 kg of body mass, after which gains declined, even into negative territory around 250 kg. In other words, the modest increases in ingested volumes of foliage that occurred at large body masses (see above) could not offset the increased energetic needs of a large bear, even given a less than 1:1 scaling of unit volume metabolic rate with body mass.

Something very similar was evident for wild bears subsisting on berries. Gains increased, peaking for bears of around 100 kg mass, and thereafter declined, even into negative territory for one c. 150 kg grizzly. To explain this pattern requires additional explanation of figure 10A. The ascending dotted red and blue lines denote the theoretical maximum rates of gain for bears eating unlimited quantities of serviceberries and huckleberries;

that is, for captive bears. But this theoretical maximum is obviously not achieved, primarily because of the limits imposed by foraging inefficiencies under field conditions; for example bite sizes and bite rates. These limits are described by the descending gray lines--the farthest left associated with a bite size of 1.7 berries and a bite rate of 55 per minute, the farthest right with a bite size of 2.5 berries and a rate of 90 per minute. The point being that foraging efficiencies take a major toll on what bears can realize from eating berries, with major implications for even modest-sized bears. Notably, though, at peak, daily gains for wild bears eating berries were over three times greater than gains for wild bears eating foliage: roughly 0.5 versus 0.15 kg per day.

There are some important implications of all this: Most important, if you are a bear weighing much in excess of 100 kg, weight gains are going to be greatest on a meat diet, not a berry or foliage diet. And much of these gains will be in lean body mass (see [Protein and energy effects](#)). So, given the consistently greater size of adult males compared to other bears--typically in excess of 150

kg--you would expect adult males to eat disproportionate amounts of meat, which is indeed the case. And, adopting such a strategy, you would expect males to grow ever larger over time, which seems to be the case as well. But all of this is with an important proviso: If you are female weighing somewhere between 100-150 kg, rates of body fat accumulation will probably be greatest on an energy-rich but protein-poor berry diet, as long as you can eat large volumes, closer to 2.5 berries per bite, at 90 bites per minute.

One important additional proviso: None of the graphs above deal with foods rich in fat, but containing adequate protein. More concretely, we don't have a clear picture of the nutritional benefits entailed for bears eating army cutworm moths and whitebark pine seeds: two of the most important bear foods in the Yellowstone ecosystem. Even so, it is not too hard to imagine that these foods are among the best bear foods of all.

Diet Meat Effects

Meat is handy shorthand for denoting a food comprised mostly of protein and fat. As I describe in the section devoted to [digestion](#), protein and fat are the most digestible of all nutrients and, because of that, the essential ingredients of an energy-rich diet. Put a slightly different way, meat is the most concentrated form of protein and fat commonly eaten by bears. Given that we can only rarely directly measure the nutrient composition of bear diets, it is useful at times to use the fraction of meat (or berries, for that matter, to denote little protein) as a proxy and, from that, get a general sense of how a protein- and energy-dense diet affects outcomes such as body size and female reproduction, which is what I address below.

It is worth noting that not all meat is equal. Fractions of water, protein, and fat vary with the season and from prey animal to prey animal. Emblematic of this variability, I've created a summary in figure 11 of variation in the mass of edibles, including body fat and metabolisable energy, for a representative source of meat: female mule deer.

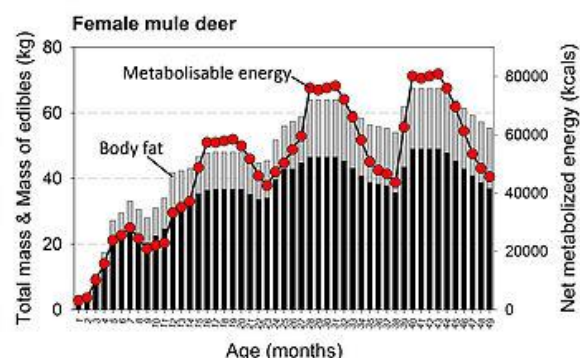


Figure 11. Total mass, amount of fat, and total metabolisable energy of female deer carcasses as a function of deer age.

The amount of edibles increases (obviously) with animal age, up to around age 4 in the case of mule deer; the fraction of body fat varies with the season; and, with all of this, the amount of metabolisable energy available to a carnivore such as bears varies substantially seasonally and with age of the prey animal.

The graphs in figures 12 and 13 show data that I assembled from North American study areas reporting both the body mass of grizzly bears captured for research purposes as well as information sufficient to determine the percent of the bear diet that was

comprised of meat. On the meat front, Garth Mowat was the primary source, based on either direct measures or estimates derived from interpolation of one form or another. I differentiate adult males from adult females, and areas where bears had access to abundant spawning salmon from those where the primary source of meat was land-dwelling herbivores. I also denote the Yellowstone area with a white-centered dot.

Figure 12 shows trends towards larger size among populations of grizzlies that consume more meat, but more so for males than for females. The trend among females that eat terrestrial meat is barely discernable, and that of salmon-eating bears is substantially greater than the trend among populations of grizzlies that eat terrestrial herbivores.

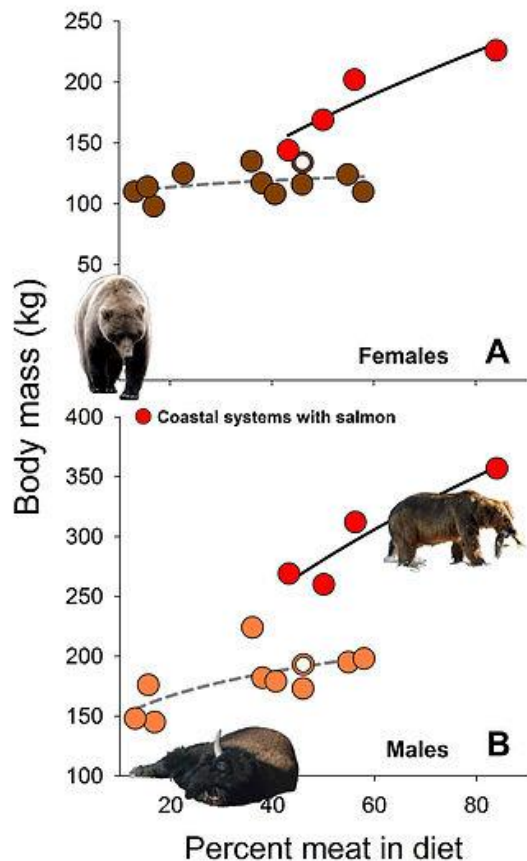


Figure 12. Population-averaged body mass of female (A) and male (B) grizzly bears as a function of population-averaged meat in the diet.

Figure 13 shows an increase in the ratio of male body mass to female body mass as the percentage of meat in the collective bear diet increases. In other words, size dimorphism of the sexes is greater where bears eat more meat, especially terrestrial meat (the burgundy dots). This is just a different way of representing the lesser

response of females versus males to increasing amounts of dietary meat, noting, again, that the trend is greater among interior versus coastal salmon-eating populations. The dampened trend for all populations, including coastal ones, is shown by the solid line whereas the trend for interior populations alone is shown by the dashed line.

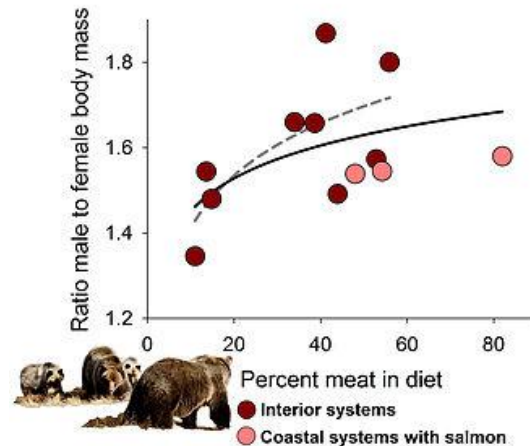


Figure 13. Ratio of population-averaged male and female body mass as a function of population-averaged meat in the diet.

The different responses of males versus females and of coastal versus interior populations to increased dietary meat beg for explanation. I can only speculate, but I suspect that differences between the sexes have to do with differences in diet within any given population, as well as differences in sex-linked physiological responses to dietary protein--all driven, in turn, by differences in the reproductive strategies of male versus female grizzlies.

More specifically, although responses of the two sexes to dietary protein have not been explicitly studied (or at least reported) for bears, we do know a fair amount about this phenomenon in two other omnivores: swine and humans. In both *Sus scrofa* and *Homo sapiens*, males and females fed the same amount of protein differ in the efficiency with which they accumulate lean body mass. Not surprisingly, males are more efficient than females. So if such were true for bears as well, this phenomenon could plausibly contribute to the greater population-level response of male versus female grizzly bears to elevated dietary meat.

Moreover, study after study has shown that, on average, male grizzlies eat more meat compared to female grizzlies in any given population. This could partly be a result of motivation and resulting dietary preferences. It could also partly be the consequence of on-average larger males being better able to dominate a

concentrated food source, as is typical of packages of meat. So, differences in diet between males and females could also explain some differences in population-averaged body size between the sexes.

But what about the differences between coastal and interior ecosystems; between areas with spawning salmon compared to areas without? As I describe in the section devoted to the effects of diet protein, bears fed as much salmon as they can eat can grow to a much larger size (albeit at a slower rate) compared to bears fed deer. As the research in that section also shows, a diet exceedingly rich in protein (as would be the case with

salmon) actually leads to less efficient accretion of body mass. But this lesser efficiency (as perhaps manifest in the lesser rate of gain among salmon-fed bears) can be more than offset by access to large volumes of food, as would certainly be the case--and for sustained periods of time--in most of the Pacific coastal areas with multiple runs of spawning salmon. So, the point here is that the greater response of population-averaged body mass to increasing dietary meat among grizzlies with access to salmon may simply be a consequence of these bears having access to a veritable glut of energy-rich food perhaps more than it has anything to do with protein content of salmon, as such.

Foraging Efficiency

The rate at which a bear of a given size can ingest, masticate, and swallow food is a critical aspect of nutrition. It sets the stage for how much can be passed through the gut, which is particularly important when it comes to vegetal foods. Bears depend upon passing large volumes of foliage through their digestive tract if they are to stay ahead energetically when eating such a fibrous food (see [Digestion](#)). And, when it comes to berries and roots, they likewise need to ingest large volumes to compensate for the very low protein content of these foods--but with the derivative benefit of ingesting relatively high concentrations of digestible energy (see [Protein & energy effects](#)).

Given this imperative to ingest large volumes when bears eat vegetal foods, it is with such foods that the consequences of fine-scale variation in foraging efficiency are starkest--at the scale of bite size and bite rate, which is why researchers such as Charlie Robbins and Lisa Shipley have focused on berries and foliage in their investigations of foraging efficiency by bears. And it is their research that I feature here, most of which was executed under Dr. Robbin's tutelage by Christy Welch and Karen Rode.

Effects of forage density & stature

Figure 14 shows the effects of berry density on the size and rate of bites by bears. Bite rate and size are perhaps self-evidently the two immediate determinants of the total rate at which food is ingested, at least as far as the mouth cavity. After that, the rate and efficiency of mastication take over; e.g., chewing.

The two graphs in figure 14 feature two berry-producing species that are of widespread importance to bears: serviceberry (*Amelanchier alnifolia*; salmon-colored dots)

and huckleberry (*Vaccinium membranaceum*; blue dots). There are substantial differences between these two species in how berries are presented to a potential forager. Serviceberries grow in attenuated terminal bunches which allow large-mouthed foragers such as bears to harvest multiple berries in a single bite. By contrast, huckleberries tend to grow singly and dispersed, which means that bears need to employ a strategy of taking numerous small bites that are often contaminated with the accompanying detritus of leaves.

These morphologic differences are clearly evident in the relations of bite rate (A) and bite size (B) to variations in berry density for each species, where each dot represents one feeding trial involving a single bear. Put succinctly, bite size, but not bite rate, increases substantially as densities of serviceberries increase. The opposite is true for huckleberry. Bite rate, but not bite size, increases with density. More to the point, different strategies are imposed on bears by physical configurations of the berries they eat. As a result, morphologic features are as important as digestible energy in determining the overall energetic benefits of exploiting different patches of berries.

The same is true for grazed foliage. Figure 15 shows how bite sizes of clover vary with both the size of the involved bear and, more to the point here, with stature of the grazed plant--this under circumstances where the clover is uniformly dense. Basically, the relatively small sizes of bites taken by small bears are essentially unaffected by the stature of the grazed plant. By contrast, even though large bears are constrained to bites no larger than those of small bears when grazing plants <9-13 cm (3.5-5") tall, they reap huge comparative benefits (at least in terms of bite size) if they can find patches of herbaceous plants that average >15 cm (6") tall.

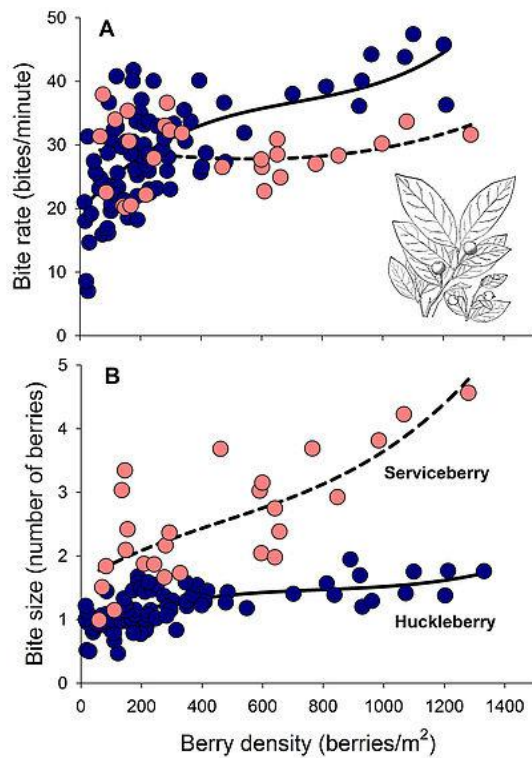


Figure 14. Bite rate and size of serviceberry and huckleberry by bears as a function of berry density.

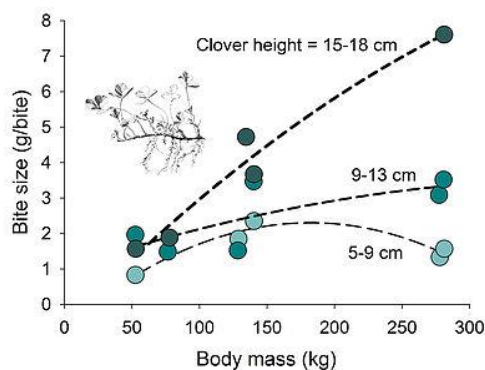


Figure 15. Size of bites of clover as a function of clover height and mass of the involved bear.

In short, the small dentition and jaws of small bears mean that they don't benefit from increases in the stature of grazed foliage, whereas the larger dentition and jaw of large bears allow them to exploit and benefit from greater vertical expression of biomass; which amounts to a constraint imposed by foliage stature on large but not small bears. This, in turn, exacerbates the intrinsic energetic problems for large bears when they try to subsist on a diet of stems and leaves. Which is to

say, they typically can't, whereas small bears more commonly can (see [Body mass effects](#)).

Bite rate vs Bite size

The relationship between bite size and bite rate further elucidates the basic mechanics of bear grazing and, along with this, some fundamental constraints imposed on bears trying to subsist on foliage. Figure 16 shows this relationship; again, each dot represents a single trial involving a single bear.

The inverse relationship is not surprising. A larger bite requires more processing time, which intrinsically constrains bite speed (i.e., bite rate). But the important feature here is the rapid diminishment in bite rates with increases in bite size.

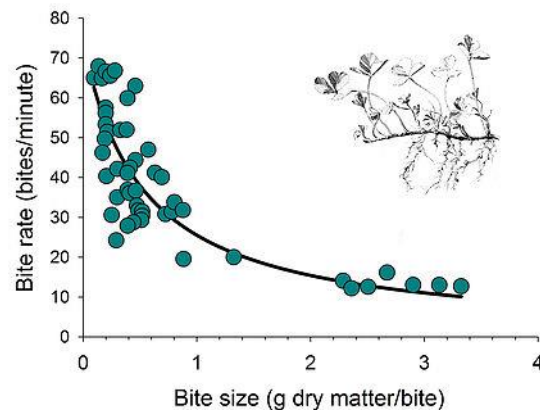


Figure 16. Bite rate as a function of bite size of clover for bears of a given size and clover of a given stature.

The implications? If a bear, it probably makes more sense to seek out patches of foliage to graze that allow for small rapid bites. And, if you are large, you are probably not going to benefit much in the end from being able to take larger bites of taller-statured foliage (as above), which partly explains why, in places such as Yellowstone, smaller bears seek out and heavily graze very dense short-statured patches of clover and bluegrass--commonly referred to as "grazing lawns."

Total rate of intake

Regardless of proximal biomechanics, the bottom line for bears is the total rate at which they can ingest foliage, berries, or any other vegetal food. Again, total rate of intake is especially critical for bears when it comes to vegetal foods (see above), in contrast to when they eat foods such as meat.

The graphs in figure 17 show total rate of intake (grams of dry matter per minute) as a function of key constraining factors. In the case of both serviceberry and huckleberry (B) intake (not surprisingly) increases with the density of each type of berry in a given patch. But the response for serviceberry is dramatically greater than the response for huckleberry because serviceberries (as I describe above) grow in terminal clumps that make it much easier for bears to harvest when compared to the more dispersed single berries of a huckleberry bush. That being said, huckleberry is considerably more digestible than serviceberry (see [Digestion](#)), which probably negates the benefits of the latter species rooted solely in ingestible volumes.

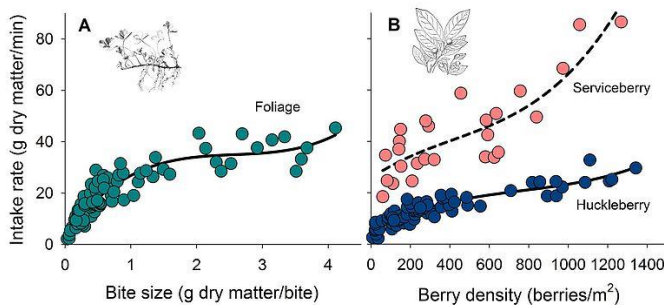


Figure 17. Intake rate of (A) clover and of (B) serviceberry and huckleberry as a function of bite size and berry density, respectively.

Figure 17A shows intake rate as a function of bite size for clover, one of the choicest of grazed bear foods. Why bite size rather than forage density? Simply because the research that produced these data essentially held density constant by insuring that bears had access to thick patches of foliage within which researchers varied composition and stature. Perhaps the point of this is that anything less would presumably be a non-starter for a food as fibrous and relatively indigestible as foliage (see [Digestion](#)). But the key point of graph A is that ingested volumes increase with bite size at first, but then rapidly reach a plateau (i.e., asymptote). This pattern is consistent with the depressive effect of bite size on bite rate (see above), ultimately rooted in the limits imposed by a need to chew foliage and then, after that, rate of passage through the gut.

Attachment 3. Primer on Taxonomy & Biogeography of *Ursus arctos* to accompany

David J. Mattson, Ph.D., Wyoming Wildlife Advocates, Comments on the US Fish & Wildlife Service proposal to remove grizzly bears in the Yellowstone ecosystem from the list of endangered and threatened wildlife protected under the US Endangered Species Act (ESA); Federal Register 81(48): 13174-13227; And Related Materials

Evolutionary relations

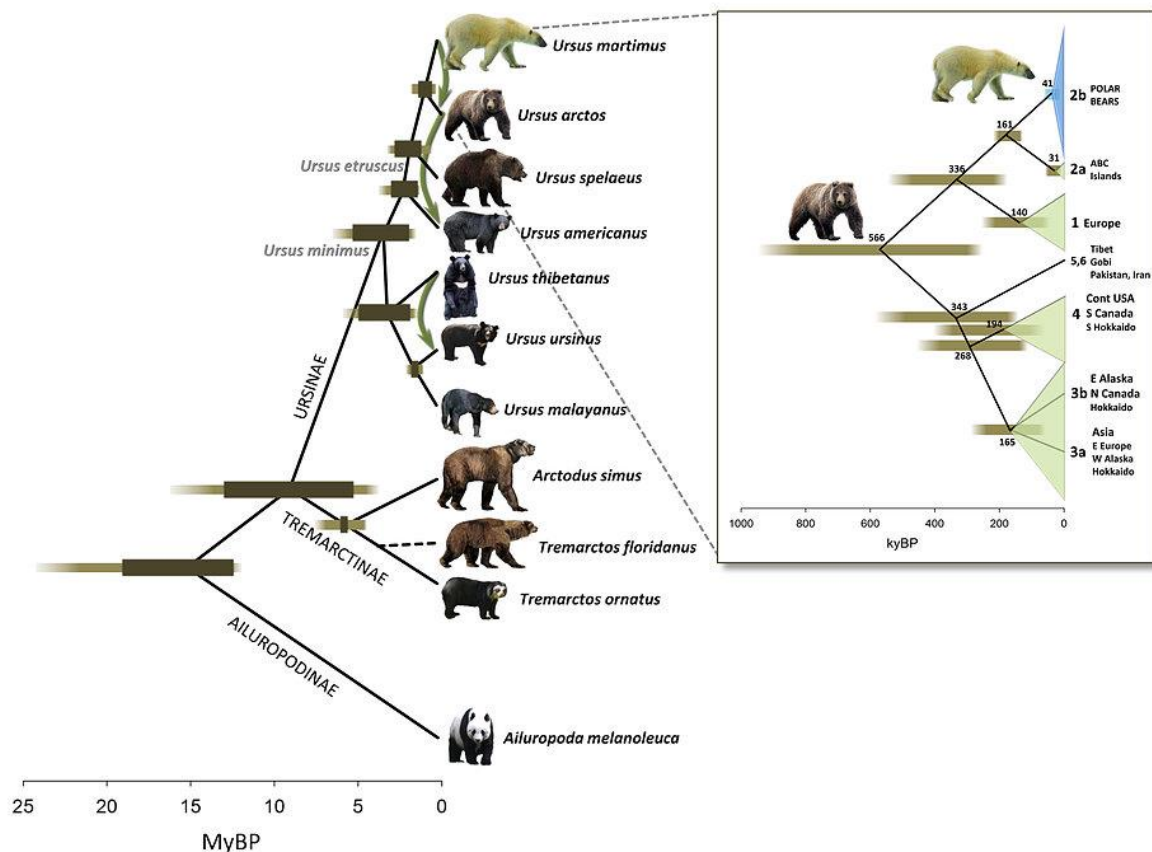


Figure 1. Consensus tree on the phylogeny of Ursidae, including an inset showing relations between *Ursus maritimus* and *U. arctos* as well as the diversification of *U. arctos* into various Clades. Gene flow subsequent to species separations is shown by the green arrows. Ranges of uncertainty in times of divergence are denoted by the length of the horizontal green bars at each node. Source are given below.

Figure 1 illustrates what taxonomists call a "consensus tree" describing relationships and timing of divergence among species within the family Ursidae, as well as (in the inset) relationships and divergence times for various subgroups of the species *Ursus arctos* (the brown and grizzly bears). The polar bear *Ursus maritimus* is included here for reasons that will be addressed shortly. This so-called consensus has been reached only within the last few

years, and may be revised in light of new research. But the main part of it will likely hold over time. An important feature to be noted, in addition to the main branching, is the green arrows. These arrows indicate on-going gene flow between "species," which has led to some of the confusion and disagreements over relations and dates of divergence among different species. Note the gene flow from polar bears to grizzly bears, and from

grizzly bears to black bears, which suggests inter-fertile breeding, albeit under presumably rare circumstances.

Surviving bear species of the family Ursidae are, for the most part, relatively recent in origin. The most ancient surviving derivative is the giant panda (*Ailuropoda melanoleuca*) which, although most closely related to bears, is so different as to have led taxonomists to put into a separate family, or even cluster it with raccoons. Another main split is between species of the subfamilies Tremarctinae and Ursinae. This split happened about 6-13 million years ago (mya), giving rise to bear species that evolved and survived mainly in North America (the Tremarctine bears), and those that evolved primarily in Eurasia (the Ursine bears). The only surviving bear of the Tremarctine lineage is the Spectacled bear (*Tremarctos ornatus*) of South America, although prior to the end of the last Ice Age a number of Tremarctine bears had existed and flourished. Perhaps the most spectacular of these bears was the Giant short-faced bear (*Arctodus simus*), which was a giant as much as 6 feet tall at the shoulder that survived until roughly 13,000 plus or minus 300 years ago (this in years corrected for bias in carbon dating).

But the main focus here is the species *Ursus arctos*, which encompasses the grizzly bears living in Yellowstone. Grizzlies and their kin the Polar bear and Eurasian cave bear (*U. spelaeus*) split from the lineage giving rise to the American black bear (*U. americanus*) roughly 3 mya. These species all shared a common ancestor called *U. minimus*, which gave rise as well to an intermediary form called *U. etruscus*. Barring the American black bear, these species are all best represented by fossils that have been found in Europe and western Asia.

More recently, the branch giving rise to the cave bears split from the brown bear lineage in Eurasia roughly 1-3 mya and, more recent yet, the polar bear lineage split from brown bears about 200-500 thousand years ago (kyBP). There is persisting disagreement among those who study phylogeny regarding when "the" polar bear split happened--some arguing as long as a million years ago, others as recent as 300 thousand years ago. The waters remain muddy because this so-called split has continued to be blurred by interbreeding among brown and polar bears. Whatever the conclusion, polar bears are closely related to brown bears.

But even before the divergence of polar bears, brown bears began to diversify into lineages, or clades, most of which have survived to the present. The major split between brown bears that live in Europe (Clade 1, along with an anomalous bunch on the ABC Islands of Alaska--Clade 2a) and brown bears that live elsewhere (Clades 3-6) occurred around 300-900 kyBP. The reasons for this complex of Clades has a lot to do with how various lineages of brown bears were split and more-or-less isolated during the course of the Ice Ages, which is covered immediately below under Evolutionary biogeography. Of particular relevance to Yellowstone's grizzlies: all of them belong to Clade 4, which appears to have been isolated in central North America when, according to Chris Stokes and collaborators, the Pleistocene ice sheets of North America coalesced across the northern span of the continent for the last time roughly 70 kyBP, albeit with what seems to have been a temporary opening around 55 kyBP. Clade 4 split from the various lineages of Clade 3 (currently concentrated in Asia and Alaska) around 200-350 kyBP. Clade 4 currently survives nowhere other than the in the center of North America and on the island of Hokkaido, which testifies to the Eurasian ancestry of all brown bears, including bears of this clade.

Information in this section is based on a host of sources, including for the carnivoran supertree, Bininda-Emonds et al. (1999) and Nyakatura & Bininda-Emonds (2012); phylogeny of Ursidae writ large, Waits et al. (1999), Lorie et al. (2004), Yu et al. (2004), Krause et al. (2008), Pages et al. (2008), and Kutschera et al. (2014); the unrelenting discourse on relations between polar bears and other bear species, Lindqvist et al. (2011), Cronin & MacNeil (2012), Hailer et al. (2012), Miller et al. (2012), Nakagome et al. (2013), Liu et al. (2014), and Cahill et al. (2015); and on divergence and nature of brown bear clades, Waits et al. (1998), Leonard et al. (2000), Shields et al. (2000), Matsushita et al. (2001), Miller et al. (2006), Hirata et al. (2013, 2014), and Solomashkina et al. (2014).

Evolutionary biogeography

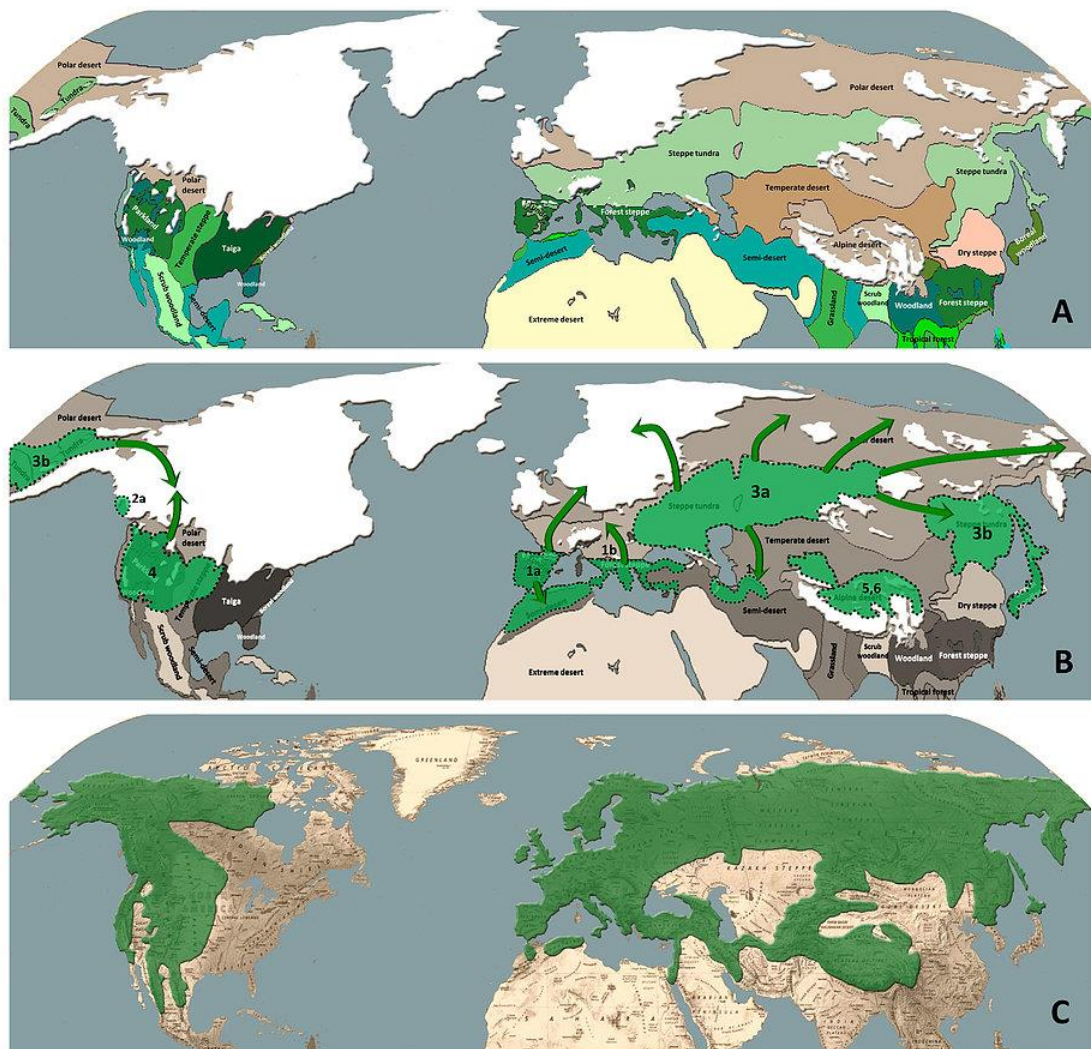


Figure 2. A somewhat speculative reconstruction of the Pleistocene biogeography of *Ursus arctos*, with (A) a reconstruction of Northern Hemispheric vegetation during the Last Glacial Maximum (LGM); (B) the LGM distribution of *Ursus arctos*, by Clade, including glacial refugia and subsequent recolonizations; and (C) the distribution of *U. arctos* circa 10,000 year bp.

The three maps in figure 2 attempt to summarize much of what's relevant to understanding the current population-level genetic diversity evident among today's brown and grizzly bears—all included within the single species *Ursus arctos*. Most of what's presented in these maps is a result of the synthesis published by Davison and his colleagues in 2011. Parenthetically, the notion of "subspecies" has

passed out of favor in application to brown bears, and been replaced instead with the concept of "clades," each of which represents enough genetic differentiation to warrant speculations about reasons for the divergence. This recent convergence by taxonomists on the notion of clades is in stark contrast to a 1918 publication of C.H. Merriam in which he described over 70 "species" of grizzly bears

in North America alone. The shift has been a result of both increased reliance on information from the genome along with increased appreciation for how plastic brown bear morphology can be (morphology of the skull was the main basis for Merriam's distinctions).

One key to understanding the current genetic diversity of brown bears resides in understanding the distribution of this species during the last Ice Age, which was, in turn, a reflection of vegetation and climate--especially the distribution of ice sheets and exceptionally harsh polar climates. Geneticists speculate that the main explanation for current differences in genomes of bears living in different parts of Eurasia and North America has to do with where their ancestors found refuge--often in isolation--during the different Ice Ages of the Pleistocene, and how they moved and mixed during warmer intervals, especially the current warm period that led to terminal melt of ice sheets between 18,000 and 6,000 years ago.

With that in mind, the map in Panel A, above, shows a plausible reconstruction of ice sheets and vegetation during the height of the last glaciation, roughly 25,000-15,000 years ago. You can see that much of the main range of brown bears in Eurasia was covered by polar desert and what many have called steppe tundra--a kind of tundra with substantially more grass than is common in boggy shrub-dominated tundras of today. This abundance of grass meant that a corresponding abundance of large herbivores could live there, including horses, mammoths, rhinos, giant bison, and more. Overall, though, the main range of Eurasian brown bears (the vast majority of the brown bears alive at the time) was quite dry and bitterly cold.

The map in Panel B shows a speculative reconstruction of the Ice Age distributions of the various modern-day clades, each denoted by its own number (see Evolutionary relations for more details). As you can see, Clade 1 was hunkered down in the southern part of Europe while Clade 3 was distributed throughout the steppe tundra of Asia. Clades 5 and 6, which persist as the genetically and morphologically distinct bears of the Tibetan Plateau and Gobi Desert, were thought to be more or less isolated in high-elevations of south-central Asia. Note that Clade 4 is the sole representative south of the North American ice sheet. More on where and when Clade 4 got there a little later. Also of interest,

the green arrows in Panel B show how each of the clades spread and colonized during the late Pleistocene and early Holocene (our current warm period). Clade 1 moved north to occupy most of Europe, but Clade 3 was the big winner, with bears of this lineage spreading into eastern Europe and surging once again into Alaska via Beringia. Clade 3 bears also moved south in North America to mingle with Clade 4 bears moving north in what is now Alberta.

The final map above, in Panel C, shows (in green) how the distribution of brown bears settled out after all of the surges and retreats that occurred with warming and ice melt--by roughly 1000-2000 years ago. Of note, brown bears occurred in the Atlas Mountains of Africa as well as in Mediterranean coastal mountains of the Middle East. They also spread south into Mexico in North America and ended up retreating to an eastern boundary on this continent that aligned with the Great Plains.



Figure 3. Somewhat speculative routes and timings of migrations by *Ursus arctos* Clades from Eurasia to North America during the late Pleistocene along with a reconstruction of ice sheets prior to the Last Glacial Maximum, including a potential ice-free corridor that could have allowed for early passage of Clade 4 bears south.

The map in Figure 3 provides a little more detail on when and how the various clades of grizzly bears represented in North America arrived. The earliest colonists were apparently of Clades 2 and 4, along with a sprig of Clade 3 called 3c. Clade 4 continued south, occupying west-central North America prior to closure of the last ice-free corridor, which some think might have happened as early as 70,000 years ago (kyBP), although with a brief opening perhaps around 55 kyBP. During this same period bears of Clade 2 (specifically, 2a) made it to the ABC (Admiralty, Baranof, Chichigof) Islands of Alaska. The early southward movement of brown bears into the region encompassing Yellowstone is evidenced by current distributions of the various clades, as well as by a single find of skeletal remains near Edmonton, Alberta, that dates to roughly 32 kyBP (corrected for bias in carbon dating).

Interestingly, of these early colonizing clades, 2a and 4 survived in their interior continental and island refuges whereas 2c and 3c eventually disappeared.

The final colonists, all across Beringia into and via Alaska, were of Clade 3. Clade 3b comprised an

earlier wave of colonization that occurred perhaps during and immediately after the last glacial maximum, whereas Clade 3a represents the most recent and last wave of migrants, arriving just prior to when the land bridge of Beringia disappeared. (Remember from the Map in Panel B above, Clade 3a bears had farther to go compared to Clade 3b bears before reaching Beringia.) Modern-day grizzly bears in eastern Alaska consist of descendants of the Clade 3b colonists, whereas those in western Alaska consist of descendants of the Clade 3a new-comers.

The main source of information for the material in this section is Davision et al. (2011), but augmented by the numerous publications that describe Pleistocene refugia and related brown bear lineages in Eurasia, including Taberlet & Bouvet (1994), Matsushashi et al. (2001), Saarma et al. (2007), Sommer & Benecke (2005), Valdiosera et al. (2007), Keis et al. (2013), Kutschera et al. (2014), and Salomashkina et al. (2014). Mathues et al. (2001) describe the *U. arctos* remains found near Edmonton, Alberta. Stokes et al. (2012) are the source for delineations of ice sheet margins prior to the Last Glacial Maximum.

Early prehistory: 70,000-10,000 years ago

Up until the early 2000s most scientists thought that grizzlies had not arrived in the middle part of North America until after the last continental Ice Sheets had melted enough to allow passage of bears from Beringia (which included all of modern-day Alaska) through an ice-free corridor along the eastern edge of the Rocky Mountains (see the maps below)--probably around 13,000 years ago (all of the ages here are corrected for biases in radiocarbon age). However, the discovery of grizzly bear remains near Edmonton, Alberta, dating to roughly 32,000 (or 32k) years ago turned this assumption on its head. Recent analyses of genetic material from North American grizzly bears have reinforced the idea that grizzlies arrived much earlier, probably during the last opening in the Alberta ice-free corridor, prior to closure at the height of the last Ice Age, roughly 55,000-18,000 years ago. Recent research by Chris Stokes and his colleagues suggests that a long-lasting opening between the Cordilleran (to the west) and Laurentide (to the east) continental ice sheets occurred between 80k and 65k years ago, with a

possible brief opening again around 55k years ago. So, grizzlies probably arrived--and presumably then persisted--as early as 70k or as late as 55k years ago.

As I noted in the previous section, figure 3, above summarizes current thinking about the several migrations of brown bears from Asia into and through North America (parenthetically, grizzlies are brown bears, all *Ursus arctos*). An early wave of bears carrying genetic material identified with Clades 2a, 2c, 3c, and 4 (roughly the equivalent of subspecies) arrived in eastern Beringia around 70k years ago, having successfully crossed over the Bering Land Bridge. Of those bears, those of Clade 4 managed to successfully complete the journey into the middle part of the continent, presumably along the eastern edge of the Rocky Mountains. They were then isolated with closure of the ice-free corridor, intermingling with other grizzlies of the newly-arrived Clade 3b only after reopening of the ice-free corridor around 14-11k years ago (see the maps below). Shortly after, the Bering Land Bridge was

closed to additional migrants by rising sea levels. Parenthetically, some researchers have theorized that grizzlies also got to the mid-continent by following ice-free coastal areas of modern-day Alaska and British Columbia--prior to the opening of Alberta's ice-free corridor. Land levels at these ice free margins were dramatically elevated as a compensatory ("forebulge") response to depression of the Earth's crust by the ice sheet farther inland. Migrating coastal grizzlies presumably subsisted largely on marine resources.

Figure 4 shows the distributions of grizzly bear remains from two different periods: In panel A, from 32-10k years ago, with all but the ones near Edmonton dating to less than 15.5k years ago; and, in panel B, from 10k to 200 years ago--up to essentially historical times. In panel A the extent of the ice sheets and bordering glacial melt lakes are shown at 13.5 and 11.5k years ago. Note Lake Agassiz (see the discussion above about climate). Most of the remains are not radiocarbon-dated.

The map in panel A constitutes pretty conclusive evidence that grizzly bears occurred in eastern North America between roughly 15.5 and 11k years ago. But by 10k years grizzlies seem to have been gone in the East. All of the specimens post-10k roughly coincide with the historical distribution of grizzlies. The one exception is the Utz site in Missouri. This specimen was apparently found during excavations of a prehistoric Indian settlement. I tried to track down the original publication documenting this find, but without success. My current suspicions are that either: (1) the specimen was misidentified or, if authentic, then (2) the result of a series of trades among tribes that transported grizzly bear remains from farther west to this site in Missouri.

In addition to the sources that I mention in the section on biogeography, I also reference Guilday (1968), Loring & Spiess (2007) and Harington et al. (2014) for more information on *Ursus arctos* in eastern North America. The Utz site is described by Berry & Chapman (1942).

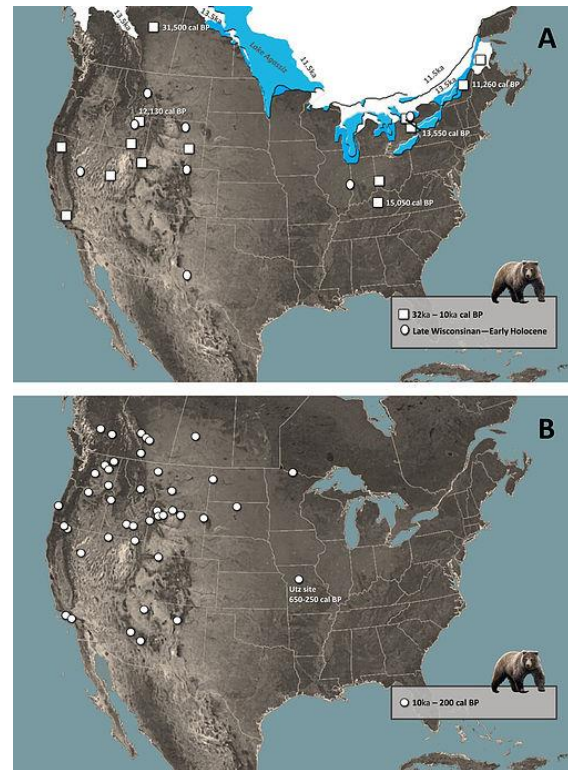


Figure 4. Locations of *Ursus arctos* remains in central North America for two different time periods: (A) 32-10k years bp; and (B) 10k-200 years bp. Locations are shown as either white dots or white squares.

Attachment B

Draft Tri-State Memorandum of Agreement (“Draft MOA”)



December 7, 2015

Daniel M. Ashe, Director
U.S. Fish and Wildlife Service
1849 C Street NW, Room 3331
Washington, District of Columbia, 20240

Dear Director Ashe:

On August 28, 2015, we wrote you regarding the overdue re-designation and delisting of the Greater Yellowstone Grizzly Bear Distinct Population Segment (DPS). We appreciate the progress and agreements we achieved during our discussions in Tucson on September 14th and your subsequent letter dated September 25, 2015 memorializing those discussions. Since then, our agencies have had several discussions with the U.S. Fish and Wildlife Service (Service) as to documentation for the delisting rulemaking process.


The Ninth Circuit determined that adequate regulatory mechanisms were in place at the time of the prior rule designating and delisting the Greater Yellowstone DPS in 2007. The regulatory mechanisms that the Ninth Circuit found adequate remain in effect today. The Interagency Grizzly Bear Study Team published findings that resolved the single deficiency found by the Ninth Circuit in the 2007 rule, and best available science continues to demonstrate the GYA population consistently exceeds recovery criteria.

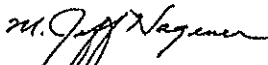
Nevertheless, we agree that additional documentation as to regulatory mechanisms will provide clarity and transparency as to how the states will coordinate with each other and federal land managers to ensure maintenance of the recovered bear population. Various signatory agencies have discussed appropriate updates to the 2007 Interagency Conservation Strategy.

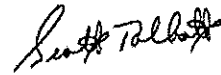
We have also enclosed a draft memorandum of agreement (MOA) among the states that we will recommend to our respective commissions for approval at meetings in the next few months following public notice. Although not necessary for delisting, this MOA memorializes how the three states will coordinate with each other, as well as with federal land managers, regarding bear management and allocation of discretionary mortality. An attachment to the MOA summarizes individual state regulatory mechanisms to manage, monitor, restrict, and adjust bear mortality. We will keep the Service apprised as to our respective commissions' approval of the MOA.

We look forward to continuing to work with you and your staff to finalize all steps necessary to delist. As we stated in our prior letter, delisting delay is needlessly straining relationships vital to responsible grizzly bear management. It is critically important that we capitalize on our tremendous progress and momentum by fulfilling the purpose of the ESA by proceeding with long overdue delisting.

Sincerely,


Virgil Moore, Director
Idaho Dept of Fish and Game
P O Box 25
Boise ID 83707


M. Jeff Hagener, Director
Montana Fish, Wildlife & Parks
P O Box 200701
Helena MT 59620-0701


Scott Talbott, Director
Wyoming Game and Fish Dept
5400 Bishop Boulevard
Cheyenne WY 82006

Enclosure

FINAL DRAFT 12-4-2015

MEMORANDUM OF AGREEMENT REGARDING THE MANAGEMENT AND ALLOCATION OF DISCRETIONARY MORTALITY OF GRIZZLY BEARS IN THE GREATER YELLOWSTONE AREA

Among

**Wyoming Game and Fish Commission, Wyoming Game and Fish Department,
Montana Fish and Wildlife Commission, Montana Fish, Wildlife and Parks,
Idaho Fish and Game Commission, and Idaho Department of Fish and Game**

This Memorandum of Agreement (MOA) is made and entered into by and among the Wyoming Game and Fish Commission and the Wyoming Game and Fish Department (collectively WGFD), the Montana Fish and Wildlife Commission and Montana Fish, Wildlife and Parks (collectively MFWP), and the Idaho Fish and Game Commission and the Idaho Department of Fish and Game (collectively IDFG), collectively referred to as the Parties.

I. Purpose

The purpose of this MOA is to define the process by which the Parties will coordinate the management and allocation of discretionary mortality of grizzly bears in the Greater Yellowstone Area (GYA). The Parties enter into this MOA in support of the re-designation of the Distinct Population Segment (DPS) of GYA grizzly bears and delisting of this DPS under the federal Endangered Species Act. The Parties intend this MOA to be consistent with the 2007 interagency *Final Conservation Strategy for the Grizzly Bear in the Greater Yellowstone Area* (Strategy) and individual state management plans, and with revisions to these documents made in conjunction with the delisting process.

II. Background

The Interagency Conservation Strategy Team, with the participation of the Parties and various federal agencies, developed the Strategy to implement regulatory mechanisms, interagency cooperation, and population and habitat management and monitoring, and other actions to ensure continued recovery of the GYA grizzly bear. The Strategy was subject to public comment and scientific peer review. The Strategy's key mechanisms for maintaining a recovered GYA grizzly population are its population and habitat standards, which are based on the recovery criteria originally set forth in the USFWS Recovery Plan. The Strategy incorporated the Parties' individual state management plans that have different, but compatible, management objectives.

On March 21, 2013, USFWS published for public comment a draft Supplement to Demographic Recovery Criteria, but USFWS has not yet finalized any such Supplement. For purposes of this MOA, the Parties assume adoption of the Demographic Monitoring Area (DMA) identified in the 2013 draft Supplement as the geographic area used to monitor continued achievement of GYA population and distribution objectives. The Interagency Grizzly Bear Study Team (IGBST) and the Yellowstone Ecosystem

Subcommittee (YES) of the Interagency Grizzly Bear Committee (IGBC) have recommended the use of the DMA for population monitoring, including mortality monitoring.

USFWS' draft 2013 Supplement kept in place the recovery criterion for a conservative total population size of at least 500 GYA bears. This minimum population size includes a conservative buffer in addition to the recommendation of Miller and Waits (2003) for a minimum population size of at least 400 bears to adequately mitigate the potential effects of genetic drift and inbreeding depression in light of the relative isolation of the GYA population. For purposes of this MOA, the Parties assume the conservative criterion for minimum population size will remain in place.

USFWS' draft 2013 Supplement also kept in place the conservative criterion for female occupancy standards in the Primary Conservation Area (PCA). For purposes of this MOA, the Parties assume this conservative criterion will remain in place.

The demographics and vital rates of the GYA population have changed over time. USFWS' draft 2013 Supplement proposed a revision to mortality standards to reflect changes in these rates to ensure a total GYA population of at least 500 bears and to meet the occupancy standard for female bears. For purposes of this MOA, the Parties identified adjustable mortality rates (see Paragraph IV. 2) to manage human-caused mortality within the DMA to levels that will sustain a population range based on the 2002-2014 Chao2 average population estimate of 674 grizzly bears within the DMA.

Adjustable mortality levels allow for higher or lower mortality rates and correspond to the upper and lower 95% confidence intervals of the 2002-2014 Chao2 average population point estimate. Adjustable mortality rates enable the Parties to address higher human-bear conflict levels that may occur when the bear population is well above the population recovery criterion. They also ensure the population stays above the recovery criterion of a minimum population size of 500 animals in the GYA. The Parties will review the population vital rates and demographics (compiled by IGBST) a minimum of every 5 years to recommend appropriate adjustments to mortality rates.

From 2002 to the present, the IGBST has used the Chao2 estimator and model averaging process to calculate population size on an annual basis. As the bear population has grown, Chao2-based estimates have become increasingly conservative (i.e., prone to underestimation). The IGBST has also made population estimates more recently using a mark-resight based technique (IGBST Report, 2012). The mark-resight approach has no known density-associated bias, and should better reflect actual bear abundance; however, current implementation of the approach is less precise than Chao2 at tracking population trend. For purposes of this MOA, the Parties assume that USFWS will, as a matter of best available science and appropriate conservatism, rely on the Chao2 estimate for assessing the population size for the post-delisting monitoring period. The Parties recognize that methods for population estimation may change in the future as circumstances warrant and new methods are scientifically vetted and accepted.

III. Definitions

1. "Discretionary mortality" is the amount of human-caused grizzly bear mortality over which agencies have discretionary authority, such as management removals and regulated harvest.
2. "Non-Discretionary mortality" is documented loss over which agencies do not have discretionary authority, such as naturally occurring mortality or human-caused mortality such as illegal shootings, defense-of-human-life shootings, and vehicle collisions.
3. "Greater Yellowstone Area" (GYA) is defined as that portion of Idaho that is east of Interstate Highway 15 and north of U.S. Highway 30; that portion of Montana that is east of Interstate Highway 15 and south of Interstate Highway 90; that portion of Wyoming south of Interstate Highway 90, west of Interstate Highway 25, Wyoming State Highway 220, and U.S. Highway 287 south of Three Forks (at the 220 and 287 intersection), and north of Interstate Highway 80 and U.S. Highway 30. This definition of GYA was used in the 2007 USFWS rule to designate a distinct population segment (DPS) of grizzly bears under the Endangered Species Act, and to delist that DPS; in 2010 USFWS vacated this rule in response to a court decision. The Parties assume USFWS will re-designate a grizzly bear DPS for the GYA geographic area as defined herein.
4. "The Recovery Zone," also known as the "Primary Conservation Area" (PCA), is the area whose boundaries are approximately depicted on the map attached hereto as Attachment A; the Recovery Zone is divided into 18 Bear Management Units.
5. "Demographic Monitoring Area" (DMA) is the area that includes the Recovery Area and an additional area surrounding the Recovery Area, approximately 19,279 mi² in area and whose boundaries are depicted on the map attached hereto as Attachment A.
6. "Chao2" is the population estimation technique currently used for the GYA population of Grizzly Bears.

IV. Responsibilities

1. The Parties will employ best science and adaptive management approaches to collectively manage grizzly bears within the GYA.
2. To achieve population criteria to support a recovered GYA grizzly bear population, the Parties will:
 - a. Maintain a minimum population size of 500 bears in the GYA.

- i. The Parties agree to achieve this criterion by managing the GYA grizzly bear population within the DMA to at least the 2002-2014 Chao2 average point estimate for total population, with 95% confidence intervals (*i.e.*, 600-747).
- b. Ensure that 16 of the 18 Bear Management Units within the PCA are occupied by at least one female with cubs over a six-year period, with no two adjacent Bear Management Units unoccupied over a six-year period.
- c. Ensure the following total mortality rates are not exceeded within the DMA for three consecutive years for independent males, independent females and dependent young, as set forth in the following table, based on the 2002-2014 Chao2 average point estimate for the total population with 95% confidence intervals (600-747).

	Total Grizzly Bear Population Estimate		
	≤674	675-747	>747
Total mortality rate for independent <u>FEMALES</u> .	7.6%	9%	10%
Total mortality rate for independent <u>MALES</u> .	15%	20%	22%
Total mortality rate for dependent young.	7.6%	9%	10%

- i. The Parties agree to achieve this criterion using an adaptive management framework that will include, but not be limited to, the following:
 - If the population is less than 600, the Parties will not allow discretionary mortality unless necessary to address human safety issues.
 - At any population level greater than 600, if total allowable independent male or female mortality is exceeded, the number exceeding the total allowable mortality will be subtracted from the next year's discretionary mortality available for harvest for that gender.
 - If a state meets any of its allocated regulated harvest limits at any time of the year, the respective state will cease hunting within the DMA.
 - If the total mortality limit for independent males, independent females, or dependent young is exceeded for three consecutive years, the Parties will evaluate alternatives to reduce discretionary mortality and request IGBST biology and monitoring review. The Parties will consider the results of the IGBST review in determining appropriate changes to the management framework.
 - If the distribution of reproductive females does not meet the criterion for Bear Management Unit occupancy, the Parties will request IGBST

biology and monitoring review. The parties will consider the results of the IGBST review in determining appropriate changes to the management framework.

3. The Parties will support the IGBST in the annual monitoring of the GYA grizzly bear population.
4. a. The Parties will meet annually in the month of January to review population monitoring data supplied by IGBST and collectively establish discretionary mortality limits for regulated harvest for each jurisdiction (MT, ID, WY) in the DMA, so DMA thresholds are not exceeded, based upon the following allocation protocol.
 - Begin with DMA Chao2 total population estimate and estimates for independent males, independent females, and dependent young (demographic classes) for the previous calendar year, as reported by the IGBST.
 - Determine the maximum allowable mortality limit for each demographic class based on the mortality rates identified in the table above.
 - Determine total mortality during the previous calendar year for each demographic class.
 - Subtract the previous year's total mortality from the maximum allowable mortality limit for each demographic class. If the difference is negative (*i.e.*, a DMA annual mortality limit is exceeded for any of the three classes), the number of mortalities above the limit will be subtracted from the corresponding DMA discretionary mortality limit for that class for the current year.
 - Allocate discretionary mortality available for regulated harvest for independent males and females to each management jurisdiction as provided in the following table. The Parties may agree to adjust the allocation of discretionary mortality based on management objectives and spatial and temporal circumstances.

Management Jurisdiction*	% of DMA outside NPS lands
WY inside DMA	58%*
MT inside DMA	34%
ID inside DMA	8%

*Four percent (4%) of the DMA outside of National Park System lands in Wyoming is under the jurisdiction of the Joint Business Council of the Eastern Shoshone and Northern Arapaho Tribes of the Wind River Reservation.

- b. The Parties will prohibit hunting of females accompanied by young, and young accompanied by females, and discretionary mortality of such animals will only occur for management removals.
- c. Each party has discretion as to how it applies its allocation of discretionary mortality pursuant to its respective regulatory processes and management plan.
- d. The Parties will coordinate with IGBST to review and make any appropriate adjustments to mortality rates at least every five years.

5. The Parties will confer with the National Park Service (NPS) and United States Forest Service (USFS) annually. The Parties will invite representatives of both GYA National Parks, the NPS regional office and GYA USFS Forest Supervisors to attend the annual meeting.
6. The Parties will monitor mortality throughout the year, and will communicate and coordinate with each other and with federal land management agencies as appropriate to minimize the likelihood of exceeding mortality limits.
7. Each party has discretion to manage grizzly bears within its jurisdiction in areas within the GYA that are outside the DMA pursuant to its respective regulatory processes and state management plan.
8. Each party will designate one representative as a respective Point of Contact for purposes of achieving the objectives of this MOA.

V. Authorities and Regulatory Mechanisms

The Parties enter this MOA pursuant to their respective state authorities as set forth in Title 87 Montana Code Annotated, Title 23 Wyoming Statutes Annotated, and Title 36 Idaho Code.

The Parties have the authority, capability and biological data to implement appropriate hunting restrictions, management relocations and removals, and population management. The Parties will use their respective individual authorities to regulate discretionary mortality as allocated to their jurisdictions under this MOA. The Parties' respective regulatory mechanisms to manage, monitor, restrict, and adjust mortality include, but are not limited to, those identified in Attachment B.

This MOA in no way restricts the Parties from participating in similar activities with other states, agencies, tribes, local governments, or private entities.

VI. No Obligation of Funds

This MOA is neither a fiscal nor a funds obligation document. Any endeavor or transfer of anything of value involving reimbursement or contribution of funds among the Parties will be handled in accordance with applicable laws, regulations, and procedures and such endeavors will be outlined in separate agreements or contracts that shall be made in writing by representatives of the Parties. This MOA does not provide such authority.

VII. Term, Termination and Effective Date

This MOA shall become effective upon the date of signature of all Parties. It shall remain in effect until it is terminated by the Parties. Any party may terminate its participation in

the MOA by providing thirty (30) days written notice to the other Parties, which notice shall be transmitted by hand or other means of delivery confirmation.

VIII. Amendment

The Parties will meet annually to review implementation of the MOA and to recommend any appropriate modifications to the MOA based on changes to the Strategy, state management plans or other pertinent regulatory documents. Any modification to the MOA will only become effective upon the written consent of all Parties.

IX. No Third Party Beneficiary

Nothing contained herein shall be construed as granting, vesting, creating or conferring any right of action or any other right or benefit upon any third party.

X. Severability

Should any portion of this MOA be judicially determined to be illegal or unenforceable, the remainder of the MOA shall continue in full force and effect.

XI. Sovereign Immunity

The states of Wyoming, Montana, and Idaho do not waive their sovereign immunity by entering into this MOA, and each fully retains all immunities and defenses provided by law with respect to any action based on or occurring as a result of this MOA.

In Witness Whereof, the Parties hereto have executed this MOA as of the last written date below.

President, Wyoming Game and Fish Commission

Date

Director, Wyoming Game and Fish Department

Date

Chairman, Montana Fish and Wildlife Commission

Date

Director, Montana Fish, Wildlife and Parks

Date

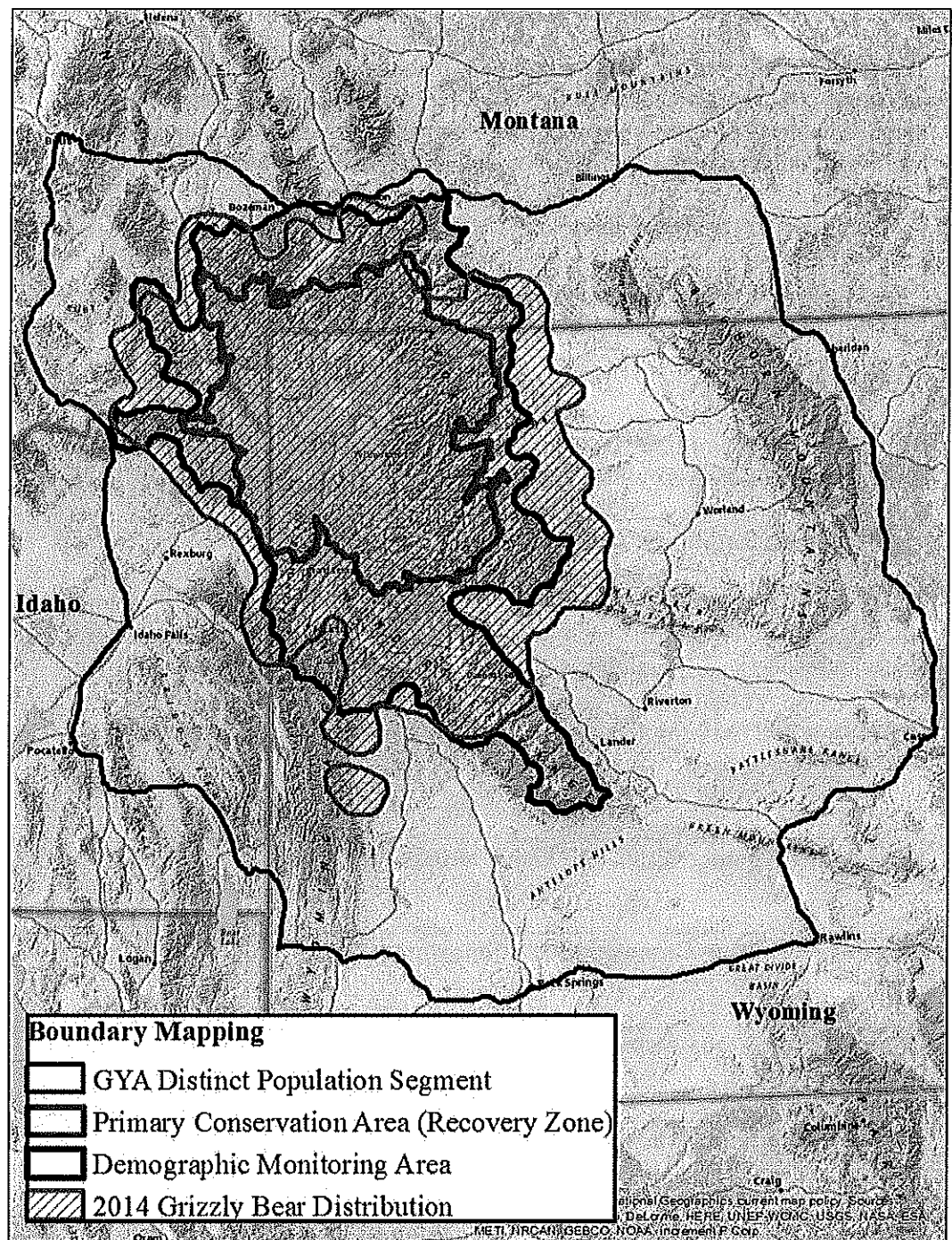
Chairman, Idaho Fish and Game Commission

Date

Director, Idaho Department of Fish and Game

Date

ATTACHMENT A



ATTACHMENT B

	Wyoming WS=Wyoming Statute WGBMP=Wyoming Grizzly Bear Management Plan	Montana MCA= Montana Code Annotated ARM=Admin. Rules of Montana MTFWC – Montana Fish and Wildlife Commission Regulation	Idaho IC=Idaho Code IDAPA=Idaho Admin. Code ISP=Idaho Season Proclamation
Protected Classification	W.S. 23-1-101 (a)(xii)(A) (classified as trophy game animal)	MCA 87-2-101 (4) (classified as a game animal)	IC 36-201 IDAPA 13.01.06.100.01(e) (classified as big game animal)
No Take without Statutory/Commission/Director Authorization	W.S.23-3-102(a)	MCA 87-1-301; MCA 87-1-304; MCA 87-5-302	IC 36-1101(a)
Commission restriction of season, location boundaries, limits, gender, age	W.S. 23-1-302(a)(ii), WGBMP	MCA 87-1-304 (1); MCA 87-5-302	IC 36-104(b)(2) seasons, locations, sex, limits, methods of take; ISP
Commission limit of harvest to automatically close season, including gender-based limits	W.S. 23-1-302(a), WGBMP	MCA 87-1-304; MCA 87-5-302	IC 36-104(b)(2); ISP
Commission authority to restrict hunter effort (e.g., controlled hunts, tag limits)	W.S. 23-1-302(a)(i), WGBMP	MCA 87-1-201(8); MCA 87-1-304 (1); MCA 87-2-702; MCA 87-5-302;	IC 36-104(b)(2) IC 36-104(b)(5) authority to designate controlled hunt IC 36-408(1),(2); ISP
Prohibition against take of females with young present	W.S. 23-1-302(a)	MCA 87-1-304; MCA 87-5-302; MCA 87-5-302	IC 36-104(b)(2) (Commission authority to prohibit in conjunction with season setting); ISP Commission authority to enact through rule (<i>see</i> IDAPA 13.01.08.300)
Requirement for license and tag	W.S. 23-3-102(a)	MCA 87-1-201(8); MCA 87-2-701; MCA 87-2-702; MCA 87 2-814; MCA 87-5-302	IC 36-401 IC 36-409(c)
Mandatory Check/Report to Monitor Harvest	W.S. 23-1-302(a)	MCA 87-1-301; MCA 87-5-302	IC 36-104(b)(3) Commission authority for rules for mandatory check and report requirements (<i>see</i> IDAPA

	Wyoming WS=Wyoming Statute WGBMP=Wyoming Grizzly Bear Management Plan	Montana MCA= Montana Code Annotated ARM=Admin. Rules of Montana MTFWC – Montana Fish and Wildlife Commission Regulation	Idaho IC=Idaho Code IDAPA=Idaho Admin. Code ISP=Idaho Season Proclamation
			13.01.08.420-422 for rules for all big game species open to harvest)
Authority for Emergency Season Closure based on Change in Conditions affecting mortality/habitat	W.S. 16-3-103(b)	MCA 87-1-304 (5); MCA 87-5-302	IC 36-104(b)(3) Commission emergency closure authority IC 36-106(e)(6) Director authority, closure in emergency effective upon written order
Permit required for response to depredation unless self-defense/defense of others/defense of property under threat to human life or domestic animals	W.S. 23-1-302(a)(viii)	MCA 87-1-201(8); MCA 87-1-304(1)(e); ARM 12.9.103(1)(d)	IC 36-1107 (carcass remains property of state)
Mandatory Education	W.S. 23-1-302(a)(xxii)	MCA 87-1-301; MCA 87-1-304 MFWC Black Bear Regulations	IC 36-412(a) Hunter education mandatory for those born after 1/1/1975 IDAPA 13.01.02.100 Recommended additional materials and exam regarding bear identification available on-line.
Penalties	W.S. 23-3-102(d), W.S. 23-6-202, W.S. 23-6-206, W.S. 23-6-208	MCA 87-6-413. (Hunting or killing over limit)	IC 36-1404(c) Misdemeanor IC 36-1404(d) Felony IC 36-1404(e) Revocation of hunting license for certain violations, including for take during closed season, exceeding bag/possession limit IC 36-1404(g): license revocation in Idaho revokes hunting privileges in all 44 states participating in the Interstate Wildlife Violator

	Wyoming WS=Wyoming Statute WGBMP=Wyoming Grizzly Bear Management Plan	Montana MCA= Montana Code Annotated ARM=Admin. Rules of Montana MTF WC – Montana Fish and Wildlife Commission Regulation	Idaho IC=Idaho Code IDAPA=Idaho Admin. Code ISP=Idaho Season Proclamation
Civil Penalty	W.S.23-6-204(e)		compact IC 36-1404(a)(3)
Procedural Aspects of State Regulatory Mechanisms	W.S. 16-3-101, Wyoming Administrative Procedures Act	MCA 2-4-101, et seq, Montana Administrative Procedures Act	IC 74- Open Meeting Requirements, including notice for all meetings of Idaho Fish and Game Commission IC Title 67, Chapter 52 (Idaho Administrative Procedure Act), requirements for public notice and comment, legislative review IC 36-105(3) Public Notice & Publication requirements for season setting

The University of Notre Dame

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Survey of Selected Pathogens and Blood Parameters of Northern Yellowstone Elk: Wolf Sanitation Effect Implications

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ABSTRACT.—The restoration or conservation of predators could reduce seroprevalences of certain diseases in prey if predation selectively removes animals exhibiting clinical signs. We assessed disease seroprevalences and blood parameters of 115 adult female elk (*Cervus elaphus*) wintering on the northern range of Yellowstone National Park [YNP] during 2000–2005 and compared them to data collected prior to wolf (*Canis lupus*) restoration (WR) in 1995 and to two other herds in Montana to assess this prediction. Blood parameters were generally within two standard deviations of the means observed in other Montana herds (Gravelly-Snowcrest [GS] and Garnet Mountain [GM]), but Yellowstone elk had higher seroprevalences of parainfluenza-3 virus [95% CI YNP = 61.1–78.6, GS = 30.3–46.5] and bovine-virus-diarrhea virus type 1 [95% CI YNP = 15.9–31.9, GM = 0]. In comparisons between pre-wolf restoration [pre-WR] (*i.e.*, prior to 1995) seroprevalences with those post-wolf restoration [post-WR] in Yellowstone, we found lower seroprevalences for some disease-causing agents post-wolf restoration (*e.g.*, bovine-virus-diarrhea virus type-1 [95% CI pre-WR = 73.1–86.3, post-WR = 15.9–31.9] and bovine-respiratory syncytial virus [95% CI pre-WR = 70.0–83.8, post-WR = 0]), but similar (*e.g.*, *Brucella abortus* [95% CI pre-WR = 0–4.45, post-WR = 0–4.74] and epizootic hemorrhagic disease virus [95% CI pre-WR = 0, post-WR = 0]) or higher for others (*e.g.*, *Anaplasma marginale* [95% CI pre-WR = 0, post-WR = 18.5–38.7] and *Leptospira* spp. [95% CI pre-WR = 0.5–6.5, post-WR = 9.5–23.5]). Though we did not detect an overall strong predation effect through reduced disease seroprevalence using retrospective comparisons with sparse data, our reference values will facilitate future assessments of this issue.

INTRODUCTION

The high mountains and plateaus of Yellowstone National Park provide summer range for an estimated 10,000–25,000 elk (*Cervus elaphus*) from 8 herds. Most of these elk winter on separate ranges outside the park, owing to snowfalls that accumulate to more than 3 m on interior plateaus. These world-renowned herds provide significant visitor enjoyment and benefits to local economies (*e.g.*, hunting). However, they also have been implicated in the transmission of diseases such as brucellosis (*Brucella abortus*), sarcoptic mange (scabies) and septicemic pasteurellosis to wildlife and domestic livestock in Idaho, Montana and Wyoming (Aguirre *et al.*, 1995; Wolfe *et al.*, 2002). These claims have led to proposals for eliminating diseases such as brucellosis from elk in the Greater Yellowstone Area by capture, test and slaughter (USDOJ and USDA, 2000).

However, management proposals should consider the potential for selective predation to reduce disease prevalence in ungulate herds through natural means (*i.e.*, a sanitation

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effect). Yellowstone supports an intact large-predator complex, including black bears (*Ursus americanus*), coyotes (*Canis latrans*), grizzly bears (*U. arctos*) and cougars (*Puma concolor*); and wolves (*C. lupus*), which were reintroduced in 1995–96. Wolves increased rapidly and during 2000–2005 reached one of the highest densities recorded worldwide (Smith *et al.*, 2003). Elk comprised 89% of wolf kills during the winters of 1995–2005 (Smith *et al.*, 2004) and elk in the northern part of the park decreased by approximately 50% (White and Garrott, 2005). Wolves and hunters each took 7–8% of adult cow elk annually (Evans *et al.*, 2006). Bears and coyotes were also significant predators of neonatal elk during this period (Barber *et al.*, 2005). If some diseases increase prey vulnerability, selective predation (Mech and Peterson, 2003) may reduce disease prevalence depending in part on the transmission dynamics of the disease (*i.e.*, animals compromised by an infectious agent are not always the most important transmitters of the agent).

Some of the diseases summarized by Mech (1970) and (Mech *et al.*, 1998) which apparently make prey more vulnerable to wolf predation include actinomycosis (a severe infection affecting jawbones), other skeletal diseases and disorders (*e.g.*, arthritis), heavy hydatid-tapeworm (*Echinococcus granulosus*) cyst infestations, and poor condition evidenced by reduced marrow-fat suggesting some serious disease condition in the prey (unless there is a lack of adequate food). However, no previous studies have examined disease prevalence in prey pre- and post-wolf restoration. Yellowstone National Park presented this opportunity.

The National Research Council (NRC, 2002) recommended for Yellowstone that “Periodic surveillance for pathogens (including brucellosis) in wild ruminants in the northern range should be continued and a more thorough understanding of population-level threshold dynamics gained.” Our first objective was to collect data to create reference values for selected pathogens and blood parameters in northern Yellowstone elk during 2000–2002 and 2005. Our second objective was to compare these seroprevalence data with: (1) data from Yellowstone elk prior to wolf restoration; and (2) data from two other elk herds in Montana to assess differences among areas and periods. We predicted the following changes in disease seroprevalences after wolf restoration: (1) decreased seroprevalence in certain diseases via wolves selectively removing elk with clinical manifestations of disease which increased their vulnerability to predation (Murie, 1944; Mech, 1966; Fuller, 1966: 36; *see* summary by Mech and Peterson, 2003:141); (2) decreased disease seroprevalence by a reduction in overall elk numbers which may reduce disease transmission if elk concentrations correspondingly change; and (3) potentially increased seroprevalence of some diseases depending on elk-herding behavior following wolf restoration (Mao, 2003) and, therefore, potentially increased disease transmission rate. Because elk in Yellowstone were already at high densities prior to wolf restoration (White and Garrott, 2005), we did not expect increased herding to be as important in disease dynamics compared to our first two predictions. Therefore, we hypothesized an overall decrease in disease seroprevalence following wolf restoration. Because the epidemiology (*i.e.*, transmission dynamics, seasonal variabilities, clinical manifestation of disease) of many diseases in wild elk remains only partially understood (Depner *et al.*, 1991; Aguirre *et al.*, 1995; Frolich, 2000; NRC, 2002; Thorne *et al.*, 2002) specific predictions with respect to particular diseases were not possible.

METHODS

Yellowstone National Park encompasses 8991 km² of Wyoming, Montana and Idaho in the western United States (44°N latitude and 110°W longitude). Our study area included the winter range of northern Yellowstone elk, which consisted of 1520 km² of foothills and

valley bottoms along the Gardiner, Lamar and Yellowstone rivers. Nearly 1000 km² of this area was within Yellowstone National Park and the remainder was on Gallatin National Forest, state and privately owned lands (Lemke *et al.*, 1998). Annual counts of elk that wintered on the northern range during 2000–05 ranged between 8335–14,539 (White and Garrott, 2005). Descriptions of the climate, topography, vegetation and diverse predator-prey complex of this range during our study were provided in White and Garrott (2005) and the references cited therein.

We captured 115 adult female elk (≥ 1 -y old) using net-guns from helicopters during either Feb. or Mar. of 2000–02 and 2005 as described by Cook *et al.* (2004). Helicopter chases of elk generally lasted less than 1 min. Animals were handled in compliance with the requirements of the Institutional Animal Care and Use Committee for the University of Minnesota and guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee, 1998). Biologists drew approximately 50 ml of blood (< 5 min after netting the elk) by puncture of the jugular vein using 16 or 18 gauge 1 $\frac{1}{2}$ " needles and a 60 mL syringe. We placed blood in sterile, 10-mL, serum tubes and centrifuged the blood within 4 h of collection. We stored serum in cryovials (2–5 mL) in a freezer (-60 C) within 1–8 h. At the completion of captures each winter, serum samples were shipped overnight with ice packs to the Wyoming State Veterinary Laboratory (WSVL; Laramie, WY, USA). We also collected about 5–10 fecal pellets from the rectum of the animal using a gloved hand. We froze fecal samples and shipped them overnight with ice packs to the WSVL for pregnancy tests for all years and for parasites during 2001–02 (Baermann's test and eggs and oocysts). During 2001–02 we also collected one nasal swab sample from each elk using either the Baxter Healthcare Culturette System (Deerfield, Illinois, USA) or the Becton/Dickinson BBL CultureSwab (Sparks, Maryland, USA) for bacteria and virus isolations. Nasal samples were maintained at 5°C and shipped within 24 h to the WSVL for bacterial evaluation. Both the fecal and nasal swab tests were considered "gold standard" tests (Thrusfield, 2005) and actual disease-causing agents were detected. We also estimated age by tooth annuli (the fourth incisor during 2000 and the upper canine during 2001–02 and 2005), nutritional condition (during 2000–02) and pregnancy status (protein B specific for pregnancy via radioimmunoassay, BioTracking, Moscow, Idaho, USA) (Cook *et al.*, 2004). Lactation and body fat data were collected during 2000–02 (Cook *et al.*, 2004).

Whole-blood and serum were sent to WSVL for analyses. We tested sera for presence of antibodies (rather than the actual pathogen itself) against *Anaplasma marginale*, border-disease virus, bovine-respiratory syncytial virus, bovine-virus-diarrhea virus type 1 and type 2, *Brucella abortus*, *Chlamydophilia*, epizootic-hemorrhagic-disease virus, infectious-bovine rhinotracheitis virus, *Leptospira* spp., parainfluenza-3 virus and *Mycobacterium paratuberculosis* during 2000–02, 2005 using tests indicated in Table 1. The WSVL summarized *A. marginale*, *B. abortus*, *Chlamydophilia*, epizootic-hemorrhagic-disease virus and *M. paratuberculosis* results as positive or negative (all evaluations were bovine-based except for *B. abortus* tests which were elk-validated and none of the tests were considered "gold standard" tests; Thrusfield, 2005). Leptospirosis exposure was evaluated at 1:100 dilution. Other disease titers were considered as follows: $> 1:16$, exposed to the disease; $= 1:16$, possibly exposed; and $< 1:16$, not exposed (except for parainfluenza-3 virus because these titers were not reported in 1:4 dilutions and, therefore, these titers were interpreted as follows: $> 1:20$, exposed; $= 1:20$, possibly exposed; and $< 1:20$, not exposed). After discussions with WSVL staff we set these conservative titer categories to avoid falsely identifying an animal as exposed to disease (see Goyal *et al.*, 1988). We constructed 95% confidence intervals for seroprevalence following Thrusfield (2005).

TABLE 1.—Disease seroprevalence tests performed on blood sampled from adult, female elk on Yellowstone’s northern range during winter 2000–02 and 2005. Unless otherwise noted all tests were conducted at the Wyoming State Veterinary Lab (WSVL)

Disease ^a	Year(s) Sample(s) Collected	Year(s) Sample(s) Analyzed	Test ^{b,c}	Comments
ANA	2000, 2002, 2005	2005	ELISA	–
BDV	2001, 2002	2001, 2002	SN	–
BRSV	2000, 2005	2005	SN	–
	2001, 2002	2001, 2002	SN	–
BVD-1	2000, 2005	2005	SN	–
	2001, 2002	2001, 2002	SN	–
BVD-2	2001, 2002	2001, 2002	SN	–
BRU	2000–2002, 2005	2000–2002, 2005	CARD, SPT, RIV ^d	–
<i>Chlamydia</i>	2000	2000	SN	Tested at the Texas Veterinary Medical Diagnostic Laboratory System, Amarillo, TX
	2001, 2002	2001, 2002	SN	Tested at the WSVL
EHDV	2001, 2002	2001, 20002	AGID	–
IBR	2000, 2005	2005	SN	–
	2002	2002	SN	–
LEPTO	2000, 2005	2005	MAT	–
	2001, 2002	2001, 2002	MAT	–
PI-3	2000–2002, 2005	2000–2002, 2005	SN	–
PTB	2000, 2005	2005	ELISA	–
	2001, 2002	2001, 2002	AGID	–

^a ANA, *Anaplasma marginale*; BDV, border-disease virus; BRSV, bovine-respiratory syncytial virus; BVD-1 and BVD-2, bovine-virus-diarrhea virus type 1 and 2; BRU, *Brucella abortus*; EHDV, epizootic-hemorrhagic-disease virus; IBR, infectious-bovine rhinotracheitis virus; LEPTO, *Leptospira* spp.; PI-3, parainfluenza-3 virus; PTB, *Mycobacterium paratuberculosis*

^b ELISA, enzyme-linked immunosorbent assay; SN, serum neutralization; CARD, card test; STP, standard-plate test; RIV, rivanol-precipitation-agglutination; AGID, standard agar-gel immunodiffusion; MAT, microscopic agglutination test

^c Tests for *Brucella abortus* were USDA/APHIS validated for elk. The other tests were bovine-validated

^d Morton *et al.* 1981

Hematology was analyzed using the Idexx QBC VetAutoread (QBC Diagnostics Inc., State College, Pennsylvania, USA) and included hemoglobin, packed-cell volume, platelets, white-blood-cell counts and differentials including segmented neutrophils, banded neutrophils, lymphocytes, monocytes, eosinophils and basophils (slides prepared at the WSVL), and mean corpuscular hemoglobin concentration. Samples from 2002 and 2005 were analyzed for serum concentrations of urea nitrogen, total protein, albumin, calcium, magnesium, inorganic phosphorus, alkaline phosphatase, creatine kinase, aspartate aminotransferase, gamma glutamyltransferase, lactate dehydrogenase, gamma globulins and glucose using the Idexx VetTest Chemistry Analyzer prior to 2003 (Idexx Laboratories Inc., Westbrook, Maine, USA) and the VetEx Autoanalyzer after 2003 (Alfa Wasserman, West Caldwell, New Jersey, USA). Total serum thyroxine was analyzed using the VetEx Autoanalyzer (Alfa Wasserman, West Caldwell, New Jersey, USA). Trace minerals including zinc, copper, iron, manganese and molybdenum from serum and selenium from blood were analyzed by

inductively coupled plasma-mass spectrometry with the Elan 6100 (PerkinElmer, Norwalk Connecticut, USA).

We compared disease seroprevalences and blood parameters during winters 2000–02, and 2005 with values reported for: (1) 143 male and female (unknown sex ratio) elk > 2-y old from northern Yellowstone that migrated outside the park and were harvested by hunters prior to wolf restoration (Aguirre *et al.*, 1995); (2) 209 female elk \geq 3-y old (blood parameter comparisons) and 913 female and male elk (disease seroprevalence comparisons) of western Montana captured in the Gravelly-Snowcrest Mountains of Montana by helicopter net driving, drug immobilization, darting from a helicopter and a hand-held net gun fired from a helicopter during 1984–1996 (Hamlin and Ross, 2002); (3) 28 adult-female elk captured from the Garnet Mountains in west-central Montana with ballistic nets fired from a helicopter during 2002–04 (2006; M. Thompson, Montana Fish, Wildlife, and Parks, pers. comm.); and (4) standards for captive female elk > 2-y old reported by the International Species Information System from 19 member institutions (ISIS, 2002).

We used two factorial analysis of variance (ANOVA) models to assess relationships between disease seroprevalence or parasite values for northern Yellowstone elk during 2000–05 and covariates including capture year, age (2–9 y old, and \geq 10-y old) and body fat (<5%, 5–10% and >10%; during 2000–2002). One ANOVA model used all the available data for a particular disease or parasite value and capture year and age covariates and a 2nd model was limited in years by the addition of body-fat data.

We used factorial ANOVA to assess relationships between individual blood parameters for northern Yellowstone elk during 2000–2005 and covariates including capture year, pregnancy status, age (2–9 y old and \geq 10-y old), body fat (<5%, 5–10% and >10%), and lactation status. We converted all continuous variables to logarithm base 10 to stabilize variance and lessen the impact of extremes for ANOVA analyses. We first added 0.5 to each monocyte, banded neutrophil, and eosinophil value because these covariates included numerous zero values (Krebs, 1999). We obtained geometric means by back-transforming the logarithms and created three factorial ANOVA models for each blood parameter. One model used all the available data, while a 2nd model was temporally limited to 2000–02 data by the inclusion of body-fat data and a 3rd model was similarly limited by the inclusion of lactation data. Only 2-way interactions were assessed among covariates due to sample-size limitations. We performed all analyses using Statistica v.6 (StatSoft, Tulsa, Oklahoma, USA) and considered differences significant at $\alpha \leq 0.05$.

RESULTS

We captured and sampled 115 adult female elk on the northern range of Yellowstone during winters 2000–02 and 2005. Seroprevalences and 95% confidence intervals follow: bovine-virus-diarrhea virus type 1, 24% (16–32%); bovine-virus-diarrhea type 2, 6% (0–12%); infectious-bovine rhinotracheitis virus, 4% (0–8%); parainfluenza-3 virus, 70% (61–79%); bovine-respiratory syncytial virus, 0%; *Brucella abortus*, 2% (0–5%); *Leptospira* spp., 17% (10–23%); *Anaplasma marginale*, 29% (18–39%); *Mycobacterium paratuberculosis*, 0%; and epizootic hemorrhagic virus, 0% (Table 2). Presence of nasal bacteria (*e.g.*, *Enterobacter*, *Streptomyces*) was low (4%, 95% CI = 0–9%), and parasites were detected in 31% (95% CI = 18–45%) of fecal samples using Baermann's test and in 57% (95% CI = 42–71%) of samples examined for eggs and oocysts (Table 3). No disease or parasite value was related to age or body fat (Table 4).

Disease seroprevalences for northern Yellowstone elk 5–10 y after wolf restoration [post-WR] compared to those prior to wolf restoration [pre-WR] were substantially lower for bovine-virus-diarrhea virus type 1 [95% CI pre-WR = 73.1–86.3, post-WR = 15.9–31.9] and

TABLE 2.—Seroprevalence of disease in adult female elk on Yellowstone's northern range during winter 2000–02 and 2005 [% positive, SE (no. positive/n) and % possibly exposed, SE (no. possibly exposed/n)] compared with hunter-killed male and female elk in Upper YNP prior to wolf restoration (Aguirre *et al.*, 1995), male and female elk combined in the Gravelly-Snowcrest Mountains, Montana during winters 1984–95 (Hamlin and Ross, 2002), and adult female elk in the Garnet Mountains, Montana during winter 2002–04 (2006; M. Thompson, MTFWP, pers. comm.)

Disease ^a	YNP elk positive	YNP elk possibly exposed	Upper YNP elk positive prior to wolf restoration ^b	Gravelly-Snowcrest Mountains elk positive ^c	Garnet Mountains elk positive ^c
Gender	female	female	male and female	male and female	female
BVD-1	23.9, 4.1 (26/109)	11.0, 3.0 (12/109)	79.7, 3.4 (114/143)	—	0.0, 0.0 (0/27)
BVD-2	5.8, 3.2 (3/52)	1.9, 1.9 (1/52)	—	—	0.0, 0.0 (0/26)
IBR	3.7, 2.1 (3/81)	12.3, 3.7 (10/81)	—	12.9, 2.6 (22/171)	0.0, 0.0 (0/27)
PI-3	69.8, 4.5 (74/106)	12.3, 3.2 (13/106)	84.6, 3.0 (121/143)	38.4, 4.1 (53/138)	—
BRSV	0.0, 0.0 (0/81)	1.2, 1.2 (1/81)	76.9, 3.5 (110/143)	—	0.0, 0.0 (0/26)
BRU	2.0, 1.4 (2/100)	3.0, 1.7 (3/100)	2.1, 1.2 (3/143)	0.4, 0.2 (4/913)	0.0, 0.0 (0/28)
LEPTO ^d	16.5, 3.6 (18/109)	—	3.5, 1.5 (5/143)	4.3, 0.7 (39/909)	32.1, 8.8 (9/28)
ANA	28.6, 5.2 (22/77)	—	0.0, 0.0 (0/143)	0.0, 0.0 (0/202)	50.0, 9.5 (14/28)
PTB	0.0, 0.0 (0/95)	0.0, 0.0 (0/95)	—	—	0.0, 0.0 (0/27)
EHD	0.0, 0.0 (0/52)	0.0, 0.0 (0/52)	0.0, 0.0 (0/143)	—	—

^a BVD-1, bovine-virus-diarrhea virus type 1; BVD-2, bovine-virus-diarrhea virus type 2; IBR, infectious-bovine rhinotracheitis virus; PI-3, parainfluenza-3 virus; BRSV, bovine-respiratory syncytial virus; BRU, *Bruella abortus*; LEPTO, *Leptospira* spp.; ANA, *Anaplasma marginale*; PTB, *Mycobacterium paratuberculosis*; EHD, epizootic hemorrhagic disease virus

^b Aguirre *et al.* (1995) considered titers 1:4 as positive for serum neutralization tests of BVD and BRSV. Had we used this titer cutoff our percents positive for BVD-1 and BRSV would have been 68.8 and 18.5, respectively. Aguirre *et al.* (1995) also used different tests for PI-3 (hemagglutination-inhibition), BRU (macroscopic agglutination), and ANA (macroscopic agglutination)

^c We were unable to obtain complete information on the types of disease tests used on serum samples from the Gravelly-Snowcrest Mountains elk and the Garnet Mountains elk. However, the only difference we could confirm was that PTB tests on the Garnet Mountains elk were done using standard agar-gel immunodiffusion during all years, whereas we also used enzyme-linked immunosorbent assay during some years

^d Number of serovars tested in Yellowstone elk, upper YNP hunter-killed elk, Gravelly-Snowcrest Mountains elk, and Garnet Mountains elk were 5, 4, 7 and 8, respectively

TABLE 3.—Other disease, bacteria, parasite, and virus profiles [% positive, SE (no. positive/n) and % possibly exposed, SE (no. possibly exposed/n)] evaluated in Yellowstone’s northern-range, adult female elk during winters 2000–02 and 2005

Pathogen	YNP elk positive	YNP elk possibly exposed	Comments
Border disease virus	7.8, 3.8 (4/51)	13.7, 4.8 (7/51)	–
<i>Chlamydia</i>	0.0, 0.0 (0/96)	9.4, 3.0 (9/96)	–
Bacteria (nasal swab)	4.0, 2.8 (2/50)	–	1 <i>Enterobacter</i> and 1 <i>Streptomyces</i> detection
Viruses (nasal swab)	0.0, 0.0 (0/52)	–	–
Parasites (fecal)			
Baermann’s test	31.1, 6.9 (14/45)	–	Mean lungworm larvae/gm = 1.43; 0.88 sd; range 0–3.46
Eggs & oocysts	56.5, 7.3 (26/46)	–	Various <i>Eimeria</i> (also non-pathogenic), small <i>Trichostrongylids</i> , <i>Moniezia</i> , <i>Trichuris</i> , and mites detected

bovine-respiratory syncytial virus [95% CI pre-WR = 70.0–83.8, post-WR = 0]) while similar (e.g., *Brucella abortus* [95% CI pre-WR = 0–4.45, post-WR = 0–4.74] and epizootic hemorrhagic disease virus [95% CI pre-WR = 0, post-WR = 0]) or higher for others (e.g., *Anaplasma marginale* [95% CI pre-WR = 0, post-WR = 18.5–38.7] and *Leptospira* spp. [95% CI pre-WR = 0.5–6.5, post-WR = 9.5–23.5]) (Table 2). Compared to other Montana elk herds (Garnet Mountains [GM] and Gravelly-Snowcrest [GS]) 95% confidence intervals for disease seroprevalences of northern Yellowstone elk following wolf restoration were higher for parainfluenza-3 virus (95% CI YNP = 61.1–78.6, GS = 30.3–46.5) and bovine-virus-diarrhea virus type 1 (95% CI YNP = 15.9–31.9, GM = 0) (Table 2).

Pregnant elk had lower monocytes ($P = 0.05$, $F_{1,42} = 4.20$) and higher albumin, calcium, gamma globulins, magnesium, and protein (all $P \leq 0.04$, $F_{1,28} \geq 4.71$). No blood values were related to lactation or body fat after accounting for capture year, age and pregnancy, except for segmented neutrophils which varied by the interaction between age and body fat ($P = 0.02$, $F_{2,35} = 4.57$) (Tables 5, 6).

DISCUSSION

The values for selected blood parameters for northern Yellowstone elk during 2000–02 and 2005 were generally similar to those from the Gravelly-Snowcrest and Garnet Mountains

TABLE 4.—Reproductive and condition characteristics (mean, SE, n) [min, max] of adult, female elk on Yellowstone’s northern range during winters 2000–2002 and 2005

Year	Age (yr)	Proportion Pregnant	Proportion Currently Lactating	% Fat
2000 ^a	7.56 (0.60, 42) [1, 15]	0.84 (0.06, 43)	–	8.85 (0.50, 40) [1.79, 14.32]
2001 ^a	11.12 (0.80, 28) [4, 18]	0.78 (0.08, 28)	0.09 (0.06, 23)	9.78 (0.80, 28) [1.80, 16.55]
2002 ^a	8.75 (0.79, 24) [1, 15]	0.83 (0.08, 23)	0.17 (0.08, 24)	10.14 (0.75, 24) [2.94, 15.03]
2005	8.32 (0.79, 17) [2.5, 16]	0.94 (0.06, 17)	–	–

^a Means for 2000–2002 were also reported by Cook *et al.* 2004. The differences in reported mean ages are due to interpretation of values such as “10+” from teeth annuli. For our analysis, we disregarded any “+” associated with estimated age

TABLE 5.—Blood parameters of adult, female elk on Yellowstone’s northern range during winters 2000–2002 and 2005 compared to age, pregnancy, lactation and body fat

Blood characteristic	Elk characteristic	P	Means (95% CI, n)
Segmented neutrophils (%)	age × body fat	0.02	age 2–9; body fat <5% = 46.48 (36.24–59.61, 3), age 2–9; body fat 5–10% = 22.36 (12.92–38.72, 8), age 2–9; body fat >10% = 23.15 (17.30–30.99, 15), age 10+; body fat <5% = 26.84 (13.17–54.66, 5), age 10+; body fat 5–10% = 41.19 (30.53–55.57, 6), age 10+; body fat >10% = 34.62 (29.82–40.20, 14)

herds, with some notable exceptions. Northern Yellowstone elk had lower mean serum urea nitrogen than elk from the Gravelly Snowcrest Mountains, the Garnet Mountains and ISIS standards. Serum urea nitrogen (SUN) is an indicator of protein quality in the diet and has been related to nutritional condition in white-tailed deer (DelGiudice *et al.*, 1987). Renal disease and hydration status can also impact SUN (Coles, 1980; DelGiudice *et al.*, 1987). Isolated interpretation of SUN is not possible as moderately high levels may indicate increasing levels of dietary protein intake (Cook, 2002), while diets with very high energy intake may have very low levels of serum urea nitrogen due to the rumen microbes more efficiently utilizing the proteins and thus, producing less urea (Harder and Kirkpatrick, 1994). Northern Yellowstone elk also had reduced lymphocytes compared to elk from the Garnet Mountains. Lymphocytes are white blood cells important in cell-mediated (T-cells) and humoral (B-cells) immune responses and both increases and decreases in lymphocytes can be signs of disease (Tizard, 1992). Thus, this finding alone cannot be interpreted to indicate either herd was in better overall condition.

Northern Yellowstone elk had higher seroprevalences of parainfluenza-3 virus, bovine-virus-diarrhea virus types 1 and 2 and brucellosis compared to those from the Gravelly-Snowcrest and Garnet Mountains herds. With greater wolf densities in northern Yellowstone, elk herd dynamics following wolf restoration may actually increase disease transmission depending on the specific epidemiology of these diseases. During winter northern Yellowstone elk were found in larger groups following wolf restoration (Mao, 2003), possibly because this may reduce predation risk via the dilution effect (Hamilton, 1971) and allow elk to more easily detect wolves through increased vigilance (Pulliam, 1973). However, aerial survey data from more recent research indicates that at least in some areas elk are found in smaller groups following wolf restoration (P. J. White, National Park Service, unpubl. data). Because elk grouping following wolf restoration is not fully understood, we cannot reliably attribute increased disease seroprevalence to increased elk herding.

Disease seroprevalences for northern Yellowstone elk were substantially lower 5–10 y following wolf restoration for bovine-virus-diarrhea virus type 1 and bovine-respiratory syncytial virus, but similar for *Brucella abortus* and epizootic hemorrhagic disease while higher for *Anaplasma marginale* and *Leptospira* spp. Determining whether wolves (through direct impacts via predation and/or indirect impacts through elk behavioral changes) caused these changes in elk disease seroprevalence would require substantially more knowledge of the epidemiology of each disease. Because only limited information is available about disease transmission dynamics and clinical manifestations in wild elk only plausible inferences are possible and causation cannot be determined.

For examples, parainfluenza-3 viruses cause mild respiratory disorders in domestic cattle and sheep that serve as initiators for secondary infections of *Pasteurella* spp., which can result

TABLE 6.—Means^a (SD, n) of blood parameters of adult, female elk on Yellowstone's northern range during winters 2000–2002 and 2005 compared with those of female elk \geq 3-y old in the Gravelly-Snowcrest Mountains, Montana during winters 1984–1995 (Hamlin and Ross, 2002), adult female elk in the Garnet Mountains, Montana during winter 2002–04 (2006; M. Thompson, MTFWP, pers. comm.) and to International Species Information System (2002) reference ranges for adult female elk > 2-y old (SD, n, animals contributing to samples)

Blood characteristic	YNP elk	Gravelly Snowcrest Mountains	Garnet Mountains	ISIS standards
Thyroxine (ug/dl)	4.36 (1.39, 77)	—	—	—
Serum urea nitrogen (mg/dl)	9.46 (4.40, 36)	18.40 (4.95, 209)	15.68 (5.50, 28)	27 (6.0, 53, 35)
Total protein (g/dl)	8.48 (1.30, 36)	7.17 (0.81, 209)	7.48 (0.58, 28)	7 (0.7, 37, 29)
Albumin (g/dl)	4.02 (0.85, 36)	4.72 (0.58, 209)	4.26 (0.31, 28)	3.7 (0.5, 37, 29)
Calcium (mg/dl)	9.55 (0.85, 36)	10.97 (1.19, 209)	10.20 (0.50, 28)	9.1 (0.8, 50, 32)
Magnesium (mg/dl)	2.66 (0.34, 36)	2.39 (0.40, 171)	2.49 (0.22, 28)	2.06 (0.34, 14, 11)
Inorganic phosphorus (mg/dl)	6.57 (1.42, 36)	5.27 (1.62, 209)	5.81 (1.07, 28)	7.0 (2.4, 50, 33)
Alkaline phosphatase (IU/L)	170.32 (297.75, 34)	140.56 (97.40, 209)	215.32 (114.22, 28)	111 (94, 50, 33)
Creatine kinase (IU/L)	308.25 (162.92, 36)	632.08 (359.97, 48)	1738.43 (2919.22, 28)	156 (114, 27, 16)
Aspartate aminotransferase (IU/L)	83.66 (25.86, 35)	107.06 (46.73, 48)	127.32 (56.09, 28)	55 (17, 43, 26)
Gamma glutamyltransferase (IU/L)	51.19 (31.67, 32)	43.08 (21.79, 48)	70.39 (33.20, 28)	31 (13, 19, 13)
Lactic acid dehydrogenase (IU/L)	562.17 (285.31, 36)	—	—	447 (306, 29, 17)
Globulins (g/dl)	4.46 (0.58, 36)	2.84 (0.83, 29)	3.22 (0.61, 28)	3.3 (0.7, 37, 29)
Glucose (mg/dl)	176.11 (31.48, 36)	171.50 (25.27, 10)	172.79 (34.98, 28)	153 (50, 54, 36)
Molybdenum (mg/dl)	0.04 (0.01, 47)	—	—	—
Zinc (mg/dl)	0.70 (0.33, 47)	—	—	—
Selenium (mg/dl)	0.14 (0.03, 22)	—	—	—
Copper (mg/dl)	0.56 (0.07, 47)	—	—	—
Iron (mg/dl)	2.91 (1.85, 46) ^b	—	—	—
Manganese (mg/dl)	0.02 (0.02, 47)	—	—	2.01 (0.42, 9, 6)
Packed cell volume (%)	51.95 (9.33, 51)	53.25 (5.60, 203)	55.48 (3.71, 28)	43.0 (9.4, 79, 51)
Platelets (K/ul)	57.18 (39.03, 44)	247.59 (92.96, 17)	—	197 (131, 22, 11)
Hemoglobin (g/dl)	18.13 (3.12, 51)	18.18 (1.55, 165)	18.70 (1.07, 28)	15.2 (3.4, 57, 40)
MCHC ^c (g/l)	35.00 (1.77, 51)	—	33.76 (1.52, 28)	34.5 (3.1, 57, 40)
White blood cells (K/ul)	2.73 (1.57, 44)	5.17 (1.83, 165)	4.99 (1.06, 28)	4.95 (2.68, 74, 50)
Segmented neutrophils (%)	32.20 (13.50, 52)	—	23.64 (9.97, 28)	—
Banded neutrophils (%)	5.61 (8.11, 52)	—	—	—
Lymphocytes (%)	35.02 (14.76, 52)	—	62.29 (12.54, 28)	—
Monocytes (%)	11.66 (12.92, 52)	—	3.0 (2.12, 25)	—
Eosinophils (%)	16.01 (12.31, 52)	—	10.75 (6.17, 28)	—
Basophils (%)	0.18 (0.94, 28)	—	2.0 (1.41, 9)	—

^a Values were reported to two decimal places unless less information was reported in the primary source

^b One case was deleted with an iron concentration of 301 mg/dl

^c Mean cell hemoglobin concentration

in bacterial pneumonia (Martin, 1996; Storz *et al.*, 2000). Whether this virus causes clinical symptoms in wild elk remains unknown. However, if elk exhibit respiratory difficulties, it is easy to imagine them being predisposed to wolf predation during a chase. Bovine-virus-diarrhea virus causes enteritis, mucosal disease, infections, and respiratory and reproductive disorders in cattle (Baker, 1995), though experimentally inoculated non-pregnant elk showed no clinical signs and remained healthy for >50 d post inoculation (Tessaro *et al.*, 1999). Therefore, if the lack of clinical signs in non-pregnant elk is similar in wild elk (including those pregnant) then it appears unlikely that elk infected with this virus would face increased vulnerability to wolf predation. Regarding anaplasmosis, significant clinical disease in elk has not been reported (mild anemia followed by recovery has been observed; Smits, 1991), although in cattle the disease can cause anemia, jaundice, and possibly death (Thorne *et al.*, 2002). While clinical signs of leptospirosis have been detected in captive red deer, only serologic evidence of infection has been reported in elk (Thorne *et al.*, 2002). Clinical signs other than death may include bloody urine and kidney disease, hemolysis and jaundice, and depression (Thorne *et al.*, 2002). If wild elk infected with *Leptospira* spp. exhibit clinical signs similar to captive red deer, it is conceivable that they may be vulnerable to increased predation by wolves. In contrast, epizootic hemorrhagic disease produced only mild fever in clinical trials of infected wapiti (Smits, 1991), which likely would not increase vulnerability of prey to wolf predation. Elk infected with *Mycobacterium paratuberculosis* may show non-specific clinical signs including poor weight gain and poor shedding of hair coat and just prior to death rapid weight loss and diarrhea may occur (Smits, 1991). Given these clinical manifestations, elk with paratuberculosis may be more vulnerable to wolf predation.

Similarly, it is possible that wolves may select for elk with brucellosis infections, at least in chronic cases, because these cases may cause bursitis, synovitis, and arthritis resulting in lameness (Thorne *et al.*, 1978; Herriges *et al.*, 1989). However, it is unclear whether this selection would result in a detectable decrease of seroprevalence because elk without chronic cases do not exhibit these symptoms. Also, elk interactions with bison in Yellowstone are important because Yellowstone bison have 50–60% seroprevalences of brucellosis (Ferrari and Garrott, 2002). Our results suggest the seroprevalence of brucellosis has not appreciably increased in Yellowstone elk during the past decade. Seroprevalence during 2000–2005 was 2% (95% CI = 0–4.74) compared to 1% (95% CI = 0–1%) in hunter-killed elk of both sexes sampled during 1991–1995 from 3 areas of Wyoming and Montana adjacent to the park (Rhyan *et al.*, 1997) and 3% (95% CI = 0–6%) in central Yellowstone adult female elk during 1996–1998 (Ferrari and Garrott, 2002). These seroprevalences are much lower than those documented among elk that used feedgrounds at the National Elk Refuge in Wyoming using similar tests to detect antibodies against *Brucella abortus* (25%, 95% CI = 20–31 as cited in Table 1 of Ferrari and Garrott, 2002).

Thirty-one percent of northern Yellowstone elk tested positive for lungworm compared to 9–43% during the 1960s (Barrett and Worley, 1966; Greer, 1968) and <20% during 1989–1995 (Foos, 1997; Rhyan *et al.*, 1997). Parasite load can affect vulnerability to predation and intraspecific competition (Mech, 1966; Davies, 1978; Anderson, 1979; Holmes, 1982). The prevalence of lungworm infection during 2000–2005 was not remarkably high (31%, 95% CI = 18–45%) and the mean larvae/gm (1.43; 0.88 sd) was moderate (Table 3). However, the relatively low intensity of infection could increase in future years given the current prevalence of approximately 31%.

Five–10 y after wolf restoration, disease seroprevalences for northern Yellowstone elk were substantially lower for bovine-virus-diarrhea virus type 1 and bovine-respiratory syncytial virus, but similar for *Brucella abortus* and higher for *Anaplasma marginale* and *Leptospira* spp.

Thus, our prediction that selective predation by wolves would reduce disease prevalence was only partly supported. For some diseases (e.g., anaplasmosis, bovine-viral-diarrhea, leptospirosis and epizootic hemorrhagic disease) wild elk may not exhibit clinical symptoms that would increase their vulnerability to wolf predation or they may only show clinical signs years after infection (e.g., bovine tuberculosis, Thorne *et al.*, 2002). If we assume that a particular disease leads to deficiencies that are exploitable by wolves, we may expect disease prevalence to decrease as a result of wolf selective predation. However, as discussed above, diseases may potentially be more readily transmitted between elk following wolf restoration if elk grouping behaviors are significant to a particular disease's dynamics. Depending on the transmission dynamics of *A. marginale* and *Leptospira* spp. in wild elk, this may explain why we observed higher prevalences in elk following wolf restoration.

Further complications in interpreting our results arise because of the limited specificity (proportion of true negatives that are detected) and sensitivity (proportion of true positives that are detected) of the disease tests themselves (in part because most of the tests we used were bovine-validated and not "gold standards") (Thrusfield, 2005). Some of the difference in comparisons between pre- and post-wolf seroprevalences may potentially be attributed to different tests and methods such as titer level interpretation (*see* Table 2). Additionally, our comparisons were hampered by limited overlap in the pathogens surveyed. Nevertheless, the fact that post-wolf seroprevalence for some diseases were so much lower suggests that wolves could be selecting individuals with those diseases and reducing their prevalence or reducing the overall herd sufficiently to reduce the transmission of this disease and therefore, the prevalence. Certainly this finding could form a valuable hypothesis for other studies to test.

This was the first detailed assessment of disease seroprevalences and blood profiles of elk in Yellowstone and, as a result, there were only sparse data available for comparison. Our reference values will facilitate more rigorous future evaluations of potential predator "sanitation" effects, especially when the epidemiology of these diseases in wild prey is more fully understood.

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REVIEW

Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes

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ABSTRACT

1. Long-term studies on large felids are rare and yet they yield data essential to understanding the behaviour of species and the factors that facilitate their conservation.

2. We used the most extensive data set so far compiled on leopards *Panthera pardus* to establish baseline reproductive parameters for females and to determine the demographic and environmental factors that affect their lifetime reproductive success.

3. We used comprehensive sightings reports and photographs from ecotourism lodges in the Sabi Sand Game Reserve, South Africa, to reconstruct life histories for 44 female leopards that gave birth to 172 litters over a 32-year period.

4. Leopards appeared to exhibit a birth pulse; most litters were born in the wet season, particularly in December. Mean age at first parturition ($n = 26$, mean \pm standard error = 46 ± 2 months, range = 33–62) was older than previously recorded, possibly due to elevated intraspecific competition. Average litter size was 1.9 ± 0.1 ($n = 140$, range = 1–3) and declined with maternal age. Age of litters at independence ($n = 52$, 19 ± 1 months, range = 9–31) was inversely related to prey abundance but did not affect the likelihood of recruitment of offspring. Interbirth intervals differed following successful litters (in which at least one cub survived to independence; $n = 55$, 25 ± 1 months, range = 14–39) and unsuccessful litters ($n = 46$, 11 ± 1 months, range = 4–36), as did the time taken to replace litters.

5. Variation in lifetime reproductive success was influenced mainly by differences in cub survival, which was related to maternal age and vulnerability to infanticide. Cub survival (37%) declined as females got older, perhaps because mothers relinquished portions of their home ranges to philopatric daughters. Male leopards were responsible for many (40%) cub deaths and females appeared to adopt several

strategies to counter the risk of infanticide, including paternity confusion and displaying a period of reduced fertility immediately after a resident male was replaced.

6. Our results suggest that the reproductive success of female leopards is regulated primarily by top-down processes. This should be taken into account in management decisions, particularly when managers are considering the implementation of invasive activities such as legal trophy hunting.

INTRODUCTION

Population persistence is ultimately a function of mortality and reproduction (Caughley 1977). Studies on the reproductive biology of species are therefore fundamental to their conservation (Holt et al. 2003). However, accurately quantifying reproductive parameters requires longitudinal data collected over multiple generations (Clutton-Brock 1988). Such data are rare, particularly for long-lived carnivorous mammals. Among the 37 extant wild felid species (Hunter & Barrett 2012), only lions *Panthera leo* (Packer et al. 1988), cheetahs *Acinonyx jubatus* (Kelly et al. 1998) and, to a lesser extent, pumas *Puma concolor* (Logan & Sweanor 2001) and tigers *Panthera tigris* (Smith & McDougal 1991) have been studied for sufficient periods to produce reliable estimates of reproductive success. Here, we present reproductive data collected over 32 years on a protected leopard *Panthera pardus* population in the Sabi Sand Game Reserve (SSGR), South Africa. Previous studies on leopard reproduction (Bailey 2005, Balme 2009, Owen et al. 2010) relied on cross-sectional surveys that suffer numerous weaknesses. Notably, they often fail to account for trade-offs that exist between reproduction and survival (Moyes et al. 2006). They may also be affected by short-term changes in the environment or population dynamics, which can artificially elevate variance in breeding success (Clutton-Brock 1988). By tracking the fate of female matriline across generations, our study overcomes these weaknesses and provides novel insight on the reproductive ecology of a species that is increasingly threatened (Henschel et al. 2008).

Although resilient in the face of human pressure, leopards have been eradicated from an estimated 37% of their historic African range, due mainly to loss of habitat, depletion of natural prey and direct killing by people (Ray et al. 2005). Large numbers of leopards are killed because of the real and perceived threat they pose to livestock (Balme et al. 2009, St John et al. 2011). In addition, 12 African countries are permitted by the Convention for the International Trade of Endangered Species to export a quota of leopard skins procured through trophy hunting (the combined annual quota for all countries is 2648; Balme et al. 2010). Without reliable estimates on reproduction and recruitment rates, it

is difficult to gauge the impacts that such human-mediated mortality may have on leopard populations. It is also impossible to estimate effective population size or model metapopulation dynamics, aspects of leopard biology that are key to the persistence of the species (McCullough 1996).

In this paper, we use the most extensive data set so far compiled on leopards to establish baseline reproductive parameters for the species. We also assess the effects of demographic and environmental factors on reproduction. Carnivore populations are typically regulated by top-down processes (e.g. natural enemies) or by bottom-up processes (e.g. resource limitation; Kissui & Packer 2004). Lions and spotted hyaenas *Crocuta crocuta* kill leopards, potentially limiting their reproductive output (Balme et al. 2009). Infanticide can similarly curtail population productivity, especially if turnover rates among adult male leopards are high (i.e. if resident males are frequently replaced; Balme et al. 2009, Packer et al. 2009). Alternatively, prey availability can affect carnivore reproduction by influencing pregnancy rates, age at maturity and levels of inter- and intraspecific competition (Tannerfeldt & Angerbjörn 1998, Schwartz et al. 2006). Food shortages can also affect offspring survival through increased starvation and abandonment (Packer et al. 1988, Kelly et al. 1998). Several researchers have examined the individual influences of these factors on carnivore reproduction (though not for leopards), but few have investigated their simultaneous effects, and the subject remains a source of debate (see Kissui & Packer 2004 for review). In addition to fluctuating ecological forces, reproductive success may vary with maternal age. In some felid species, older, more experienced mothers have a higher likelihood of raising cubs to independence (Packer et al. 1998, Pettorelli & Durant 2007), but they can also suffer from the increased energetic costs of rearing offspring (Logan & Sweanor 2001). Age at primiparity and reproductive senescence also partly determine the number of litters a female can produce during her life (Schwartz et al. 2003, Zedrosser et al. 2009). Accordingly, we calculate age-specific maternity rates for female leopards and estimate their lifetime reproductive success (LRS). Our results enhance the understanding of leopard biology and facilitate improved management of the species throughout its range.

METHODS

Study area

The SSGR (625 km²; midpoint: 31°29' E, 24°49' S) is situated in the lowveld region of the Mpumalanga Province, South Africa (Fig. 1). It comprises 20 privately owned properties that have been managed collectively as a conservancy since 1961. There are no internal fences between individual properties, and the eastern boundary fence that separates the SSGR from the Kruger National Park was removed in 1993. Hence, animals range freely across a protected landscape of >22000 km². The prevailing vegetation is open to semi-wooded savanna dominated by *Combretum*, *Terminalia* and *Acacia* species, interspersed with grasslands and wooded grasslands. It is a semi-arid ecosystem characterized by a warm, dry winter from April to September and a hot, humid summer from October to March, which includes the rainy season. Average annual rainfall is 650 mm and mean monthly temperatures range from 19 to 33 °C. Numerous waterholes have been created to supplement the two perennial rivers that flow through the SSGR. Consequently, there is little seasonal fluctuation in populations of wild

mammals (with the exception of elephants *Loxodonta africana*; Thomas et al. 2008). Forty-five species of large mammals (excluding rodents and bats) have been recorded on the SSGR, including the entire indigenous large carnivore guild (Radloff & du Toit 2004).

Data collection

The SSGR includes 21 lodges that run as high-end destinations for photographic safaris. Clients are taken on two game drives daily, in the early morning and late afternoon (c. 0530–0930 and 1600–2000 h). Game drives are conducted by an experienced guide accompanied by a trained tracker. Charismatic species such as leopards are highly sought after and guides maintain radio contact with each other to maximize the opportunity of locating such animals. Success rates are high; clients at lodges viewed at least one leopard on 337 ± 15 (mean \pm standard error) days per year during the study (range = 310–363). Because of the high number of vehicles active in the SSGR and its long history of protection, leopards have become habituated to the presence of game drives. As a result, guides are familiar with the leopards that use their traversing area (individuals can be distinguished by their unique spot patterns; Miththapala et al. 1989) and have been able to monitor their fates over time (see Hes 1991, Hancock 2000, Kure 2003).

Guides from all lodges are required to record daily sightings of leopards, although the frequency of reporting varies. Owners of some lodges require guides to transcribe detailed ecological information (e.g. location of individuals, predatory behaviour and social interactions) after every game drive, while others simply require significant reproduction and mortality events to be recorded. The oldest records date back to 1979, but consistent reporting throughout the SSGR has taken place from 2000 onwards. We collated all long-term sightings records from the lodges and used these to reconstruct life histories of individual leopards in the SSGR. Female leopards are philopatric (Bailey 2005) and were thus likely to remain in the study area for their entire life. Consequently, we have far more complete data for females than for males, which often dispersed away from the SSGR (G. A. Balme, unpublished data). The home ranges of individual leopards usually overlapped the traversing area of game drives from several lodges ($n = 44$, mean = 4.1 ± 0.3 lodges, range = 1–7), which allowed us to evaluate the consistency of reports. There was no discrepancy in the number of litters reported for individual females or in the fate of litters, but the recorded timing of events sometimes differed (although never by more than four months). In such cases, we used the median date between records. To ensure that maternity of litters was correctly assigned, we collected photographs taken by guides of females together with their offspring. In total, we amassed >3500 photographs

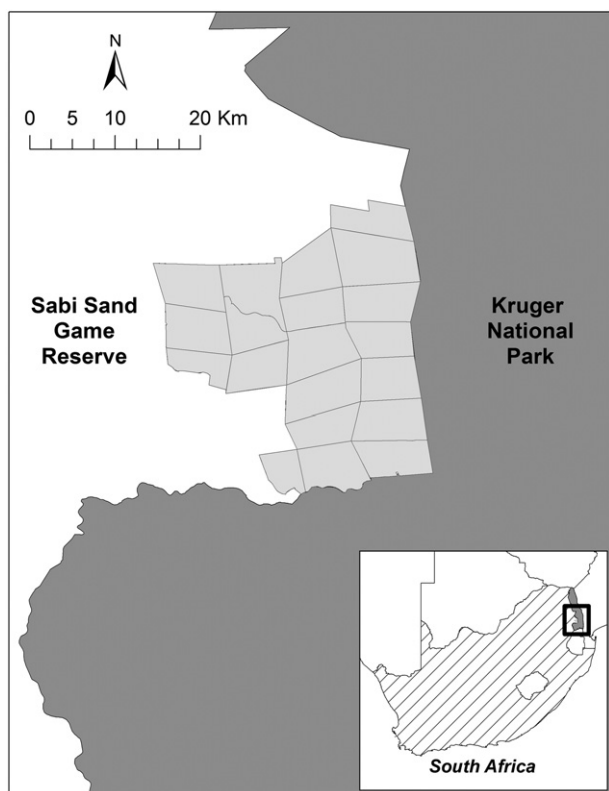


Fig. 1. Map of the Sabi Sand Game Reserve study area (pale grey; showing internal property boundaries) in relation to the Kruger National Park (dark grey), South Africa (hatched area in inset map).

that included 85% of cubs that survived to independence ($n = 118$). By using reports from multiple sources and confirming the identity of individuals through photographs, we were confident of the veracity of our data.

Reproductive parameters

We used sightings records collected by guides between January 1979 and December 2010 to estimate the following reproductive parameters for female leopards: age at first parturition, litter size, age of the litter at independence and interbirth intervals for successful and unsuccessful litters. We defined successful litters as those with at least one cub that survived to independence. Age at primiparity was only estimated for known-age females (i.e. those first observed as cubs under four months old). Litter size in our study was determined earlier ($n = 140$, mean = 49 ± 4 days after birth, range = 1–270) than previously documented (Bailey 2005, Balme 2009, Owen et al. 2010), but it still represents a minimum estimate as some cubs may have died prior to detection. Interbirth intervals were only calculated for females seen on at least a monthly basis and for litters first observed when under four months old. This reduced the chances of excluding litters that died at an early age and ensured that errors associated with our interbirth interval estimates were negligible. Young leopards were considered independent when they were no longer seen associating with their mothers. However, individuals that disappeared suddenly at a young age were excluded from the analysis because they were likely to have died (newly independent leopards were typically observed in their natal area for several months before they dispersed; G. A. Balme, unpublished data). Age at independence was estimated for litters rather than cubs, as mothers typically left siblings at a similar time. To determine if age at independence affected recruitment, we established whether individuals survived to breeding age. Subadults that dispersed from the study area before 46 months (mean age at first parturition; Table 1) were censored.

Data were also extracted on the copulatory behaviour of leopards. We calculated the length of consortships (though this was a minimum estimate as mating may have begun before and continued after leopards were encountered), the frequency of consortships and the number of different males that females were observed mating with between successive litters.

Cub survival

We used the Kaplan–Meier method (Pollock et al. 1989) to estimate age-specific survivorship for all cubs born during the study. We assigned the median litter size of two to litters that disappeared before cubs could be counted and

Table 1. Baseline reproductive parameters for female leopards *Panthera pardus* in the Sabi Sand Game Reserve, South Africa, 1979–2010. Successful litters were defined as those in which at least one cub survived to independence

Parameter	N*	Mean	SE	SD	Min	Max
Age at first parturition (months)	26	46	2	8	33	62
Litter size	140	1.9	0.1	0.6	1.0	3.0
Age of litter at independence (months)	52	19	1	5	9	31
Interbirth interval after successful litters (months)	55	25	1	7	14	39
Interbirth interval after unsuccessful litters (months)	46	11	1	6	4	36

*Sample size.

Max, maximum estimate; Min, minimum estimate; SD, standard deviation; SE, standard error.

right-censored individuals still alive at the end of the study. The Kaplan–Meier method assumes that survival times are independent among individuals (Pollock et al. 1989); however, siblings were frequently killed in the same incident. Hence, we also calculated litter survival to 18 months. We used log-rank tests to compare survival curves of male and female cubs and of cubs born during the wet and dry seasons (Pollock et al. 1989).

The causes of cub mortality were not always apparent. We only included records in which the actual mortality event was observed or could be unambiguously determined by post-mortem and evidence collected at the site. We calculated the mean proportions of litters lost and the average age of cubs affected by the different sources of mortality.

Reproductive success

Past studies of leopard reproduction included only breeders in estimates of fecundity (Balme 2009, Owen et al. 2010), so the reproductive potential of populations is likely to have been overestimated (Clutton-Brock 1988). We calculated age-specific fecundity as the number of offspring born to females in a particular age class divided by the total number (breeders and non-breeders) of females monitored in that age class (Packer et al. 1998). In this way, we estimated maternity rates for the entire population. We estimated female survivorship to determine whether reproductive senescence occurred before maximum longevity.

We also calculated the LRS of female leopards with complete reproductive histories (i.e. those monitored from birth until death). LRS is generally considered the sum of all recruits produced by an individual in its lifetime (Clutton-Brock 1988). However, data on the number of leopards reaching breeding age were incomplete; hence, we used the

number of cubs reaching independence as the metric of LRS, acknowledging that this is an overestimate. We applied the model developed by Brown (1988) to assess the relative importance of the different components of LRS (reproductive longevity, fecundity and cub survival). To allow comparison with other studies, we restricted our analysis to females that raised at least one cub to independence.

Correlates of reproductive success

We used the Kullback–Leibler information-theoretic approach (Burnham & Anderson 2002) to test the effects of different demographic and environmental covariates on litter size, age of litters at independence and reproductive success (i.e. the likelihood of at least one cub surviving to independence). For each analysis, we constructed a set of candidate models based on alternative *a priori* hypotheses. We performed model selection using Akaike's Information Criterion (AIC) corrected for small sample size (Burnham & Anderson 2002). We determined the maximum log likelihood for each candidate model and calculated the values for AIC, delta AIC ($\Delta AIC_i = AIC_i - \min. AIC$, the minimum AIC value of all models) and the Akaike weight (w_i , the weight of evidence that model *i* is the best approximating model given the set of candidate models considered). Where several models competed for the top rank (i.e. $\Delta AIC_i < 2$), we used multimodel inference to assess the relative strength of predictors (Burnham & Anderson 2002). We calculated the unconditional standard error and the 95% confidence intervals of each covariate, and those variables whose standard error excluded zero were deemed significant (Mazerolle 2006). We used the variance inflation factor ($\hat{c} = \text{residual deviance}/\text{residual degrees of freedom}$) to test the data for overdispersion and Cook's distances to identify potential outliers (Mazerolle 2006).

We limited our analyses on reproductive correlates to 2003–10 ($n = 101$ litters) as we had data on lion and leopard numbers in the SSGR for this period. Mean annual rainfall was calculated for each year of the study. Rainfall might influence leopard reproduction through effects on vegetative cover, which affect leopard hunting success (Balme et al. 2007) and may affect the vulnerability of cubs to predation (Bailey 2005). It can also influence prey availability but we found no correlation between impala *Aepyceros melampus* numbers and mean annual rainfall in our study (Pearson's correlation coefficient = 0.062, $n = 8$, $P = 0.761$). We included seasonality (either of birth or independence) as an additional covariate as it may have similar effects to rainfall (Laundré & Hernandez 2007). Impala comprised >50% of leopard diet in this area (Bailey 2005), so we used impala population size throughout the SSGR (as determined by annual aerial censuses) as a proxy for relative prey abundance (Sabi Sand Wildtuin, unpublished data). Each year,

guides submitted estimates of the lion and leopard populations using their traversing area to the SSGR management based on the numbers of known and unknown individuals that they viewed (Sabi Sand Wildtuin, unpublished data). We used these estimates as measures of inter- and intraspecific competition. They are relatively coarse indices of abundance; however, sampling effort (the number of game drives active) remained constant throughout the study period ($\chi^2_7 = 5.469$, $P = 0.603$), as did the number of sightings per season ($\chi^2_7 = 0.750$, $P = 0.993$) and the ratio of known to unknown leopards observed ($\chi^2_7 = 11.910$, $P = 0.104$). Lion and leopard numbers were negatively correlated (Pearson's correlation coefficient = -0.776 , $n = 8$, $P = 0.024$) and were thus excluded from the same analyses. For models relating to reproductive success, we included a dichotomous covariate describing the relative vulnerability of female leopards to infanticide. Females were considered vulnerable if an infanticide event occurred in an adjoining home range and if they had at least one dependent cub less than or equal to six months old (76% of cubs killed through infanticide were less than or equal to six months old; Table 5) or if they gave birth within three months of the event (assuming a gestation period of 101 days; Skinner & Chimimba 2005). Demographic covariates used in models included maternal age, litter size and the number of cubs reaching independence. The identity of the mother was included as a random factor.

We calculated all analyses and statistical computations using IBM SPSS 19.1 (SPSS Inc., Chicago, Illinois, USA). We tested all variables for normality and transformed data where appropriate. Significance was measured at $P < 0.05$ and two tailed. We present means with standard errors as a measure of precision.

RESULTS

Reproductive parameters

Female leopards began displaying signs of oestrus (scent marking and calling; Wielebnowski & Brown 1998) at 26 ± 2 months ($n = 9$, range = 18–36) and were first recorded mating at 35 ± 3 months ($n = 11$, range = 24–46). Mean age at first parturition was 46 ± 2 months (Table 1), suggesting that females successfully conceived for the first time at approximately 43 months. Age at primiparity was not related to leopard abundance ($R^2 = 0.034$, $F_{1, 14} = 0.488$, $P = 0.496$). Mating pairs were typically observed associating for 2.4 ± 0.2 days ($n = 41$, range = 1–7). The mean number of consortships observed between consecutive litters was 2.8 ± 0.5 ($n = 72$, range = 1–10), but the minimum number that must have occurred (including successful consortships that were not observed) was 3.3 ± 0.4 . On average, female leopards mated with 1.3 ± 0.1 males (range = 1–3) between successive litters.

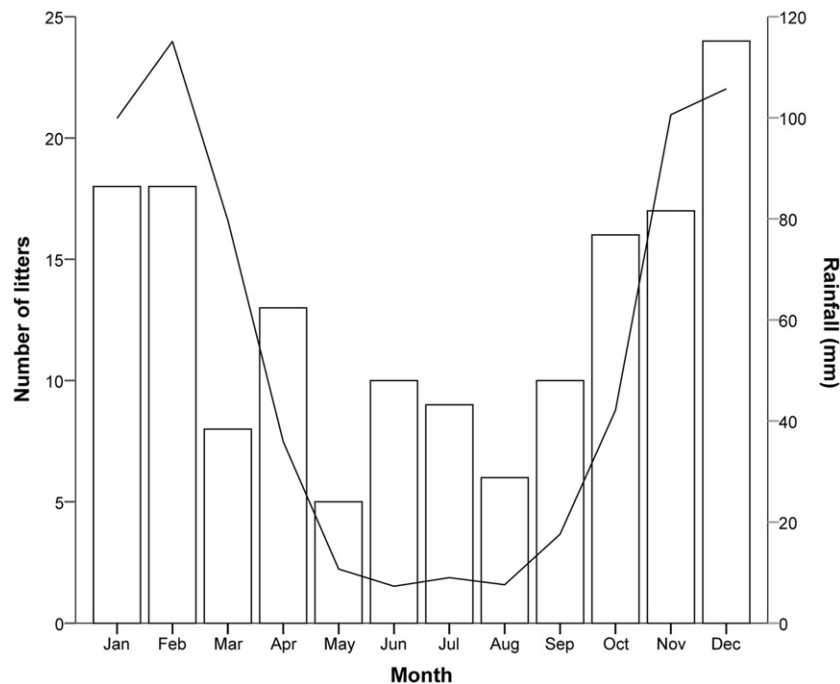


Fig. 2. Number of leopard litters recorded (bars) and mean rainfall (line; millimetre) in each month of the year in the Sabi Sand Game Reserve, South Africa, 1979–2010. The wet season spans October to March; the dry season spans April to September.

Leopards gave birth in all months of the year ($n = 154$ litters), but births were more frequent in the wet than in the dry season ($\chi^2_1 = 14.961$, $P < 0.001$), and peaked in December (Fig. 2). The number of litters born per month was related to rainfall ($R^2 = 0.630$, $F_{1, 11} = 17.020$, $P = 0.002$). Thirty-one litters (22%) comprised a single cub, 95 litters (68%) comprised twins and 14 litters (10%) comprised triplets (Table 1). Our regression analyses suggested that the best predictor of litter size was maternal age (Table 2). Litter size appeared to remain relatively constant until females were 13 years old and thereafter declined, although sample sizes for older age groups were relatively small (Fig. 3). There was no difference in the size of primiparous ($n = 32$, mean = 1.9 ± 0.1 , range = 1–2) and multiparous litters ($n = 108$, mean = 1.9 ± 0.6 , range = 1–3; $U = 1748.000$, $P = 0.904$). Although leopard and impala abundance were also included in models with $\Delta\text{AIC} < 2$, their influence on litter size was weak (Table 2). The ratio of male ($n = 86$) to female cubs ($n = 83$) did not differ from parity ($\chi^2_1 = 0.053$, $P = 0.818$).

Average age at independence of litters in our study area was 19 ± 1 months (Table 1). Five models had $\Delta\text{AIC} < 2$ but the only variable exhibiting a strong effect was impala abundance (Table 3), which was negatively correlated with age at independence (Fig. 4; $R^2 = 0.161$, $F_{1, 51} = 9.612$, $P = 0.003$). There was no difference in the age that mothers abandoned litters with single cubs ($n = 33$, mean = 19 ± 1 months, range = 9–31) and two cubs ($n = 19$, mean = 18 ± 1 months, range = 9–25; $U = 293.000$, $Z = -0.391$, $P = 0.696$), or male ($n = 34$,

mean = 19 ± 1 months, range = 9–31) and female cubs ($n = 38$, mean = 18 ± 1 months, range = 9–29; $U = 746.500$, $Z = 1.137$, $P = 0.255$). Timing of litter independence was also random; similar numbers of litters were left in the wet and dry seasons ($\chi^2_1 = 0.380$, $P = 0.579$). The likelihood of

Table 2. *A priori* regression models and model averaged parameters predicting the effect of demographic and environmental factors on leopard litter size in the Sabi Sand Game Reserve, South Africa, 2003–10

Model no.	Model set	K†	AICc‡	ΔAIC_c	wi§
1	Maternal age	2	83.915	0	0.204
2	Maternal age, leopard abundance	3	84.477	0.562	0.154
3	Maternal age, impala abundance	3	84.157	0.730	0.144

Parameter	Estimate	SE	Confidence interval	
			Lower	Upper
Maternal age*	0.014	0.007	0.001	0.028
Leopard abundance	9.496	7.855	–5.901	24.893
Impala abundance	7.426	7.335	–6.951	21.802

*Parameter deemed significant as confidence interval excludes 0.

†The number of estimable parameters.

‡Akaike Information Criteria adjusted for small sample sizes.

§Akaike weight.

Explanations of the predictors included are provided in the text. Only candidate models with $\Delta\text{AIC}_c < 2$ are shown.

SE, standard error.

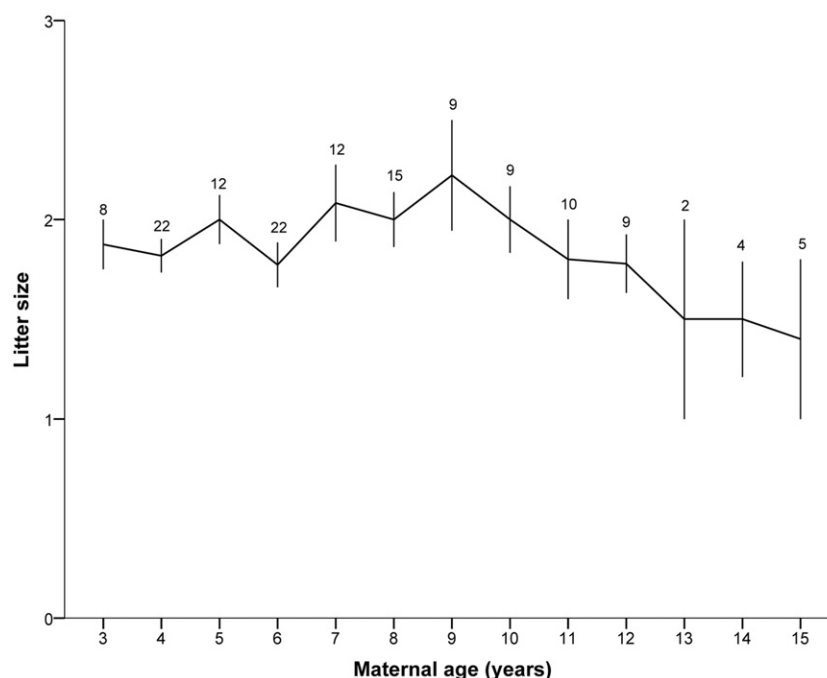


Fig. 3. Mean litter size (line) recorded for female leopards aged 3–15 years in the Sabi Sand Game Reserve, South Africa, 1979–2010. Bars represent standard errors; numbers above bars denote the sample sizes for the means (number of litters recorded for each maternal age class).

recruitment into the adult breeding population did not appear to be influenced by age at independence (recruited: $n = 31$, mean = 18 ± 1 months, range = 9–26; not recruited: $n = 9$, mean = 17 ± 2 months, range = 9–29; $U = 152.500$, $Z = 0.424$, $P = 0.679$).

The interval between births of successive litters differed when at least one cub survived to independence and when no cubs survived to independence (Table 1, $U = 2383.000$, $Z = 7.631$, $P < 0.001$). Similarly, the time taken by females to replace litters differed for successful and unsuccessful litters ($U = 580.500$, $Z = -2.489$, $P = 0.013$). Female leopards

generally gave birth 6 ± 1 months ($n = 37$, range = 1–19) after their previous litter became independent or 8 ± 1 months ($n = 46$, range = 2–22) after a litter was lost (although females resumed mating from 12 days after losing a litter). No female cared for more than one litter simultaneously, but at least 41% were pregnant when accompanied by old cubs.

Cub survival

Only 47% of known cubs ($n = 251$, we censored eight cubs that were still alive at the end of the study) survived to inde-

Table 3. *A priori* regression models and model averaged parameters predicting the effect of demographic and environmental factors on the age at independence of leopard litters in the Sabi Sand Game Reserve, South Africa, 2003–10

Model no.	Model set	K	AIC _c	ΔAIC _c	w _i
1	Maternal age, impala abundance	3	304.554	0	0.245
2	Maternal age, impala abundance, annual rainfall	4	304.753	0.199	0.222
3	Impala abundance	2	305.492	0.938	0.153
4	Impala abundance, annual rainfall	3	306.136	1.582	0.111
5	Maternal age, impala abundance, seasonality	4	306.519	1.965	0.092

Confidence interval				
Parameter	Estimate	SE	Lower	Upper
Maternal age	0.001	0.001	−0.001	0.003
Impala abundance*	−1.354	0.412	−2.160	−0.547
Annual rainfall	0.342	0.244	−0.135	0.820
Seasonality	0.050	0.067	−0.081	0.181

*Parameter deemed significant as confidence interval excludes 0.

Explanations of the predictors included are provided in the text. Only candidate models with ΔAIC_c < 2 are shown. Abbreviations as in Table 2.

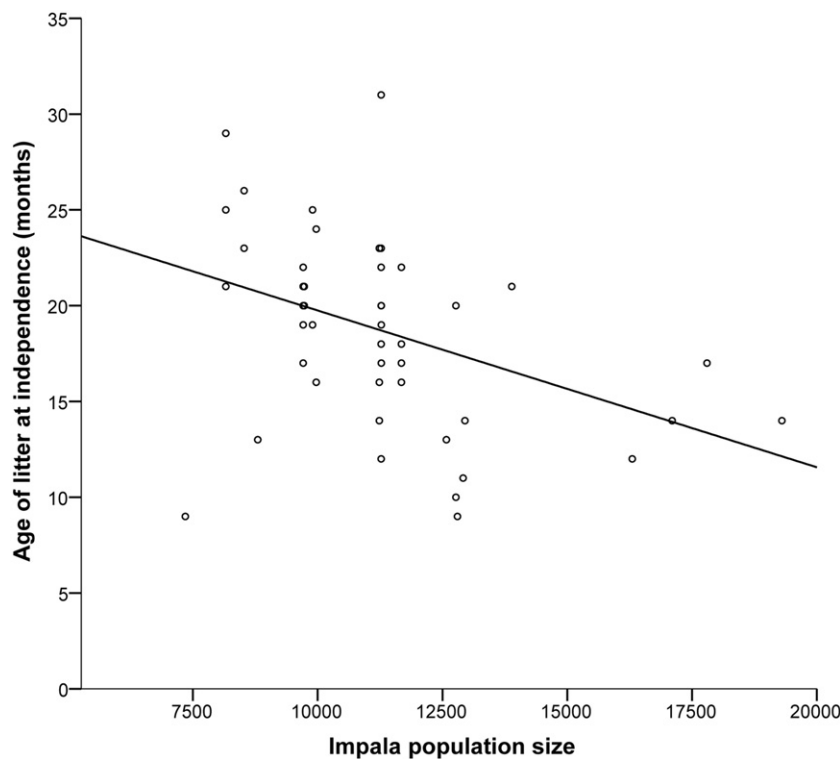


Fig. 4. Relationship between the estimated abundance of impala *Aepyceros melampus* (the main prey of leopards) and age at independence of litters for leopards in the Sabi Sand Game Reserve, South Africa, 1979–2010 ($R^2 = 0.161$, $F_{1, 51} = 9.612$, $P = 0.003$).

pendence. If we include estimates for litters that disappeared before cubs were counted ($n = 33$), survivorship to independence dropped to 37%. Cumulative cub survival declined rapidly with age (Fig. 5a). Only 55% of cubs survived their first three months, 44% survived to six months, 40% to nine months, 38% to 12 months and 37% survived to 18 months. There was no difference in survival of male and female cubs ($\chi^2_1 = 0.319$, $P = 0.572$) or of cubs born in the wet and dry seasons ($\chi^2_1 = 2.867$, $P = 0.090$). Litter survival showed a similar trend to cub survival; at least one cub survived to independence in only 49% of litters ($n = 166$, six litters censored), and most mortality occurred in the first three months (Fig. 5b). Our logistic regression models suggested that exposure to infanticide and maternal age were the only significant factors affecting litter success (Table 4). Cub survival declined once females were 9 years old and then dropped rapidly after 14 years (Fig. 6).

We were able to determine the cause of death for 98 cubs (Table 5). Infanticide accounted for most mortality, followed by predation by lions and spotted hyaenas. Only male leopards were recorded committing infanticide. Cubs killed by lions and leopards were a similar age, but those killed by hyaenas tended to be younger ($\chi^2_2 = 11.632$, $P = 0.003$). Two cubs, aged four and six months, presumably starved when their mothers died, as did a three-month-old cub that was separated from its family by a flooding river. Only one other cub (aged six months) was

abandoned by its mother, but it was adopted by another female leopard (its grandmother) and survived to independence (Balme et al. 2012a). African rock pythons *Python sebae* preyed on three cubs in their dens, and a 12-month-old cub died after being bitten by a Mozambique spitting cobra *Naja mossambica*. Two litters (aged two months) drowned in their dens during heavy storms. Except for a six-month-old female that contracted and died from mange, disease was not recorded as a mortality factor of cubs. The likelihood of at least one cub in a litter surviving a mortality event increased significantly with age (Table 6; Spearman's $\rho = -0.507$, $P < 0.001$).

Reproductive success

Female leopard survival was lowest in the first year, continued to decline until 7 years, stabilized temporarily and then decreased again after 16 years (Fig. 7). The oldest known-age female was 18.6 years. The oldest female we recorded giving birth was 16.3 years. The highest number of litters documented for a single female was 11, comprising 19 cubs, of which four survived to independence. After females reached sexual maturity, maternity rates remained relatively constant throughout their lives (with peaks at 4, 6, 8 and 11 years corresponding to a 25-month interbirth interval), only decreasing notably at 16 years old (Fig. 8). Maximum per capita cub production occurred at 8 years.

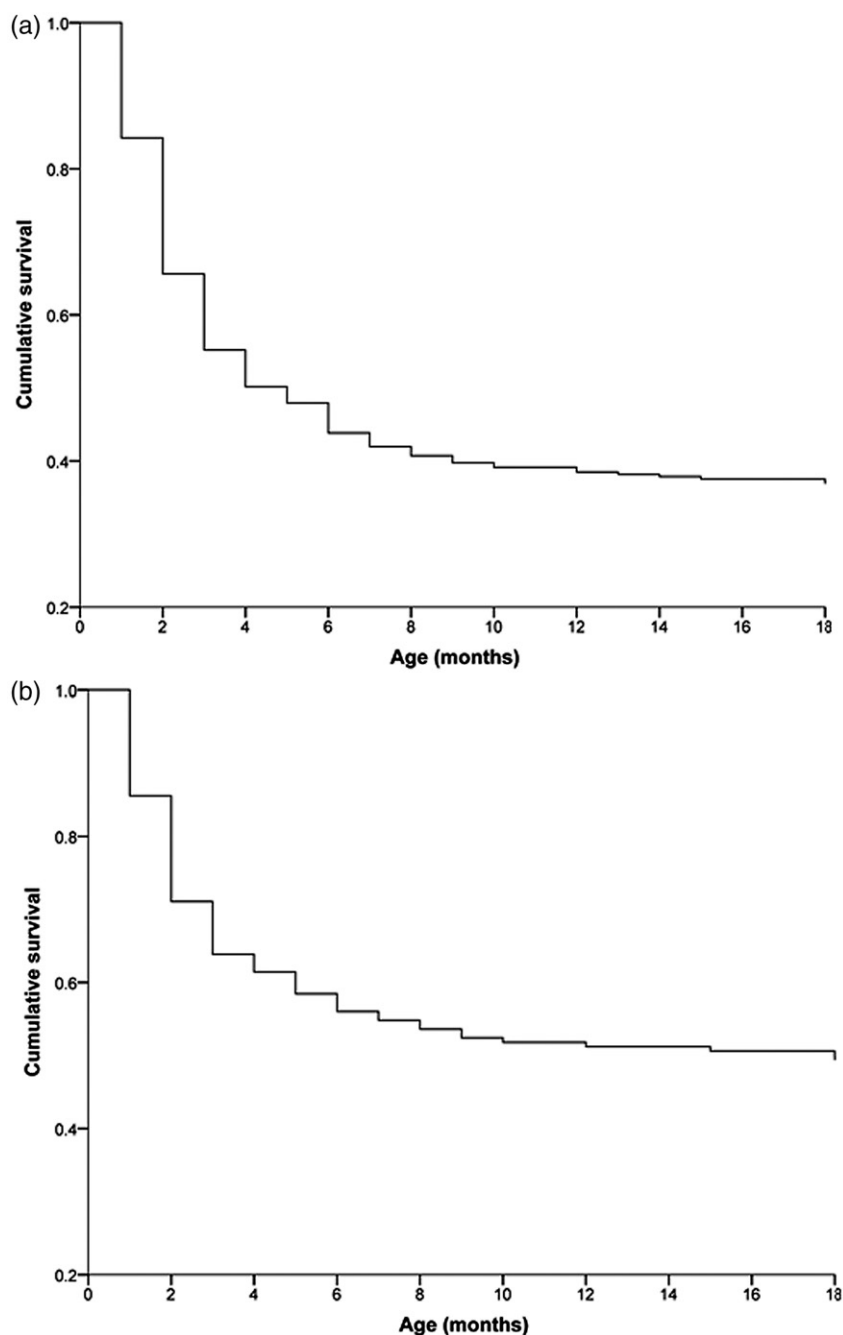


Fig. 5. Cumulative survival of leopard (a) cubs and (b) litters in the Sabi Sand Game Reserve, South Africa, 1979–2010. Successful litters were those in which at least one cub survived to independence.

We documented complete reproductive histories for 15 female leopards that had at least one cub survive to independence. The average LRS for females was 4.1 ± 0.8 (Table 7a). Although all three life history traits made substantial contributions to LRS, cub survival appeared the most important, accounting for 62% of the variance if longevity and fecundity were set equal to their means (Table 7b). Percentage contributions of all three traits totalled more than 100 because longevity and fecundity

were both negatively correlated to cub survival and to each other. LRS was negatively related to the proportional number of female cubs raised to independence ($R^2 = 0.474$, $F_{1,14} = 11.708$, $P = 0.005$).

DISCUSSION

Our study is the first to examine comprehensively the environmental and demographic factors affecting leopard

Model no.	Model set	K	AIC _c	ΔAIC _c	w _i
1	Maternal age, exposure to infanticide, lion abundance	4	119.438	0	0.531
2	Maternal age, exposure to infanticide, impala abundance, lion abundance, litter size, annual rainfall, seasonality	8	120.065	0.627	0.388

Parameter	Estimate	SE	Confidence interval	
			Lower	Upper
Maternal age*	−0.092	0.036	−0.162	−0.022
Exposure to infanticide*	−2.293	0.552	−3.375	−1.212
Impala abundance	−0.709	1.776	−4.190	2.772
Lion abundance	12.603	7.088	−1.289	26.495
Litter size	−0.963	0.535	−2.012	0.086
Annual rainfall	9.773	7.312	−4.559	24.105
Seasonality	−0.765	0.537	−1.818	0.288

*Parameter deemed significant as confidence interval excludes 0.

Explanations of the predictors included are provided in the text. Only candidate models with ΔAIC_c < 2 are shown. Abbreviations as in Table 2.

Table 4. *A priori* regression models and model averaged parameters predicting the effect of demographic and environmental factors on leopard litter success (i.e. the likelihood that at least one cub in a litter survived to independence) in the Sabi Sand Game Reserve, South Africa, 2003–10

reproduction in a stable, protected population. It therefore represents a baseline for comparison with future research and to inform management decisions pertaining to the species.

Reproductive parameters

Leopards in the SSGR appeared to exhibit a birth pulse; the majority of litters were born during the wet season, particularly in December. Bailey (2005) documented a similar peak

in leopard births in the adjoining Kruger National Park and suggested that females synchronized births to take advantage of impala lambs born at a similar time. Lactation is the most energy demanding part of the reproductive cycle, since mothers must maintain themselves as well as produce milk for their offspring (Bronson 1989). Females must also restrict their movements around den sites while nursing young cubs. Hence, timing births when food is predictably abundant and vulnerable should be an adaptive strategy that enhances cub survival (Logan & Sweanor 2001).

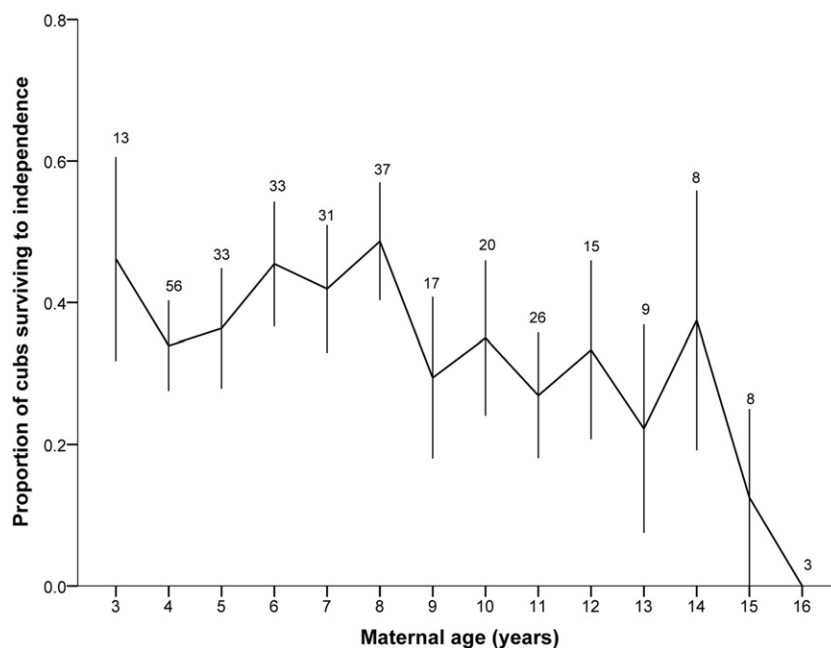


Fig. 6. Mean proportion of cubs surviving to independence (line), produced by female leopards aged 3–16 years in the Sabi Sand Game Reserve, South Africa, 1979–2010. Bars represent standard errors; numbers above bars denote the sample sizes for the means (total number of cubs recorded for each maternal age class).

Table 5. Causes of mortality, proportions of litters lost and mean ages at death for leopard cubs in the Sabi Sand Game Reserve, South Africa, 1979–2010

Cause of mortality	No. of deaths		Proportion of litter lost		Age of cub at death (months)			
	N	%	Mean	SE	Mean	SE	Min	Max
Infanticide	39	40	0.7	0.1	5	1	1	15
Lion	27	28	0.7	0.1	4	1	1	18
Spotted hyaena	14	14	0.6	0.1	2	0	1	5
Abandoned	4	4	0.7	0.3	5	1	3	7
Drowned	4	4	1.0	0	2	0	2	2
Snake	4	4	0.8	0.2	4	3	1	12
Banded mongoose <i>Mungos mungo</i>	2	2	1.0	0	1	0	1	1
Nile crocodile <i>Crocodylus niloticus</i>	1	1	0.3	–	9	–	–	–
Martial eagle <i>Polemaetus bellicosus</i>	1	1	0.5	–	3	–	–	–
Honey badger <i>Mellivora capensis</i>	1	1	0.5	–	2	–	–	–
Disease – mange	1	1	1.0	–	6	–	–	–

Min, minimum; Max, maximum; SE, standard error.

However, we detected no difference in survival rates among leopard cubs born in the wet and dry seasons. Habitat modification and the creation of numerous artificial water sources in the SSGR during the last 30 years have reduced seasonal fluctuations in impala numbers, resulting in a stable year-round prey base for leopards (Owen-Smith & Ogutu 2003). Therefore, the benefits of seasonal breeding in our study area were probably diminished, but insufficient time may have elapsed for female leopards to adapt to the altered conditions.

Primiparity among female leopards appears to be influenced by social as well as physiological factors. Females in our study were first recorded mating at approximately 3 years old. At this age, they are still in the process of establishing territories and, although physiologically capable of conceiving, it is unlikely that they could successfully raise cubs until settled (Bailey 2005). Most females have established residency by 4 years, securing access to the resources necessary for pregnancy, lactation and cub rearing. Delayed primiparity may also have evolved as an inbreeding avoidance mechanism. Philopatric female leopards may have postponed reproduction until their fathers were ousted from their territories and replaced by unrelated

males. Such behaviour has been documented in several mammalian species where subadult females remain in contact with male relatives (Pusey & Wolf 1996, O'Riain et al. 2000). Mean male leopard tenure in our study area was 4.6 ± 0.6 years (Balme et al., in prep.); hence, there was considerable opportunity for sexually mature daughters to mate with their fathers. However, such incidents comprised only 5% of observed consortships and levels of inbreeding appeared low (mean coefficient of relatedness between consorting pairs = 0.04 ± 0.01 ; Balme et al., in prep.). Mean age at first parturition was older in our study (46 months) than recorded for two lower density leopard populations in South Africa (Karongwe Game Reserve: 37 months, Owen et al. 2010; Phinda Game Reserve: 40 months, Balme 2009). Intraspecific competition is generally less intense at low population densities, which may allow females to establish territories earlier and give birth when younger (Festa-Bianchet et al. 1998).

Mean litter size observed in our study (1.9) was slightly larger than reported elsewhere (Serengeti National Park, Tanzania: 1.4, Schaller 1972; Kgalagadi Transfrontier Park, South Africa: 1.5, Bothma & le Riche 1984; Chitwan National Park, Nepal: 1.7, Seidensticker et al. 1990; Karongwe Game Reserve: 1.6, Owen et al. 2010; Phinda Game Reserve: 1.6, Balme 2009). This may be a reflection of the earlier age that cubs were first encountered in our study, assuming high levels of pre-emergent cub mortality. Nonetheless, our median litter size of two concurred with that of other studies. The energetic costs involved in producing large litters may have been excessive for old female leopards, possibly explaining the decrease in litter size after 13 years. Lions in Serengeti National Park show a similar drop in litter size at the same age (Packer et al. 1998). Unlike in many other carnivore species (Tannerfeldt & Angerbjörn 1998, McDonald & Fuller 2001), litter size in leopards was not related to prey abundance. Management intervention in the SSGR ensured that impala numbers were artificially

Table 6. Age-specific likelihood of an entire leopard litter being lost during a mortality event in the Sabi Sand Game Reserve, South Africa, 1979–2010

Age (months)	No. of mortality events	No. of litters lost	Probability of whole-litter loss (%)
0–2	64	50	78
2–4	36	15	42
4–6	11	3	27
>6	11	1	9
Total	122	69	57

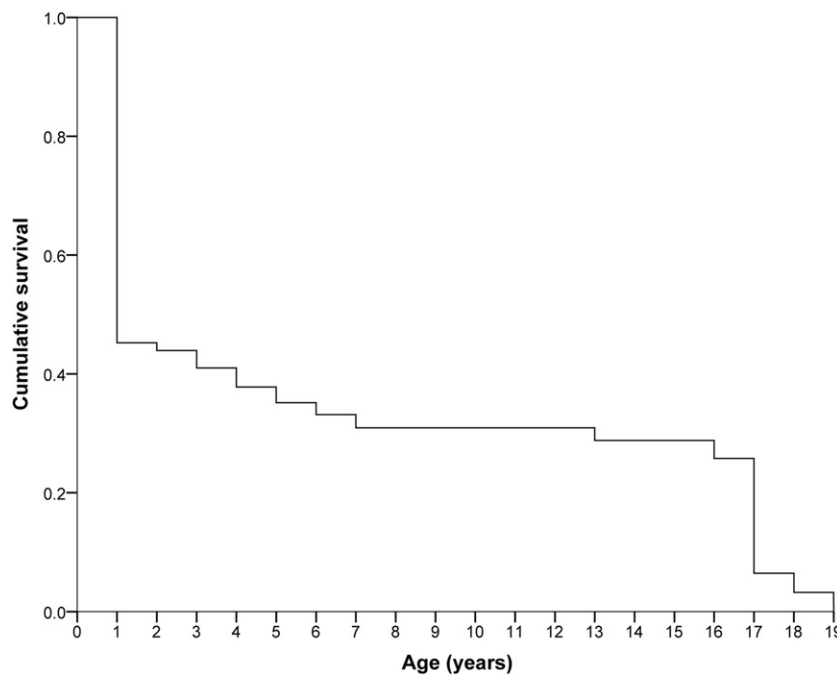


Fig. 7. Cumulative survival of female leopards in the Sabi Sand Game Reserve, South Africa, 1979–2010.

high and, even during lean periods, it is unlikely that the leopard population was resource limited. However, very large sample sizes are required to assess the demographic and environmental determinants of litter size accurately because there is limited variation in the number of young born to carnivores (Schwartz et al. 2006).

There was considerable variation in the age that cubs became independent. We could not determine the fate of all

independent youngsters; however, cubs that stayed with their mothers for longer did not appear any more likely to be recruited into the breeding population. Even though females spent a small proportion of their time with cubs of over one year old, associating mainly at kills, they gave birth again only once their previous litter was independent. No female in our study cared for more than one litter concurrently (although this has been reported anecdotally from

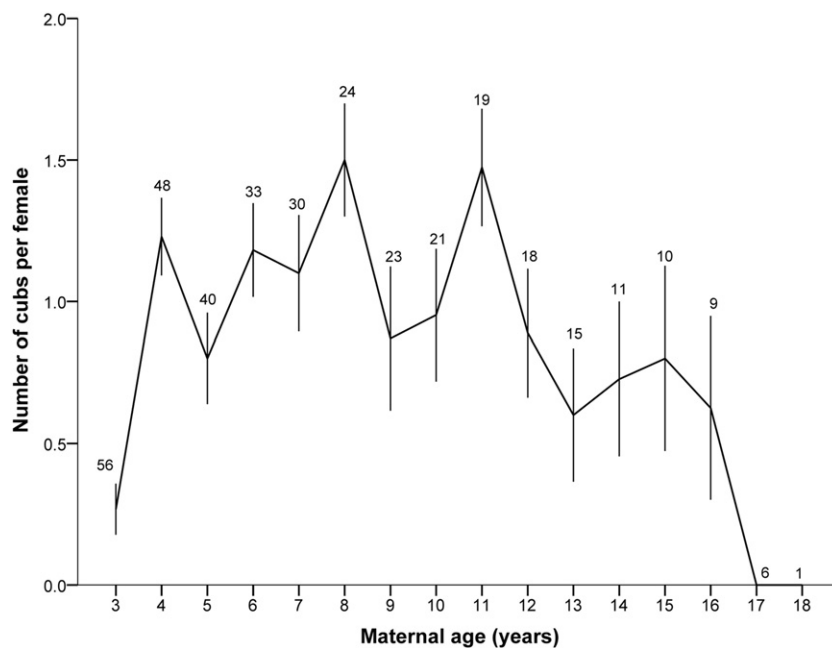


Fig. 8. Mean numbers of cubs produced per year (line) by female leopards aged 3–18 years in the Sabi Sand Game Reserve, South Africa, 1979–2010. Bars represent standard errors; numbers above bars denote the sample size for the means (total number of breeding and non-breeding females in each age class).

Table 7a. Means and variances of individual components of lifetime reproductive success and their products for female leopards in the Sabi Sand Game Reserve, South Africa, 1979–2010

Component	Mean	Variance
Longevity	9.3	23.2
Fecundity	1.36	0.4
Cub survival	0.4	0.1
Longevity × cub survival	10.8	37.5
Longevity × fecundity	3.8	7.0
Fecundity × cub survival	0.4	0.1
Lifetime reproductive success	4.1	10.1

Table 7b. Percentage contribution of individual components of lifetime reproductive success (LRS) to variation in LRS for female leopards in the Sabi Sand Game Reserve, South Africa, 1979–2010 (see Brown 1988)

Component	Longevity	Fecundity	Cub survival
Longevity	45		
Fecundity	–33	42	
Cub survival	–27	–54	62

other areas; Scott & Scott 2003, V. Athreya, pers. comm.). Therefore, females that left cubs earlier were likely to produce more litters and have higher LRS. However, our results suggest that increased fecundity must be balanced with food availability. Given their relative inexperience, it seems likely that the survival of newly independent cubs increases with prey abundance. Mothers may therefore be more inclined to leave cubs during prey-rich periods. Moreover, increased food supply may accelerate growth and shorten time to maturation (Owen et al. 2010). Mean age at independence in our study (19 months) was older than that recorded in Karongwe Game Reserve (12 months; Owen et al. 2010) and Phinda Game Reserve (13 months; Balme 2009). Although prey abundance in these areas was comparable to SSGR, leopard population density was lower, which should result in higher per capita food availability.

Cub survival

Although there are few reliable data for comparison, cub survival in our study (37%) was lower than previously documented for the species (Kruger National Park: 50%, Bailey 2005; Phinda Game Reserve: 58%, Balme 2009; Karongwe Game Reserve: 53%, Owen et al. 2010). Again, this may be a result of litter size being underestimated in other studies. Even our estimates of survivorship were conservative, as some cubs or even whole litters may have died undetected. Leopard cubs were most vulnerable during their first four months. This spans the time that cubs are confined to dens (usually for six to eight weeks after birth)

and when they are first led to kills by their mothers (Le Roux & Skinner 1989). Dens are focal points of activity as females move back and forth between hunting and nursing. Such activity is likely to generate visual, auditory and olfactory cues that increase the chances of predation. The relative immobility of young cubs and their inability to climb trees until two months old (GA Balme, pers. obs.) also increases their vulnerability, as evidenced by the high proportion of litters lost at this age.

Infanticide was the most common source of cub mortality, accounting for 40% of known-cause deaths. Our multivariate analysis similarly showed that exposure to infanticide was a key determinant of litter success. Although there are several hypotheses explaining why infanticide evolved (e.g. nutritional gain, competitive exclusion, parental manipulation of progeny and sociopathology; see Hrdy 1979 for review), sexual selection appears the primary driver for the behaviour in leopards. On most occasions, infanticide was committed by incoming (assumedly unrelated) males that later established home ranges overlapping those of affected females. A transient individual (a male leopard that subsequently left the area without breeding) was responsible for only one of the 27 incidents of infanticide where the perpetrator was identified. Most attacks, particularly those involving cubs less than four months old, resulted in the complete loss of litters. This prompted females to return to oestrus and shortened the interval between litters (although actual replacement time was longer). Infanticide was therefore likely to improve the fitness of male leopards by accelerating their opportunity to father offspring, which extended their reproductive life spans (Packer et al. 1988).

Female leopards appear to adopt several strategies to counter the threat of infanticide. Our observations showed that females often courted multiple males between the births of successive litters. Polyandrous mating has been documented in several carnivore and primate species and is thought to be a mechanism employed by females to increase paternity uncertainty (Wolff & Macdonald 2004). Cub survival may be enhanced in such cases, as males should be less inclined to kill cubs that they may have sired. In addition to increased promiscuity, female lions display a period of reduced fertility immediately following the takeover of a pride by a new male coalition (Packer & Pusey 1983). This potentially allows lionesses to assess the fitness of new males and postpone conception until the threat of further takeovers has diminished. We do not have conclusive data for leopards in the SSGR, but the time taken for females to replace litters lost to infanticide was longer than the time following successful litters, even though females were recorded mating soon after losing cubs. Balme et al. (2009) showed that leopard mating success (defined as the number of litters produced per mating bout observed) in Phinda

Game Reserve was lower during a period of high male turnover than during a more stable period. Although female leopards in our study typically attempted to defend their cubs from incoming males, they were almost always unsuccessful. Solitary carnivores appear more susceptible to infanticide than social species simply because they cannot rely on cooperative defence (Packer et al. 2009).

Our analyses showed that cub survival was also influenced by maternal age. Intuitively, older female leopards should be better mothers, and reproductive success has been positively linked to experience in cheetahs (Pettorelli & Durant 2007). However, cub survival in our study decreased once females reached 9 years old and dropped notably after 14 years. Dispersal in leopards is generally sex biased; females are philopatric and males disperse long distances from their natal area (Bailey 2005). As with other carnivores that form matrilineal assemblages (Logan & Sweaner 2001, Goodrich et al. 2010), female leopards often relinquish parts of their home range to establishing daughters (Fattebert et al., in prep.). Consequently, the home ranges of females that raise several daughters to independence should contract as they get older, potentially to the point where resource limitation impacts cub survival. Unfortunately, we do not have sufficient long-term spatial data to demonstrate such range contraction; however, LRS was lower for mothers that raised proportionally more female cubs to independence. Since male leopards usually disperse, they are unlikely to affect their mother's access to resources and consequently her ability to raise cubs. This seemingly altruistic behaviour by female leopards presents a possible illustration of kin selection, where an individual enhances its inclusive fitness by assisting a relative, even though its own reproduction may suffer as a result (Hamilton 1964).

Reproductive success

Maternity rates for leopards mirrored the classic bell-shaped productivity curve evident in many carnivore species (Schwartz et al. 2003). Cub production increased rapidly during sexual maturity, reached a peak between 8 and 11 years and declined gradually thereafter, only dropping off at 16 years. Females suffered increased mortality from 3 to 7 years presumably while they secured their newly established territories (Bailey 2005). This may explain why cub production only peaked at 8 years even though most females began breeding at 4 years old. Reproductive senescence approximated physical longevity in our study. It is possible that old females had lower fertility, as cub survival among this age class was lower than for prime-aged females; however, shorter interbirth intervals and correspondingly higher fecundity would then be expected but did not occur. Even so, it seems unlikely that reproductive senescence would have much effect on the intrinsic growth of leopard popula-

tions (Packer et al. 1998, Schwartz et al. 2003). It occurred late in life, the number of individuals surviving to this age was small and their overall contribution to recruitment was minimal.

The LRS of leopards (4.1 ± 10.1) was comparable to that of other large felids (lion: 3.8 ± 7.8 , Packer et al. 1988; cheetah: 3.5 ± 4.9 , Kelly et al. 1998; tiger: 4.5 ± 11.5 , Smith & McDougal 1991). When we partitioned LRS into its separate components, variation in cub survival was the most important contributor to variation in LRS. We presumably underestimated the importance of cub survival because we defined reproductive success as the number of individuals reaching independence when it should be the number of cubs recruited into the breeding population (Clutton-Brock 1988). Several studies have shown that offspring survival after independence can have a significant effect on variation in LRS (Clutton-Brock et al. 1988, Fitzpatrick & Woolfenden 1988). This suggests that parental care extends beyond the weaning period, which in female leopards is likely to be manifested through the kin-related spatial structure of females (Støen et al. 2005). Cub survival was inversely related to fecundity because females that lost their cubs resumed breeding more rapidly than those that successfully raised litters to independence. Cub survival and reproductive longevity were also negatively correlated, presumably reflecting the inferior reproductive performance of older female leopards. The negative relationship between fecundity and longevity may be a statistical artefact that arose from excluding non-breeders (Packer et al. 1988). Individuals that died soon after maturity had disproportionately high fecundity because of their relatively short life spans.

CONCLUSION

Our results suggest that the reproductive success of female leopards in the SSGR is regulated primarily by top-down processes. Offspring survival was the most important variable affecting LRS, and predation (predominantly by male leopards, lions and spotted hyaenas) accounted for 91% of cub mortality. Similarly, our logistic regression models showed that exposure to infanticide was a key factor determining the likelihood of a female successfully raising cubs to independence. This has significant management implications. The leopard population in the SSGR appeared capable of withstanding the high incidence of infanticide observed in our study (the population remained relatively stable throughout the study period); however, activities such as trophy hunting that artificially elevate turnover among breeding males may increase rates of infanticide to unsustainable levels (Whitman et al. 2004, Packer et al. 2009). It seems unlikely that cub survival would adjust through some compensatory response; infanticide was not related to

population density and starvation was a minor cause of mortality. A safe harvest could potentially be ensured by restricting hunting of leopards to males over 7 years old (Packer et al. 2009), and aging criteria exist that enable hunters to identify suitably aged individuals (Balme et al. 2012b). Alternatively, quotas should be reduced to conservative levels [e.g. $\leq 3.8\%$ of the total population (Caro et al. 2009) or an offtake of ≤ 1 leopard/1000 km² (Packer et al. 2011)] and effort made to ensure hunting pressure is equitably distributed throughout available leopard range (Balme et al. 2010). Less direct, bottom-up processes did have some impact on leopard reproduction. Age at independence was influenced by impala abundance, and maternal age, which presumably was linked to home range size and access to resources, affected litter size and success. Prey availability may play a larger role in the reproductive success of female leopards in less productive habitats (Stander et al. 1997) or in populations below carrying capacity (Owen et al. 2010).

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Applicability of Age-Based Hunting Regulations for African Leopards

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Abstract

In species in which juvenile survival depends strongly on male tenure, excessive trophy hunting can artificially elevate male turnover and increase infanticide, potentially to unsustainable levels. Simulation models show that the likelihood of safe harvests can be improved by restricting offtakes to males old enough to have reared their first cohort of offspring to independence; in the case of African leopards, males were ≥ 7 years old. Here, we explore the applicability of an age-based approach for regulating trophy hunting of leopards. We conducted a structured survey comprising photographs of known-age leopards to assess the ability of wildlife practitioners to sex and age leopards. We also evaluated the utility of four phenotypic traits for use by trophy hunters to age male leopards in the field. Our logistic regression models showed that male leopard age affected the likelihood of survey respondents identifying the correct sex; notably, males < 2 years were typically misidentified as females, while mature males (≥ 4 years) were sexed correctly. Mature male leopards were also more likely to be aged correctly, as were portrait photographs. Aging proficiency was also influenced by the profession of respondents, with hunters recording the lowest scores. A discriminant model including dewlap size, the condition of the ears, and the extent of facial scarring accurately discriminated among male leopard age classes. Model classification rates were considerably higher than the respective scores attained by survey respondents, implying that the aging ability of hunters could theoretically improve with appropriate training. Dewlap size was a particularly reliable indicator of males ≥ 7 years and a review of online trophy galleries suggested its wider utility as an aging criterion. Our study demonstrated that an age-based hunting approach is practically applicable for leopards. However, implementation would require major reform within the regulatory framework and the hunting industry.

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Introduction

Trophy hunting has the potential to generate substantial financial returns, which may foster tolerance towards large carnivores and enhance opportunities for their conservation outside formally protected areas [1,2]. However, poorly managed trophy hunting can drive population declines [3,4]. Felids are especially susceptible to overexploitation due to their complex social systems that depend on the stability of long-term relationships [5]. An artificial increase in turnover and immigration rates can increase contact between unfamiliar individuals and promote intraspecific strife [6,7]. Unnaturally high turnover among adult males may also increase infanticide, potentially to unsustainable levels [8,9]. Solitary species appear particularly sensitive to infanticide as females cannot rely on cooperative defence against incoming males [9]. Simulation modelling has suggested that trophy hunting can be sustained by restricting offtakes to males old enough to have reared their first cohort of offspring [8–10]. Such an approach eliminates the need for numerical quotas typically derived from unreliable population estimates [11]. Here, we explore the practical application of age-based hunting regulations for leopards *Panthera pardus*.

Leopards contribute 8–20% of gross national trophy hunting income in East and southern Africa [12] and yet, despite their declining status [13], there is little scientific input on the allocation

of harvest quotas or the implementation of hunting practices. Although advances in survey methodologies enable accurate estimates of leopard numbers, few authorities employ these techniques in setting quotas [14]. Hunting effort is also frequently distributed unevenly across available leopard range [4,15]. Such clumped offtake can create localised population sinks that have a disproportionate impact on metapopulation viability [7,16]. Hunter selectivity additionally appears poor, with female and young male leopards regularly included in trophy harvests, even though it is often illegal to do so [15,17]. It is difficult to gauge the impacts of such actions, but poorly regulated trophy hunting contributed to high mortality and low recruitment in one intensively-monitored leopard population in South Africa [7] and was instrumental to population declines in Tanzania outside the Selous Game Reserve [4]. More generally, leopards have disappeared from at least 37% of their historical African range [13], prompting the IUCN to recently list the species as Near Threatened [18].

Packer et al. [9] demonstrated that harvesting male leopards ≥ 7 years old had little impact on population persistence, regardless of offtake. Male leopards have usually left their mothers by 2 years old and can start breeding from 3 years, but typically reach their reproductive peak from 4–6 years, by which time they have held tenure sufficiently long for at least one litter to potentially reach

independence [19]. Implementing a strict 7-year age minimum for trophy leopards would dramatically reduce the risk of unsafe harvests despite uncertainties in population sizes. It should also ease pressure from inequitable distribution of quotas as local population recruitment will improve. However, for an age-based system to be applied effectively, hunters must be able to age (and sex) leopards reliably in the field. To date, age determination of leopards has been restricted to the examination of tooth eruption and wear [20], which can only be applied after rather than before an animal is hunted.

In this study, we conduct a structured survey comprising photographs of known-age leopards to assess the ability of wildlife practitioners to sex and age leopards correctly. Contemporary hunters routinely use remotely-triggered cameras to judge the trophy quality of leopards [21]; hence, a photographic survey should provide a reasonable reflection of aging proficiency, as well as demonstrate the age classes hardest to distinguish and the conditions that facilitate accurate aging. We also evaluate the utility of four phenotypic traits for use by trophy hunters to age male leopards in field conditions. The results of the photographic survey indicate the *current* aging ability of hunters while our age determination exercise reveals *potential* aging ability. Finally, we review online trophy galleries to determine whether our aging criteria are pervasive across leopard range.

Methods

Photographic Survey

High resolution (minimum 300 ppi) photographs of 31 known-age and sex leopards were sourced from a long-term study in the Sabi Sand Game Reserve (midpoint: 31°29' E, 24°49' S) adjacent to the Kruger National Park, South Africa. This population has been monitored intensively for >30 years [22,23] and only photographs of individuals first viewed at <4 months old were included. The survey consisted of two sections; a sexing component comprising 14 photographs of male and female leopards, and an aging component with 44 photographs of male leopards only (Fig. S1). Two types of photograph presentation were used; portrait photos showing the full face of the leopard including the ears (Fig. 1A), and side-profile photos showing the entire body (Fig. 1B). In the first section, participants were asked only to identify photographs as either male or female leopards. In the second section, participants were asked to assign male leopards to one of four age classes: i) <2 years, ii) 2–3 years, iii) 4–6 years, and iv) ≥7 years. The four age classes were represented roughly equally throughout the survey. After thorough pre-testing, the survey was sent to wildlife practitioners from three different professions: i) professional hunters (clients undertaking leopard hunts must be accompanied by a certified professional hunter), ii) photo-tourism guides, and iii) professional felid biologists. Survey participants were randomly selected from the membership lists of national professional hunting (including at least 10 representatives from each of the seven main leopard-hunting countries [15]) and guiding (from South Africa, Zimbabwe and Botswana) associations, and the IUCN Cat Specialist Group (only African-based members) and African Lion Working Group. In addition to sexing and aging leopards, participants were asked to provide information on where they had worked in Africa, the number of years they had worked in their respective fields, and for hunters only, the number of leopards they had successfully hunted. The survey data were analysed anonymously.

We used univariate analyses to explore how the aging proficiency of respondents was affected by profession, age class of leopards, and type of photograph presentation. In addition, we

used generalized linear models with a binary logistic response to assess the likelihood of respondents assigning photographs to the correct sex and age categories. Included as predictors were the profession of the respondent (hunter, guide or biologist), respondent experience (number of years), the age class of the photograph (for sexing, five categories were used - the four male age classes plus female), and the type of photograph presentation (portrait, side-profile, and for aging analyses only, paired photos where both portrait and side-profile photos of the same individual at the same age were presented). Respondent identity was included as a random factor. We used odds ratios to measure effect size and the Wald statistic to gauge levels of significance [24]. Model fit was evaluated by assessing residual deviance and likelihood ratio tests [24]. We also applied generalized linear models to hunters separately to determine whether discrepancies existed between this subset of the data and the total sample. We substituted years of experience with number of leopards hunted as a predictor since they were strongly correlated (Pearson's correlation coefficient = 0.515, $P < 0.001$).

Age Determination

We collated 97 paired photographs of 41 known-age male leopards from the Sabi Sand GR displaying facial features and body dimensions. The following phenotypic traits were scored on a sliding scale (Fig. 1): i) extent of facial scarring, from 1 (no scarring evident, the fur above the muzzle appears smooth and glossy) to 5 (heavily scarred, fur has thinned and appears pock-marked); ii) ear condition, from 1 (no wear, ear lobe intact) to 5 (heavily worn, ear lobe extensively notched; the scores for each ear were added, resulting in a maximum score of 10); iii) nose colour, categorised into four classes (pink, pink-grey, pink-spotted, and black; Fig. S2); and iv) dewlap size, scored from 1 (no dewlap visible) to 5 (well-developed dewlap easily recognisable extending from the underside of the maxilla to the upper chest). Two graduate students unfamiliar with the study scored 48 photographs to test repeatability of the method [25]. Their scores were comparable to those given by GB ($F_{47, 96} = 37.72$, $P < 0.001$, $R = 0.924$), suggesting repeatability was high.

To reduce interrelatedness among variables and avoid redundancy in subsequent analyses, we ran a principal component analysis (PCA) based on a correlation matrix of the four phenotypic traits assessed. The factor scores of the first PCA axes that explained >80% of the cumulative data variation were then applied in a discriminant analysis (DA) to determine whether the phenotypic traits could be reliably used to assign male leopards to their respective age classes [26]. The discriminant model was built using a randomly selected 70% of the dataset. The remaining 30% of the data were used to validate the model [26]. Accuracy was assessed by computing the proportion of correctly classified individuals. The likelihood of successful classification can be influenced by the *a priori* probabilities of an observation belonging to a discriminant class; hence, we assumed equal probability of a leopard belonging to any age class (i.e. probability = 0.25 for each age class [27]). When an individual contributed two or more pairs of photographs from the same age class, we averaged its PCA factor scores before including it in the DA, thus avoiding pseudoreplication [26]. We also conducted a separate DA using dewlap size as the only predictor.

We calculated all analyses and statistical comparisons using SPSS 19.0 (SPSS, Chicago, USA). Significance was measured at $P \leq 0.05$ and two-tailed. We tested all variables for normality and used non-parametric tests where data could not be normalized. We present means with standard error as a measure of precision.

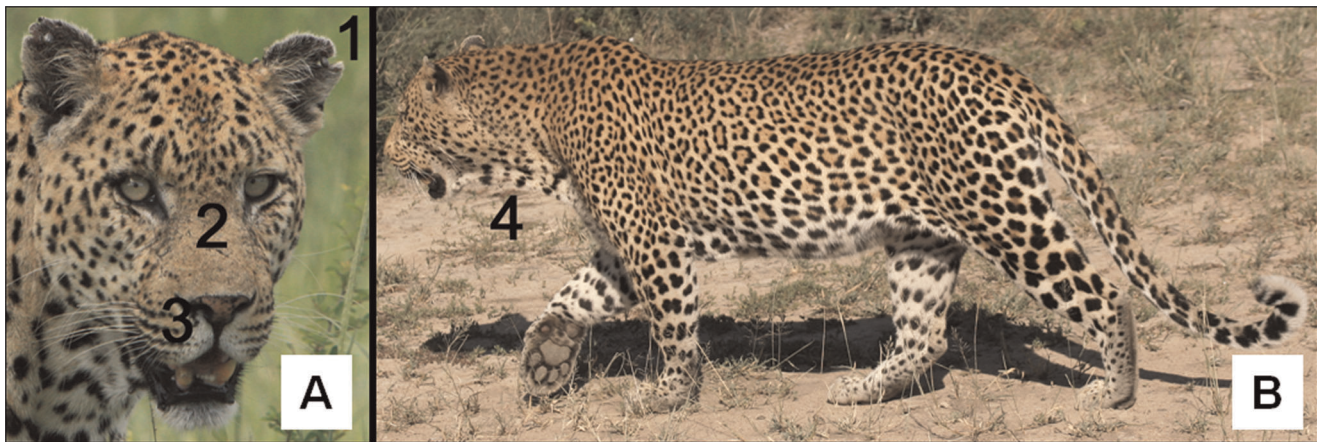


Figure 1. Photograph presentation types used in the survey to test sexing and aging ability. (A) Portrait photo of a 10.3-year male leopard showing the condition of the ears (1; score = 9), facial scarring (2; score = 3) and nose pigmentation (3; score = pink-spotted); (B) side-profile photo of a 7.5-year male showing dewlap size (4; score = 5) (photo credits: A. Bachelor).
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Results

Photographic Survey

The survey was sent out to 357 people and completed by 225 participants (guides: $n = 96$, biologists: $n = 59$, hunters: $n = 70$). Overall, respondents were more successful at sexing leopards (mean percentage correct [MPC] = 68.95 ± 0.76) than at aging male leopards (MPC = 47.98 ± 0.57 ; $Z = -12.749$, $P < 0.001$). Sexing proficiency was similar among professions (guides: MPC = 70.16 ± 1.08 , biologists: MPC = 68.64 ± 1.27 , hunters: MPC = 67.55 ± 1.62 ; $\chi^2_2 = 1.712$, $P = 0.425$) and types of photograph presentation (portrait: MPC = 69.72 ± 0.94 , side profile: MPC = 67.93 ± 1.09 ; $Z = -1.116$, $P = 0.264$) but varied between age classes ($\chi^2_3 = 404.796$, $P < 0.001$). Respondents misidentified 73% of <2 year males as females (Fig. 2). In contrast, $>90\%$ of male leopards in the 4–6 year and ≥ 7 year age classes were sexed correctly (Fig. 2).

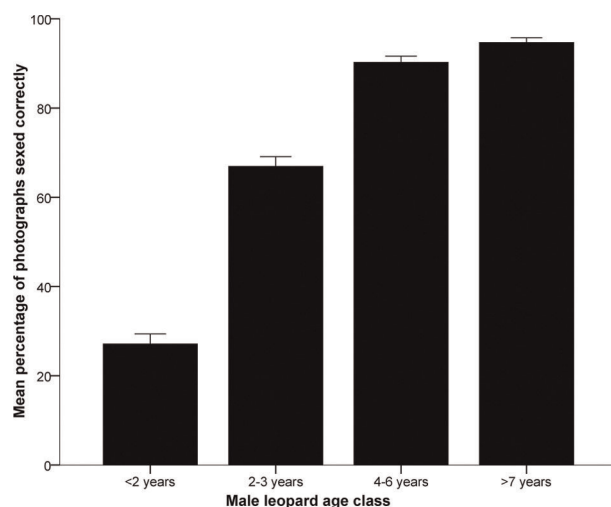


Figure 2. Mean percentage of male leopard photographs in different age classes sexed correctly by survey respondents. Bars show standard error ($n = 225$).
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Our logistic regression models supported the results of the univariate analyses by suggesting that male leopard age was the only significant factor affecting sexing ability (Table 1). Male leopards in the <2 age class reduced sexing accuracy (odds ratio = 0.140, $\chi^2_1 = 200.054$, $P < 0.001$), while males in the 4–6 year age class (odds ratio = 4.464, $\chi^2_1 = 77.460$, $P < 0.001$) and ≥ 7 year age class (odds ratio = 8.592, $\chi^2_1 = 96.932$, $P < 0.001$) improved sexing ability. The ratio of residual deviance to degrees of freedom was 0.905, suggesting no over dispersion, and the fitted model differed from the intercept-only model (likelihood ratio $\chi^2_{11} = 643.206$, $P < 0.001$). Male leopard age remained the only significant predictor when we analysed hunters separately (Table S1).

Respondent aging ability varied among professions ($F_{2, 224} = 3.674$, $P = 0.027$). Hunters (MPC = 46.04 ± 0.85) performed poorly compared to guides (MPC = 49.51 ± 1.00 ; $P = 0.028$) but were similar to biologists (MPC = 47.78 ± 0.93 ; $P = 0.433$). Aging proficiency also varied depending on age classes ($\chi^2_3 = 77.695$, $P < 0.001$). Respondents were more successful at distinguishing male leopards in the 4–6 year (MPC = 53.24 ± 1.06) and ≥ 7 year (MPC = 54.40 ± 1.34) age classes than in the <2 year (MPC = 42.41 ± 1.41) and 2–3 year (MPC = 40.03 ± 1.04) age classes (Fig. 3). Respondents were also more likely to correctly age portrait photographs (MPC = 60.18 ± 0.93) than side-profile (MPC = 42.80 ± 0.76) or paired photographs (MPC = 35.68 ± 1.18 ; $\chi^2_2 = 185.297$, $P < 0.001$).

Table 1. Results of generalized linear models assessing the likelihood of survey respondents correctly identifying the sex of leopards in photographs.

Predictor	Wald chi-squared	Degrees of freedom	P
Respondent profession	1.161	2	0.560
Respondent experience	3.135	4	0.536
Leopard age class	452.716	4	<0.001
Photograph presentation	2.043	1	0.153

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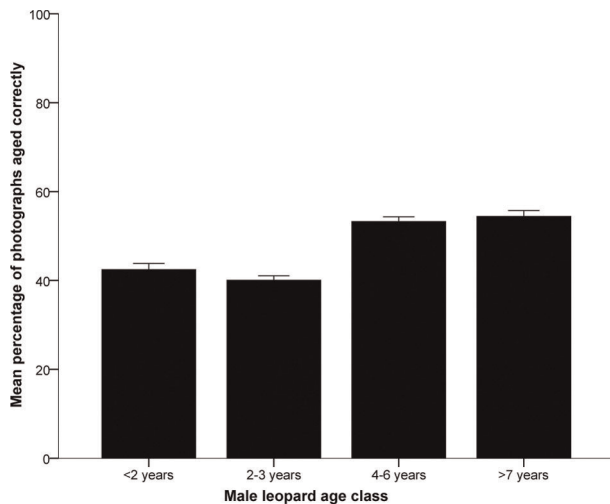


Figure 3. Mean percentage of male leopard photographs assigned to their correct age classes by survey respondents. Bars show standard error ($n = 225$). doi:10.1371/journal.pone.0035209.g003

Our logistic regression models suggested that respondent profession, male leopard age, and photograph presentation were all significant predictors of aging ability (Table 2). Hunters were the worst affected of the three professions, significantly reducing the likelihood of a correct answer (odds ratio = 0.858, $\chi^2_1 = 5.747$, $P = 0.017$). Male leopards in the 4–6 age class (odds ratio = 1.602, $\chi^2_1 = 52.125$, $P < 0.001$) and the ≥ 7 year age class (odds ratio = 1.681, $\chi^2_1 = 63.301$, $P < 0.001$) were more likely to be aged correctly, as were portrait photographs (odds ratio = 1.988, $\chi^2_1 = 188.517$, $P < 0.001$). Model fit was good (ratio of residual deviance to degrees of freedom = 1.492; likelihood ratio $\chi^2_{11} = 466.792$, $P < 0.001$). Male leopard age and photograph presentation remained as significant predictors when we analysed hunters separately (Table S2).

Age Determination

All four phenotypic traits varied between age classes (dewlap size: $\chi^2_3 = 53.309$, $P < 0.001$; facial scarring: $\chi^2_3 = 29.396$, $P < 0.001$; ear condition: $\chi^2_3 = 47.112$, $P < 0.001$; nose pigmentation: $\chi^2_3 = 18.018$, $P < 0.001$). Post hoc analyses revealed significant differences between the ≥ 7 year age class and all other age classes for dewlap size ($P = 0.002$) and ear condition ($P < 0.001$). Male leopards ≥ 7 years old generally had well developed dewlaps; only one individual in this age class ($n = 15$) had a dewlap score of less than 4 (Fig. 4A). Ear condition

Table 2. Results of generalized linear models assessing the likelihood of survey respondents assigning photographs of male leopards to their correct age class.

Predictor	Wald chi-squared	Degrees of freedom	P
Respondent profession	6.003	2	0.050
Respondent experience	2.446	4	0.654
Leopard age class	125.634	3	<0.001
Photograph presentation	312.133	2	<0.001

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varied considerably among ≥ 7 year old leopards but usually at least one ear showed some degree of wear, whereas in younger age classes there was little wear (Fig. 4B). Facial scarring tended to increase with age but there was considerable overlap between the 4–6 year and ≥ 7 year age classes (Fig. 4C). Only black and pink-spotted noses were observed in the ≥ 7 year age class, but these pigmentation categories were also found in other age classes (Fig. 4D).

The first two factors of the PCA explained $>80\%$ of the data variation and were included in the DA. The first factor primarily represented dewlap size, ear condition, and facial scarring and accounted for 70% of variance (eigenvalue = 2.814). The second factor mainly represented nose pigmentation and only accounted for 16% of variance (eigenvalue = 0.649). Only factor 1 contributed significantly to the DA (Wilk's Lambda = 0.137, $F_{3, 45} = 94.637$, $P < 0.001$), not factor 2 (Wilk's Lambda = 0.948, $F_{3, 45} = 0.825$, $P = 0.487$). Similarly, only the discriminant function strongly correlated to factor 1 (structure correlation coefficient = 1.000) was statistically significant (Wilk's Lambda = 0.130, $\chi^2_6 = 91.885$, $P < 0.001$), explaining 99% of the discriminatory power of the model (eigenvalue = 6.309). Overall, our general model classified 67% of cases correctly, with success rates ranging from 50% for the 4–6 year age class to 83% for the ≥ 7 year age class (Table 3). Our validation model showed a 7% reduction in overall success but classification rates for the ≥ 7 year age class remained high (100%). Classification rates for our reduced discriminant model using dewlap size as the only predictor were similarly high for male leopards ≥ 7 year old (91–100%).

Discussion

Sexing Leopards

The superior ability of respondents to sex rather than age leopards is unsurprising given the genus *Panthera* exhibits the most striking sexual dimorphism among extant wild felids [28]. In our study area, adult male leopards weigh at least 60% more than females [29] and the same is true across most of the species' range [30]. Such marked size dimorphism extends to the cranial morphology (males have longer and broader skulls than females), body length, neck circumference, chest girth, and shoulder height of leopards (Table S3). Although it is difficult to gauge body size from photographs, the relative dimensions are clearly apparent. Our survey showed that almost all respondents could differentiate mature (≥ 4 years) male leopards from females. In contrast, there was considerable confusion in distinguishing females from <2 year old males. At this age, male leopards superficially resemble females; they are a similar size (Table S3) and lack many of the distinctive features of adult males (e.g. well-developed chest and neck musculature, a prominent dewlap, etc.). None of the photographs in our survey displayed primary sexual characters (i.e. the scrotum or nipples). Although hunters may be able to use the external genitalia to distinguish young male leopards from females, the scrotum tends to become more conspicuous with age, and it may not be immediately obvious in males <2 years old (G. A. Balme personal observation).

Aging Male Leopards

Respondents performed poorly at aging male leopards, with less than 50% of photographs classified correctly. Hunters recorded the lowest scores, which presumably reflects the relative amount of time they spend observing leopards. A professional hunter will rarely lead >5 leopard hunts a year (and usually only 1–3

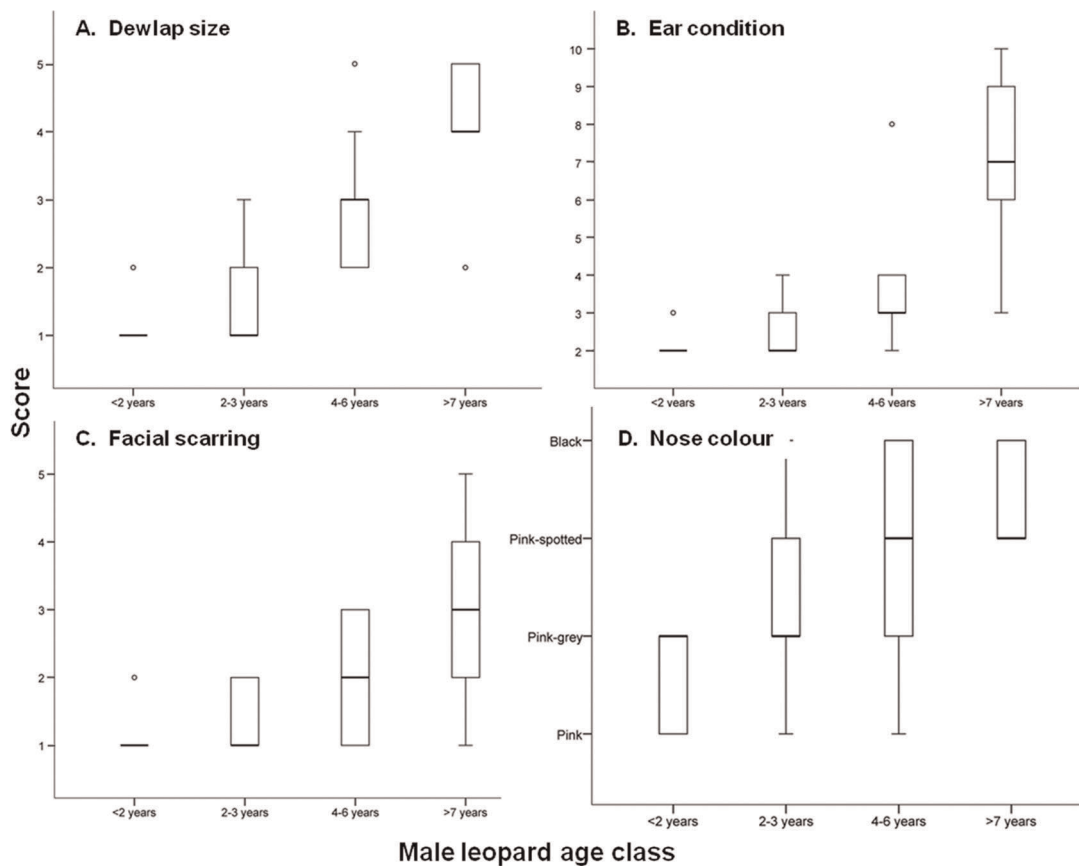


Figure 4. Relationships between four phenotypic traits and age classes of male leopards. Boxes indicate the lower, median and upper quartiles, vertical lines represent the sample minimum and maximum, and open circles correspond to outliers.
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depending on the country), whereas photo-tourism guides may view leopards weekly, or in some areas like our study site, daily [22]. Biologists also typically do not observe leopards on a regular basis, although they are at least likely to be familiar with the aging cues associated with felids since many are shared among species [31]. Importantly, our multivariate analyses showed that aging (and sexing) ability was not related to levels of experience; hence, with appropriate training, it should be possible to educate hunters and other wildlife practitioners to age leopards more reliably [32,33].

Portrait photographs appeared to increase aging proficiency. This may be due to the larger number of aging cues exhibited in portrait photos compared to side-profile photos. Portrait photographs show the condition of the ears, facial scarring, nose pigmentation, the relative 'broadness' of the skull, and occasionally tooth wear of leopards. In contrast, side-profile photos only show relative body dimensions and dewlap size (though our age determination analyses suggest this should be sufficient). We expected that paired photos should perform the best as they present the most cues but this was not the case in our study. There

Table 3. Relative success rates of discriminant models classifying male leopards into their respective age classes based on principal component factor scores for dewlap size, ear condition, and facial scarring.

Age class	Full model (predictors: dewlap size, ear condition, facial scarring)		Reduced model (predictors: dewlap size)	
	General	Validation	General	Validation
<2 years	66.7 (15)	83.3 (6)	84.6 (13)	100.0 (8)
2–3 years	64.3 (14)	50.0 (6)	25.0 (16)	25.0 (4)
4–6 years	50.0 (8)	20 (5)	27.3 (11)	50.0 (2)
≥7 years	83.3 (12)	100.0 (3)	90.9 (11)	100 (4)
Total	67.3 (49)	60.0 (20)	54.9 (51)	77.8 (18)

Discriminant functions were built using 70% of the data with the remainder used to validate models. Rates are presented as percentages with samples sizes in parentheses.

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is no obvious explanation for this result except perhaps that respondents focused mainly on the larger, side-profile photograph in paired examples, indicating a potential flaw in the survey design.

Respondents were more successful at distinguishing leopards in adult age classes (4–6 years and ≥ 7 years) than subadults (2–3 years) or juveniles (< 2 years). Our discriminant models confirmed that ≥ 7 year old males were the easiest to identify but, contrary to the results of the survey, 4–6 year males registered the most misclassifications. The classification rate recorded for this age class in the general model (50%) was nevertheless similar to that achieved by respondents in the survey (53%), suggesting that our aging methodology is unlikely to improve hunters' ability to recognise 4–6 year old leopards. However, there appears considerable scope for improvement among the other age classes. Classification rates in the full model were significantly higher for < 2 year, 2–3 year, and ≥ 7 year males than the respective scores attained by respondents in the survey.

The condition of the ears, facial scarring, and dewlap size were all related to the significant discriminant function in our model; only nose colour appeared a poor predictor of male leopard age. It is worth noting that we did not measure the extent of nose pigmentation quantitatively as was done for lions *Panthera leo* [8]; we simply categorised the overall colour of noses visually. This method is admittedly susceptible to human error or subjective differences of opinion. However, our goal was to determine whether hunters could use nose colour and the other phenotypic traits assessed as mechanisms to reliably age leopards in the field. Moreover, we demonstrated that repeatability among observers was high. Therefore, we feel that our method of visual assessment was valid within the context of our study.

Most leopards are hunted over baits at a distance of 50–80 m in low light conditions (regulations vary between countries regarding the legal timing of hunts and use of artificial lighting [34,35]). It may be impractical for hunters to assess the facial characteristics of leopards under such circumstances (although the increasing use of remotely-triggered cameras by hunters should facilitate this). However, the dewlap is a conspicuous feature easily discernible from a distance. Our analyses showed that there was little overlap in dewlap size between ≥ 7 year males and younger age classes. Furthermore, our reduced discriminant model demonstrated that dewlap size on its own was a reliable predictor of male leopard age. We identified males with well-developed dewlaps in all of the main leopard hunting countries during our online review of trophy galleries (Fig. 5). The ages of trophy leopards were not known but, in instances where these cues were visible, the condition of the ears and facial scarring often correlated with dewlap size. Our results therefore suggest that at least in the savanna regions of East and southern Africa where most leopards are hunted [15], dewlap size could be used as a practical criterion to identify suitably-aged individuals. Further site-specific research is nevertheless required regarding the relationship between dewlap size and age, particularly from forest and semi-arid environments where leopard morphology varies considerably from savanna habitats [30]. Dewlap size is related to physical condition in some species (e.g. Bali cattle *Bos javanicus* [36]) and the same may be true in leopards (Fig. S3). However, this will not affect its usefulness in improving hunter selectivity; some old leopards in poor condition may be overlooked but it will not result in younger animals being harvested.

Conservation Implications and Recommendations

It is illegal in most countries (with South Africa being a notable exception) to hunt female leopards, but compliance appears low. Genetic analyses showed that females comprised 27% of 77 leopard trophies shot in Tanzania between 1995 and 1998, even

though only males are legally harvested there [17]. Our review of trophy galleries also revealed a remarkable number of hunted female leopards on hunting company websites (and this is an optimistic representation of trophy quality as operators are likely to display their best specimens for marketing; Fig. S4). According to our survey results, stipulating a minimum trophy age of ≥ 7 years for male leopards will essentially eliminate the possibility of hunters mistakenly harvesting females. Several polygynous felids are resilient to disturbance if the prime reproductive female life-stage remains intact [37,38]. Since one male can mate with numerous females, fewer males are required to maintain the same levels of reproduction. Hunting adult females carries the additional risk of dependent cubs dying when their mother is killed [6]. Male leopards also disperse over greater distances than females [29], enabling more efficient replacement of hunted individuals. A population viability analysis conducted for the South African leopard population showed that risk of extinction almost doubled when females were included on quota [34]. The '7-year age rule' for leopards was also derived under the assumption of a male-only harvest [9].

The overall predictive power of our discriminant models (55–67%) was mediocre (although they were at least as accurate as others proposed to age carnivores [26,39,40]), but confidence levels for discerning males ≥ 7 years old were high (83–100%). This suggests that a minimum age threshold for leopard trophies could practically be applied to ensure sustainable hunting. However, it would require strict enforcement by government authorities to be effective [41]. The age of every leopard trophy will have to be independently validated. The same criteria used by hunters to estimate leopard age can be used by authorities to evaluate trophies (with the addition of tooth wear; see Fig. S5). Unsuitable trophies (a female leopard or male < 7 years old) can be confiscated [4]. Alternatively, hunting operators that take unsuitable trophies could be penalised by a reduction in quota the following year, while operators that harvest suitably-aged individuals can be rewarded with an increase in quota the following season. Such an incentive-based approach has been used to regulate trophy hunting of lions in Niassa National Reserve in northern Mozambique [42]. Hunting oftakes in Niassa have subsequently declined to sustainable levels, trophy quality has improved and the local lion population has increased [42]. The production of a comprehensive leopard aging guide (similar to that compiled for lions [31]) should help improve the aging ability of hunters. Leopard aging techniques could also be incorporated in the curricula of appropriate hunting courses with the successful completion of an examination a prerequisite for licensing (as is the case in the United States for mountain lions *Puma concolor*; <http://wildlife.state.co.us/Hunting/HunterEducation/MtnLionEduc/Pages/MountainLionExam.aspx>, accessed November 2011).

The implementation of age-based hunting regulations for leopards would not necessarily disadvantage hunters. Provided age-limits are strictly adhered to, the number of animals available to hunt (≥ 7 year old males comprised roughly 8% of our study population; G. A. Balme unpublished data) exceeds that proposed for sustainable population-based quotas (3.8% of the population [5]). Indeed, Whitman et al. [8] showed that the cumulative number of 'high-quality' lion trophies harvested was greatest when recommended age minimums were adhered to. The minimum length of leopard safaris (mean = 10–14 days [43]) could also be extended to accommodate the increased selectivity demanded of hunters. Individual operators stand to gain as their clients are typically charged a daily rate regardless of whether hunts are successful.

The results of our study have implications that extend beyond hunting. Age determination is an important prerequisite for most

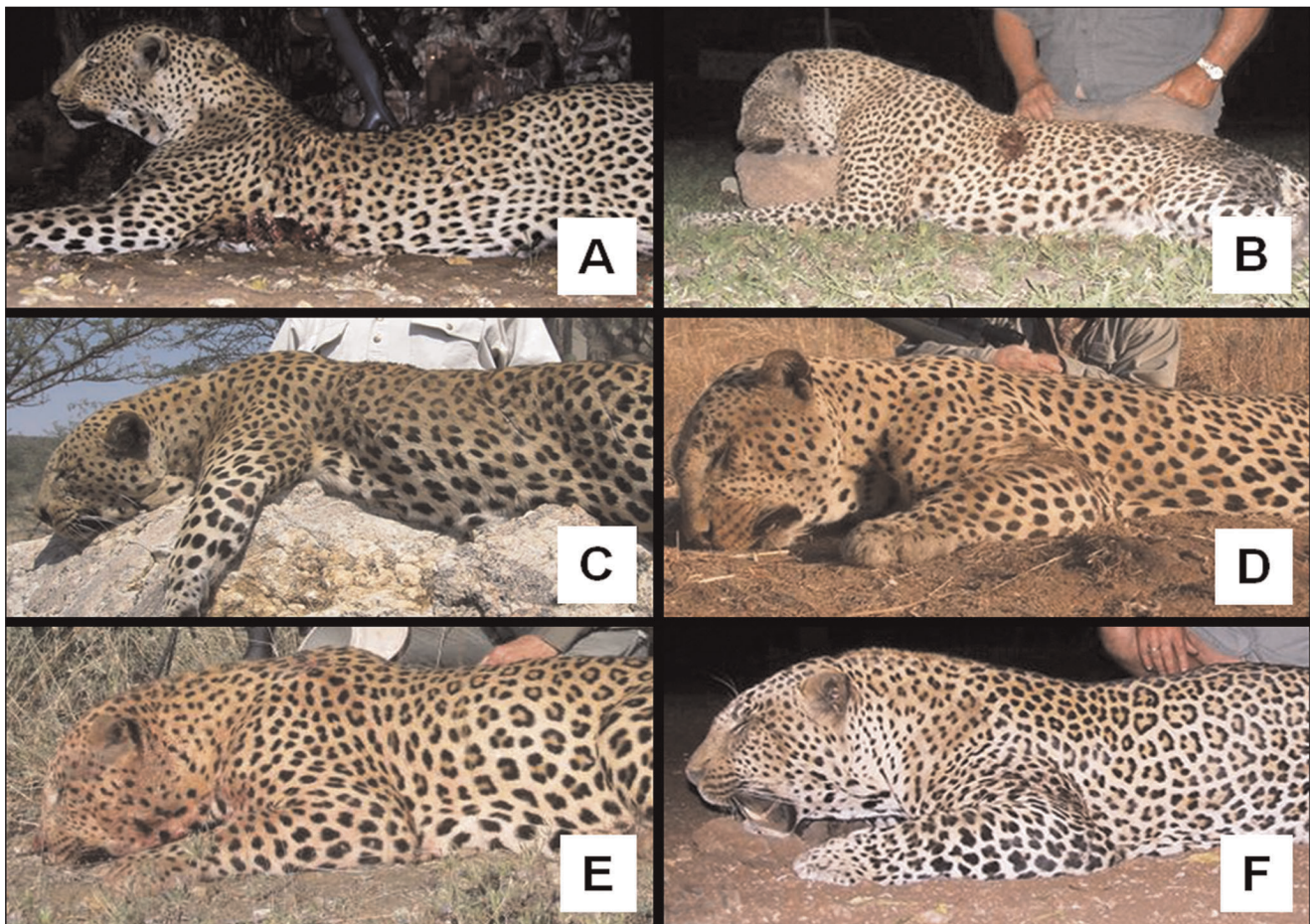


Figure 5. Examples of male leopard trophies exhibiting well-developed dewlaps from the main leopard hunting countries. (A) Botswana; (B) Mozambique; (C) Namibia; (D) Tanzania; (E) Zambia; (F) Zimbabwe. These countries (with the addition of South Africa) are permitted under the Convention for the International Trade in Endangered Species (CITES) to export >100 leopard trophies annually from hunting [15]. doi:10.1371/journal.pone.0035209.g005

large carnivore research. Variation in life history traits is closely related to age, as is the social behaviour and spatial patterns of individuals [6,29]. Our aging criteria provide an accurate and non-invasive method for aging leopards easily replicable across sites. Camera-trap surveys are widely used to estimate leopard abundance [14,44,45] and our methodology enables a robust assessment of population structure as well as size. It can similarly be used to estimate the age of telemetered individuals or leopards captured during problem-animal-control operations. Such knowledge is vital to understanding population dynamics and informing management activities.

For trophy hunting to serve as a conservation tool, it is essential that it be conducted in a manner that is scientifically robust and sustainable in the long term [46]. We demonstrate that the potential exists for the practical application of an age-based hunting system for leopards, which would reduce the risks of over-harvest and deleterious impacts on hunted populations. Hunting operators also stand to benefit as trophy quality is likely to improve (without necessarily an associated reduction in quota) and longer hunts can be offered. However, the successful implementation of an age-based hunting approach requires major reform within the regulatory framework and among the hunting industry. It remains to be seen if such changes are realistic.

Supporting Information

Figure S1 Survey used to test the ability of wildlife practitioners to sex and age leopards. The survey comprises three sections: 1) respondents must sex photographs of male and female leopards, 2) respondents must assign single photographs of male leopards to one of four age classes (<2 years, 2–3 years, 4–6 years, or ≥ 7 years), and 3) respondents must assign paired photographs of the same individual male leopard to their respective age class. (PDF)

Figure S2 Examples of nose colour categories used in the age determination analyses. (A) 11-month male: nose colour category = pink; (B) 2.8-year male: nose colour category = pink-grey; (C) 5.3-year male: nose colour category = pink-spotted; (D) 9.0-year male: nose colour category = black. (TIF)

Figure S3 Effect of body condition on dewlap size in male leopards. The same individual male leopard camera-trapped in July 2009 (A) and August 2010 (B) in Niassa National Reserve, Mozambique (Photo credits: Niassa Carnivore Project). It is unknown what caused the deterioration in condition. (TIF)

Figure S4 Examples of leopard trophies from different countries exhibited on hunting company websites that are likely females or <2 year males. (A) Botswana; (B) Mozambique; (C) Namibia; (D) Tanzania; (E) Zambia; (F) Zimbabwe. (TIF)

Figure S5 Protocol for collecting data from trophy hunted lion and leopard. (TIF)

Table S1 Results of generalized linear models assessing the likelihood of professional hunters correctly identifying the sex of leopards in survey photographs. (DOC)

Table S2 Results of generalized linear models assessing the likelihood of professional hunters assigning photographs of male leopards to their correct age class. (DOC)

Table S3 Morphological measurements of radio-collared leopards from the Phinda-Mkhuze Complex (PMC) in northern KwaZulu-Natal, South Africa [19]. (DOC)

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Author Contributions

Conceived and designed the experiments: GB LH. Performed the experiments: GB. Analyzed the data: GB AB. Contributed reagents/materials/analysis tools: GB. Wrote the paper: GB LH AB.

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Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food

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Abstract

Many areas have experienced disproportionate increases in the number of conflicts between large carnivores and humans, and this is especially true in western North America where urban sprawl has encroached into regions that have historically contained large carnivores. Yet, globally there is a paucity of studies of temporal changes in behavioural and ecological parameters of carnivores associated with human-induced perturbations at the same location. We capitalized on the extent to which human population growth and its coincident food stores offer a quasi-experimental setting to test hypotheses about the impact of novel food resources. Using black bears *Ursus americanus* and garbage, measures of behaviour and ecology were contrasted between individuals living in urban–wildland interface (‘experimental’) and in wildland (‘control’) settings at the interface of the Sierra Nevada Range and the Great Basin Desert in the western United States. A temporal dimension was included by comparing our data to those from the same population lacking areas of human encroachment 10–15 years earlier. Specifically, an examination was made of the impacts of garbage on bear time budgets, patterns of activity, and den chronology. Individuals at urban interface areas relative to wildland conspecifics were: (1) active for significantly fewer h per day (8.5 vs 13.3 h; $P < 0.01$); (2) shifted their activities to nocturnal periods ($P < 0.001$); (3) entered dens significantly later and remained in them for significantly fewer days ($P < 0.05$). Our results are contrasted with selected carnivores from sites where attendant changes in behaviour and ecology have accompanied landscape changes associated with human activity. Our findings suggest alterations in carnivore ecology may be rapid and occur within shorter periods than had been previously assumed.

Key words: *Ursus americanus*, behaviour, human-altered landscapes

INTRODUCTION

As the world’s human population increases, the resulting patchwork of urban sprawl and modified environments will dominate most landscapes (Western, 2001). The maintenance of biological diversity at the urban–wildland interface will be a challenge because for some taxa, including carnivores, populations tend to decrease as human influences increase (Vucetich & Creel, 1999; Woodroffe & Ginsberg, 2000). Little information is available about how carnivores co-exist with humans and the extent to which, if any, behavioural adjustments occur. This is particularly true if we restrict our analyses to situations not associated with livestock as the disturbance.

In some places, perturbations have compromised the viability of wildlife populations. Corbett (1995) reported that domestic dogs associated with human encroachment into areas of Australia have threatened dingoes *Canis lupus dingo* through hybridization. The introduction of domestic livestock and pets has led to an increase in diseases in some carnivore populations (e.g. Gascoyne *et al.*, 1993; Roelke-Parker *et al.*, 1996). In western North America for example, the presence of garbage in suburbs has led to a tremendous recent increase in the number of conflicts between humans and black bears *Ursus americanus* (e.g. Beckmann, 2002; Beckmann & Berger, 2003). Additionally, bears in Yellowstone have taken advantage of garbage for > 100 years (see Craighead, Sumner & Mitchell, 1995). Further, the supplemental feeding of deer in some areas of western North America has concentrated animals near urban centres. As a result, humans may be inadvertently, but rapidly, altering the distribution of cougars *Puma concolor*, an issue that clearly

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warrants further attention. A comprehensive understanding of the impacts of urban sprawl on carnivores will not only require information on spatial and demographic parameters of populations (e.g. Torres *et al.*, 1996; Ferreras *et al.*, 2001), but also data on the behaviour of individuals living inside and adjacent to these urban areas.

Effects of urban environments on the home-range size and activity patterns of meso-carnivores, most notably coyotes *Canis latrans*, have been determined (Andelt & Mahan, 1980; Shargo, 1988; Quinn, 1995; Grindler & Krausman, 2001). For larger carnivores, shifts in behaviour for species such as brown bears *Ursus arctos* in areas with high rates of contact with humans have been documented (Mattson, Knight & Blanchard, 1987; Mattson, Blanchard & Knight, 1992; Olson, Gilbert & Squibb, 1997; Gibeau *et al.*, 2002). Bears avoided areas with high road densities, salmon streams near lodges during extended lodging seasons, and mortality rates were significantly higher in areas of contact with humans.

Black bears are generally thought to shift to crepuscular and nocturnal activity when daylight activities are disrupted (Reimchen, 1998). The principal factors currently thought to promote this shift are the presence of either humans or brown bears and the role of food. Although ecologists have suggested that shifts in behaviour and activity patterns occur for black bears in areas with high levels of human activity, most of the evidence is anecdotal and few, if any, comparative studies exist or have been published.

The effect of a novel food resource (i.e. garbage) on the behaviour of black bears was assessed in urban interface areas in two ways: (1) using both spatial and temporal contrasts; (2) focusing on contact zones involving black bears and humans at the Sierra–Great Basin interface in Nevada in western North America.

As urban food resources are being exploited for the first time, changes in behaviour and ecology may occur because garbage alters the abundance and distribution of food at a landscape level. In an area where food is limited, introduction of garbage should result in shorter periods of foraging activity on a daily basis, and shorter periods in dens (Schooley *et al.*, 1994). Garbage is a good resource for bears because: (1) it is always available regardless of season or environmental conditions; (2) it is predictable in both space and time (i.e. trash cans were always set out the same day of the week); (3) it is highly clumped (e.g. in residential areas) so that little energy is required to move from patch (i.e. dumpster) to patch; (4) it is always replenished after use. We assumed, *a priori*, that urban interface areas would not be food or resource limited, whereas surrounding wildlands would be. We predicted that urban bears would shift to nocturnal activity owing to disruption of activities by humans during diurnal periods.

Study area and species

Black bears are large (50–200 kg) carnivores that have the capacity to kill ungulates, but primarily survive as omnivores subsisting on vegetation. Their current

distribution in Nevada is restricted to the Carson Range of the Sierra Nevada, Sweetwater Range, Pine Nut Range, and the Wassuk Range in extreme western Nevada. These four mountain ranges cover an area of *c.* 1400 km² and are characterized by steep topography with high granite peaks, deep canyons and are separated by desert basins that range from 15 to 64 km across (Grayson, 1993). These desert basins are often large areas of unsuitable desert habitat (e.g. large expanses of sagebrush *Artemisia* spp.) that bears do not use in the western Great Basin Desert (Goodrich, 1990; Beckmann, 2002). However, bears will occasionally make relatively short movements through areas comprised of sagebrush to reach patchily distributed suitable habitat (e.g. cone-producing trees) in this arid landscape. Historically, black bears in Nevada enter dens in mid-November and emerge from March to April (Goodrich, 1993).

MATERIALS AND METHODS

Bears were captured in culvert traps (Teton Welding, Chateau, Montana) from 1 July 1997 to 1 April 2002 and tranquilized with a mixture of Telazol/Xylazine. Each bear was weighed and radio-collared with mortality sensors were attached to adults (Advanced Telemetry Systems, Isanti, Minnesota). Age was estimated from annuli of the first upper premolar (PM₁), the tooth that is routinely removed for age analysis in black bears (Matson's Laboratory, Milltown, Montana; Stoneberg & Jonkel, 1966) and animals were classified as cubs (< 1.5 years), juveniles (1.5–3 years) or adults (> 3 years). All research was conducted under the University of Nevada, Reno Animal Care and Use Protocol no. A99/00–02. Bears wore radio-collars from 1 July 1999 until they were removed in June 2002.

Animals were located weekly, weather permitting, from a Cessna 206 fixed-wing airplane from 1 July 1999 to 1 April 2002, and from the ground. Most flights occurred from 05:00 to 16:00 Pacific Standard Time. Universal Transverse Mercator coordinates were assigned to each location from a global positioning system unit on-board the aircraft.

A priori bears were considered urban individuals if $\geq 90\%$ of their location points were inside urban areas (defined by town and city delineation on coverage maps in ArcView 3.2 software) and wildland bears if $\geq 90\%$ of their locations were outside urban areas (Carson City, Incline Village, Glenbrook, Stateline, Minden, and Gardnerville, Nevada and South Lake Tahoe, California). Urban bears were captured in each of these cities, while wildland bears were trapped in the 4 adjacent mountain ranges (see above) outside of city limits. Trapping was specifically designed to catch 2 different types of bears, those entirely in urban areas and those outside urban areas. Based upon our operational definition, there was never a questionable case whether a bear was an urban or wildland individual. As evidence of this, urban bears almost always had 100% of their location points within urban areas, whereas wildland bears almost always had 100% of their

location points outside urban areas (Beckmann & Berger, 2003). Urban bears were truly urban, as 6 of them denned under the decks of homes in the Lake Tahoe basin and 29 urban bears denned within 100 m of a building structure inside city limits.

Patterns of activity and time budgets

Ten adult urban and 10 adult wildland bears were followed for 24-h and the number of active hours recorded at 30-min intervals (beginning at 05:00) for a total of 48 data points per individual. Twenty individual bears were followed for 24 h each resulting in 480 h of observations (20 individuals \times 24 h). Of the 20 bears, 5 were urban males, 5 urban females, 5 wildland males, and 5 wildland females. If a bear was lost during a 24-h sampling period, the data were discounted and a new 24-h sampling period begun; this happened 4 times. Bears were considered active at the beginning of each hour in which a movement was first recorded. For example, if a bear moved between data collection points at 09:30 and 10:00, then the bear was considered to have begun activity during the 09:00 h.

If a bear remained in the same spot for > 2 h and it could not be seen, no activity was assumed at the time of the first location at the spot. Thus, activity was defined solely as movement between successive 30-min intervals, while inactivity was defined as no movement for > 2 h. It is possible that the period of activity for bears that foraged in a small area for several hours was underestimated, especially if activity could not be confirmed visually. A bear foraging in a small area for several hours would not move enough distance to be detected as active by telemetry alone, thus their activity would be underestimated. However, it was assumed that the direction of error (i.e. underestimating activity) was consistent across bears. Further, keeping visual contact with bears in urban areas foraging in dumpsters was relatively easy owing to their shorter movements, greater illumination, and more open terrain (e.g. parking lots behind fast food restaurants and shopping centres). Because wildland bears tended to travel more, it is probable that their activity levels were not underestimated, and although urban bears moved short distances between garbage dumpsters in a given night, the ability to establish visual contact minimized error when estimating their activity levels. Artificial light from a 1.5 million candle-watt spotlight was occasionally used for brief periods (< 30 s) to try to visually locate bears during sampling. Observations were made as far away as possible from bears (> 50 m), especially in urban areas, while maintaining visual contact, to avoid influencing their behaviour. It was never obvious that observations disturbed their natural foraging, as bears were used to feeding in garbage with some attendant level of human disturbance and because they continued to feed. Keeping constant visual contact was impossible, even in urban areas, so standard triangulation methods were heavily relied upon (Heezen & Tester, 1967; Hupp & Ratti, 1983; Samuel & Fuller, 1994) to determine an individual's location and movement and thus its activity.

Data were recorded from 25 July 2001 (late summer) to 23 September 2001 (early autumn) because these dates coincide with the stage of the annual cycle when bears have maximum caloric intake requirements as they prepare to enter dens for the winter (Brody & Pelton, 1988). Thus, any differences in either their level of activity or their use of resources would be most pronounced during this time, making it easier to detect any differences that might exist in the use of these 2 types of food resources. While data on foraging activities were gathered for 480 h during autumn, they were not gathered in spring, although supplemental food probably has a marked effect during that time as well. However, since bears achieve their maximum body masses in autumn before entry into winter dens, data gathered during this hyperphagic period was assumed to be representative of periods when individuals elect to forage most, including spring.

Den chronology

Den entry and emergence dates were estimated during 3 winters (1999–2000, 2000–1, 2001–2) as midway between the first location at the den and the previous location, and the date midway between the last location at the den and the following location. The time period between these locations never exceeded 2 weeks. Means ± 1 SD and Wilcoxon paired-sample tests (t) or Wilcoxon rank-sum tests (W) were used for contrasts. Alpha was set, a priori, at 0.05 for all statistical comparisons.

RESULTS

Patterns of activity

The mean hour that urban bears began activity ($19:00 \pm 2.33$ h) differed from that of wildland bears ($08:00 \pm 1.62$, $t = 55$, $P = 0.0007$; Fig. 1). Similarly, mean activity rate (number of hours active) differed between urban bears ($\bar{X} = 8.50 \pm 2.64$) and wildland bears ($\bar{X} = 13.3 \pm 2.67$, $t = 145$, $P = 0.0037$; Fig. 1). Urban bears generally began their activity during the evening and during nocturnal periods, while wildland bears were more diurnal. However, because bears in both areas spent several h active, overlap in activity occurred during crepuscular periods (Fig. 1).

Den chronology

Of 38 urban bears, five (13%) never denned, whereas all wildland bears did. For urban bears, mean Julian date of entry into hibernacula was 1 January vs 4 December for wildland conspecifics (day 338, $P < 0.0001$; Table 1). The pattern of urban bears entering dens on average 1 month later held for both sexes, but for females there was not a statistical difference (Table 1), although this result probably had reduced power owing to a small sample size.

Table 1. The mean Julian date of entry into dens for urban interface and wildland black bears *Ursus americanus* and the mean number of days in dens for bears in the two study areas in western Nevada. Julian dates > day 365 correspond to the equivalent Julian date the subsequent year. Urban interface bears are those that were located > 90% of the time inside urban areas. Wildland bears are those that were located < 10% of the time inside urban areas. All comparisons were made using the non-parametric Wilcoxon rank-sum test (*W*)

	Urban-interface bears		Wildland bears		<i>W</i>	<i>P</i> -value
Sex	Sample size	Mean \pm 1 SD	Sample size	Mean \pm 1 SD		
Mean Julian date of entry into den						
Males	29	367.55 \pm 13.85	17	337.06 \pm 16.28	196	0.0001
Females	4	356.75 \pm 16.26	9	340.44 \pm 19.75	36.5	0.1194
Combined	33	366.24 \pm 14.34	26	338.23 \pm 17.24	454.5	0.0001
Mean number of days in den						
Males	19	76.74 \pm 19.62	9	109.00 \pm 21.85	193.5	0.0024
Females	3	74.33 \pm 27.39	6	132.00 \pm 27.51	7	0.0444
Combined	22	76.41 \pm 20.05	15	118.60 \pm 25.91	418.5	0.0001

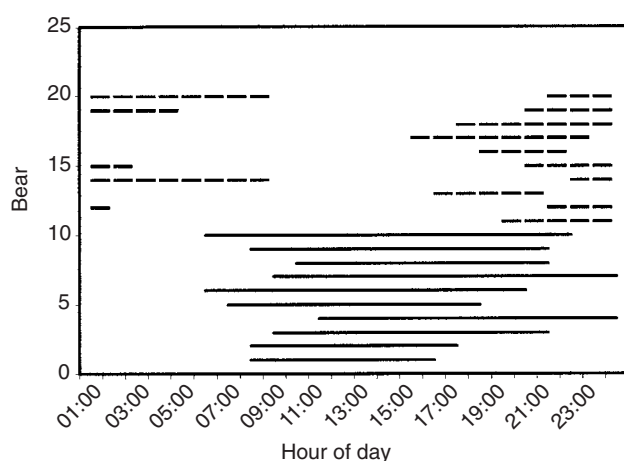


Fig. 1. The number of hours active and the patterns of activity for 10 adult (≥ 3 years) urban interface (dashed lines) black bears *Ursus americanus* and 10 adult wildland (solid lines) bears in western Nevada. Urban interface bears are those that were located > 90% of the time inside urban areas. Wildland bears are those that were located < 10% of the time inside urban areas. Five males and five females were followed for 24 h in both urban and wildland areas during late summer and early autumn 2001.

Den exit dates were similar. As a result, urban bears ($n = 22$) spent, on average, 42 days fewer in dens than wildland bears ($n = 15$, $P = 0.0001$; Table 1). This pattern held true for both males and females ($P < 0.05$; Table 1). Mean age of urban and wildland bears monitored for this analysis did not differ ($\bar{X}_{\text{urban}} = 6.95 \pm 3.67$, $\bar{X}_{\text{wildland}} = 7.95 \pm 4.59$, $W = 700.5$, $P = 0.2829$).

DISCUSSION

To maintain populations of large carnivores adjacent to urban areas, city planners must become more knowledgeable about biological diversity, and carnivores in

particular, so that issues pertaining to wildlife resources can be considered before development, such as the expansion of sub-divisions or addition of roads that encroach into wildland areas. The problem of urban expansion or appropriation of previously undeveloped habitat is widespread globally, including many regions throughout the western United States such as California, Arizona, Colorado, Montana, and Nevada. Contributing to the conflicts between carnivores and humans is a lack of ordinances, laws, or other forms of regulation prohibiting the deliberate or non-intentional feeding of wildlife. The result of the availability of urban food resources is the current situation where black bears in the western U.S.A. and other parts of North America are becoming increasingly reliant upon food sources supplied by humans in the form of garbage.

Our findings underscore consistent variation between urban and wildland bears in three behavioural parameters: (1) pattern of daily activity; (2) amount of daily activity; (3) denning chronology. These differences do not seem to be random, but the result of an underlying difference in resource availability. In addition, other rapid behavioural and ecological changes were documented that have occurred during the past 10–15 years owing to the presence of garbage.

The following points are noted at our specific study area relative to earlier work on the same population (Goodrich, 1990, 1993; Goodrich & Berger, 1994). Whereas urban bears were absent 10–15 years ago, they now not only occur but, relative to wildland bears, urban bears experience: (1) 70–90% reductions in home-range size; (2) an average 30% increase in body mass; (3) > threefold increases in densities relative to baseline levels (e.g. 10–15 years ago) (Beckmann, 2002; Beckmann & Berger, 2003). Additionally, (4) a rapid depopulation of bears from wildland areas owing to profitable foraging in urban areas has occurred with a coincident 10-fold decrease in wildland bear densities (20–40 bears/100 km² a decade ago vs 3.2 bears/100 km² currently); (5) sex ratios skewed heavily towards males in urban areas (4.25 times more skewed vs wildland areas); (6) changes have occurred in female reproductive success (see Beckmann, 2002;

Beckmann & Berger, 2003). Understanding these behavioural and ecological changes associated with human-induced perturbations is essential if we are truly to understand the impact of human activity on carnivore populations.

Shifts in patterns of activity and time budgets

Black bears are generally thought to shift to crepuscular and nocturnal activity when daylight activities are disrupted (Reimchen, 1998), and it was assumed that shifts in the patterns of activity towards crepuscular and nocturnal activity during this study were the result of human activities in urban areas. Our data offer an empirical verification of the assumption that shifts in patterns of activity occur when black bears are in urban areas. These data also suggest that shifts in behaviour, at least as assayed by time budgets, are owing not only to direct disruption from human activities, but also to anthropogenic sources of food. Our data further suggest that garbage was not a limiting resource because urban bears were active for 36% less time compared to wildland bears in late summer to early autumn. At this period of the annual cycle, black bears are achieving their maximum caloric intake (Brody & Pelton, 1988), and our analyses suggest that urban bears were meeting their caloric intake requirements more quickly than wildland bears. Further, urban bears became satiated and stopped foraging even though garbage was still available.

Changes in den chronology

Goodrich (1990) found that 10 wildland bears that he monitored in this region, hibernated by 5 December, and all collared bears entered dens, though date of entry was unknown for several bears. Bears in the Carson Range typically entered dens earlier than bears in the more xeric Pine Nut and Sweetwater Ranges, probably owing to higher snowpack depths and earlier snowfall (Goodrich, 1990). In contrast, during this study, urban bears, primarily from the Carson Range, entered dens later than wildland bears in the Carson, Pine Nut, and Sweetwater Ranges. This was a complete reversal of the situation a decade ago, despite deeper and earlier snowpack in the Carson Range than in the other Great Basin mountain ranges (USDA, 2002).

Although den entrance dates have shifted for urban bears over baseline levels in the past decade, the exit dates for urban bears were similar to wildland bears during this study and during Goodrich (1990) and Goodrich & Berger's (1994) studies. Adult males exited dens first in March to early April and adult females with cubs of the year exited last from early April to May. Similarly, Shideler & Hechtel (2000) documented four brown bears feeding on anthropogenic foods who entered dens a month later than bears of similar age that fed on wildland foods at the Prudhoe Bay, Alaska oil fields.

Temporal datasets and conservation

As humans continue to expand their distribution globally into regions that have historically contained carnivores, there will be a more pressing need for temporal datasets examining changes in both behavioural and ecological parameters of carnivores. Currently, such information exists for only a handful of carnivore species at the same location. Such broad gaps in knowledge of the temporal impacts of human perturbations on large carnivores makes conservation of these species difficult. Without long-term datasets, conservationists generally do not have a good idea of the patterns of population change, both in terms of numbers or distribution at landscape levels. However, certain attributes of carnivores can be used as major predictors for what species are likely to change. Obviously, large-bodied species that range over extensive areas and that are ecological specialists (e.g. Siberian tigers *Panthera tigris altaica*) are more likely to be negatively impacted. In contrast, generalist carnivores, such as black bears and coyotes, may actually profit in many ways through commensal relationships with humans in altered landscapes. Without baseline levels of behavioural and ecological parameters, biologists are often left guessing as to the targets of recovery for many large carnivore species. If biological diversity that includes a large mammalian carnivore is to be retained, more must be done about both education and policy to move traditional wildlife management towards conservation and at levels that involve not only citizens but public officials across multiple jurisdictions. We suggest that an effective strategy to reduce human–bear conflicts in western North America is to begin extensive public education, similar to that carried out in numerous areas, states, and parks. Also, areas that contain black bears should pass laws, ordinances, and regulations against the intentional or non-intentional feeding of bears or any wildlife that may inadvertently bring bears into an area. These areas should pass ordinances requiring private landowners and businesses to obtain and use bear-proof garbage containers.

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Grizzly Bear Hunting: Frequently Asked Questions

Fish, Wildlife and Habitat Management Branch

7 October 2010

British Columbians have widely varying views on the ethics and ecology of Grizzly Bear hunting in the province. This document is not intended to address differences in ethical viewpoints. Instead, it provides answers to some of the most common questions we receive from the public and stakeholders regarding the sustainability of BC's Grizzly Bear hunt. It also explains the Ministry's science-based harvest management practices that are designed to ensure that BC continues to be home to some of the healthiest Grizzly Bear populations in the world.

1) What is the history of the Grizzly Bear hunt in British Columbia?

Other than a brief moratorium in the spring of 2001, Grizzly Bears have been hunted in British Columbia since before European settlement. Prior to modern wildlife management, when Grizzly Bears were not considered a game species, bounties were paid for their hides. Non-resident hunting of Grizzly Bears in British Columbia has a long history with several notable hunter naturalists, such as Sheldon, Edwards, and Hornaday recording their hunting experiences in well known books. The Grizzly Bear was identified as a game species in the mid-1900s, and since then management programs have been put in place to ensure that the hunt is sustainable. Today, the Grizzly Bear hunt is the most rigidly and conservatively controlled hunt in the province.

Prior to Limited Entry Hunting (LEH: a lottery system where a controlled and limited number of hunting authorizations are available), Grizzly Bear hunting for residents and non-residents was managed through General Open Seasons (GOS) where the harvest was controlled through season dates and restrictions on sex/age classes. LEH was introduced in 1977 when a portion of the provincial Grizzly Bear GOS hunt was replaced by LEH. By 1996, all Grizzly Bear hunting in the province was put on either a LEH system for resident hunters or a quota system for non-resident guides. The Grizzly Bear is now the only species in British Columbia that is managed entirely through LEH and quota.

The Ministry of Environment has been collecting detailed harvest data for Grizzly Bears since 1976. This data, combined with inventory, research, monitoring, and habitat assessments provides vital information on the sustainability of the hunt. Figure 1 shows the trend in the Grizzly Bear harvest over the past 34 years. This, along with a number of other measures described throughout this document, has lead Ministry scientists to conclude that the Grizzly Bear harvest is sustainable.

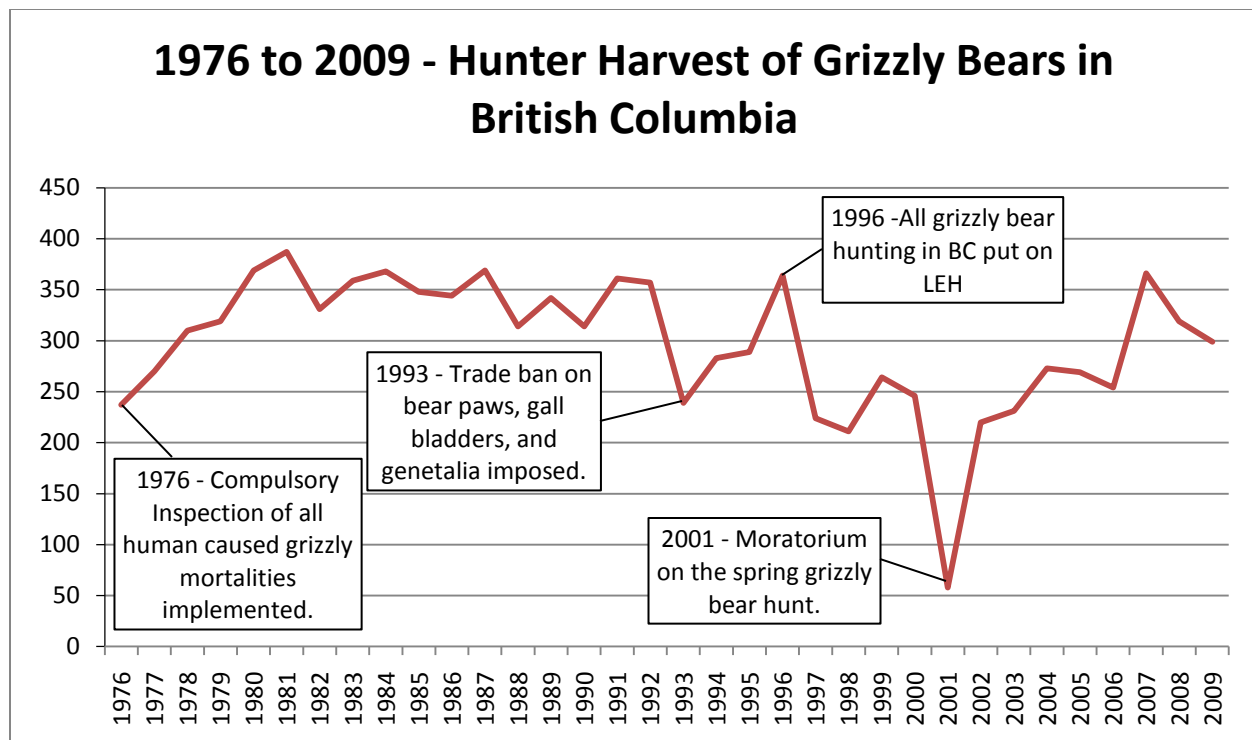


Figure 1: 1976 to 2009 Provincial Grizzly Bear Harvest. Since 1976 hunters have harvested an average of 297 Grizzly Bears annually.

2) What are Grizzly Bear Population Units (GBPUs)?

Grizzly Bears in BC are not part of one large interbreeding population, but rather are comprised of 57 discrete or nearly discrete population units (referred to as Grizzly Bear Population Units or GBPUs (see Figure 2). Grizzly Bears are managed by GPBU in order to ensure local conservation and management objectives are being met and to reflect known and suspected fractures in Grizzly Bear distribution. GPBU's have been used for setting land use priorities for Grizzly Bear conservation during strategic land use planning and are currently being used to direct population recovery. GBPUs are the primary unit for establishing Annual Allowable Harvests (AAH) for viable populations that can sustain a harvest.

Grizzly Bears in the Northern Peace region live in habitats with different ecological characteristics than those in the Southern Kootenays. Hunting in the north has no impact on Grizzly Bear populations in the south. Similarly, the very intensive recovery effort for Grizzly Bears required in Southwest BC is very different from the management and conservation focus for bears in the Kootenay area on the north coast. In addition to the 57 GBPUs, there is a large area of BC that has either never been occupied by Grizzly Bears or where adult female Grizzly Bears no longer inhabit.

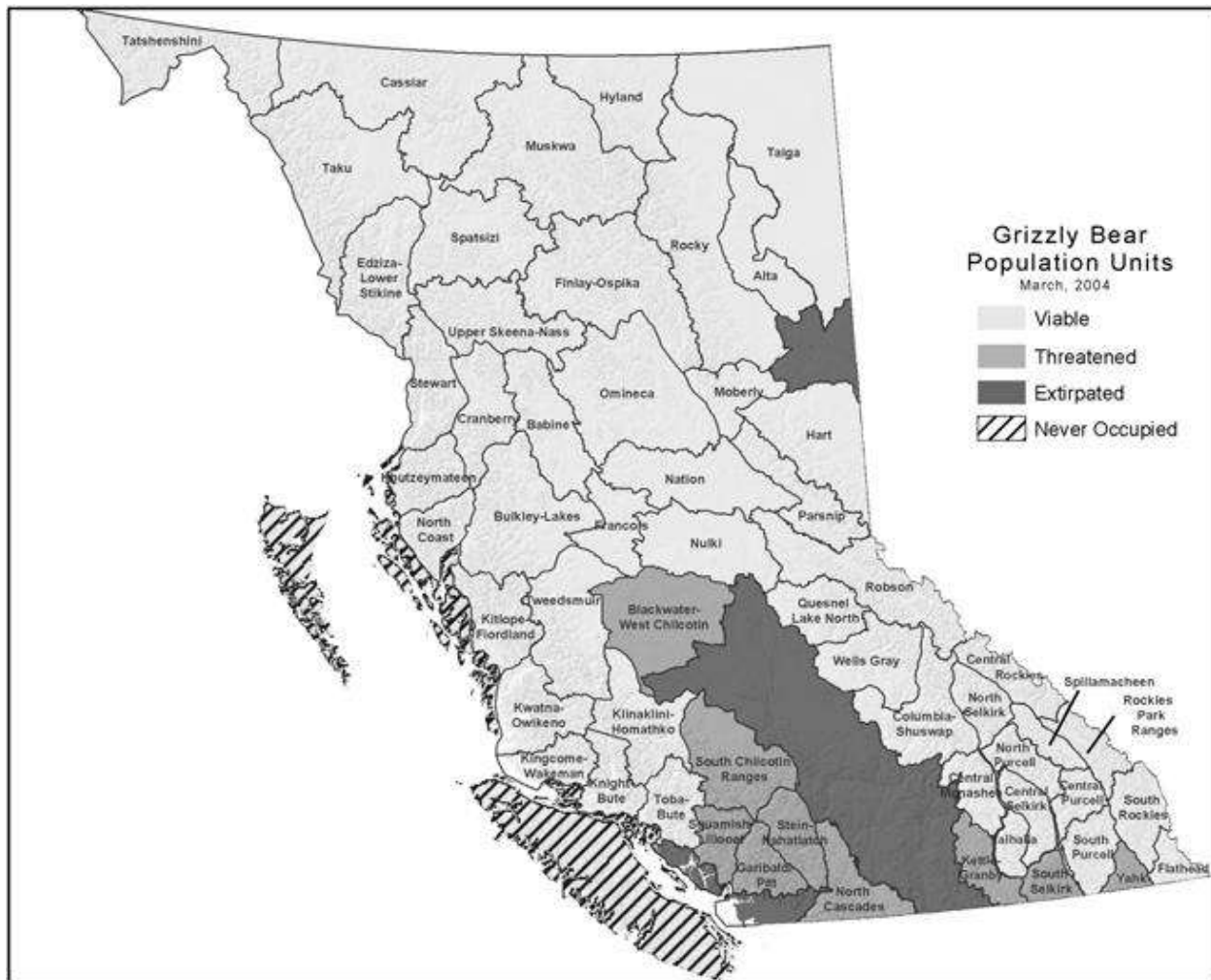


Figure 2. Grizzly Bear Population Units (GBPUs) in British Columbia.

3) *What is the conservation status of BC's 57 GBPUs, and how were they determined?*

The Ministry and its partners have invested over \$7 million in Grizzly Bear inventory to estimate BC's Grizzly Bear abundance and distribution and to assist biologists in determining the conservation status of each GBPU. GBPUs are classed as Threatened or Viable (Figure 3). This status is based on the difference between the current population estimate, and the estimated population capability for the GBPU, as determined through population and habitat modelling. Capability is defined as the inherent, idealized ability of the land to support a specific density of Grizzly Bears independent of human influence. If the current estimate is less than 50% of capability (i.e. the population is less than 50% of the number of animals that the habitat could support), the GBPU is designated as Threatened. There is no hunting allowed in Threatened GBPUs. The primary objective in these units is to recover the population to sustainable levels.

4) How does the Ministry estimate the number of Grizzly Bears in each GBPU?

Wherever possible, Grizzly Bears are inventoried using Mark-Recapture that relies on systematic hair-snagging within a grid (survey area) for subsequent DNA and statistical analysis. To date, over 30 Grizzly Bear mark-recapture inventories have been conducted in BC. Individual hair snags are set up in cells ranging from 25km²-100km², and survey areas composed of numerous cells cover multiple watersheds within GBPU's.

The sampling method, first used for bears in British Columbia, and published in peer-reviewed scientific journals, combines traditional mark-recapture methods and individual recognition through unique DNA profiles. The genetic signature of each bear is the “mark” and that bear’s pattern of detection on the grid across a defined time period are the potential “recaptures”. As a sampling session progresses, the number of “new” bears detected on the grid declines vs. the number of recaptures and that ratio and other measures are used to help determine a population estimate with a “confidence interval” (an estimate of reliability) around it. Inventories are designed to take advantage of natural or human-caused fractures in Grizzly Bear distribution in order to ensure “closure”, such that bears are restricted from coming into, or leaving the survey area during the hair sampling sessions and confounding results as a consequence.

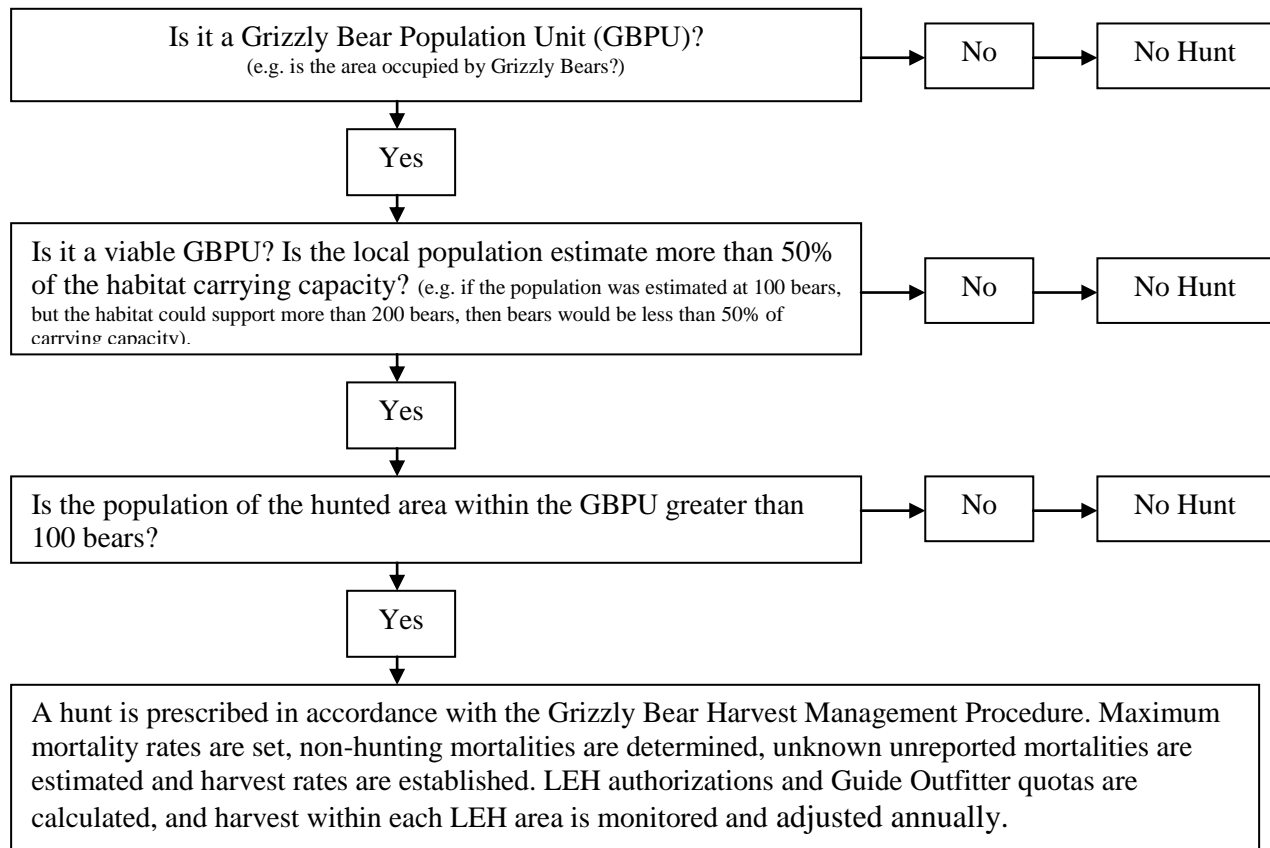
Where direct inventory is not possible, the Ministry estimates densities using a Multiple Regression Model that relates known densities from inventories to a list of environmental, geographic and human influences. This model can then be used to predict Grizzly Bear densities within GBPU's that have not been surveyed. For coastal British Columbia, a different model (termed the Expert Based Model) also considers the proportion of Pacific salmon in the diet as a factor that determines bear density, but the coastal model is more subjective than the interior model. Additional modelling is currently underway to reduce this subjectivity.

Periodic surveys enable some populations to be monitored over time to determine if their numbers are increasing, stable or declining. For example, 2009 was the 11th year of systematic aerial surveys of Grizzly Bears in the Kimsquit River in mid-coastal BC. That work is proving valuable in helping determine the potential impact of an apparent decline in Pacific salmon on Grizzly Bear numbers and productivity. The Ministry has recently undertaken a comprehensive GBPU-specific priority-setting exercise for future inventory, monitoring and distribution projects.

5) Why are some GBPU's open to hunting while others are closed? How is this decision made?

Viable GBPU's are subject to LEH only when the population is greater than 100 bears. A hunt may be allowed within an entire GBPU, or only within a portion of the GBPU. Portions of the viable unit may be closed to hunting if the current population is below acceptable levels compared to what the habitat can support, or if a Grizzly Bear No Hunting Area (GBNHA) has been designated. GBNHAs are established as representative benchmarks and typically surround large protected areas or conservancies. For example, the large Skeena-Nass GBNHA surrounds the Khutzeymateen Park, Canada's first official Grizzly Bear sanctuary.

The process for determining where hunting for Grizzly Bears will be open and where hunting will be closed is described by the flow diagram below:



6) *How much of the province is open to a Grizzly Bear hunt?*

Approximately 65% of the province (not including Vancouver Island or Haida Gwaii which are not within the historic range of Grizzly Bears), is currently open to Grizzly Bear hunting (see Figure 3).

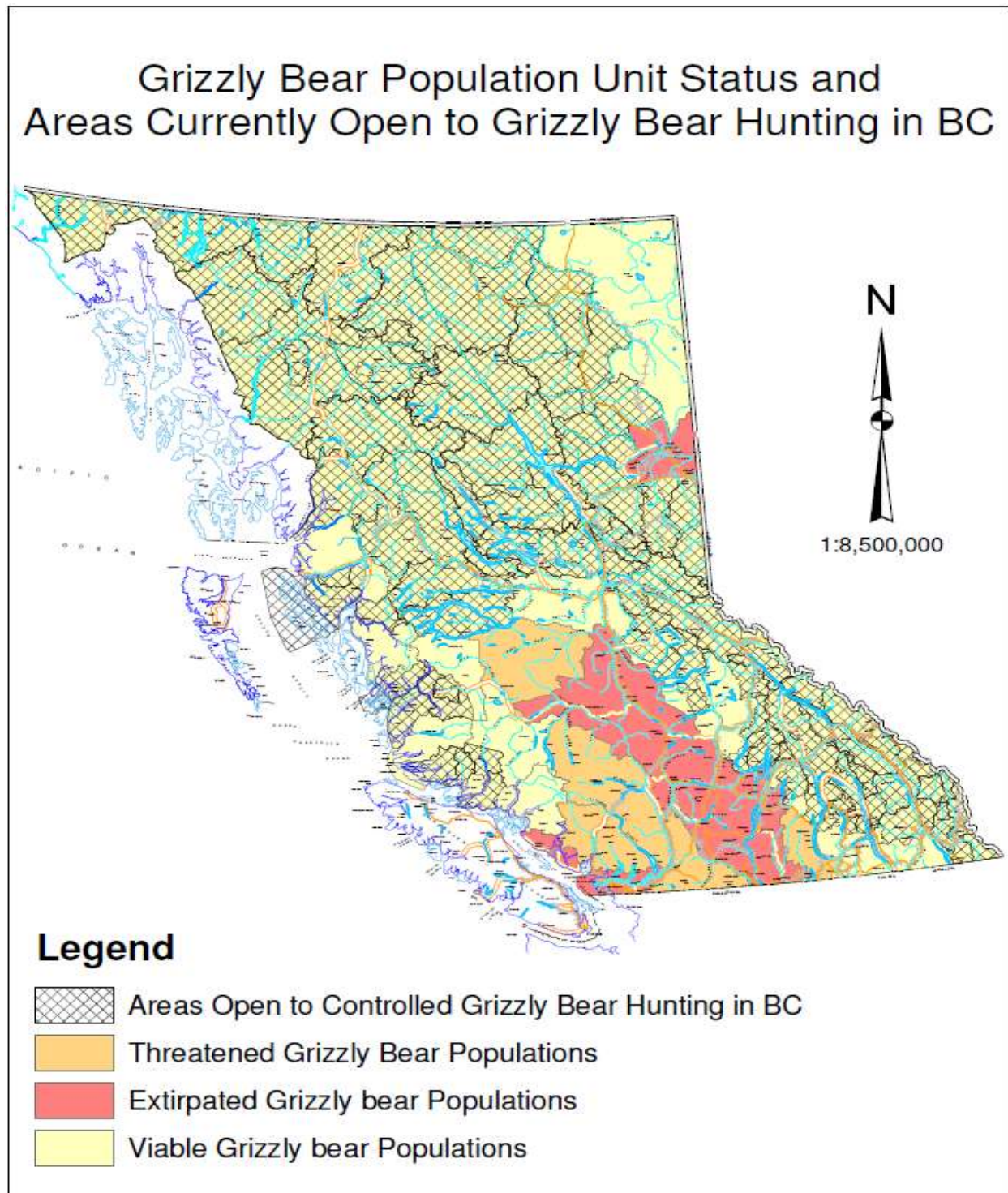


Figure 3: Grizzly Bear Population Unit Status and Areas Currently Open to Grizzly Bear Hunting in BC.

7) How does the Ministry determine the level of hunting mortality that is sustainable?

The proportion of a Grizzly Bear population that can be harvested by humans without creating a population decline was discussed in detail by the original Grizzly Bear Conservation Strategy Scientific Advisory Committee, and the subsequent Scientific Advisory Panel, see http://www.env.gov.bc.ca/wld/documents/gbear_finalspr.pdf.

The Panel Report contained the following (pages 11-12):

“A model involving the sustained yield concept discussed above may be used to estimate sustainable harvest rates, and then these rates can be applied to a population estimate to obtain an estimate of sustainable hunting mortality. Outputs from such models vary with the assumptions used. The B.C. government relies on results of a modeling exercise performed by Harris (1986b) that estimated maximum sustainable harvest mortality at 6%. This model used reproductive and mortality rates believed typical of “southern interior” Grizzly Bear populations and included density-dependent effects resulting from the increased survival of young in response to the removal of males. Miller (1990a) estimated the maximum sustainable harvest of Alaskan Grizzly Bears at 5.7% based on a model that did not include density-dependent effects. In all likelihood, differences between models used to estimate sustainable harvest rates for bears are insignificant compared to the typical magnitude of error in estimates of total population size. We note, however, that both the Harris and Miller models did not consider the effect of sampling error on the estimations of population size or demographic parameters on the estimated harvest rate.”

The Panel commissioned Dr. P McLoughlin to assess the risks of decline for hunted populations of Grizzly Bears given uncertainty in population parameters. That study (see http://www.env.gov.bc.ca/wld/documents/gbear_mcl.pdf) concluded that most Grizzly Bear populations in North America can tolerate approximately 3 – 5% total annual harvest before declines in probability of persistence accelerate to unsatisfactory levels. Given more recent estimates of demographic parameters for Grizzly Bears, the results of that study are now considered to have been conservative.

Based on the above information and demographic information collected by Dr. Bruce McLellan in the Flathead River in SE BC, the Ministry revised the Grizzly Bear Harvest Procedure in 2007 (see http://www.env.gov.bc.ca/wld/documents/grizzlybear_harvest_mgmt_proc_2007.pdf) to include the following:

“In general, GBPU's will be managed so as not to exceed the cumulative Annual Allowable Mortality (AAM) or female AAM over the course of an allocation period. The AAM for each GBPU will typically be calculated by using a maximum allowable mortality rate of 6%, unless a written rationale (that is consistent with stated management objectives) is available and supports the use of a higher or lower maximum allowable mortality rate. This rationale may consider such factors as:

- uncertainty in the population estimate,
- knowledge of the population's natural growth rate,
- location of the area within the species' distribution, or
- a difference between the estimates of population size and current carrying capacity.”

The procedure also includes a provision for females which states:

“The female AAM will be calculated as 30% of [overall] AAM” [that is, no more than 30% of the 6% can be female].

To date, this policy over-ride has only been invoked on one occasion – for the Tweedsmuir GBPU, LEH zone 5-08C, the Bella Coola Valley, by varying the management objective for the valley.

The 6% maximum, total human-caused mortality rate, applied on a five-year (allocation period) basis, remains fundamental to Grizzly Bear harvest management in BC. In practice, the rate as applied in over 135 different LEH zones and Wildlife Management Units, varies from 1.3% (Francois GBPU) to 5.7% (Stewart, Spatsizi, Upper Skeena-Nass, and Kwatna-Owikenno GBPU) and averages 4.2 % over the area of BC where there is an open Grizzly Bear hunt. Rates are directly proportional to bear population productivity – higher rates are applied only where there is evidence of a healthy, higher density population.

More recent research on Grizzly Bear population demographics in Alaska and in Yellowstone Park supports the currently applied BC maximum of 6% for all human-caused mortality as sustainable and likely conservative for bears occupying good quality habitats. Computer modelling, based on recently documented reproductive and survival rates for Grizzly Bears, also indicates that 6% human-caused mortality is conservative and that rates up to or even exceeding 9% can be sustainable for some populations.

One of the major uncertainties associated with determining human-caused mortality limits has been the lack of conclusive evidence of density-dependent effects. Recent work on Black Bears in Northern Alberta advocates “the inclusion of density dependence in population projection models for bear populations”. However, density dependence would have less influence where Grizzly Bear populations are held below carrying capacity by human caused mortality.

Management Statement

The Ministry of Environment has adopted a 6% maximum allowable human-caused mortality rate as sustainable and likely conservative for Grizzly Bears occupying good quality habitats. The limit of all human-caused mortalities at 6%, supplemented by a procedural rule that no more than 30% of all human-caused mortalities can be females, and a regulation that stipulates there is no open season on any bear less than two years old or any bear in its company (thereby protecting females and their dependent offspring), provides sufficient safeguards to ensure that BC’s Grizzly Bear hunt is sustainably managed.

Legal harvests are closed when either (or both) the 6% total or the 30% female limits are exceeded. In practice, managers have adopted maximum allowable human-caused mortality limits of between 1.3 and 5.7% in recognition of the highly variable population productivity across the province.

8) What are the human-caused mortality rates for Grizzly Bears in British Columbia?

The Ministry sets a specific allowable human-caused mortality rate for each hunted GBPU based on a variety of GBPU characteristics. For example, higher density populations are able to withstand higher levels of human-caused mortality. While it is not uncommon for mortality in an individual year to exceed the annual allowable mortality for a GBPU, this does not represent a conservation concern or overharvest as adjustments are made in the following years to ensure total mortality over a five year period is not exceeded. It is extremely rare for mortality rates over a five year period to be in excess of the allowable mortality, and in these situations the mortality rates over the next five year period are significantly reduced or eliminated to compensate for the overharvest in the previous five year period.

Currently, 50% of the of the province's 135 Grizzly Bear hunts are set at 6% maximum allowable human-caused mortality, 24% are set at 5%, and 26% are set at 4%. (see Figure 4).

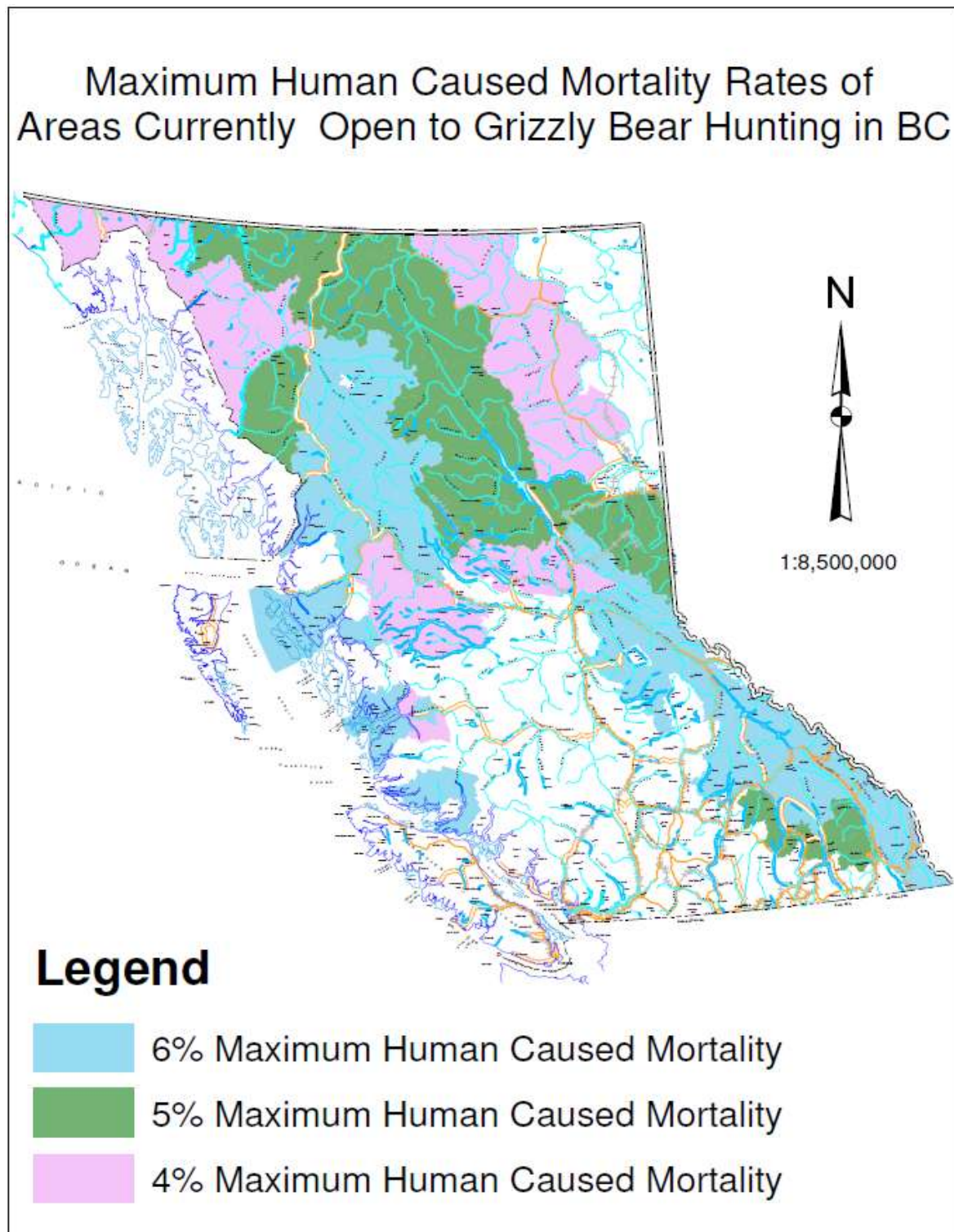


Figure 4: Maximum Human-Caused Mortality Rates of Areas Currently Open to Hunting in BC, as of spring, 2010.

9) How are the hunter harvest rates determined for Grizzly Bears in BC?

Once the maximum human caused-mortality rate is established, a series of calculations known as “step-downs”, are used to determine the Annual Allowable Harvest (AAH) rate. These calculations include subtracting the First Nations harvest rate, and the estimated unreported mortality rate from the maximum human caused-mortality rate. The procedure also factors in the expected number of reported non-hunting mortalities that will occur in the future (typically conflict bears) based on the previous records of reported non-hunting mortalities in that GBPU. Only after all of these step-downs are made is the AAH rate determined. Although this rate is calculated on an annual basis, it is applied over a five year period to allow for annual variation and to reflect natural population processes.

10) How does the province record the actual human-caused mortality levels for Grizzly Bears?

Human caused mortality of Grizzly Bears includes both legal hunting and other human-related causes.

Known human-caused mortality of Grizzly Bears includes the licensed harvest, bears removed through animal control activities, and animals that have died from other related human causes, such as collisions with motor vehicles or trains. Known illegally-taken animals are also included.

Mortality records are collected and kept within the Ministry’s Compulsory Inspection database. Compulsory Inspection for Grizzly Bears was initiated in 1975, and all reports submitted after 1976 are considered to be both complete and accurate. From 2004 to 2009, there were 2,138 reported human-caused Grizzly Bear mortalities in the province of which 358 (16.7%) were related to motor vehicle collisions, illegal kills, railway mortality, and animal control incidents.

Other sources of human-caused mortality, such as poaching, are less well known. The harvest by First Nations is also largely unknown, as traditional rights and title of First Nations on traditional territory exempts them from the requirement to report their harvest. However, using local knowledge, inventory and research, the Ministry has developed an estimate for these unreported causes. Generally, 0.3% to 2.0% of Grizzly Bears are believed to be killed and not reported in the province each year.

11) How many bears are killed in the province each year through human activities? Is it within sustainable limits?

The current maximum human-caused mortality for all hunted populations in BC combined is set at 682 bears per year. Of the 682 bears that can be sustainably removed from the hunted populations of the province, 120 are estimated as unreported mortality, leaving a sustainable mortality of 562 bears that could be removed through hunting, control kills, road-rail collisions, or other causes. From 2004 to 2009, the average reported mortality of Grizzly Bears in the province has been 297 per year, approximately 53% of the maximum limit. However, while this provides a “big picture”, mortality distribution is a critical component to the responsible diligent management of Grizzly Bears.

As described under question five, harvest is determined for each viable GBPU with a hunting season. In addition, many GPBUs have more than one LEH zone (total of 135 for the province) where desired harvest levels are established and monitored. In summary, human-caused mortality is tracked, calculated, and assessed first for each of the 135 LEH zones, and then for each of the 43 viable hunted GBPU.

Of the 43 Grizzly Bear Population Units where a hunt exists, total mortality is below the maximum allowable human-caused mortality in 38 units as determined for the period from 2004 to 2009 (see Figure 5).

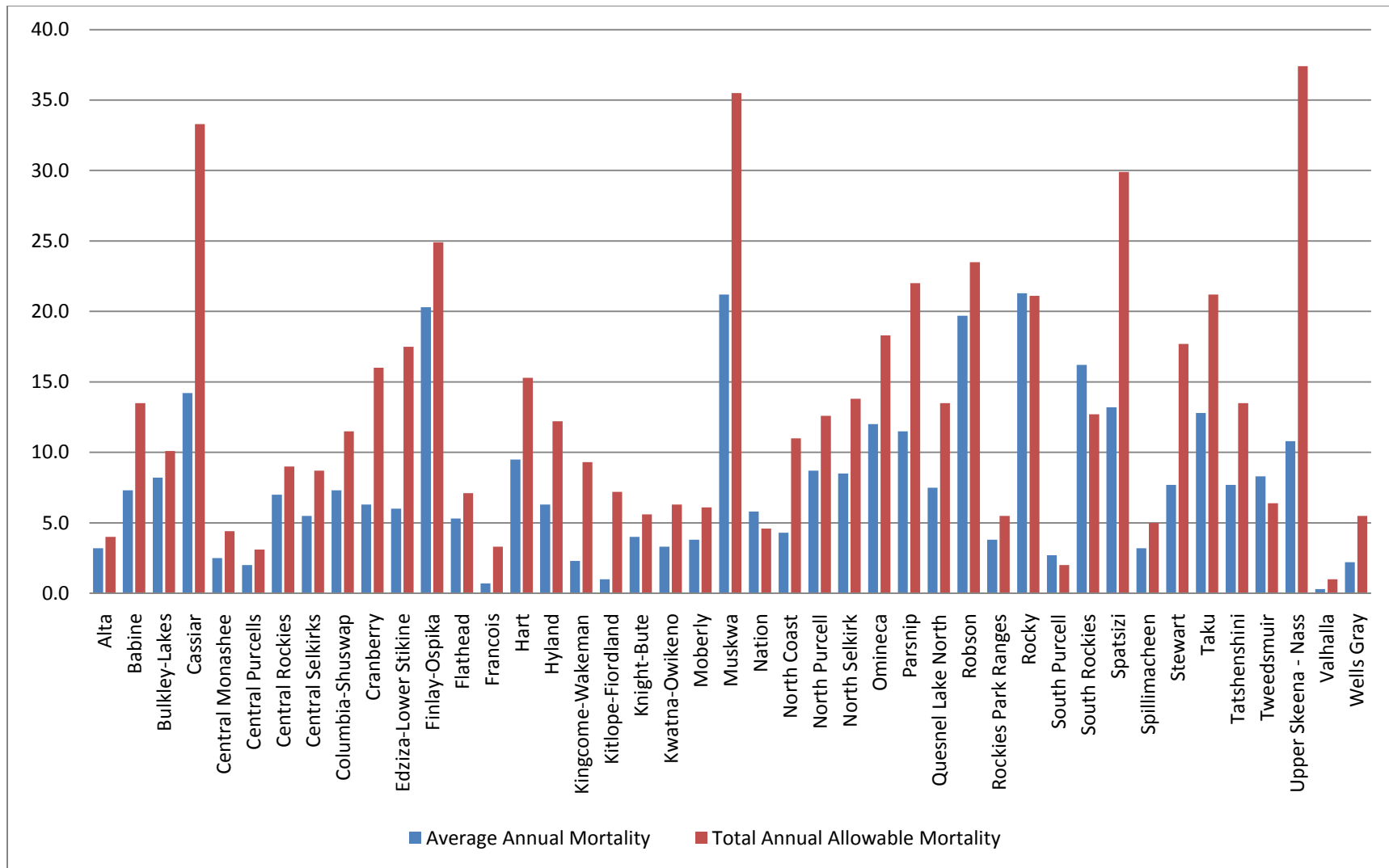


Figure 5: 2004 to 2009 average annual Grizzly Bear mortality compared to allowable Grizzly Bear mortality. Where the red line is taller than the blue line, it means that average annual mortality rates are below maximum mortality rates.

12) Which viable GBPU's are currently of highest management concern?

As shown in Figure 5, there are 5 GBPU's (Nation, Rocky, South Purcell, South Rockies, and Tweedsmuir) that are above the maximum allowable human-caused mortality, primarily as a result of high levels of non-hunting mortality (primarily motor vehicle/train collisions and conflict kills). Actions have been taken, and further actions are being considered, including further restricting or closing specific hunts, in order to reduce human-caused mortality within these 5 GBPU's to sustainable limits within the 5 year allocation period. The Ministry is concerned about these 5 units, which are described in more detail below

Nation GBPU: The population for the hunted portion of the Nation GBPU is estimated at 241 bears. The maximum human-caused mortality rate for the Nation GBPU is 4%. Once unreported mortality is factored in, the total Annual Allowable Mortality of Grizzly Bears in the hunted portion of the Nation GBPU is calculated at 4.6 bears per year. The average reported human-caused mortality within the hunted portion of the Nation GBPU from 2004 to 2009 was 5.8 bears per year. The hunted portions of the Nation GBPU are divided into 7 separate LEH zones; each zone has both a spring and a fall hunt. The average success rate in this GBPU over the past 5 years is 0.83%, which means that, on average, one bear is harvested for every 120 authorizations given. The Ministry has responded to increased mortality rates in the Nation GBPU by dropping the number of LEH authorizations from 51 in 2008 to 26 in 2009, and then further decreasing authorizations to 14 (1 authorization per zone per season) in 2010.

Rocky GBPU: The population for the hunted portion of the Rocky GBPU is estimated at 729 bears. The maximum human-caused mortality rate for the Rocky GBPU is 4%. Once unreported mortality is factored in, the total Annual Allowable Mortality of Grizzly Bears in the hunted portion of the Rocky GBPU is calculated at 21.1 bears per year. The average reported human-caused mortality within the hunted portion of the Rocky GBPU from 2004 to 2009 was 21.3 bears per year, a difference of 0.2 bears per year. The hunted portions of the Rocky GBPU are divided into 9 separate LEH zones; each zone has both a spring and a fall hunt. The average success rate in this GBPU over the past five years is 6.9%, which means that one bear is harvested, on average, for every 15 authorizations given. The Ministry has responded to increased mortality rates in the Rocky GBPU by dropping the number of LEH authorizations from 138 in 2008 to 127 in 2009, and then further decreasing authorizations to 84 in 2010.

South Purcell GBPU: The population for the hunted portion of the South Purcell GBPU is estimated at 68 bears. The hunted population within this GBPU is less than 100 bears; for most areas this would mean that the GBPU is closed. However, the boundary between this GBPU and adjacent GBPU's is "soft", meaning there is significant enough immigration and emigration between the South Purcell GBPU and surrounding areas that this GBPU is managed on a larger scale than the GBPU boundary. The maximum human-caused mortality rate for the South Purcell GBPU is 5%. Once unreported mortality is factored in, the total Annual Allowable Mortality of Grizzly Bears in the hunted portion of the South Purcell GBPU is calculated at 2 bears per year. The average reported human-caused mortality within the hunted portion of the South Purcell GBPU from 2004 to 2009 was 2.7 bears per year. The South Purcell GBPU has one hunted LEH zone with only a spring season. The average success rate for this zone over the past five years is 27.3%; which means that one bear is harvested, on average, for every 4 authorizations. The Ministry has responded to increased mortality rates in the South Purcell GBPU by dropping the number of LEH authorizations from 3 in 2008 to 1 in both 2009 and 2010.

South Rockies GBPU: The population for the hunted portion of the South Rockies GBPU is estimated at 301 bears. The maximum human-caused mortality rate for the South Rockies GBPU is 5%. Once unreported mortality is factored in, the total Annual Allowable Mortality of Grizzly Bears in the hunted portion of the South Rockies GBPU is calculated at 12.7 bears per year. The average reported human-caused mortality within the hunted portion of the South Rockies GBPU from 2004 to 2009 was 16.2 bears

per year. The South Rockies GBPU is divided into 5 separate LEH zones with only a spring season. The average success rate for this GBPU over the past five years is 38%; which means that, on average, two bears are harvested for every 5 authorizations. The Ministry has responded to increased mortality rates in the South Rockies GBPU by dropping the number of LEH authorizations from 27 in 2008 to 25 in both 2009, and then further decreasing authorizations to 15 in 2010.

Tweedsmuir GBPU: The population for the hunted portion of the Tweedsmuir GBPU is estimated at 174 bears. The maximum human-caused mortality rate for the Tweedsmuir GBPU is 4%. Once unreported mortality is factored in, the total Annual Allowable Mortality of Grizzly Bears in the hunted portion of the Tweedsmuir GBPU is calculated at 6.4 bears per year. The average reported human-caused mortality within the hunted portion of the Tweedsmuir GBPU from 2004 to 2009 was 8.3 bears per year. The Tweedsmuir GBPU is currently divided into 3 separate LEH zones; each zone has both a spring and a fall hunt. In 2009, one of the zones within the Tweedsmuir GBPU (Zone C of Management Unit 5-09) was closed as it was encompassed by the Khutze-Kitlope-Kimsquit and Upper Dean-Tweedsmuir GBNHAs developed through the coastal Land and Resource Management Planning tables and implemented by the Ministry of Environment.

The situation regarding Grizzly-human conflict in BC is at its most significant in the Bella Coola Valley. A large number of Grizzly Bears are residents of the side tributaries and main valley. In addition, collaring studies have shown that transient bears travel vast distances to take advantage of the huge numbers of spawning salmon in the Bella Coola and Atnarko river systems. The valley bottom habitats are superlative coastal Grizzly habitat in any season, and it is not uncommon that bears are either displaced into human settlements and valley farms or deliberately seek human and vehicle presence to protect themselves from other bears. Conflicts in 2008 and 2009 were unusually high, likely due to lower abundance of spawning salmon. As many as 25-30 Grizzly Bears were destroyed in direct conflict situations over this two year period.

Bella Coola staff from the Environmental Stewardship Division have joined with the Conservation Officer Service and have received funding support from the Grizzly Bear Trust Fund and Bear Aware for a local Bear Aware education program to be delivered by the British Columbia Conservation Foundation (BCCF). Conflict response will be co-ordinated through the Ministry Call Centre (1-877-952-7277) and is the responsibility of the Conservation Officer Service office in Williams Lake. The local Bear Aware coordinator will be available for immediate, low-level conflict response and has a strong mandate for community education and outreach, with a focus on attractant reduction.

13) Who hunts Grizzly Bears?

Ministry policy identifies conservation as the highest priority, then First Nations use, followed by resident and non-resident use. First Nations may choose to exercise their right to harvest Grizzly Bears for food, social or ceremonial purposes. Residents are only eligible to hunt if they have a LEH authorization. Non-residents seeking to harvest a Grizzly Bear are required to hire the services of a licensed guide outfitter. Guide outfitters are given an annual quota for Grizzly Bears which, along with the resident harvest, is factored into the calculation of the Annual Allowable Harvest. The balance between resident and non-residents hunting opportunities is determined through a publicly consulted and approved Wildlife Allocation Policy.

From 2004 to 2009, resident hunters harvested an average of 191 bears per year, while non-residents harvested an average of 106 bears per year; a split of 64% for resident and 36% for non-resident hunters.

14) What are the hunting seasons for Grizzly Bears?

There are no General Open Seasons for Grizzly Bears in British Columbia. Rather, resident hunters must apply for and receive a Limited Entry Hunting (LEH) authorization in order to hunt Grizzly Bears. LEH is a random draw system where hunters submit applications to hunt for a certain species, during a specific time, in a specific area. Any hunter who has an outstanding fine under the *Wildlife Act* is not permitted to apply for a LEH authorization. The Grizzly Bear harvest is often referred to as a controlled hunt, as it restricts the number of LEH authorizations available to resident hunters, and thus controls the level of harvest.

Hunters that are not residents of British Columbia must hire the services of a licensed guide outfitter to hunt for Grizzly Bears. Guide outfitters receive a quota which stipulates the number of Grizzly Bears that their clients may harvest in their guide outfitting area during a licence year.

15) What assurances are there that Grizzly Bears will not be over-harvested?

There are 3 primary mechanisms that the Ministry uses to ensure that Grizzly Bears will not be overharvested. These include: (1) LEH/Quota; (2) Protection of females with dependent young; and (3) a female harvest limit.

LEH/Quota

The LEH/Quota system is very effective at controlling the Grizzly Bear harvest, and ensuring that an overharvest does not occur. The number of permits issued is set to achieve the Annual Allowable Harvest for resident hunters, based on their average success rate. The average 2004 to 2008 success rate for resident hunters was approximately 10.5%, but varies by GBPU. A 10% success rate means that for every 10 resident hunters in possession of a LEH Grizzly Bear authorization, on average only 1 will actually harvest a bear. If the allowable harvest of Grizzly Bears in an area was 10 for resident hunters, and the hunter success rate for that area was 50%, then 20 LEH authorizations would be available. If there is an anomaly, and success rates in a given year are higher than the previous five year average, the number of authorizations available the following year is reduced to account for the change in success rates.

By policy, the minimum success rate factored into the LEH permit calculations is 5%. That is, if success rates are lower, (e.g. 2%), the same number of permits are issued as if the success rate was 5%. This precaution further limits the number of LEH authorizations available in a season, decreasing the chances of a higher than average success rate resulting in excessive harvest. Additionally, there is a legislated Range of Authorizations (RoA) for each specific hunted zone in the province; 97% of the hunted zones in the province have a RoA of 1-50 per season, the remaining 3% are between 1-50 and 1-100. This additional restriction on the number of LEH authorizations serves two purposes: to reduce crowding and reduce the risk of excessive over-harvest due to extremely high numbers of authorizations.

Example: Say the target harvest of a LEH zone is 5 Grizzly Bears in a season, the average success rate over the preceding 5 years is 2%, and the maximum number of authorizations is 50. Based on the actual success rate, 250 authorizations could be sustainably issued for this zone (5/2%). However, the minimum success rate of 5% is used, which would result in 100 authorizations (5/5%). As this number is outside the legislated RoA for this zone, the actual number of authorizations available in this scenario would be further reduced to 50. Based on the actual success rate of 2%, the actual harvest should be 1 Grizzly Bear.

Similarly, the restricted quota that enables Guide Outfitters to take non-resident Grizzly Bear hunters is a responsive system. If harvest in an area has met or exceeded target levels, Grizzly Bear hunting opportunities for non-residents is closed.

Protection of females with dependent young

Another important management tool for assuring that Grizzly Bears are not overharvested is the regulation, passed in 1975, that states “it is unlawful to hunt a Grizzly Bear less than 2 years old, or any bear in its company.” This regulation protects family groups (mothers with yearlings or cubs) and thus ensures that young animals as well as a significant proportion of adult females are protected from harvest each year.

Female Harvest Limit

Grizzly Bear populations are extremely sensitive to human-caused mortality of females, and the Grizzly Bear harvest procedure stipulates that the maximum female mortality must not exceed 30% of the Annual Allowable Harvest (AAH). If female mortality is in excess of 30% of the AAH measures are taken to reduce mortality in following years. Since the fall of 2008, every hunter in possession of a Grizzly Bear LEH authorization has been provided with an informational document on why it is important to select a male Grizzly Bear and tools on how to distinguish between males and females.

16) Is the Grizzly Bear harvest in the “Great bear Rainforest” sustainable?

Much attention has been placed on the Grizzly Bear hunt in the Great Bear Rainforest (GBR). The population estimate for the entire GBR is approximately 2,000 bears. From 2004 to 2009 there has been an average of 24 reported mortalities within the GBR annually, representing 1.2% of the GBR population, most of which occurred as non-hunting mortality in the Bella Coola Valley. Even after factoring in other human-related causes of mortality, actual mortality is well within the sustainable mortality limits for the coastal GBPU's.

Approximately 53% of the GBR is open to hunting, leaving 47% that is closed. Included in the closed area are 470,000 hectares of Grizzly Bear No Hunting Areas (also referred to as Grizzly Bear Management Areas (GBMAs) in the Coastal Land and Resource Management Planning Process), which were previously open to Grizzly Bear hunting and prescribed closed through coastal Land and Resource Management Plans and subsequent Government to Government agreements with Coastal First Nations. Of the portion of the GBR that is open, the current population estimate is 970 bears. The average reported human-caused mortality within this area, from 2004 to 2009, was 21, or approximately 2.1% of the population. Of the 21 reported mortalities of Grizzly Bears per year, an average of 8 were non-hunting mortalities, and 13 were harvested by hunters. Harvest rates are well below sustainable limits for all coastal GBPU's with the exception of the Tweedsmuir GBPU which, because of its high occurrence of non-hunting mortality, is being managed under a slightly modified process. The Ministry is aware of, and concerned about the potential decline in Pacific salmon and the subsequent effect on coastal Grizzly Bears. As a result, we are planning and undertaking additional population monitoring of coastal populations.

17) Are Grizzly Bears harvested in BC Parks and Protected Areas?

In total, 14.3% of British Columbia's land base is protected. Since the establishment of the first Provincial Park at Strathcona in 1911, the system has grown to over 900 designated parks and protected areas, totalling over 13,000,000 hectares. Each BC Park has a management plan which, through a process of public consultation, guides how a protected area will be managed over the next ten to twenty years. The plan sets out objectives and strategies for conservation, development, interpretation and operation of a protected area. A management plan relies on current information relating to such subjects as natural

values, cultural values, and recreation opportunities within a protected area and resource activities occurring on surrounding lands.

Hunting is a recognized outdoor recreational opportunity that is permitted in many BC Parks, provided the activity is approved through the Park Management Planning Process. Policy provides that hunting in parks is more conservative than on crown land outside of parks.

From 2004 to 2009 there was an average of 33 Grizzly Bear mortalities per year in BC Parks and protected areas, of which an average of 28 were hunting mortalities, and 5 were non-hunting mortalities.

18) What is being done to manage Grizzly Bear mortalities in un-hunted areas?

Approximately 35% of British Columbia (not including Vancouver Island, the Sunshine Coast, the Lower Mainland or Haida Gwaii) is closed to grizzly hunting. Within these areas, the objective is to have no human caused Grizzly Bear mortality. However, non-hunting mortality (e.g. control kills, motor vehicle/train collisions) does occur in these areas, and the Ministry is concerned about these mortalities.

Areas where Grizzly Bear hunting is closed to hunting fall into three categories:

- 1) *Closed areas within viable GBPU's.* Area closures within viable GBPU's may occur for 1 of 3 reasons. These include:
 - a) *Grizzly Bear No Hunting Areas (GBNHAs):* In 2003 the Grizzly Bear Scientific Panel recommended the establishment of one Grizzly Bear Management Area (GBMA) in each of the 9 Ecoprovinces in BC. These areas are now referred to as Grizzly Bear No Hunting areas (GBNHAs); since one of the objectives for these areas is to establish benchmarks for non-hunted bear populations that can be used for further research and comparison with hunted populations. In 2008, through direction from the North and Central Coast Land and Resource Management Planning process, three GBNHAs, totalling 1.16 million hectares (470,000 hectares of which was previously open), were established within the Coastal Ecoprovince of BC. These include the Khutzamateen, Ahnuhati, and Nass-Skeena areas. There are 5 Ecoprovinces where GBNHAs have not been implemented and are under review.
 - b) *Closed areas because of specific vulnerability:* The estuaries of Knight Inlet, Kingcome Inlet, and Wakeman Sound are all closed to Grizzly Bear hunting due to vulnerability of Grizzly Bears in open estuaries with high visibility.
 - c) *Small, localized closures to reduce potential conflicts between hunting and commercial bear viewing operations:* Glendale Cove in Knight Inlet is one of the most recognized Grizzly Bear viewing areas in British Columbia. In 1995 a 17 km² Grizzly Bear hunting closure was implemented surrounding the viewing area of Glendale Cove.
- 2) *Total area closures within threatened GBPU's (areas closed to Grizzly Bear hunting).* Management efforts are focussing on recovering these populations to sustainable population levels. For example, under the Sea to Sky Land and Resource Management Plan, the associated Land Use Plans of local First Nations and the subsequent motorized access management plan for the Sea to Sky area, 11 seasonal motorized access closures have been implemented under the *Wildlife Act* to protect Grizzly Bears in the spring.
- 3) *Total area closures within extirpated areas.* Extirpated areas provide limited opportunities for recovery, largely because of human activities associated with urbanization, agriculture, and

transportation infrastructure that are not compatible with Grizzly Bears. An example of this is the lower reaches of the Fraser River and its estuaries which were once exceptional Grizzly Bear habitat. The population has been extirpated, and recovery is unlikely as the social tolerance for Grizzly Bears in urbanized and rural agricultural areas is very low. This is also true for most of the major agricultural zones, urban centers, and transportation corridors throughout the province. Minimal recovery efforts are being pursued in these areas as human developments have altered habitats to the extent that the modified environment will no longer support, or tolerate, Grizzly Bears.



Rates and Causes of Grizzly Bear Mortality in the Interior Mountains of British Columbia, Alberta, Montana, Washington, and Idaho

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RATES AND CAUSES OF GRIZZLY BEAR MORTALITY IN THE INTERIOR MOUNTAINS OF BRITISH COLUMBIA, ALBERTA, MONTANA, WASHINGTON, AND IDAHO

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Abstract: Trends of grizzly bear (*Ursus arctos*) populations are most sensitive to female survival; thus, understanding rates and causes of grizzly bear mortality is critical for their conservation. Survival rates were estimated and causes of mortalities investigated for 388 grizzly bears radiocollared for research purposes in 13 study areas in the Rocky and Columbia mountains of Alberta, British Columbia, Montana, Idaho, and Washington between 1975 and 1997. People killed 77–85% of the 99 grizzly bears known or suspected to have died while they were radiocollared. In jurisdictions that permitted grizzly bear hunting, legal harvest accounted for 39–44% of the mortalities. Other major causes of mortality included control killing for being close to human habitation or property, self-defense, and malicious killings. The mortality rate due to hunting was higher ($P = 0.006$) for males than females, and subadult males had a higher probability ($P = 0.007$) of being killed as problem animals than did adult males or females. Adult females had a higher ($P = 0.009$) mortality rate from natural causes than males. Annual survival rates of subadult males (0.74–0.81) were less than other sex–age classes. Adult male survival rates varied between 0.84 and 0.89 in most areas. Survival of females appeared highest (0.95–0.96) in 2 areas dominated by multiple-use land and were lower (0.91) in an area dominated by parks, although few bears were killed within park boundaries. Without radiotelemetry, management agencies would have been unaware of about half (46–51%) of the deaths of radiocollared grizzly bears. The importance of well-managed multiple-use land to grizzly bear conservation should be recognized, and land-use plans for these areas should ensure no human settlement and low levels of recreational activity.

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Key words: Alberta, British Columbia, grizzly bears, hunting, Idaho, Montana, poaching, problem wildlife, protected areas, survival rates, *Ursus arctos*, Washington.

Due to late maturation and a low reproductive rate, the trend of a grizzly bear population is most sensitive to a change in female survival (Knight and Eberhardt 1985, McLellan 1989, Eberhardt et al. 1994, Hovey and McLellan 1996, Mace and Waller 1998). Grizzlies, however, are vulnerable to several forms of human-caused mortality. They are prized trophies for hunters and a valuable source of Asian medicine (Mills and Servheen 1994). During some encounters with people, grizzlies are viewed as a threat and shot in self-defense. These bears are also attracted to human habitation where they are often destroyed or captured and moved.

Minimizing grizzly bear mortality, particularly of adult females, is the key to grizzly bear conservation in small, threatened populations (U.S.

Fish and Wildlife Service 1993, Mattson et al. 1996). Limiting mortality to a sustainable level is the primary management objective in other areas (Alberta Fish and Wildlife Division 1990, Province of British Columbia 1995). Managers usually set a maximum acceptable human-caused mortality rate of 2–6% of the estimated population (Alberta Fish and Wildlife Division 1990, Miller 1990, Province of British Columbia 1995) but must guess at the number and causes of undetected deaths. Knowing the actual causes and rates of grizzly bear mortality is critical to grizzly bear conservation.

Because grizzly bears are difficult to capture, frequently lose radiocollars, and usually have low mortality rates, individual research projects rarely collect sufficient information on mortality factors to make general inferences. In addition, factors influencing mortality rates and causes

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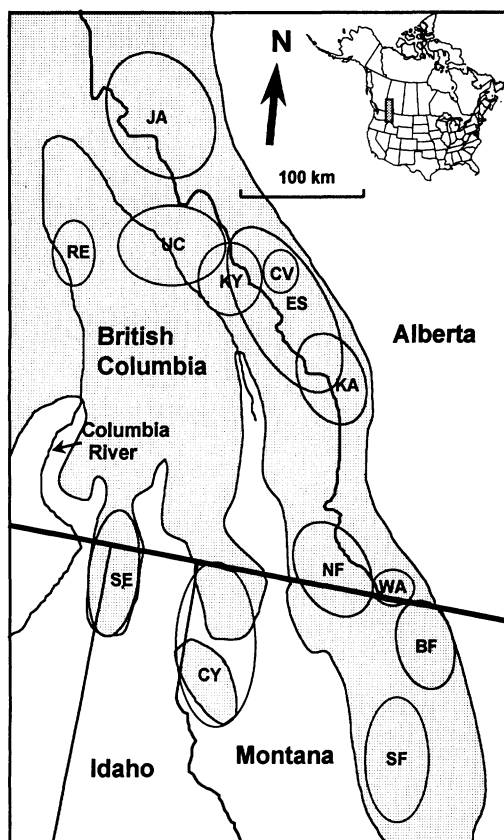


Fig. 1. Location of 13 study areas providing data on mortality rates and causes for grizzly bears in the Rocky and Columbia mountains, 1975–97; where JA is Jasper National Park, RE is Revelstoke, UC is Upper Columbia, KY is Kootenay–Yoho National Parks, CV is Cascade Valley, ES is Eastern Slopes, KA is Kananaskis, SE is Selkirk Mountains, CY is Cabinet–Yaak Mountains, NF is North Fork of the Flathead River, WA is Wapiti National Park, BF is Blackfoot Indian Reservation, SF is South Fork of the Flathead River. The shading represents the approximate distribution of grizzly bears in the area.

may vary among areas, making extrapolations potentially misleading. We used data from several telemetry-based studies in areas with a variety of management goals to estimate and compare grizzly bear mortality rates and causes. We also estimated the proportion and types of grizzly bear deaths that would not have been recorded by management agencies unless the grizzly bears had been radiocollared.

STUDY AREA

We used data from 13 study areas in the Rocky and Columbia mountains of British Columbia, Alberta, Montana, Idaho, and Washington collected between 1975 and 1997 (Fig. 1). Topography of all study areas was mountainous,

but climate and resulting ecosystems varied from relatively mild and wet habitats near Revelstoke, British Columbia (Achuff et al. 1984) to dry, cold ecosystems in Jasper National Park (Holland 1976). Although grizzly bear diets varied among areas, they generally relied on roots and tubers, graminoids (Cyperaceae, Gramineae), horsetails (*Equisetum* spp.), and members of the carrot family (Umbelliferae) in the spring. During summer and fall, huckleberries (*Vaccinium* spp.) and buffalo berries (*Shepherdia canadensis*) dominated their diet. Grizzly bears in all study areas consumed ungulates when encountered, but none had access to anadromous salmon (*Oncorhynchus* spp.; Mace and Jonkel 1986, Hamer and Herrero 1987, McLellan and Hovey 1994).

Study areas contained varying amounts of protected areas and a diversity of human activities. Studies in Cascade Valley, Alberta, (Hamer and Herrero 1987) and Waterton, Alberta, each focused on 2 female grizzly bears that remained almost exclusively in national parks. The Eastern Slopes, Yoho–Kootenay, and Jasper studies were based in national parks but also included lands outside park boundaries. The Upper Columbia and Kananaskis (Carr 1989, Wielgus and Bunnell 1994) study areas were almost equally in and out of parks. The Eastern Slopes and Upper Columbia study areas contained rural and urban settlements both in and outside park boundaries.

The remaining 6 study areas were primarily outside protected areas, but radiocollared grizzly bears used adjacent parks and designated wilderness. Intensity of human uses varied among these 6 areas. In the South Fork of the Flathead River (SF Flathead) study area, multiple-use lands with extensive forest management and outdoor recreation met an abrupt transition with rural and urban areas (Mace and Waller 1997a). Rural settlement, ranching, and some oil and gas development occurred within the Blackfoot study area. There was limited human settlement in and adjacent to the Cabinet–Yaak, North Fork of the Flathead (NF Flathead), and Selkirk study areas. Timber harvest was common in these areas, as was gas exploration in the NF Flathead. There was only 1 residence in the Revelstoke study area, but timber harvest was common.

Grizzly bear hunting was regulated by a quota for guides and their nonresident clients and a limited entry draw or lottery for resident

hunters in Alberta and British Columbia. A strict quota system was permitted in Montana, excluding the Cabinet–Yaak areas, until 1991, when hunting was closed. Grizzly bear hunting was not permitted in Idaho or Washington. The NF Flathead and Revelstoke studies were the only areas that had grizzly bear hunting over most of the study area and over the duration of study. Hunting for other species was permitted in all study areas, excluding portions in national and some provincial parks.

METHODS

Grizzly bears were captured for research purposes with foot snares or in culvert traps set throughout the study areas, and immobilized to allow handling. Some grizzly bears were darted from a helicopter. No grizzly bears were first captured as problem animals. A premolar was removed from subadults and adults for aging (Stoneberg and Jonkel 1966), and grizzly bears were classified as cubs (<1 yr old), yearlings (1 yr old), subadults (2–5 yr old), and adults (≥ 6 yr old). Except for bears captured and radiocollared before 1980, radiocollars were attached with a canvas connector that decomposed and allowed the radiocollar to drop from the grizzly bear after a planned amount of time (1–5 yr). Not only did these canvas connectors result in fewer neck injuries, but radiocollars were usually shed when transmitting; hence, fates of grizzly bears at the end of the monitoring period were clear. Most radiocollars were sensitive to movement and changed pulse rate after 4–6 hr of inactivity, after the radiocollar was shed, or the grizzly bear had died.

Cause of death of radiocollared grizzly bears was determined by a variety of methods. The Cascade Valley and Waterton studies relied on ground tracking, but none of the grizzly bears in those studies died while being monitored. In the other studies, radiocollared grizzly bears were located from fixed-wing aircraft 2–8 times/month in addition to supplemental ground tracking. If a change in radio pulse rate was detected, the site was investigated, usually within 1 week, and the dropped radiocollar retrieved or the cause of mortality determined. Because radiocollars on hibernating grizzly bears often switch pulse rates, 2 grizzly bears that died during or near to the denning period were investigated several months after they had died. Grizzly bears killed as problem wildlife, for defense of life or property, taken legally by hunt-

ers, and some illegal killing were reported to or investigated by conservation officers.

Mortalities were first classified as natural, human-caused, or unknown. Deaths were classified as natural when a natural cause was evident. In 3 cases, deaths were classified as natural without clear evidence of a natural cause, but the carcasses were found in locations rarely if ever visited by people. In some cases, it was not possible to determine whether a death was natural or human-caused. These mortalities were classified as unknown.

Mortalities classified as human-caused were further categorized by the apparent reason: (1) legal hunting; (2) malicious, where the animal was shot and left for no apparent reason; (3) management problem, when the bear was near buildings, camps, or livestock, and killed or removed by a wildlife official; (4) citizen's problem, when a citizen shot the bear for being near buildings, livestock, or a camp; (5) self-defense, when a person thought their safety was threatened; (6) poached, when the animal was hunted but killed illegally; (7) accident, such as a vehicle collision; (8) unknown, when a radiocollar had been cut off; and (9) research, when death was capture-related. Deaths due to research were excluded from analyses. The legality of killings was not specifically addressed, because of different laws among jurisdictions and inconsistencies in legal systems.

Suspected human-caused deaths were recorded when the radio signal from a grizzly bear that had been located near human residences or camps disappeared prematurely. For example, when 2 radiocollared subadults that traveled together disappeared concurrently after being located in an area with many homes, their deaths were suspected. In another case, not only was the radiocollared grizzly bear located near a hunting camp before the radiocollar disappeared, but a blood trail was found at the camp.

For each confirmed or suspected grizzly bear mortality, we determined whether or not the management agency would have recorded the death if the animal had not been radiocollared. Unrecorded cases were those only reported by researchers after the radiocollar changed pulse rate and the site was investigated. There was a chance that some of these dead grizzly bears may have been found and reported. However, after cause of death was ascertained, carcasses were usually left in the field, and in no cases

were they later reported. Similarly, grizzly bears were not discovered if they were killed and had their radiocollars cut off and discarded.

Although we assumed grizzly bears monitored during each study were representative samples for that time and place, we were forced to pool data because of small sample sizes. Data were pooled by study areas into groups with similar management goals and geographic proximity. The Jasper, Cascade Valley, Eastern Slope, Upper Columbia, Yoho–Kootenay, and Kananaskis studies were based in the contiguous Canadian national and provincial park complex. Some radiocollared bears moved between 2 or more of these study areas, so data were pooled into the study area group called Mountain Parks. Because Waterton and the Blackfoot Indian Reservation are adjacent and some bears moved between study areas, they were pooled and called the Blackfoot–Waterton. Although the Cabinet–Yaak is geographically separated from the Selkirks, we pooled data from these studies because management objectives were similar. The NF Flathead and SF Flathead study areas were geographically isolated and had large enough sample sizes to remain separate. Data from Revelstoke grizzly bears were not used in survival rate calculations, because sample sizes were small and geographic isolation prevented pooling with other studies. Revelstoke data were used in cause of death analyses.

Survival rates were estimated for each sex–age class (ad M, ad F, subad M, subad F) from each study area group via censored data from grizzly bears that were tracked for a minimum of 20 days. We used the following Kaplan–Meier estimator described by Hovey and McLellan (1996) to determine annual survival rates (\hat{S}_i):

$$\hat{S}_i = \prod_{j=1}^{n=52} \left[1 - \left(\frac{D_{ij}}{R_{ij}} \right) \right], \quad (1)$$

where D_{ij} was the number of recorded deaths, and R_{ij} was the number of animals at risk for age class i during week of the year j ($j = 1$ [Jan 1–7], $j = 2$ [Jan 8–15], . . . , $j = 52$ [Dec 24–31]).

We applied Equation 1 to our data by using the following procedure. For each grizzly bear, the dates radiotracked were partitioned into week of the year. The sample at risk (R_{ij}) was increased by 1 for every week that a grizzly bear was radiotracked. Grizzly bears that were radio-

tracked >1 year had 1 record added to R_{ij} for every year they were monitored during week j . If the grizzly bear died, then D_{ij} was also increased by 1. Grizzly bears that lost radiocollars during week j were treated as censored and R_{ij} was reduced. If these individuals were recaptured, they were added to the sample at risk as a new record. Because grizzly bears were not radiocollared simultaneously, we treated the radiotracked sample as a staggered-entry design (Pollock *et al.* 1989). We used 5,000 bootstrapped samples (Efron and Gong 1983) to estimate bias and standard errors.

We tested differences in survival rates among study area groups and sex–age classes via an unbalanced, 2-way analysis of variance (ANOVA; Montgomery 1991). We performed a prospective power analysis of this ANOVA to determine appropriate sample sizes for future research based on our results (Cohen 1977). For the power analysis, both minimum and maximum power curves were derived via the mean square error of the ANOVA, with the experimentwise error rate and detectable difference set to 0.05. Differences in mortality rates associated with different causes were analyzed as a 1-way ANOVA with sex–age class as the design factor. We used the method of least-significant difference (Milliken and Johnson 1992) to test for pairwise differences between levels of significant factors. For these tests, we used Bonferroni's correction to determine the significance level. The power analysis and calculation of F -ratios, t -statistics, and P -values were performed with SAS programs (SAS Institute 1988) we developed for these analyses.

Because each jurisdiction had different management goals, practices, and laws, it is most valuable to discuss results by jurisdiction. For this reason, we summarized causes of mortality by jurisdiction. Unfortunately, survival rates could not be estimated for each jurisdiction, because radiocollared grizzly bears frequently moved among them. Instead, we calculated survival rates by sex–age class for each study area group.

RESULTS

A total of 388 grizzly bears was radiocollared and monitored for a total of 704.4 radiotracking years in the 13 telemetry studies. Of these grizzly bears, 90 (23%) were known to have died and 9 (2.3%) were suspected to have died while radiocollared. Seven of the 90 known deaths

Table 1. Estimated annual survival rates of adult and subadult (excludes radiocollared cubs and yearlings and Revelstoke data) grizzly bears of each sex by groups of study areas in the Rocky and Columbia mountains, 1975–97.

Age-sex Study area	No. bears	Mortalities (suspected)	Radio-years	Survival rate	SE
Adult female					
Mountain Parks	41	6	65.5	0.905	0.036
NF Flathead	31	4	89.9	0.959	0.021
SF Flathead	14	6	50.0	0.888	0.043
Selkirk–Yaak	18	3	57.9	0.952	0.026
Blackfeet–Waterton	14	0(2)	22.4	0.918	0.055
Combined	118	19(2)	285.7	0.926	0.006
Adult male					
Mountain Parks	50	7	55.8	0.891	0.038
NF Flathead	24	4	35.1	0.887	0.054
SF Flathead	12	3	25.4	0.888	0.062
Selkirk–Yaak	18	5	27.8	0.842	0.066
Blackfeet–Waterton	7	3	7.0	0.625	0.180
Combined	111	22	151.1	0.877	0.006
Subadult female					
Mountain parks	14	1	17.8	0.954	0.045
NF Flathead	25	3	46.5	0.935	0.036
SF Flathead	18	5	35.2	0.872	0.054
Selkirk–Yaak	10	1	9.5	0.929	0.070
Blackfeet–Waterton	13	3	19.5	0.859	0.077
Combined	80	13	128.5	0.923	0.008
Subadult male					
Mountain parks	29	8	24.6	0.742	0.078
NF Flathead	36	5(4)	36.4	0.782	0.063
SF Flathead	11	4	15.4	0.784	0.095
Selkirk–Yaak	16	4	18.7	0.807	0.090
Blackfeet–Waterton	17	3	12.1	0.798	0.106
Combined	109	24(4)	107.2	0.801	0.007

were due to research. Survival rates differed among sex–age classes ($F_{3,351} = 3.89$, $P = 0.009$), but not among study area groups ($F_{3,351} = 0.69$, $P = 0.559$). The interaction between sex–age and study area groups was not significant ($F_{9,351} = 0.52$, $P = 0.861$). The annual survival rates of adult males, adult females, and

subadult females were not different, but all were greater than the survival of subadult males (Table 1). Given the variability in survival rates and time that grizzly bears carried functioning radiocollars, our results indicated that about 42 grizzly bears should be radiocollared in each of the 16 sex–age study group categories to be 80% sure of detecting a survival rate difference of 0.05 (Fig. 2).

Depending on how the 9 suspected deaths and 5 deaths from unknown causes were treated, people caused 77–85% of the grizzly bear deaths (Table 2). Reasons that people killed grizzly bears varied among jurisdictions. Grizzly bear hunting was legal in British Columbia and Alberta, but it was only a major cause of mortality of radiocollared bears in British Columbia, where it accounted for 39–44% of the deaths. Ungulate hunters killing grizzly bears in self-defense, hunters mistaking a grizzly bear for a black bear (*Ursus americanus*), and malicious killing were major causes of grizzly bear deaths in Montana. Being shot or translocated by wildlife officials or shot by a citizen for killing live-

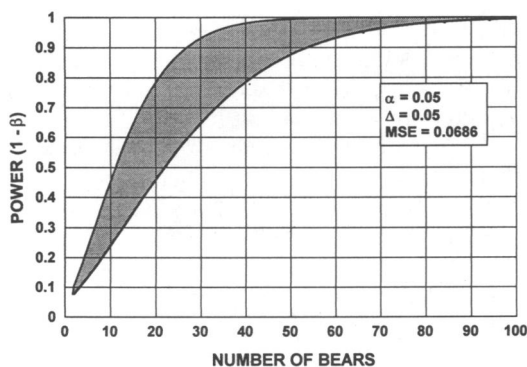


Fig. 2. Maximum (upper curve) and minimum (lower curve) statistical power as a function of sample size in each sex–age by study area group category for a 2-way analysis of variance F -test. The power curves were determined with $\alpha = 0.05$ (experimentwise error rate) and $\Delta = 0.05$ (detectable difference).

Table 2. Number of known mortalities of radiocollared grizzly bears in the Rocky and Columbia mountains, 1975–97, that would have been recorded by the management agency in each jurisdiction, including the number of additional known () and suspected mortalities [] that would not have been detected without the aid of radiotelemetry.

Cause of death	Jurisdiction						Total
	Alberta	British Columbia	Idaho	First Nation	Montana	Washington	National park
Natural	0	(8)	0	0	(4)	0	(14)
Unknown	0	(2)	0	0	(3)	0	(5)
Human-caused							
Hunter kill	1	15	0	0	0	0	16
Citizen problem	0(1)	0(1)[1]	0	1(1)	1	0	2(3)[1]
Management problem	1	1	0	2	5	0	10
Misidentification	0	0	0(1)	0	2(2)	0	2(3)
Self defense	1	1	0	0	3(1)	0	5(1)
Accident	0(1)	0	0	0	0	0	1(1)
Poach	0(1)	2(1)	1	0	0	2	5(2)
Malicious	0	1	0	0(2)	0(4)	0	1(6)
Unknown	0	(2)[3]	(1)[1]	(1)[2]	(2)	0	0(6)[8]
Total: human-caused	3(3)	20(4)[4]	1(2)[1]	3(4)[2]	11(9)[2]	2	42(22)[9]
Total: all deaths	3(3)	20(14)[4]	1(2)[1]	3(4)[2]	11(16)[2]	2	42(41)[9]

stock or being near homes or camps was a major mortality factor in several jurisdictions. Poachers rarely killed radiocollared grizzly bears, and there was no evidence of a radiocollared grizzly bear dying after being wounded by a hunter (wounding loss). People killed grizzly bears for unknown reasons in most studies.

Without the aid of radiotelemetry, management agencies would have been aware of only 46–51% of radiocollared grizzly bear deaths and 54% (if the 5 unknowns and 9 suspected were killed by people) to 66% of human-caused deaths. A large proportion of radiocollared grizzly bears in British Columbia was killed legally and reported by hunters, but even in British Columbia the management agency would have recorded only 53–59% of the mortalities and 67–83% of the human-caused deaths. In Montana, where there was little legal hunting of grizzly bears while radiocollared grizzly bears were being monitored, and no radiocollared grizzly bears were shot by hunters, agencies would have recorded 38–41% of the deaths and 44–55% of the human-caused deaths.

Mortality rates due to hunting differed among sex-age classes ($F_{3,425} = 4.17$, $P = 0.006$), with adult and subadult males having similar rates that were higher than adult or subadult females. Mortality rates due to a combination of management and citizen control killing also differed among sex-age classes ($F_{3,425} = 4.06$, $P = 0.007$), with subadult males having a higher rate than the other 3 age classes. Mortality rates from a combination of the clearly illegal categories of poaching, malicious killing, and killing for unknown reasons (radiocollars cut off) did not differ among sex-age classes ($F_{3,425} = 1.89$, $P = 0.131$). Mortality rates from other human causes (accidents, misidentification, self defense) differed among sex-age classes ($F_{3,425} = 2.80$, $P = 0.040$). Adult males had a higher rate than adult females, as 5 adult males but no adult females were shot in self-defense (Table 3). Natural mortality rates differed among sex-age classes ($F_{3,425} = 3.83$, $P = 0.010$), with adult females having a higher rate than adult or subadult males. Twelve females died of natural causes: 3 in rock or snow avalanches, 1 in a collapsed den, 5 apparently by conspecifics, and 3 by unknown causes (Table 3).

DISCUSSION

Grizzly bears, particularly those without access to anadromous salmon, occur at low den-

Table 3. Age–sex class of known mortalities of radiocollared grizzly bears that would have been recorded by the management agency, including the number of additional known () and suspected mortalities [] that would not have been detected without the aid of radiotelemetry.

Cause of death	Age–sex class				Total
	Adult female	Adult male	Subadult female	Subadult male	
Natural	(10)	0	(2)	(2)	(14)
Unknown	(2)	0	0	(3)	(5)
Human-caused					
Hunter kill	2	10	0	4	16
Citizen problem	0	(1)	1	1(2)[1]	2(3)[1]
Management problem	1	3	1	5	10
Misidentification	1	0	1(3)	0	2(3)
Self defense	0	4(1)	0	1	5(1)
Accident	0	(1)	1	0	1(1)
Poach	1	1(1)	1	2(1)	5(2)
Malicious	1(1)	(1)	(2)	(2)	1(6)
Unknown	(1)[3]	(1)	(2)[1]	(2)[4]	(6)[8]
Total: human-caused	6(2)[3]	18(6)	5(7)[1]	13(7)[5]	42(22)[9]
Total: all deaths	6(14)[3]	18(6)	5(9)[1]	13(12)[5]	42(41)[9]

sities (McLellan 1994, Miller *et al.* 1997) but require adult female survival rates of about 0.90 or greater to persist and be available for study (Eberhardt 1990, Mace and Waller 1998). Due to low densities and high survival rates, it is difficult to collect sufficient survival data for comparisons in an ecologically meaningful spatial and temporal scale. For example, after 10 years of research in the SF Flathead, Mace and Waller (1998) determined that the grizzly bear population had most likely been decreasing ($\lambda = 0.977$, 95% CI = 0.875–1.046). In contrast, after 15 years of research in the NF Flathead, Hovey and McLellan (1996) found the population had been rapidly increasing ($\lambda = 1.085$, 95% CI = 1.032–1.136). Even for these 2 populations with very different trends, we still could not detect a significant difference in adult female survival rates, particularly when 2 other study area groups were added to an ANOVA.

The power analysis further demonstrates this problem. A 5% difference in survival rate is biologically significant for grizzly bears (Eberhardt 1990), but we should have monitored many more grizzly bears of each sex–age class in each of the study area groups to detect this difference. Due to the difficulty of detecting statistical significance for the biologically significant phenomenon of a small difference in grizzly bear survival rates, we believe it is valuable to identify important trends even if statistical confidence may be lacking.

Subadult male grizzly bears had lower survival rates than other sex–age classes, and this rate

was consistent among study areas. Perhaps due to their large ranges (Blanchard and Knight 1991, Mace and Waller 1997b) and inexperience, young males are more prone to encounter human attractants and be killed as problem bears than other sex–age classes. Where hunting was permitted, both subadult and adult males were more likely to be legally harvested than females. Different vulnerability to hunting was likely due to females with cubs or yearlings being legally protected, males having larger ranges, and some hunters selecting large-bodied males.

Although grizzly bear hunting selects males over females and was permitted in some study area groups but not others, adult males had similar mortality rates in all areas except the Blackfoot–Waterton, where sample sizes were very small. Survival rates of adult males in our study areas were similar to the 0.84 recorded in a hunted population on Chichagof Island (Titus and Beier 1994), but higher than the 0.75–0.80 recorded in the Susitna Drainage of Alaska. The Susitna population was being intentionally reduced in an attempt to increase survival of moose (*Alces alces*) calves (S. D. Miller, Alaska Department of Fish and Game, unpublished data).

Survival rates of adult females were similar to rates of adult males in the Mountain Parks and SF Flathead study areas, and also similar to the 0.89–0.92 recorded for adult females in the grizzly bear reduction area of the Susitna Drainage, Alaska (S. D. Miller, Alaska Department of

Fish and Game, unpublished data). Adult female survival rates in the NF Flathead and Selkirk-Yaak, however, were similar to that of females on Chichagof Island (0.96; Titus and Beier 1994) and appeared to be higher, although not statistically so, than in the Mountain Parks and SF Flathead.

The lack of difference or perhaps even higher survival rates of adult females in some multiple-use landscapes (e.g., NF Flathead, Selkirk-Yaak) compared to areas dominated by protected areas (e.g., Mountain Parks) is an important consideration in developing conservation strategies. Although few radiocollared grizzly bears died when inside park boundaries, grizzly bears had high mortality rates on the periphery. The high mortality rate along park boundaries is likely an indirect result of nearly 1 million people (i.e., Calgary metropolitan area) within a 1–2-hr drive, and approximately 43,000 residents and 28,000 hotel beds in occupied grizzly bear habitat of the Mountain Park study areas. Similarly, within the SF Flathead study area, Mace and Waller (1998) found that grizzly bears with home ranges entirely within multiple-use areas had higher survival rates than grizzly bears that also used rural settlements or designated wilderness areas. We suggest that the long-term conservation value of protected areas is not only related to the amount and quality of habitat they contain and their grizzly bear management programs, but also the number and activities of people using the protected area and adjacent lands. Multiple-use lands remote from human population centers may be critical to the long-term conservation of grizzly bears, provided that they are managed for low-density human use.

Most radiocollared grizzly bears died because people killed them. Hunting was a significant factor only in British Columbia, where it accounted for less than half the deaths. In more remote areas, a higher proportion of grizzly bear deaths probably would be from legal hunting because, with less human settlement, control killing would be reduced (Miller and Chihuly 1987). Results from remote study areas in Alaska suggest that between 78 and 100% of the human-caused deaths of radiocollared grizzly bears were from hunting (Schoen and Beier 1990, Reynolds 1993, Sellers 1994).

Biases

Using radiocollared bears to estimate survival rates and causes of death has potential biases.

First, study areas were not located randomly. To obtain sufficient sample sizes, telemetry studies were sometimes located in or at least included areas where grizzly bears were relatively abundant and human influences less common. The NF Flathead and SF Flathead studies, which together contributed about half of the data, had little human settlement. Although a large proportion of grizzly bears likely lives in similar unsettled valleys, it is probable that grizzly bears in unsettled areas have higher survival rates and are legally shot by hunters or die naturally more often than grizzly bears that live closer to people.

A second potential bias of using radiocollared grizzly bears is that people may be less likely to shoot radiocollared grizzly bears but more likely to report the radiocollared grizzly bears that they do shoot. Radiocollars used were black or brown and were difficult to see on a living grizzly bear; however, some hunters or poachers may have avoided killing radiocollared grizzly bears. Due to these biases, it is likely that actual survival rates were less than reported here, and even a higher proportion of deaths were unknown to management agencies.

Finally, pooling data from several studies will weigh areas and time periods unequally; thus, results may not be representative of the entire study area group. The Mountain Parks study area group contained data from 6 studies, each with insufficient data to test if pooling was justified. Because most data came from 2 geographically large and recent projects (Eastern Slopes, Upper Columbia) and management goals have remained the same over the duration of all studies, we believe the data are representative of the area.

MANAGEMENT IMPLICATIONS

Reducing or controlling grizzly bear mortality is central to grizzly bear management in the southern extreme of their distribution. Managers must not only understand why grizzly bears are being killed, but what proportion of deaths is detected. Undetected deaths were usually due to nonhunting human causes. Development and implementation of comprehensive access, recreation, and settlement plans is essential in occupied grizzly bear habitat to maintain a low density of people, particularly those who engage in activities that put grizzly bears at risk (McLellan 1990, Mattson et al. 1996, Mace and Waller 1997a).

Black bear and ungulate hunters killed a relatively high proportion of the radiocollared grizzly bears. Misidentification, self-defense, and problems associated with attractants such as garbage, food, and ungulate carcasses in hunting camps were often the reason for killing grizzly bears. Enforcement of existing rules on clean camping and stressing techniques for hunting in grizzly bear country during hunter training courses and in regulation synopses may reduce the number of grizzly bear mortalities associated with big game hunting seasons.

Managers should incorporate appropriate estimates of unreported kills in estimates of acceptable harvest rates. These estimates, however, remain uncertain but appear to depend on the amount of legal hunting and the degree that grizzly bears and people share habitat. In remote areas with legal hunting, managers will likely be aware of >70% of the grizzly bears killed by people. In areas without legal hunting and where people commonly live, work, and recreate in occupied grizzly bear habitat, the unreported number of bears that people kill is likely similar to the number reported.

Protected areas that are close to large human population centers may not always be suitable cores for grizzly bear conservation. Such protected areas may require intensive management of recreation, industry, and human settlement along their periphery to ensure long-term viability of local grizzly bear populations. The importance of well-managed multiple-use land should be recognized during conservation planning processes. If land-use plans for multiple-use areas can ensure no human settlement and low levels of recreational activity, then these areas may serve as source populations.

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BACKGROUND AND PROPOSED STANDARDS FOR MANAGING GRIZZLY BEAR HABITAT SECURITY IN THE YELLOWSTONE ECOSYSTEM

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INTRODUCTION

The Endangered Species Act requires that managers anticipate and minimize negative human effects on threatened and endangered species to the extent necessary for insuring viability. This stipulation is especially relevant to grizzly bears (*Ursus arctos horribilis*) given that direct human-caused mortality is the arguable cause of virtually all grizzly bear population declines and extinctions (see Storer and Tevis 1955, Craighead and Mitchell 1982, Brown 1985, Servheen 1989a, and Mattson 1990), and that human access is a primary mediator of this mortality (Mattson 1990, McLellan 1990, Mattson and Knight 1991a).

A wealth of information concerning the responses of grizzly bears to humans has accumulated especially within the last 10 years. During this same time the Interagency Grizzly Bear Study Team, National Park Service, and Wyoming Game and Fish have collected information that is specific to bear behavior and survival in the Yellowstone ecosystem. However, there has not been a recent summary or interpretation of this information in terms relevant to grizzly bear management and, more importantly, in terms applicable to derivation of road density standards. I have attempted to serve these purposes in this paper.

This paper is organized into four sections. The first constitutes a review and summary of literature pertaining to the responses of grizzly bears to humans. The second provides a rationale and parameters for what I call "micro-scale" security areas - areas that are functional at the scale of individual foraging bouts. The third section provides methods for calculating standardized road densities in a way that reflects access by motorized vehicles and the presence of cover. The fourth and last section provides a rationale and parameters for

grizzly bear road density standards in the Yellowstone area and, in addition, sets forth a conceptual frame-work for relating Yellowstone-specific standards to the global situation.

SECTION 1 -- Grizzly Bear Responses to Human Activities: A Summary and Interpretation

This section presents a summary and interpretation of existing literature concerning the responses of grizzly bears to humans. I have organized this information first as basic observations, and then as direct inferences that integrate and reconcile these observations. I included not only information concerning the immediate behavioral responses of grizzly bears to humans, but also population-level responses that were mediated through direct human-caused mortality. I limited the scope of my review to North American grizzly bears, although I have included results from Eurasian brown bear studies where there was some compelling relevance.

Basic Observations

Immediate Responses.--

- Some grizzly bears readily habituate to humans, especially if humans are associated with high quality human-origin or natural foods (Braaten and Gilbert 1990; Warner 1987; Fagen and Fagen, in press; McArthur Jope (1983); Jope (1985); Olson et al. 1990; Tracy 1977; Herrero 1985).
- Proportionally more of resident grizzlies habituate to humans when human use is spatially and temporally predictable, and the bear population protected from hunting (McArthur Jope 1983, Jope

1985, McLellan and Shackleton 1989, Kendall 1983, Jope and Shelby 1984).

- Grizzly bears are more likely to use roads, recreational trails, and areas near human residences (campsites or front-country facilities) at night or when unoccupied (Nadeau 1989, Harting 1985, McLellan and Shackleton 1988a, Gunther 1990, Hoak et al. 1983, Zager 1980).

- Grizzly bears are more prone to flight from humans in the back-country than most other large vertebrates (Chester 1980).

- Flush distances vary from 44m to 370m, on average, primarily depending on whether the bear is in or out of cover and whether the bear or human(s) approach prior to the bear detecting the human(s). Flush distances tend to be closer in cover or when the bear approaches people unaware of their presence (Jope 1985, McLellan and Shackleton 1989, Schleyer et al. 1984, Haroldson and Mattson 1985).

- Grizzly bears move away or flee from people during 25-100% of encounters, primarily depending on whether the bears population is hunted, they encounter people on foot, whether the bear is in the open, or whether the encounter is near facilities receiving high levels of predictable human use. Flight is less frequent when bears are in cover compared to in the open, part of a protected-unhunted population, near human access that has higher levels of spatially and temporally predictable human use, or when encountering humans in moving vehicles rather than on foot (Jope 1985, Gunther 1990, McLellan and Shackleton 1989, Chester 1980, Albert and Bowyer 1991).

- Grizzly bears tend to flee farther (>1km, and up to 1.4-3.0(8.6)km) after relatively unpredictable encounters with humans on foot in back-country areas, especially in the open (McLellan and Shackleton 1989, Schleyer et al. 1983, Haroldson and Mattson 1985, Gunther 1990).

- Flight from encounters in open areas is consistently towards cover (Gunther 1990, McLellan and Shackleton 1989, Schleyer et al. 1984, Haroldson and Mattson 1985, Smith 1978).

- Aggressive responses to encounters are more likely when a female with dependent young is involved, when the population is unhunted, and when the encounter occurs in areas where there is less human activity that tends to be less spatially and temporally predictable (McArthur-Jope 1983, Jope 1985, Herrero 1985, Jope and Shelby 1984, Gunther 1990, McLellan and Shackleton 1989, Albert and Bowyer 1991, Olson et al. 1990).

- Most of this variation in flight response and aggression is ultimately attributable to the degree of wariness or human-habituation among bears in the respective study area, with habituated bears exhibiting less flight response and less aggression in day-light encounters (Braaten and Gilbert 1990, Warner 1987, McArthur-Jope 1983, Jope 1985, McLellan and Shackleton 1989, Albert and Bowyer 1991, Kendall 1983, Jope and Shelby 1984, Olson et al. 1990).

- Fewer bear conflicts and human-injuries occur when human use is regulated so that it becomes more temporally and spatially predictable, and restricted to specified levels (Warner 1987; Fagen and Fagen, in press; Albert and Bowyer 1991; Dalle-Molle and Van Horn 1989).

- A large portion of human fatalities caused by grizzly bears is attributable to human-habituated and food-conditioned bears; and a substantial portion of these fatalities occur at campsites during the night (Herrero 1985, Herrero and Fleck 1990).

Population-Level or Demographic Responses.--

Conflicts and Mortality.-

- Number of conflicts between grizzly bears and humans is positively correlated with levels of human use as it changes seasonally or among years, especially in areas where human activity is unregulated and/or where the bear population is protected from hunting (Fagen and Fagen, in press; Mattson et al. 1992; Keating 1986; Titus and Beier 1992; Albert and Bowyer 1991; Kendall 1983; Smith et al. 1989; Dalle-Molle and Van Horn 1989).

- Number of human-caused grizzly bear mortalities is positively correlated both spatially and

temporally with increased human access and activity, and the resulting increased contact between bears and humans. This relationship is evident in both protected and hunted populations, but is most pronounced where hunting is allowed (Mattson et al. 1992, Mace et al. 1987, Titus and Beier 1992, Mattson and Knight 1991a, Smith et al. 1989).

- Known human-caused mortality occurs disproportionately more often within 1.5-1.6km of a road compared to areas more remote from roads, or is negatively correlated with distance to the nearest road (Mattson and Knight 1991a, McLellan and Shackleton 1988a, Dood et al. 1986, Aune and Kasworm 1989).

- Few grizzly bear population ranges include major town-sites or recreational developments, however those populations that do exhibit disproportionately the greatest mortalities in association with these features (Servheen 1989b, Mattson and Knight 1991a).

- Habituated or food-conditioned grizzly bears are much more likely to be killed by humans than bears that remain wary, especially where human activity is relatively unregulated and/or hunting allowed. Conversely, survival of habituated bears is relatively high in more remote but unhunted areas where human activity is highly controlled (Mattson et al. 1992, Meagher and Fowler 1989, Dau 1989, Braaten and Gilbert 1990, Warner 1987, Albert and Bowyer 1991, Olson et al. 1990).

- Subadults and adult females with young are disproportionately common among habituated bears that range near humans, with the exception of Glacier National Park's back-country. In a few studies females with young tended to avoid areas near humans, probably because they were avoiding the adult males concentrated on high quality food sources that were also located near the human facilities (as at Brooks River Falls) (Braaten and Gilbert 1990; Warner 1987; Fagen and Fagen, in press; Mattson et al. 1992; Jope 1985; McArthur Jope 1983; Tracy 1977; Olson et al. 1990; Dau 1989).

- Subadult males were disproportionately killed by humans in most study areas, most often by hunters, in conflicts over livestock, or as a consequence of

risks posed to humans (Dood et al. 1986; Dood and Pac 1993; Nagy and Gunson 1990; Mace et al. 1987; McLellan and Shackleton 1988b; Bunnell and Tait 1980, 1985). This vulnerability is partly attributable to wider-ranging movements (Bunnell and Tait 1980) and long-range dispersal into unfamiliar habitats (Blanchard and Knight 1992, Mattson 1990).

- Proportionately more bears from hunted populations are killed illegally or to resolve conflicts in areas that contain or are near more resident humans (McLellan and Shackleton 1988b, Mace et al. 1987, Nagy and Gunson 1990).

- Ungulate hunters accounted for a large portion of defense-of-life-and-property (DLP) kills in several study areas (Titus and Beier 1992, Smith et al. 1989), including the Yellowstone ecosystem since 1988, or most illegal kills occurred during the big-game hunting season (Knick and Kasworm 1989).

Distribution and Behavior.-

- Habituated bears are proportionately most active and most common near human facilities such as roads, viewing areas, and recreational developments, especially in unhunted populations (Braaten and Gilbert 1990; Warner 1987; Fagen and Fagen, in press; Mattson et al. 1992; Jope 1985; McArthur Jope 1983; Albert and Bowyer 1991; Tracy 1977; Olson et al. 1990; Dau 1989; Herrero 1985).

- Grizzly bears consistently under-use habitat within 100-500(914)m of roads. This under-use does not vary substantially with use levels or whether the road is paved or unpaved, and is exhibited at very low levels of traffic (0.5-1.9 vehicles hr⁻¹) (Aune and Kasworm 1989, Kasworm and Manley 1990, Mace and Manley 1993, Archibald et al. 1987, McLellan and Shackleton 1988a, Mattson et al. 1987). Similarly, grizzlies under-use habitat where open road densities exceed 1 mile/mile² (Mace and Manley 1993), and observations of bear sign are negatively correlated with km of road (Elgmork 1978).

- Grizzly bears under-use habitat within 400-2000m of occupied back-country campsites and cabins by

40-67% (Gunther 1990, Elgmork 1983). Bear also tend to use back-country foraging areas at different times than humans where human activity is not highly controlled (Olson et al. 1990, Gunther 1984).

- Grizzly bears substantially under-use habitat near town-sites and major recreational developments in the Yellowstone ecosystem. This under-use extends out to between (1)4-5km, and impairs daytime use by between 46-94% within this zone, depending on the season, food, and development (Mattson et al. 1987, Mattson and Knight 1992, Reinhart and Mattson 1990).

Inferences and Implications

- Immediate responses of grizzly bears to humans are arguably a function of the bear's wariness/habituation, the setting (whether in cover or at an atypical site), whether the encounter is with a vehicle, and whether the bear or human approached immediately prior to detection. Encounters between wary bears and humans on foot, especially in the open and in atypical situations, will likely result in a more extreme response by the bear characterized by either aggression or long-range and rapid flight. Aggressive responses are more probable if this type of encounter involves a female with dependent young.

- Habituation will be more common among bears in any given area or population if the bears are unhunted and protected, if levels of human use are high, and if that human use is spatially and temporally predictable.

- Habituation allows grizzly bears to more fully use habitat that is near human facilities, and lessens the probability of an extreme response during encounters with humans. However, the fact that an habituated bear is more likely to range near people will predictably result in a much higher rate of close encounters with humans. Habituated bears will pose the least threat to human safety where there is the tightest control of human activity with the intent of creating consistent and highly predictable spatial and temporal distributions.

- Because habituated bears are more vulnerable to hunting and poaching, and are often perceived to be a threat to human safety, they are typically killed at a higher rate than wary bears. Thus, habituation typically increases mortality risk for individual bears except where human activity is closely regulated and the bear population is unhunted.

- Areas near human facilities can constitute short-term refuges for females with young and subadults, with the attendant condition that these animals become habituated to humans. This refuge effect will have varying beneficence to the population depending on how lethal habituation is to individual bears. In turn, lethality will be a function of whether hunting is allowed and how closely regulated humans are.

- Under-use of habitat near human facilities will predictably be a function of individual range sizes, harvest rates, and the distribution of human facilities with respect to productive habitat; and would be greater in populations that have larger ranges and are well below ecological carrying-capacity because of historically high harvest rates, and where human facilities are located in the poorest habitat. Greater under-use would ultimately be attributable to a lower frequency of habituated bears and more opportunities for the remaining warier bears to meet their energetic needs without using habitat near humans. This interpretation suggests that hunting might reduce human-bear conflicts not so much by instilling fear in bears, but by selecting for the survival of wary bears and by providing more individual foraging space for the bears that survive.

- Proportionately more of sustainable harvest rates will be attributable to illegal causes or control actions as the numbers of resident humans in or near occupied grizzly bear habitat increases. Thus, as populations of resident or recreating humans increase, proportionately more bear mortality will be irreducible or resistant to ready management. In this type of situation, management will be much less responsive to population declines than where the majority of mortality is caused by legal hunting. There appears to be trade-off between hunting opportunities and management flexibility on the one-hand and numbers of resident or recreating humans on the other.

- Over-all mortality risk will increase as miles of open roads and numbers of town-sites or major recreational developments increases in occupied grizzly bear habitat. This risk could be substantially reduced by termination or reduction of hunter-harvest. If mortality risk implicit to these human facilities is at or below sustainable levels, then exhibited under-use of habitat should remain stable. If attendant mortality risk is greater than sustainable levels, then under-use would predictably increase, with a possible attendant decrease in human-bear conflicts. Thus, declining levels of human-bear conflict that might be attributed to successful management could alternatively be attributed to over-harvest.

- If habituation is lethal to bears, as in the Yellowstone area, and current levels of non-hunting mortality are at or near sustainable levels, then the bear population's future prospects will likely be determined simply by the over-all frequency of contact between bears and humans, mediated through the level, dispersal, and predictability of human use. Greater numbers of unpredictably dispersed and armed humans will result in higher mortality risk for the population given the same levels of over-all human use.

- Mortality risk for bears will increase substantially as the number of big-game hunters in grizzly bear habitat increases. Risk attributable to big-game hunters is disproportionately high because hunters are armed, often dispersed in an unpredictable way across the landscape, and typically associated with animals remains that attract bears.

SECTION 2 -- Micro-Scale Security Areas for Yellowstone Grizzly Bears

Rationale

Historically, North American grizzly bears did not persist in areas with even moderate densities of humans or domestic livestock (Mattson 1990). Grizzly bears continue to be killed by humans for numerous reasons, most commonly because of conflict over common resources (e.g., livestock and other human foods) or because the bear is perceived as a physical threat (Craighead et

al. 1988). Human-bear conflicts often revolve around bears habituated to humans as they pursue natural or human-food related feeding opportunities near humans (Meagher and Fowler 1989; Mattson et al. 1992; Section 1). By inference, as human access and activities increase in an area, increasing numbers of bears are forced to come into contact with and tolerate humans as they use their natural habitat. Circumstantial evidence suggests that this results in an increased frequency of bears habituated to humans (McArthur-Jope 1983; Mattson 1990; Mattson et al. 1992; Section 1), and increased bear mortality either because of chance encounters with humans, where humans claim self-defense, or because management agencies judge the bear's tolerance to be a risk to humans (Mattson et al. 1992).

History has demonstrated that grizzly bear populations survived where frequencies of contact with 19th and 20th-century technological humans were very low (Storer and Tevis 1955; Brown 1985; Servheen 1989). Although grizzly bear mortality can be regulated and influenced by changes in human attitudes, it seems unlikely that humans will generally tolerate much contact with an animal, like the grizzly bear, that is a direct competitor for foods (Mattson 1990) and a potential hazard (Herrero 1985). Thus there is a strong case for preserving areas where grizzly bears will be secure from encounters with humans; where bears can meet their energetic requirements while at the same time choosing to avoid people. Such areas would foster the wary behavior in grizzly bears that most managers consider to be desirable. In conjunction with management of attractants around human facilities and town sites, security areas could help to significantly reduce the incidence of poached bears, and bears killed out of self-defense or killed by management agencies because of undesirable behavior.

In this section I describe the rationale for parameters and identification of what I call "micro-scale" security areas. These areas are functional at the scale of individual foraging bouts, as distinguished from security more directly relevant at the scale of a bear's life-time range. By implication, managers need to provide security not only at the "micro-scale" but also somehow relate these security areas to the goals of viability and recovery. By the conceptualization presented here,

this linkage can be achieved through access standards and security area networks (Section 4).

Parameters

Existing analyses of telemetry data from radio-collared grizzly bears provide a basis for postulating dimensions and spacing of security areas, suitable for the scale of an individual bear's home range. Wary bears consistently avoid areas within 2 km of major roads and 4 km of major human developments or town-sites (Mattson et al. 1992), while bears that use areas near roads and developments exhibit disrupted foraging behavior out to these same distances (Mattson et al. 1987). By implication, micro-scale security areas would consist of a 2-4 km wide buffer surrounding a core area corresponding in size to the average 24-48 hour foraging radius of a Yellowstone grizzly bear. This would hypothetically allow a grizzly bear the space to forage while concurrently maintaining its wariness of humans. Results of a 1984-1985 study where grizzly bears were radio-relocated on an hourly basis for periods of 48-96 hours (Schleyer et al. 1984; Haroldson and Mattson 1985) suggested that the average 24-48 hour foraging radius of Yellowstone grizzlies was ca. 0.96 km. Thus, micro-scale security areas should be an absolute minimum of 6 km in diameter or 28.3 km² (ca. 7,000 acres). If these areas were roughly pentagonal in shape, radii would vary from a maximum of 3.4 to a minimum of 2.8 km.

Ideally, spacing of these security areas would allow for safe and unimpeded movement of wary bears among secure habitats. Thus, one hypothesized configuration of security areas would place them on average ca. 2x the mean 48-hour foraging radius apart. After accounting for angular irregularities, this distance averages 1.8 km. If an entire analysis area or bear home range (averaging 884 km² for an adult female life range [Blanchard and Knight 1991]) were apportioned by these guidelines, ca. 57% would be in security areas. Under less favorable conditions, existing or planned security areas would ideally be contiguous and part of a functional network rather than scattered and isolated.

Identification

For practical reasons security areas should have identifiable characteristics, in addition to dimensions and spacing, that relate to the level and nature of human use within. The literature review in Section 1 and the experimental conditions under which relevant data were collected are logical points of reference for identifying these characteristics. First, there should be minimal dispersed use by armed humans, especially associated with attractants such as animal remains. Encounters between humans and bears under these conditions are potentially most lethal to bears (Section 1). Second, there should be no open roads and only low densities of closed roads and/or trails within a security area. This is in accord with the study area conditions during which the data were collected that were used to derive security area dimensions. Unfortunately, there is no readily accessible basis for empirically estimating the densities of trails/closed roads that are compatible with maintaining adequate security within a security area. However, this issue is potentially addressed indirectly through road density standards, and the identification of related allowable densities of trails and closed roads (Section 4).

To facilitate use and recognition by bears, security areas should logically be secure for some minimum period of time. Optimally, a security area would remain secure indefinitely. In situations where management necessitates spatially and temporally varied human activity, then the duration of security areas should arguably relate to the time required for a female to mature and replace herself (i.e., one generation length) without habituating herself or her cubs to humans. This can be calculated as $\Sigma x l_x m_x / \Sigma l_x m_x$, and averages ca. 11 years for wary female Yellowstone grizzly bears (unpublished data).

Whatever the criteria, security areas can be identified by a series of map overlays done either manually or by a GIS. The optimal sequence would be (1) an initial screening with respect to existing open roads, (2) a subsequent screening to identify high-priority security areas containing high-quality bear habitat, and (3) a final screening to identify candidate areas where sufficient road-closures could create a security area. Furthermore, these areas should be evaluated to determine the

temporal sequencing of networks given schedules of planned human activities.

SECTION 3 -- Conversion Factors for Standardized Calculations of Road and Trail Densities

Rationale

Human access has varying impacts on grizzly bears depending on the presence of hiding cover, the intensity of use by humans, and whether motorized vehicles are employed (Kasworm and Manley 1990; Archibald et al. 1987; Schleyer et al. 1984; Haroldson and Mattson 1985; McLellan and Shackleton 1989; Chester 1980; Gunther 1990; and others, see Section 1). These varying degrees of impact are reflected in the zones of influence (ZOI) and "disturbance coefficients" (DC) defined for different types of human activities and access in the publication: *Cumulative Effects Analysis Process for the Yellowstone Ecosystem* (USDA For. Serv. 1985).

Road density standards have become an important part of grizzly bear management in the contiguous United States. Usually only one standard has been applied in any given area. However, as pointed out above and in Section 1, the impacts of any given mile of road will vary according to the amount of associated hiding cover, the level of use, and whether the road is closed to motorized traffic. Trail systems are also commonly ignored in road density calculations, despite the fact that these features also facilitate human access and have demonstrated or likely impacts on resident bears. We need to have some means of accounting for these variables, as well as recreational trail systems, in conjunction with road density standards.

The Cumulative Effects Analysis (CEA) handbook referenced above (USDA For. Serv. 1985) provides a means of dealing with these complexities. By using the ZOIs and DCs for different types of access and activities we can calculate conversion factors that can render miles of road or trail under various conditions into a common standard. Thus, we can add up "equivalent miles" of trails and roads subject to different management and cover to compare to a

road density standard derived with respect to the same common standard. In the following section I detail the calculations used to derive conversion factors and give factor values for roads and trails with and without associated hiding cover. I have treated "closed roads" as trails in this approach, thereby giving a more realistic means of dealing with closed roads rather than dropping them from consideration as soon as they are barricaded. This approach is in accord with the direction specified in the CEA handbook (USDA For. Serv. 1985).

Methods and Parameters

I used the latest revised summer values for ZOIs and DCs from the CEA handbook, as follow:

Activity Group	ZOI Distance	Cover DC	Noncover DC
Motorized linear low use	0.5 mile	0.90	0.71
Nonmotorized linear low use	0.25 mile	0.92	0.83

Total relative habitat alienation (HA_{ij}) associated with each of the above categories was calculated as:

$$HA_{ij} = ZOI_i * (1 - DC_{ij}).$$

Using either roads with cover or a weighted average of roads with and without cover as a standard (i.e., $CF = 1.00$), equivalencies or conversion factors (CF_{ij}) were calculated as follows:

$$CF_{ij} = HA_{ij} / HA_{\text{motorized-cover}}; \text{ or}$$

$$CF_{ij} = HA_{ij} / (0.75 * HA_{\text{mot.-cover}} + 0.25 * HA_{\text{mot.-noncov}}).$$

The calculated CF_{ij} s are as follows:

Access Type	CF	CF
	Mot.-cover as standard	Wgt. ave. as standard
Roads in cover	1.00	0.70
Roads in noncover	2.80	1.90
Trails or closed roads in cover	0.40	0.30
Trails or closed roads in noncover	0.80	0.60

It is very important to realize that use of the 2 different equivalency standards depends on how road density standards were derived for any given area. In the Yellowstone ecosystem the proposed road density standard (see Section 4) was developed in the context of an environment with ca. 75% cover. Thus the CFs based on 3/4 weighting cover would be most appropriate.

These CFs should be used as weighting factors for total miles (TM_{ij}) added under each category. After weighting, equivalent miles would be added across all categories to calculate "standardized road density" (SRD), which would then be compared against the road density standard, where:

$$SRD = (CF_{11} * TM_{11}) + (CF_{12} * TM_{12}) + (CF_{21} * TM_{21}) + (CF_{22} * TM_{22}).$$

These CFs should be updated as our conceptualization of the problem improves and new information becomes available that allows us to more accurately specify impacts associated with different types of human access.

SECTION 4 -- Perspective and Rationale for Proposed Road Density Standards in the Yellowstone Ecosystem

Management of human access is currently viewed by most managers as the most critical element of grizzly bear habitat conservation. Road density standards have consequently become a key part of most grizzly bear management plans. In this capacity, road density standards logically identify thresholds of acceptable change in grizzly bear habitat. These thresholds ideally reflect acceptable levels of habitat alienation and mortality risk that in turn fulfill objectives for population persistence mandated by the federal Endangered Species Act.

However, most grizzly bear road density standards have until very recently been based on elk (*Cervus elaphus*) models (for example, see Lyon 1979, 1983), and none of these standards have demonstrated ties to explicit population persistence or viability objectives. These are important issues for at least two reasons. First, the hypothesis that elk-based road density standards are adequate to insure security for grizzly bears is

implicitly not as defensible as the alternate hypothesis that elk-based standards are deficient in this regard. This conclusion is suggested by the following observations: (1) elk are generally more fecund, (2) consistently exist at higher densities, and (3) are extant in a larger portion of their former range compared to grizzly bears in the contiguous United States. Second, viability-based road density standards are critical because no other standards exist to insure that grizzly bear habitat is not degraded beyond some level compatible with long-term population persistence (Mattson and Knight 1991b; Servheen 1992). Grizzly bear population status is currently monitored strictly through demographic indices (Servheen 1992) that are inherently insensitive to habitat conditions because of the explicit metric and implicit somatic averaging that affects them. Thus, it is imperative that methods be developed for deriving road density standards that are specific to grizzly bears and that can be explicitly tied to population demography. This section presents an initial effort to reach these ends.

Concerns and Considerations

Habitat Alienation and Mortality Risk. -- Most people accept that road density *per se* has little impact on grizzly bears. Only a trivial amount of any landscape is directly obligated to road prisms and surfaces. In fact, some research results have suggested that the physical road structure may, in a proximal sense, enhance bear habitat; by increased foraging opportunities associated with roadside seedings of clover (*Trifolium* spp.) and graminoids (Jonkel and Cowan 1971), and by facilitating the travel of individual bears that are willing to use roads, typically at night (Zager 1980; McLellan and Shackleton 1988a). Rather, most managers and researchers emphasize road density because it is assumed to be highly correlated with more critical factors such as frequency of human-bear contact (Bunnell and Tait 1980; Section 1).

Human-bear contact is typically thought to manifest primarily in two negative ways: (1) habitat alienation or avoidance and (2) mortality risk. Numerous studies have documented under-use of habitat near roads that is typically attributed to avoidance (Section 1), while fewer studies have associated higher levels of grizzly bear mortality

either with areas near roads or areas impacted by higher road densities (Section 1). I argue that these two factors are inter-related and that mortality risk is the more important consideration (1) because of its direct and substantive manifestation in population demography and (2) because of the likelihood that habitat alienation is largely a direct function of differential mortality rates that are selective against human-habituated (i.e., less wary) bears that would otherwise be able to fully use habitat near roads (Mattson et al. 1992; Section 1).

If my contentions are correct, then behavioral-based results (i.e., under-use or alienation of habitat near humans) may be a compromised basis for deriving road density standards unless coupled with some estimate of the role that habituation played among the sampled bears. Based on this hypothesis, I would predict that habitat alienation and mortality risk are not linearly correlated in space, and that because of this nonlinearity, behavioral-based density standards will be higher than mortality-risk based standards. This is to be expected because mortality risk is not realized instantaneously, and as a consequence areas near humans would be used at proportionately higher rates than expected by mortality risk, especially given that a relative surplus of resources in these areas would predictably recruit new resident bears. Thus preliminary spatial results of behavioral-based studies such as Mace and Manley (1993) may over-estimate road densities that are compatible with long-term population persistence.

Scale of Analysis. -- The documented responses of grizzly bears to human facilities will predictably be strongly scale dependent. This derives from the fact that most results are relative in nature (e.g., proportional use of habitat strata) and consequently prone to change as study area bounds are changed. For example, the larger perspective involving mortality risk gradients associated with transitions from wildlands to settled agricultural lands has not been explicitly captured in any study to date and has consequently not been used in conceptualizing road density standards. Furthermore, most analyses that have addressed the hypothesis of habitat alienation have focused on scales of <1-5 km, within the range where habituated or less wary bears may be prevalent (Mattson et al. 1992). The full spatial pattern of mortality risk is likely to manifest only at much broader scales, including areas >1-5 km from road

access, where encounters with humans are likely to be infrequent, and wary bears consequently more common (Mattson et al. 1992).

Inclusion of these more remote areas is critical because most under-use of habitat attributable to lower survivorship of habituated or less wary bears will be manifest as the differential in use of habitat compared to that expected between areas far from humans, where wary bears are more numerous, and areas nearer humans where unwary bears are predictably more common. This differential would be a direct reflection of higher mortality risk associated with human access played out primarily through the loss of fear among vulnerable bears.

Results from the Yellowstone ecosystem suggest the appropriate scale of analysis for capturing broader scale phenomena is approximately 10x the size of the average female life range. In Yellowstone, patterns of mortality risk, habitat use, and distribution by behavior were not fully expressed in an area <9,000 km² (e.g., Mattson et al. 1987; Mattson et al. 1992); approximately equal to 10 x 884 km² average female life ranges (Blanchard and Knight 1991).

However, at this broader scale, analysis is potentially confounded by several important factors. For one, differences in habitat productivity or support capability need to be explicitly accounted for in estimates of "expected" bear use in any given zone (i.e., area alone is not a good indicator of expected use). Trapping effort should also not be biased towards more accessible, potentially more impacted areas; and trapping success should not be biased towards more habituated animals. In either case, behavioral data will likely under-estimate impacts associated with access, while demographic data will be unduly pessimistic with respect to the entire population. A spatially structured analysis using trapping effort as a covariate may address spatial biases, while a behaviorally-spatially structured demographic analysis may address some effects attributable to trapping bias with respect to bear behavior or accessibility.

Variable Road Density Standards. -- There are at least four hypothesized reasons why road density standards should vary among ecosystems or bear management units in accord with differences in attendant risk to individual bears.

First, allowable road densities should logically vary with average bear range sizes. All other things equal, a wider-ranging bear is predictably at greater risk from a given road density compared to a less mobile bear (Bunnell and Tait 1980). Thus, road density standards should compensate for this greater implicit risk, and be lower in areas with wider-ranging typically lower density (see Nagy and Haroldson 1990) bear populations.

Second, road density standards should vary with local human attitudes and levels of traffic. Again, all other things equal, an individual bear will predictably be at greater risk at a given road density where humans are more hostile towards grizzly bears and/or where there are higher levels of human traffic. Local attitudes could be readily determined through surveys, although the exact relationship between attitudes thus determined and bear demography would be difficult to establish. Furthermore, it could be argued that there is a subsidiary but important positive relationship between hostility and restrictiveness of road density standards that could modify the simple proposed relationship superficially suggesting that lower road density standards are needed where humans are more hostile.

Third, unless some means of incorporating the presence of cover into road density calculations can be achieved, mortality risk will predictably vary with the amount of cover at the same road densities, with bear populations with less cover at greater risk. This follows from the greater apparent vulnerability of bears in the open, and their orientation towards cover for security (Section 1).

Fourth, unless some means of incorporating trails and closed roads into road density calculations can be achieved, mortality risk will predictably vary with the additional miles of this type of access at the same open road density, with bear populations in areas of greater closed road

or trail densities at greater risk. This follows from the fact that many bears are killed by armed humans during hunting season, and from the general proposition that area access for these people is facilitated not just by open roads, but in some areas more importantly by trails and closed roads (see Section 1).

Propositions

For reasons expounded above, I offer the following 5 propositions related to derivation of road density standards for grizzly bear management:

- (1) Road density standards should vary among ecosystems as a function of bear range sizes and local human attitudes, with lower allowable densities where ranges are larger and/or human attitudes more negative.
- (2) Road density standards should reflect mortality risk more than habitat alienation; and if behavioral data are used as a basis for road density standards then the spatially explicit effects of habituation and/or intra-specific spacing on mortality risk should be accounted for.
- (3) Road densities should be calculated so as to account for the effects of variable cover and road closures (Section 3).
- (4) Trails should also be incorporated into road density calculations on the basis of pro-rated equivalencies (Section 3).
- (5) Studies of the relationships between road densities and bear behavior or demography should ideally encompass an area equivalent to ca. 10 female life ranges, including areas not impacted by roads, and should include enough data to allow spatially structured analyses of life expectancy and population growth rate.

Proposed Approach

In this section I outline an approach to deriving road density standards for grizzly bear habitat in the Yellowstone Ecosystem that is attentive to the previous 5 propositions. Given the paucity of relevant empirical data, my approach is more conceptual than empirical in nature. It also relies upon the methods presented in Section 3 for calculating equivalent miles of roads and trails in a way that reflects the presence of cover and road closures; thus all road densities are expressed in terms of equivalent miles.

Rationale. -- Mortality risk in the Yellowstone ecosystem is much higher for bears that are habituated to humans, regardless of whether bears are seeking out natural or human-origin foods near humans (Mattson et al. 1992). Furthermore, habituated bears are disproportionately common within 2 km of roads and 4 km of major developments. Following the logic for micro-scale security areas, the spatial extent of "secure" habitats will largely be a function of the area that is sufficiently buffered to maintain wariness, which is apparently key to preserving high survivorship (Mattson et al. 1992). Thus, it is reasonable to postulate that long-term persistence of the Yellowstone grizzly bear population will be contingent upon the proportion of the recovery zone that is >2 km from an open road and >4 km from a major development or town site (cf. Craighead 1980; Mattson 1990).

The extrapolation of results primarily from bears responding to major roads in Yellowstone Park to secondary road systems on National Forest lands is potentially problematic. However several results support the hypothesis that such results are extrapolable, and may even be conservative with respect to areas impacted by secondary road systems. First, behavioral responses of bears to road traffic seem to reach an asymptote at very low traffic levels; bear responses appear to be much the same whether traffic frequency is 0.5 or 100 vehicles per hour (Section 1). Even though the relative importance of different mortality causes varies between parks and National Forests (Mattson and Knight 1991a), it is arguable that many of these causes are compensatory. In other words, many of the bears that exhibit habituation around primary roads in Yellowstone Park are killed at or near developments by managers, while this same

type of bear is killed near secondary roads in National Forests, more often by poachers or in DLP (Mattson and Knight 1991a). Thus, park roads and developments, in combination, are similarly lethal as Forest Service road systems to less wary or habituated bears; and, indeed, this hypothesis seems to be borne out by the available data (Mattson and Knight 1991a). Accordingly, we would expect under-use of habitat near secondary roads on National Forests and primary roads in parks to be similar, given the assumption that this under-use as well as the spatial distribution of habituated bears is an artifact of both mortality rates and the degree to which mortality is selective against habituation (see above).

Open Road Density Standards. -- This approach assumes that micro-scale security areas are the building blocks important to preserving wariness among bears and the higher survivorship associated with this behavior. Accordingly, if an entire Yellowstone Bear Management Unit (see Weaver et al. 1986) were apportioned to minimum-sized (ca. 28 km²) security areas, approximately 10% of the unit would be sufficiently buffered to meet criteria for maintaining high levels of wariness among resident bears. This level of security would correspond to a road density of approximately 0.4 km/km² or 0.6 miles/mile². This is arguably the highest road density compatible with retaining resident bears in any area for any substantive period of time. To achieve 50% security, road densities would have to be approximately 0.16 km/km² or 0.26 miles/mile². The general relationship between percent secure habitat (PSH) and road density (RD in km) would be negative, and for the range RD = 0.04-0.40 km/km² would be approximated by:

$$\arcsin(\text{PSH}) = 90 - 119\text{RD}^{0.538}.$$

Given that the "population" growth rate exhibited by Yellowstone's habituated bears is highly negative, and exceeding in degree the slightly positive growth rate of the wary bear "population" (manuscript in preparation), it is reasonable to postulate that road densities at the scale of an adult female's life range (ca. 884 km² [Blanchard and Knight 1991]) should be less than 0.26 miles/mile². In other words, at least 50% of available habitat should be adequately buffered to preserve wariness and provide security in any given Bear

Management Unit. Accordingly, I recommend the following road density standards for the Yellowstone ecosystem: open road densities should not exceed 0.6 miles/mile² over some fraction of a bear's life range, and furthermore average no greater than 0.26 miles/mile² over the entire range. In other words, some areas could have road densities averaging 0.6 miles/mile², but other areas comprising the bear's range would have to compensate with average densities substantially less than 0.26 miles/mile².

Spatial Frame-Work for Calculating Road Densities. -- There have been many problems associated with spatial referents for road density calculations, given that densities will vary if roads are non-randomly distributed and analysis areas are delineated with regard to road aggregations. Fundamentally, there is concern that density calculations will be capricious if analysis boundaries change for each analysis, and that calculations will be arbitrary with respect to the needs of bears. These concerns can be resolved by permanently fixing the boundaries of analysis areas according to criteria that reflect discontinuities in habitat use by bears, and by sizing analysis areas such that they capture the scale at which grizzly bears operate. In other words, these concerns can be alleviated by making the spatial referents as attentive as possible to the scales and patterns of bear movements, rather than to management concerns defined by a particular project.

The Yellowstone ecosystem has already been stratified in a way that directly reflects documented patterns and scales of grizzly bear movements. These strata constitute the Bear Management Units (BMU) and Subunits (BMUS) used in Cumulative Effects Analysis (Weaver et al. 1986). Each BMU was delineated according to observed discontinuities in the distributions of radio-marked grizzly bears, and roughly corresponds in size to an adult female's life range (ca. 200,000 - 400,000 acres). Each BMU is characterized by high observed fidelity (70-90% [Mattson 1987]) by individual adult females and captures the spatial range of options available to females that reside there. Thus, from a grizzly bear's perspective, it makes the most sense to calculate road density by BMU and to apply road density standards at this scale; with the proviso that these standards provide sufficient security to insure long-term population persistence, or, at a

minimum, $r > 0$. **In this context, I propose that road densities should average less than 0.26 miles/mile² at the scale of a BMU.**

BMU subunits typically delineate finer-scale discontinuities in habitat, often areas of seasonally important habitats. However, virtually all grizzly bears range over areas larger than a BMUS during their life-time, and exhibit lower fidelity to these strata. Thus it is reasonable to postulate that bears could co-exist with higher road densities within a given BMUS as long as road densities in other BMUSs of the same BMU were low enough to keep the BMU average within its more restrictive standard. **In this context, I propose that road densities could average as high as 0.6 miles/mile² within a given BMUS, but only as long as the BMU average remained less than 0.26 miles/mile².**

Closed Road and Trail Densities. -- As pointed out earlier, trails and closed roads also facilitate human access to grizzly bear habitat. Accordingly, their impacts need to be considered when assessing the adequacy of management and the sufficiency of habitat security. Unfortunately, there are few empirical results that relate to the impacts of these linear features on mortality risk for bears. The results of Mace and Manley (1993) based on behavioral responses of bears, suggest that absolute densities of open roads, closed roads and trails should be cumulatively no greater than twice the absolute densities of open roads. Given the conversion factors presented in Section 3, **this result suggests that total densities of open roads and closed roads or trails, expressed in terms of equivalent miles, should be no more than 1.38x open road density standards at both the BMU and BMUS scale; or 0.36 miles/mile² and 0.8 miles/mile², respectively.**

Relationship of Proposed Standards to Actual Densities. -- Road densities discussed here are expressed in terms of standardized miles (see Section 3). Standardized miles will deviate from actual miles of roads or trails on the landscape depending on the amount of cover and whether roads are open or closed. As a consequence, actual miles will rarely equal standardized miles and actual densities will rarely equal standardized densities. Thus, any given BMU subunit may meet road density standards with varying mileage of linear features. Figure 1 illustrates the potential

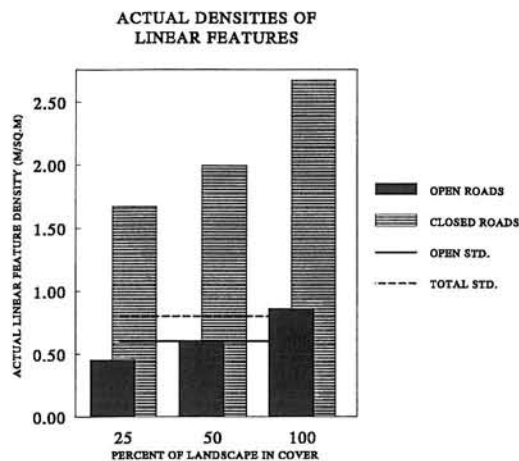


Figure 1. Range of actual linear feature densities possible when meeting proposed BMU subunit standards, given varying levels of cover and open road densities.

range of actual linear miles that could exist in a given area, and meet density standards, depending on the level of cover and road closures. For example, with 100% cover and closure of all roads to motorized traffic, a total density standard of 0.8 miles/mile² could be met with many as 2.67 miles/mile² of existing closed roads and trails. At the other extreme, if there were 25% cover and open roads were maintained at maximum allowable densities (e.g., 0.6 miles/mile²), total density of linear features would have to be approximately 0.87 miles/mile² to meet density standards.

Variation in Road Densities Among Ecosystems. -- At a given road density (RD), miles of road intersected by a bear's range (MR) would increase approximately by the power of -2 (square root) of home range size (HR) as follows:

$$MR = 2 * HR^{-2} * RD.$$

We can postulate a similar relationship between range size and mortality risk, assuming that they are linearly and positively related. Correspondingly, road density standards would hypothetically decrease as average range sizes increase approximately according to:

$$RD = MR / (2 * HR^{-2}).$$

Thus, road density standards proposed here are not likely to be applicable in other ecosystems unless the scale of bear movements is similar. However, this formulation constitutes a hypothesis that is testable if risk-based road density standards are derived for several ecosystems characterized by different bear range sizes. Similarly, it provides a rational frame-work for comparing road density standards from different ecosystems.

Figure 2 illustrates the potential differences in road density standards among ecosystems as a function of female life range size expressed in square miles. It is important to note that range sizes of Yellowstone females are among the largest described for grizzly bears in North America. It is also important to note that average life range size of Yellowstone's adult female grizzlies was 3.1x larger than average annual range size (Blanchard and Knight 1991).

Mace and Manley (1993) are the only other researchers to relate levels of grizzly bear habitat use to different densities of open and closed roads. They found under-use of habitat in areas with open road densities >1 mile/mile². They also estimated average annual range size of adult females to be 48 miles². Assuming that the same relationship between life and annual range size documented in the Yellowstone area holds in their study area, then predicted average life range size would be 151 miles². This corresponds to a

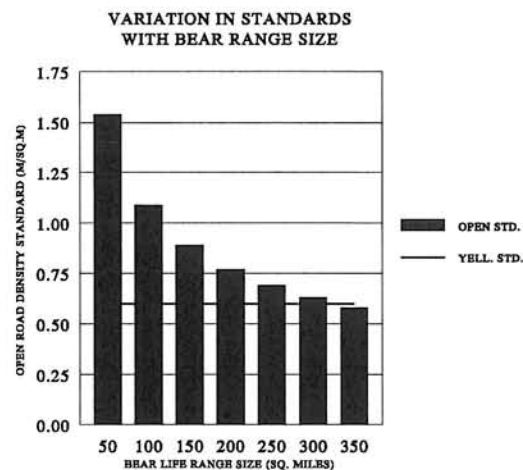


Figure 2. Predicted variation in open road density standards as a function of adult female life range size. The proposed Yellowstone standard (YELL. STD.) is also indicated.

predicted open road density standard (0.9 miles/mile²[Fig. 2]) that is in remarkable accord with the apparent tolerances of grizzly bears (<1 mile/mile²) documented during their study to date. This single comparison supports my hypothesis that (1) road density standards will vary among ecosystems, (2) standards will be higher in areas where bears exhibit smaller ranges, and (3) standards will vary inversely to $2 \cdot HR^{-2}$.

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Review

Complex Challenges of Maintaining Whitebark Pine in Greater Yellowstone under Climate Change: A Call for Innovative Research, Management, and Policy Approaches

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Abstract: Climate suitability is projected to decline for many subalpine species, raising questions about managing species under a deteriorating climate. Whitebark pine (WBP) (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem (GYE) crystallizes the challenges that natural resource managers of many high mountain ecosystems will likely face in the coming decades. We review the system of interactions among climate, competitors, fire, bark beetles, white pine blister rust (*Cronartium ribicola*), and seed dispersers that make WBP especially vulnerable to climate change. A well-formulated interagency management strategy has been developed for WBP, but it has only been implemented across <1% of the species GYE range. The challenges of complex climate effects and land allocation constraints on WBP management raises questions regarding the efficacy of restoration efforts for WBP in GYE. We evaluate six ecological mechanisms by which WBP may remain viable under climate change: climate microrefugia, climate tolerances, release from competition, favorable fire regimes, seed production prior to beetle-induced mortality, and blister-rust resistant trees. These mechanisms suggest that WBP viability may be higher than previously expected under climate change. Additional research is warranted on these mechanisms, which may provide a basis for increased management effectiveness. This review is used as a basis for deriving recommendations for other subalpine species threatened by climate change.

Keywords: climate change; whitebark pine; resource management; policy; Greater Yellowstone Ecosystem

1. Introduction

Impending climate warming is perceived as a major threat to the many species that are adapted to subalpine habitats [1–3]. Upper subalpine and tree-line species have a number of traits that make them challenging to manage under climate change. These species are especially vulnerable to climate change because many mountain ranges have decreasing area at higher elevations and upslope movement

of suitable climates often results in range loss or “mountain-top extinctions” [4]. Potential change in climate suitability for these species has high uncertainty due to the narrow distributions of these species, small sample sizes, and technical difficulties in modeling climate at the fine spatial scales relevant to these species [5,6]. The ecology of these species is typically less studied and less understood than commercially valuable species and management experience is often limited. Within the U.S., the ranges of these species are often within restricted federal lands such as Proposed or Designated Wilderness and Wilderness Study Areas (hereafter termed wilderness) where management is constrained by law and policy [7]. Finally, similar to other species, these projected changes in climate suitability for tree-line species are often much larger in spatial scales (e.g., sub continental) than the scales of management jurisdictions, necessitating interagency collaboration [8].

Resource managers of locations where a species is projected to undergo declining climate suitability face difficult decisions as to appropriate management strategies. Agency policy often promotes retention of viable populations of native species [9,10]. Yet, ecological theory would suggest that species are unlikely to persist in areas that are outside of the species’ climate tolerances [11]. New perspectives on research, policy, and management are needed to maintain the viability of many subalpine species under climate change. To illustrate these perspectives, we have selected an iconic high-elevation tree species in one of the most iconic areas in the United States.

Whitebark pine (WBP) (*Pinus albicaulis*) crystallizes the complex challenges that natural resource managers will likely face for many subalpine species in the coming decades [12]. WBP is a member of the montane and subalpine forest community in western North America and is considered a keystone species for the unique ecosystem services it provides including facilitating increased forest cover, enhanced persistence of snowpack and runoff, and providing seeds that are an important food for threatened Grizzly bear (*Ursus arctos*) and many other wildlife species [13–15]. Because of these benefits, there is concern over the forest die-off that is underway. WBP is declining throughout its range because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion management policies, and the introduced disease white pine blister rust (causal agent *Cronartium ribicola*) [13]. In addition to these current threats, climate suitability is projected to decline over much of the species current range [16–18].

The Greater Yellowstone Ecosystem (GYE) in the U.S. Northern Rocky Mountains has a cold continental climate and supports extensive stands of WBP in the subalpine zone [19], and WBP individuals in the sub canopy of forests in the montane zone. Some 53% of the aerial extent of WBP in the U.S. is located in the GYE [20,21]. The GYE WBP population has been particularly hard hit in recent years with over 95% mortality of cone bearing trees [22,23] in some areas due to factors related to warming climate [24]. Beyond the current forest die-off, scientists are projecting that the area of suitable habitat for WBP in GYE will decline dramatically in the coming century under changing climate [25–28]. Consequently the U.S. Fish and Wildlife Service listed WBP on its U.S. Candidate species list [29]. An interagency committee was formed in 2000 (called the Whitebark Pine Subcommittee of the Greater Yellowstone Coordinating Committee, or GYCC WBP Subcommittee) and has begun implementing a strategy for WBP management in the GYE [30]. The potential effectiveness of this strategy under climate change has not been evaluated.

Assessing the risk of climate change to population viability of WBP in the GYE and the potential effectiveness of management is difficult because the species is influenced by a complex array of interacting ecological factors [13]. These include the direct effect of climate on WBP and the indirect effects of climate on competing tree species, fire regimes, mountain pine beetles, and white pine blister rust, all of which interact and limit WBP viability. In this paper we synthesize current knowledge on the complex interactions that impact WBP in the GYE and summarize current management approaches taken by federal land managers as coordinated by the GYCC WBP Subcommittee. We then evaluate evidence regarding new perspectives on the complex WBP system that may allow opportunities for WBP persistence in the face of climate change. We conclude by offering recommendations for research, policy, and management to increase likelihood of persistence of WBP in the GYE. Although

the ethical implications of some management options have been discussed elsewhere for example, see discussions of assisted migration in [31,32], our goal here is not to debate philosophical views on active management under climate change, but to present management recommendations that might make sense if active management of WBP were an agreed upon goal. This synthesis of a well-studied species that is currently responding to climate change is relevant to the many other subalpine species around the world that are likely to face similar threats in coming decades. Thus, we end with recommendations for research, climate-informed management, ecological forecasting, re-evaluation of policy, and interagency collaboration that may improve the viability of other subalpine species vulnerable to climate change.

2. Complex Interactions that Limit WBP under Climate Change

Research on WBP in the past decade provides a basis for a conceptual model of the complex interactions by which future climate change may directly and indirectly influence the demography of WBP (Figure 1). The population growth rate of any species is a consequence of vital rates in each life-history stage. Climate change influences WBP viability through its direct effects on establishment, growth, survival, reproduction, and dispersal and through its indirect effects on biotic interactions and disturbance.

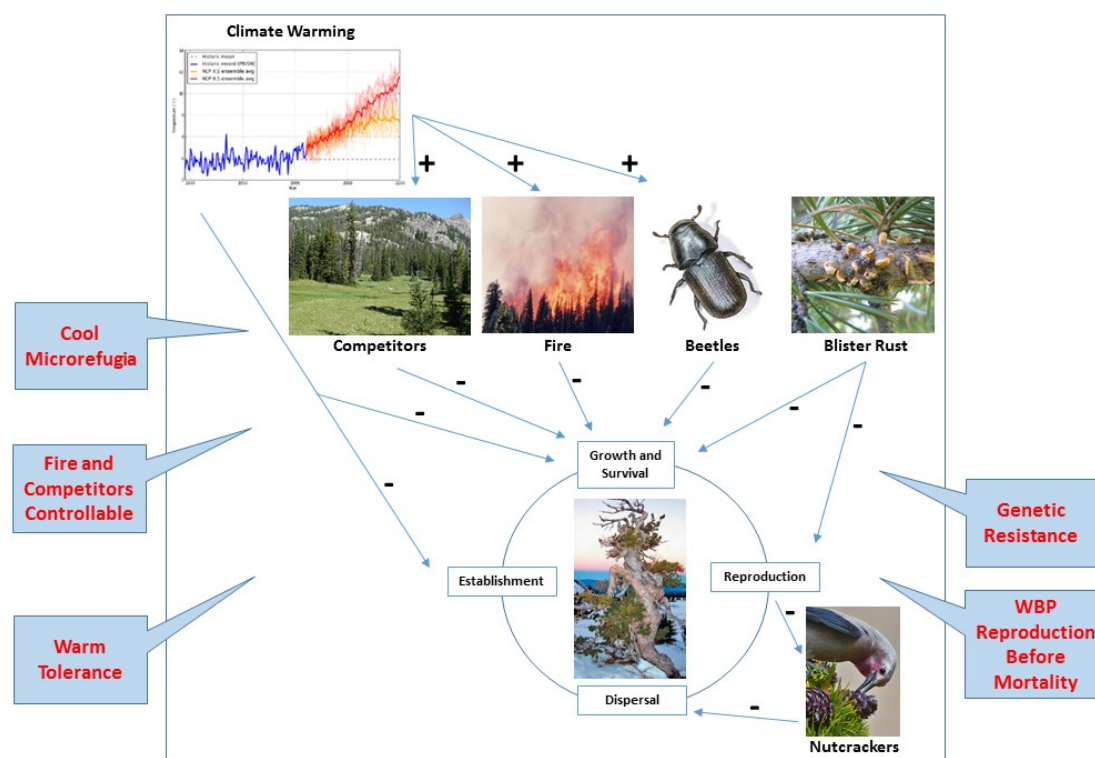


Figure 1. (Inner box) Conceptual model of the projected direct and indirect effects of climate warming on WBP demography based on the current literature. Positive and negative signs denote the nature of the effect. Climate warming reduces whitebark pine (WBP) establishment, growth, and survival directly by exceeding WBP physiological tolerances and indirectly by favoring competing vegetation, severe fire, and mountain pine beetles. White pine blister rust negatively influences WBP growth, survival, and reproduction. However, the influence of climate change on white pine blister rust in the Greater Yellowstone Ecosystem (GYE) is not currently understood. (Outer Box) Ecological mechanisms that may allow WBP to remain viable in GYE in the face of projected climate warming and related threats (red text in call-out boxes). Picture and figure credits from left to right and top to bottom are: Tony Chang, Andrew Hansen, Yellowstone National Park Photo Archive, Colleen Kimmet, Grav Skeldon, Louisa Willcox, Karen Rentz.

2.1. Climate Suitability

Climate suitability is an important determinant of the distribution of many tree species, hence the climate characteristics of where a species is found is often used to infer climate tolerances and potential effects of future climate change [33,34]. The subalpine locations where WBP is present in the GYE are characterized by low maximum July temperatures, low summer minimum temperatures, and deep April snowpack [25,26]. Climatically-suitable habitats for WBP are projected to decrease substantially by the end of the century across the species range [17,18,35] and within the GYE [25,26]. As a result, WBP was ranked as most vulnerable to climate change based on climate suitability among eight conifer species in the Northern Rockies [36]. Based on the most recent climate projections, mean annual temperatures across the GYE are projected to rise 3–7 °C above the 100-year historical mean by the end of the century and snowpack in the subalpine zone is projected to decrease by 20%–30% [26]. The area within the GYE where climate is projected to be suitable for WBP in reproductive size classes (>20-cm diameter at breast height or DBH) by 2100 was 82% less than at present under a moderate warming scenario (RCP 4.5) and 97% less under a higher warming scenario (RCP 8.5) by 2100 [26].

2.2. Competition

In addition to its physiological tolerances to climate, the performance of WBP in the GYE is structured by competition with lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). At the highest elevations, climates are mostly unsuitable for competitors, allowing WBP to persist in pure stands [24,37,38]. At lower elevations in the montane zone, the other conifer species typically grow faster than WBP, and by mid to late seral stages, there is reduced growth, reproduction, and survival of WBP through competition [38]. Under future climate scenarios in the GYE, climate suitability for all the conifer species is projected to shift upslope [39]. Locations where WBP is currently dominant are projected to increase in climate suitability for Douglas-fir, lodgepole pine, subalpine fir, and Engelmann spruce [39]. The highest elevations in the GYE, which are now not occupied by trees are projected to be suitable in climate for subalpine fir as well as WBP. Thus, the effects of competition on WBP may increase under future climates.

2.3. Fire

Nearly all effects of competition on WBP are mediated by wildland fire. Severe fire kills all species of montane and subalpine trees, including WBP [13]. WBP regenerates well in burned areas and is among the tree species that initially colonize these open sites and persist in them for decades until outcompeted by other conifer species [40]. WBP's higher resistance to fire [41] delays succession under mixed-severity fire regimes through the preferential removal of competitors such as subalpine fir and Engelmann spruce by fire [24].

Over much of the WBP range, humans have excluded fire in the past several decades resulting in shifts to greater dominance of later seral stages, to the detriment of WBP [13]. In the West Big Hole Range of Idaho and Montana, for example, Murray *et al.* [42] found that nearly half of all stands have shifted to later seral stages since 1753, possibly due to fire exclusion. The fire regime within the montane zone of the GYE is characterized by infrequent, high-severity fires [28]. This has likely favored WBP in the decades following severe fires because its seed is bird dispersed allowing great dispersal distances [43]. There is no evidence, however, that fire exclusion activities have altered the fire return interval within this zone in the GYE [44].

Climate change is expected to affect fire regimes throughout the range of WBP and, in turn, WBP dynamics [45]. In western Montana, increasing frequency of severe fires is projected to reduce the abundance of WBP, but not as much as its competitors e.g., [46]. In the GYE, fire is projected to increase in both frequency and size [47], which probably will result in increases of WBP mortality rates as well as competing species. A simulation modeling study by Clark *et al.* [48] in the montane zone of

the GYE projected substantial reductions in lodgepole pine and Douglas-fir stand age and basal area under changing climate and increased fire severity. Such studies have not been done in the subalpine zone, where WBP is most dominant. The potential effects of frequent severe fire on WBP relative to competing species are not known. However, it is likely that stand size and stand age for all conifer species will be much reduced.

2.4. Mountain Pine Beetle

Mountain pine beetle is a native species that has periodically irrupted in western forests in the past and caused significant mortality to western pine species [49]. During most of the past century, mountain pine beetles have typically been at endemic levels in WBP ecosystems, causing little host mortality because of inhospitable cold temperatures [50,51]. While periodic outbreaks have occurred during warm periods in the past, 1730s, 1819, 1887, 1930's, and 1970s [52], these outbreaks were typically short-lived. In the GYE, cold winter temperatures have limited the severity of outbreaks in WBP forests due to negative impacts on beetle development [50]. The current outbreak, which is more severe than any in recorded history, is thought to be the result of favorable forest conditions, perhaps resulting from fire exclusion [22], as well as shortened mountain pine beetle generation times linked to recent above-average temperatures [50,53].

Mountain pine beetles are cambial feeders, which along with associated fungi typically kill their host in order to complete their life cycle. Time of development is variable and is driven largely by temperature [54]. In WBP systems, development can take up to two years because of prolonged cold temperatures. Recent milder winters and warmer summers have allowed beetles to complete an entire life cycle in one year or less, rapidly increasing the rate of population growth and the severity of the outbreak [50]. The current decline of WBP in the GYE is largely due to the abnormally severe mountain pine beetle outbreak. During 1999–2007, some 95% of WBP stands had adult mortality levels exceeding 50% [23]. Future projections show increased climate suitability for mountain pine beetle in the WBP zone of the GYE in the coming century, provided there are sufficient living host trees [53,55].

2.5. White Pine Blister Rust

White pine blister rust is an invasive pathogen native to Asia and introduced to North America circa 1910. Since initial invasion, it has followed a typical pattern of slow establishment leading to exponential growth, and now endemic persistence [56]. For decades, the pathogen has attacked white pine populations in waves but the recent spike in blister rust infection as well as high mortality rates of WBP of all ages are unprecedented [57]. The fungus is now found across almost the entire distribution of WBP, with highest levels in the north western Rocky Mountains, likely due to cool, moist climate conditions favored by the pathogen [24].

The multiple stage, five spore life cycle of white pine blister rust alternates between WBP and mainly *Ribes* species [56]. This advantageous life cycle allows for genetic diversity, short and long distance dispersal, longevity, and annual amplification [56]. WBP is susceptible to infection by *C. ribicola* at any life stage. Infection of the needles occurs first, with the fungus then spreading to branches and stems, girdling and eventually killing the tree. The pathogen is most destructive when infecting mature individuals as it cuts off and kills the upper, cone-producing canopy.

Within the past few decades blister rust infection rates have increased dramatically within much of the range of WBP. During a 17-year study monitoring blister rust infection in northern Idaho, over 75% of originally uninfected WBP became infected [57]. The GYE has seen lower infection rates, mainly 20%–30% [58]. A model of blister rust prevalence based on data from 1968 to 2008, however, projected that blister rust infection and subsequent mortality will be widespread across the GYE over the next 20 years [59].

2.6. Seed Predation and Dispersal

WBP seeds are dispersed by a species of bird, the Clark's nutcracker (*Nucifraga columbiana*) [60]. The birds store WBP seeds as a food source in caches that can be up to 32 km from the parent tree [61]. Some of the cached seeds germinate and the result is a relatively rapid dispersal of WBP [61,62]. Thus, WBP is able to colonize patches opened by fires, avalanches, and other disturbances relatively rapidly and establish new populations [13]. Although species other than Clark's nutcracker harvest and store WBP seeds in middens, uneaten seeds seldom become established because the microhabitats of the middens do not provide suitable conditions [63]. Whether WBP seeds are lost to predators or are dispersed by nutcrackers is governed by various interacting relationships. In years of low cone production, most seeds are consumed by predators [63]. In areas of high WBP mortality or in years of small WBP cone production, the crop may be too small for nutcrackers to find adequate food and they relocate to more productive areas [64]. Additionally, trees stressed by competition, beetles, blister rust or unfavorable climates are less capable of producing the large seed crops that are required to swamp seed predators and allow for WBP establishment. Consequently, WBP populations under climate change may be on the path to extinction long before the last individual dies because of the lack of dispersal and regeneration due to abandonment by nutcrackers [13] in high mortality areas.

In total, the conceptual model of the WBP in GYE (Figure 1) suggests the potential for continued population declines under future climate change. Little of the current range is projected to remain suitable in climate for WBP populations based on statistical models. Effects of climate warming on competitors, fire regimes and mountain pine beetle populations, especially in the presence of white pine blister rust, are expected to further reduce WBP vital rates. Nonlinear effects of WBP abundance on seed dispersal by nutcrackers could cause threshold declines in dispersal and reproduction as the population size decreases. Alternatively, increases in fire would lead to more open areas suitable for WBP regeneration and thereby favor future population viability [12], if adequate adult trees survive the fires and provide seed sources.

3. Current Management Approach and Status

In recognition of the many cross-boundary issues in the GYE, federal agencies in the region collaborate to manage WBP forests via the GYCC WBP Subcommittee. The subcommittee formed to "work together to help ensure the long-term viability and function of whitebark pine in the Greater Yellowstone Area" [30]. The subcommittee initially focused on mapping and monitoring WBP across the GYE. Substantial mortality of WBP was observed by 2004 leading the subcommittee to address the need for management of the species, culminating in the publication of the *Whitebark Pine Strategy for the Greater Yellowstone Area* [30].

The Strategy is organized around four goals and specific treatments are identified for each goal [65].

- **Monitoring.** The goal is to quantify the status and trends in WBP condition and use results to guide management. This goal is achieved by monitoring WBP survival, reproduction, and mortality agents.
- **Protection.** The goal is to prevent or minimize damage to existing trees and stands from insects, disease, and fire. Strategies to realize this goal include protecting genetically disease resistant trees, cone-producing trees, and trees exhibiting blister rust resistance through use of anti-aggregation pheromones (verbenone), insecticides (carbaryl), and pruning. Additionally, blister rust resistant trees and stands are protected from wildland fire.
- **Restoration.** The goal is to restore WBP stands by replanting or by creating conditions that favor natural regeneration and dominance of WBP. Methods include planting blister-rust resistant seedlings, creating openings conducive to the natural regeneration of WBP, and removing competing vegetation.

- **Tree Improvement.** The goal is to identify and propagate genotypes that have resistance or tolerance to adverse factors such as drought and white pine blister rust. This is realized by collecting seeds from WBP trees having potential resistance to white pine blister rust, propagating the seeds in nurseries, testing for blister rust resistance, and using seeds from trees that show resistance to populate a seed orchard to produce resistant seedlings for planting.

The Strategy was not formulated in the context of projected climate change because of a lack of climate science information at the time. Rather, the Strategy stated, “As scaled regional models or more detailed predictive mapping become available, this information will be incorporated into the annual work plan and future revisions of the Whitebark Pine Strategy” [30].

The potential for applying management treatments across the GYE varies with federal agency and land allocation type. The majority of WBP distribution in the GYE (68%) lies in wilderness (Table 1) where the enabling legislation or current policy dissuades active management. Twenty three percent of the WBP range in the GYE is within Inventoried Roadless Areas, where lack of mechanized access constrains management feasibility [66]. Only 8% is within multiple use lands where active management is permitted and logistically feasible.

Table 1. Aerial distribution of WBP in GYE by federal land allocation type. Not shown is the 0.21% of the WBP distribution that is on tribal and other land allocation types.

Land Allocation Type	Agency	Legal Direction/Management Philosophy	Proportion of GYE WBP Aerial Extent
Multiple Use	National Forest Service; Bureau of Land Management	Multiple use while maintaining ecological integrity	8.09%
Non-wilderness	National Park Service	Preserve unimpaired natural resources for the enjoyment, education, and inspiration of this and future generations.	0.14%
Wilderness (Designated, Proposed, Recommended, Study Area)	National Forest Service; Bureau of Land Management; National Park Service; U.S. Fish and Wildlife Service	Maintain natural and untrammeled conditions	68.18%
Inventoried Roadless Area	National Forest Service	Roads and timber harvest prohibited. Forest health treatments allowed.	23.38%

The distribution of WBP management activities coordinated by the GYCC WBP Subcommittee to date reflects these land allocation constraints. While research and monitoring plots are well distributed across land allocation types (Table 2), the majority of protection and restoration treatments were done on multiple use lands, with intermediate levels of treatment in roadless areas and very low levels of treatment in wilderness. Importantly, the estimated minimum area treated to date (*ca.* 2227 ha) is much less than 1% of the WBP aerial extent in GYE.

In summary, while considerable progress has been made in WBP management in the GYE, the scale and scope of the effort is likely inadequate considering current WBP mortality levels and future climate projections. Federal agencies have been collaborating for some 15 years and the interagency working group has prepared a comprehensive strategy document, deployed research and monitoring efforts, developed a genetically-improved seedling program, and implemented protection and restoration activities. This implementation, however, has been done on a small proportion of the GYE WBP range. Moreover, the GYE WBP Strategy, while using the best available science at the time, was not developed in the context of the projected direct and indirect effects of climate change on WBP viability. The projected loss of climate suitability over most of the GYE and potential exacerbation of the effects

of bark beetles, competition, and fire under climate change are likely to substantially reduce WBP viability in GYE. Thus, the potential long-term effectiveness of the GYE WBP Strategy as currently applied is unknown.

Table 2. Estimated minimal extent of monitoring and management treatments for WBP for federal lands in the GYE by land allocation type as coordinated by the GYCC WBP Subcommittee. Data are estimates provided by the GYCC WBP Subcommittee with most of the U.S. Forest Service data compiled from the Forest Service Activity Tracking System (FACTS) in September 2015. Research/monitoring plots are described in [67].

Management Activity	Land Allocation Type		
	Multiple Use	Wilderness ¹	Inventoried Roadless Areas
Research/monitoring	101 plots	105 plots	83 plots
Reforestation monitoring	700 ha total	0 ha	351 ha
Protection from mountain pine beetle	688 trees and 890 ha annually	398 trees and 34 ha annually	76 trees and 157 ha annually
Planting seeds/seedlings	302 ha total	4 ha total	351 ha total
Mechanical pruning/thinning	428 ha total	0 ha total	8 ha total
Targeted fire suppression	0 ha total	0 ha total	0 ha total
Wildland/prescribed fire use	53 ha total	0 ha total	0 ha total
Seed collection	166 bushels total	20 bushels total	101 bushels total

¹ Designated, Proposed, Recommended, or Study Area.

4. New Perspectives on WBP Dynamics under Climate Change

If the abundance of large cone-producing WBP has declined dramatically in the GYE over the past decade and climate suitability is projected to deteriorate in the future, does this portend the extinction of WBP in the GYE and render efforts at management futile? It is currently unknown what rates of establishment, growth, reproduction, survival and dispersal are necessary for a minimum viable population of WBP in the GYE. Our increasing understanding of the complex WBP system, however, focuses attention on existing and new perspectives on mechanisms by which the species may persist in the GYE under future conditions, probably in younger age classes and smaller population sizes (Figure 1). Improved knowledge about these potential mechanisms of persistence may improve management effectiveness. In this section we identify and evaluate six key mechanisms that may allow WBP population persistence (Table 3).

Table 3. Ecological mechanisms that may favor WBP population persistence under climate warming. Weight of evidence is based on current knowledge from the literature. Research needs and management implications are discussed in Sections 5 and 6.

Limiting Factors	Mechanism	Weight of Evidence (Citations)	Research Needs	Management Implications (Citations)
Climate change	WBP persistence in microrefugia	Strong [68–72]	Finer resolution modeling to identify microrefugia and monitoring of WBP performance	Remove competing species in cold/wet settings; protect from mountain pine beetles in cold/dry settings; protect microrefugia from severe fire [71,73]
Climate tolerances	Fundamental temperature niche broader than currently perceived	Moderate [71,74–76]	Physiological studies of temperature, precipitation limits	Remove competing species to reduce competitive exclusion of WBP in warmer settings [12,13,24,30,65,77]
Competing tree species	Release from competition improves WBP viability	Strong [40,78,79]	Species/age specific competitive effects on WBP	

Table 3. Cont.

Limiting Factors	Mechanism	Weight of Evidence (Citations)	Research Needs	Management Implications (Citations)
Fire	Enhanced moderate severity fire favors WBP	Weak [77,80]	Projections of fire severity in WBP habitat; WBP sensitivity to fire	Protect rust-resistant trees, especially those whose seeds are being harvested; allow more wildland fire use fires during moderate years; [12,13,48,65,81]
Mountain Pine Beetle	Medium sized WBP ¹ resist beetles and reproduce	Strong [82–85], Figure 4	Rates of reproduction and survival of medium sized WBP ¹ relative to minimum population size	Remove competing vegetation and perhaps thin existing WBP to increase vigor of reproducing trees [12,13,65,86]
White Pine Blister Rust	Natural and artificial selection allows persistence	Well known [87,88]	Long term monitoring of rust resistance	Plant rust-resistant seedlings; protect known rust-resistant individuals from MPB and fire [89,90]

¹ 18–25 cm diameter at breast height.

4.1. Microrefugia

Projected loss of climate suitability for WBP may fail to adequately consider variation in microclimate. “Microrefugia” are defined as localized landscape settings that support suitable climate conditions amidst unfavorable regional climate [91]. Evidence for species survival in microrefugia in the Holocene suggests that microrefugia might allow cold-adapted species to persist under future climate warming [92]. Under this mechanism, localized landscape settings in the GYE could remain climatically-suitable and serve as microrefugia for WBP persistence under future warming.

Microrefugia may be missed by bioclimate envelope analyses if the resolution of the climate projection is coarser than the climatic factors that influence spatial patterning of the organism [93]. Fine scale variation in aspect, slope, elevational extremes, topographic shading, and cold air or water drainage may influence plant distributions [5]. For example, consideration of cold-air pooling and projected climate warming resulted in 6 °C differences in modeled temperature between nearby locations in the Cascade Mountains [68]. Analyses of the effects of spatial resolution on projected climate suitability found that coarse scale models (e.g., >4 km) predicted loss of climate suitability while fine-scale models (e.g., ~90 m) projected persistence for some species [70,93]. Simply put, the finer resolution models were able to identify meaningful climatic variability in mountainous terrain that could not be resolved by the coarse scale models. In the case of WBP in GYE, the 800-m resolution used by Chang *et al.* [26], while state of the art for climate projection, may be too coarse to accurately model a narrowly distributed species like WBP by missing small areas of locally suitable habitat.

We speculate that two types of landscape positions may serve as microrefugia for GYE populations of WBP. The first are locations with relatively cool and wet conditions where temperatures may stay within the tolerances of WBP and mortality due to mountain pine beetle may be lower. Mortality of WBP from mountain pine beetle in GYE was found to be positively associated with mean minimum temperature [73] and with climate water deficit, a measure of aridity [72]. The effect of aridity was especially strong for larger WBP trees. Increases of 75 mm in climate water deficit were associated with a 20% increase in mortality rates for trees >20 cm DBH. Similar results were obtained for WBP in eastern California [71]. High elevation depressions, north-facing slopes, and medium to fine-textured soils with higher water holding capacity are areas in the GYE [72] that may possibly maintain relatively cool temperatures and higher water availability and serve as microrefugia for WBP.

In the absence of mortality from mountain pine beetles, colder and drier landscape positions represent potential microrefugia where climate conditions could remain suitable for WBP but be too harsh for competing tree species or for white pine blister rust. At upper tree line, WBP is able to

establish and survive in more exposed sites than subalpine fir or Engelmann spruce, presumably because of its: phenotypic traits to increase stress tolerance (e.g., higher soluble sugar concentrations, lower specific leaf area) and improve carbon balance (e.g., greater water use efficiency, lower respiration) [69]; higher photosynthetic tolerance for the frequent frost and bright sunlight [94]; and tolerance of wind-induced drought [95]. Such microrefugia are most likely found in wind-swept, high elevation sites where WBP currently forms the upper tree line. These drier and cooler sites are also less favorable for white pine blister rust attack on WBP [96].

4.2. Temperature Niche

Bioclimate envelope modeling only identifies the climate conditions where a species is present today and uses this to predict where it will be under climate change [34]. To the extent that competition with other conifer species restricts the presence of WBP in warmer settings in the GYE, the species may be able to tolerate warmer and drier conditions than where it is currently distributed and thus be better able to persist under warming climate than projected by bioclimate envelope models.

The upper temperature tolerances of WBP are not well known. The single study done in the GYE [76] suggested that WBP can tolerate warmer conditions than those where it currently is found. In laboratory experiments under well-watered conditions, optimal photosynthesis of WBP occurred at 20 °C with upper and lower limits of 0 °C and 35 °C. Root growth and germination ranged from 10–45 °C to 10–40 °C, respectively. Currently, only about 5% of WBP trees are growing where temperatures are near the optimum for photosynthesis identified by Jacobs and Weaver [76]. Thus, mean summer temperatures where WBP currently occur in GYE may be lower than the physiologically limiting temperatures for the species, at least when adequate moisture is available. In support, studies elsewhere in the range of WBP found that the species increased in growth rate with increasing minimum temperature [71] and increased in density and basal area in response to warmer, wetter conditions [74].

A recent paleoecological reconstruction in GYE [75] also suggests that the fundamental niche of WBP is broader than its current realized niche. WBP was most abundant (as evidenced by pollen) at a time prior to about 7500 years ago with the warmest summers and lowest effective moisture of the past 15,000 years, albeit colder winters. In the mid-late Holocene, WBP declined as summer temperatures decreased, winter temperatures and precipitation increased, and lodgepole pine increased. This persistence of WBP in the GYE since the last glacial maximum suggests that the species can tolerate a much wider range of climatic variation than its current distribution would suggest, particularly under lower levels of competition from other tree species. A caveat of this study, however, is that pollen of WBP cannot be separated from the closely related limber pine (*P. flexilis*) that tolerates much warmer conditions than WBP and the presence of limber pine in GYE during the Holocene is poorly known [75].

4.3. Release from Competition

If the distribution and abundance of WBP are influenced by competition, then ecological theory would suggest that reducing competition may increase vital rates such as establishment, growth, survival, and reproduction. This release can be initiated by humans (e.g., thinning, harvesting) or by disturbances (e.g., fire, disease).

It is well established that WBP is often limited by competition at lower elevations within its range. A study in British Columbia found that WBP was inhibited early in post-fire succession by lodgepole pine and later in succession by subalpine fir and Engelmann spruce [40]. In lower elevations in western Montana, WBP and subalpine fir individuals are found further apart than expected if the trees were distributed randomly, implying competition, whereas at high elevations, the two are found closer together [78]. The most direct evidence comes from experimental removal of competitors. Among 45 WBP trees aged 51–395 years released from competition, 31 trees exhibited a significant

increase in growth rate in the first five years post-thinning, with a mean increase in radial growth of 64% [79] (Figure 2). This increase was higher for trees in stands with high tree density before thinning.

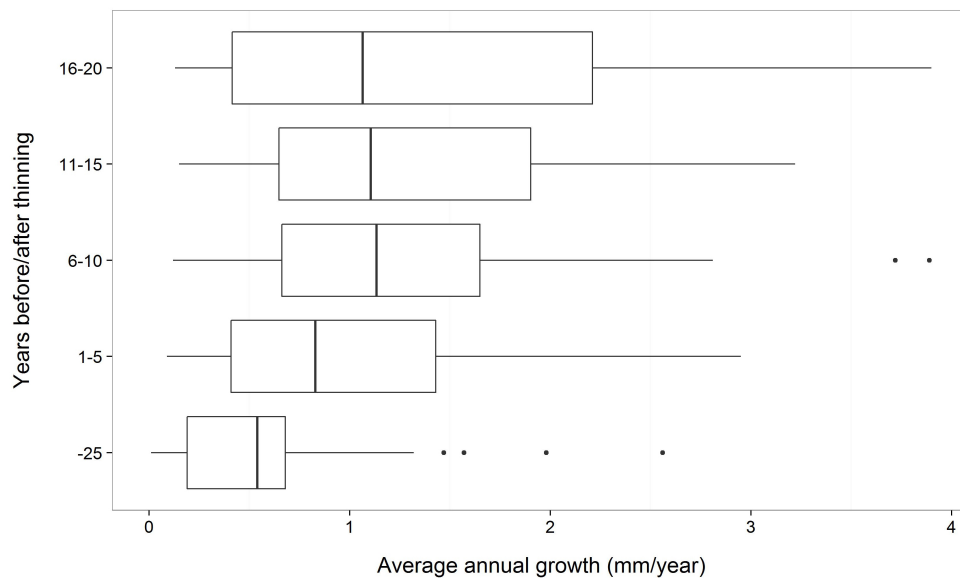


Figure 2. Average annual growth of WBP before and after thinning of competitors. Data from Keane *et al.* [79].

Competition is thought to play a more important role at lower elevations of WBP's range, as abiotic conditions are favorable for both WBP and its competitors [38]. At higher elevations, climate is less favorable for competitors, whose absence releases WBP from competition [24,37,38]. Consistent with these predictions, the elevational distributions of tree species in GYE illustrates that the prevalence of species potentially competing with WBP is reduced at higher elevations (Figure 3).

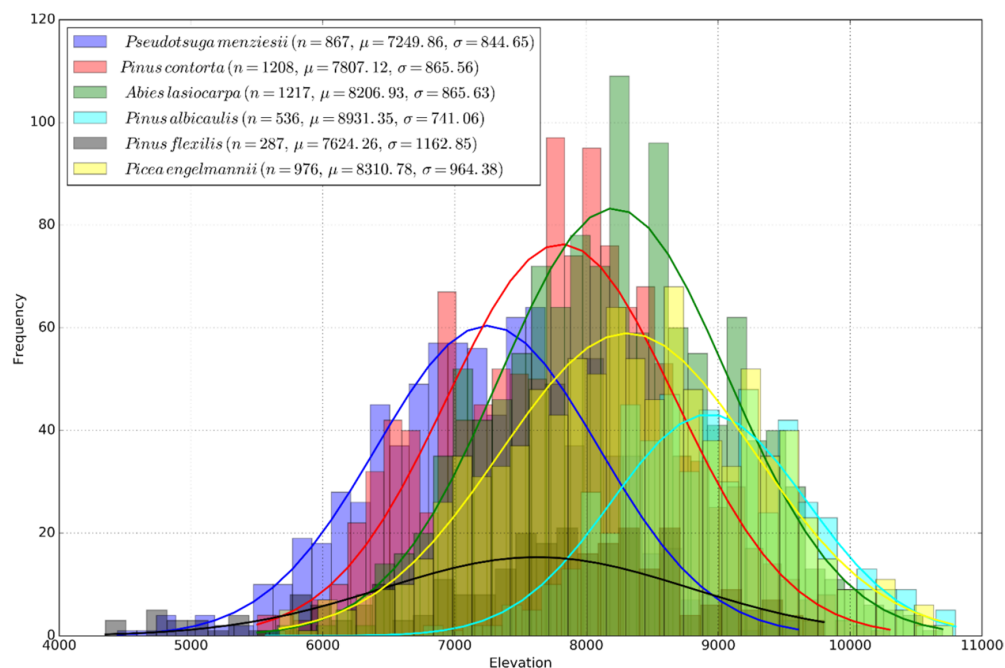


Figure 3. Frequency of occurrence of the major conifer species along the elevational gradient in the GYE as derived from Forest Inventory and Analysis data [20,21].

4.4. Shifting Fire Regime

The influence of fire on WBP varies with fire severity. Mixed-severity fire may benefit established WBP trees by killing competitors while severe fire often kills WBP along with its competitors. WBP may benefit by release from competition if climate change increases mixed-severity fire in the subalpine zone.

WBP is generally assumed to be more tolerant of fire than its competitors [97,98]. Following moderate-severity fire, Barmore *et al.* [80] found a 35% mortality rate of mature WBP, but much higher rates in Engelmann spruce (47%) and subalpine fir (59%). In contrast, experiments with prescribed fire found little difference in fire-caused mortality between WBP and subalpine fir [77], suggesting that WBP fire tolerance may be highly dependent on stand structure.

As is the case for western forests in general, climate warming is expected to increase fire frequency in the GYE. Based on the statistical relationship between past climate and fire, Westerling *et al.* [47] projected for mid-century that fire rotation will be reduced to <30 years from the historical 100–300 years for montane forests in the GYE using a statistical approach. A study that additionally included feedbacks from vegetation to fire projected a decrease in fire rotation of 16%–76% from the modeled historic period on the Yellowstone Plateau [48]. Neither study reported changes in fire severity, however. It is plausible that light fuel loads in upper subalpine environments and in previously burned areas will limit fire severity in subalpine settings under a warming climate to the benefit of WBP. But current knowledge does not allow strong inference on the potential influence of climate-induced shifts in fire regimes on WBP viability in the GYE.

4.5. Mountain Pine Beetle Escape

In well-studied pine species such as lodgepole pine, resistance to mountain pine beetle attack is known to be highest in vigorously growing individuals which are able to shunt more energy into defense tactics [99–102]. Because vigor often declines with age and size, resistance to beetles is often lower in larger, older trees. If similar patterns hold for WBP, some individuals may reach the age of reproduction and produce cones before reaching a size class where they become highly susceptible to mountain pine beetles.

Several studies across the range of WBP and in the GYE have found mortality rates due to bark beetles increase with tree age and size [82–85]. The increasing susceptibility to mountain pine beetles with increasing WBP tree size and age is likely related to the tree's reduced capacity to mobilize carbohydrates for defense as it matures [103].

One of the authors of this paper (K. Legg) has been working with the Greater Yellowstone Whitebark Pine Monitoring Working Group [67] and provided unpublished data indicating that some of the small and medium sized WBP trees survive mountain pine beetle attacks at higher rates than larger trees and are capable of producing cones. During 2004–2007, live WBP trees (>1.4 m tall) ($n = 4742$) were tagged within 176 transects distributed across the GYE. These transects were selected using a probabilistic, two-stage cluster design where whitebark pine stands were the primary sample units and 10×50 -m transects were the secondary sample units [104]. Tagged trees were visited at least twice from 2011 to 2014 to measure survival and whether the trees were bearing cones in addition to other variables such as presence of blister rust and mountain pine beetle indicators. We tallied survival rates by diameter class and evidence of cone bearing among trees alive at the end of 2014. By the end of the resample period, 30% of the trees were dead, with survival rates declining in larger size classes; mortality rates exceeded 50% in trees >20 cm DBH (Figure 4). The percentage of live trees in the resample period that showed evidence of cone bearing was low for the smallest DBH class (2%), moderate for the 10–18 cm DBH class (34%), and was substantially higher for larger diameter classes (82%). These results suggest that survival rates of WBP under beetle attack decline with increasing size while proportion of individuals that are cone bearing increases. Thus, intermediate size classes have moderate rates of both survival and cone bearing. This study did not quantify total cone production, which is known to increase with diameter and canopy volume [97]. McKinney *et al.* [105] estimated that

a threshold level of ~1000 cones/ha is needed for a high likelihood of seed dispersal by nutcrackers, and that this level of cone production can be met by forests with live WBP basal area > 5.0 m²/ha. Additional research is needed to determine if reproduction by mid-sized WBP trees is sufficient to allow population persistence during beetle outbreaks that lead to high mortality of larger individuals.

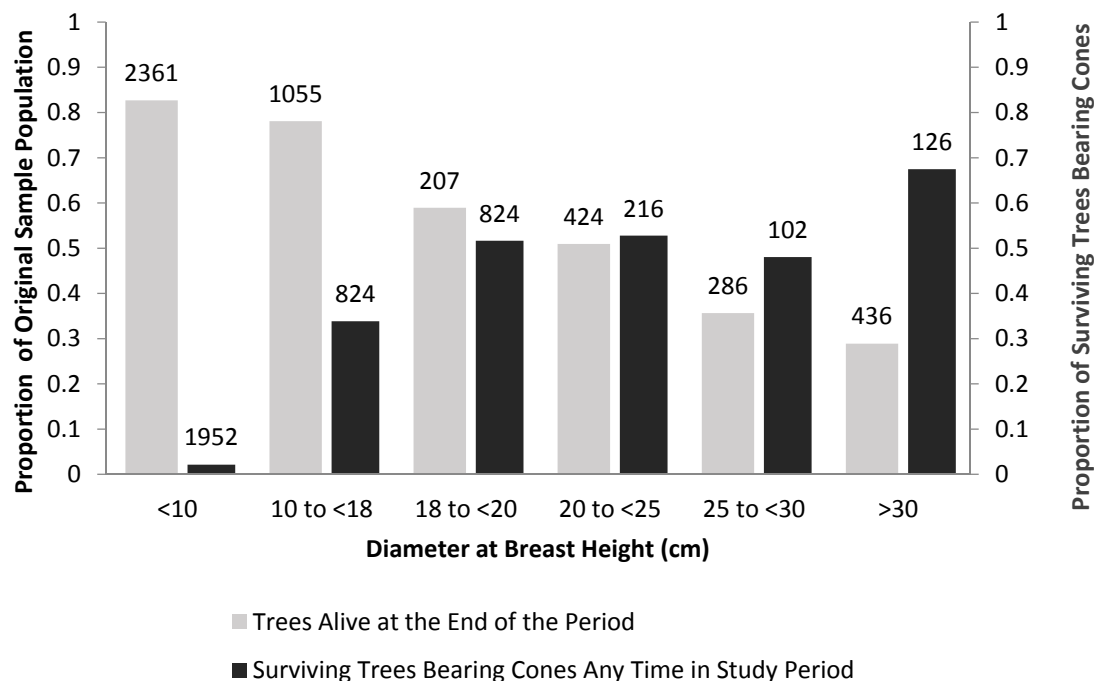


Figure 4. Results for a sample of whitebark pine trees that were living in the 2004–2007 study initiation period and monitored through a 2012–2014 resample period. Rates of tree survival during the study period are shown by the gray bars and the left Y axis. Sample size in each diameter class is displayed above the gray bars. Potential reproduction as indicated by evidence of cone bearing (cones, conelets, or cone scars present) for trees alive at the end of the period is shown by the black bars and the right Y axis. Sample size in each diameter class is shown above the black bars. Data from the Greater Yellowstone Whitebark Pine Monitoring Working Group [106].

4.6. White Pine Blister Rust Resistance

Genetic resistance to white pine blister rust and natural selection processes could potentially counter rising infection rates and offer an opportunity for increased potential for species persistence. Some individual WBP typically survive blister rust attacks and this resistance or tolerance to infection is thought to be genetically determined [89]. Trees monitored in Mount Rainier National Park, for example, have shown a promising long-term resistance to blister rust, surviving infection periods for decades [88]. Moreover, in seedling trials, survival rates for rust-exposed individuals after four years averaged from 7.7% to 17.1%, with some related individuals showing a 30% to 68.5% survival rate [88]. This purported durable resistance has important implications for species viability; rust resistance may spread through the WBP under natural selection. In support, WBP typically have high regeneration rates in stands attacked by blister rust and differential mortality of regenerating seedlings appears to favor those that are rust resistant [87].

Genetic resistance also provides the basis for artificial selection for genetic resistance through planting of genetically resistant WBP seedlings. Genetically resistant parent trees are now being utilized in the collection and screening of genetically resistant stock [87]. Rearing genetically resistant WBP seedlings provides a basis for planting WBP in locations where natural regeneration is low [107]. Thus, both natural and artificial selection may increase resistance to white pine blister rust across the GYE WBP population.

In sum, these six mechanisms and supporting evidence suggest that WBP distribution, survival, and reproduction may be higher than previously expected under the direct and indirect effects of climate change.

5. Research, Management, and Policy Needs

Progress to date on WBP ecology and management and the new perspective on the WBP system reviewed above provide a basis for developing a comprehensive climate adaptation program for WBP in the GYE. The Climate-Smart Conservation framework [108] is being widely embraced by U.S. federal land managers as a conceptual framework for integrating research and management to sustain natural resources under climate change. The approach assesses what species and places are vulnerable to climate change, identifies and evaluates adaptation options, and implements the options in an adaptive management [109] fashion where management effectiveness is monitored and results used to modify adaptation options to best meet objectives. We next examine the research, management, and policy needs for a comprehensive climate adaptation program for WBP in the GYE.

5.1. Research Needs

The specific research suggested by each of the ecological mechanisms reviewed above is described below and summarized in Table 3.

Analysis is needed of the areal extent of the two types of potential microrefugia described above under future climate scenarios. The problem involves how to downscale climate with adequate accuracy to the spatial resolution that is appropriate to capture actual WBP microrefugia in the GYE. Some fine-scale climate phenomena are difficult to model across complex landscapes [5] and weather station data in GYE may be too sparse to validate fine-scale projections. If downscaling climate below the 800-m scale currently used, perhaps to 90 m or 30 m, proves feasible, then the topographic effects on microclimate and soil water balance could be analyzed. Future climate scenarios could then be downscaled to these finer resolutions and used as a basis for bioclimate envelope modeling to more accurately determine the aerial extent and locations of potential suitable habitat for WBP.

The tolerances of WBP to warmer and drier conditions need to be better understood. Greenhouse and field experiments could be used to better determine the physiological tolerances of WBP establishment, growth rates, and survival rates to temperature, precipitation, and water balance. The findings on those tolerances could be validated through management experiments where WBP seedlings are planted across gradients in habitat conditions and survival and growth monitored.

Managers are capable of controlling the strong effects of competing species on WBP. Doing so in select locations could allow WBP to have a higher chance for viability. Experiments involving thinning, prescribed fire, and allowing wildfire under prescribed conditions are underway and expansion of these experiments could be used to refine understanding of the upper level of competition that still allows WBP adequate vigor to tolerate warmer temperatures and resist pests. Again, this could be done in the context of adaptive management where the treatments are monitored to determine the requirements for WBP growth, survival, and reproduction.

The role of fire in influencing WBP survival relative to competing species is not adequately understood, nor is the possible change in fire severity in subalpine habitats under projected climate change. Prescribed burning trials could be done to better determine levels of fire severity that allow WBP to survive but kills competing species. More dendrochronological paleo-fire studies of WBP would be insightful, including those that reconstruct past fire activity and post-fire vegetation dynamics. Interactions among competing tree species, fire severity, and fuel loads under projected climate change can perhaps best be estimated with spatially-explicit mechanistic models such as Fire-BGCv2 [46] or LPJ-GUESS [110]. These models simulate establishment, growth, reproduction, and mortality of individuals within species as a function of climate, soils, and disturbance. Applications of these models across gradients in elevation, climate, and soils could help to identify geomorphic settings where projected future fire regimes are more favorable to WBP.

With regards to the currently devastating effects of mountain pine beetle, more research is needed on the relationships between WBP tree age, vigor, age of reproduction, susceptibility to mountain pine beetle attack, and levels of reproduction required to allow for WBP persistence under future climates. A combination of field observation of WBP age of reproduction, vigor, and mortality and spatially explicit population viability modeling [111] may be the best means of addressing these knowledge gaps. Such analyses will need to consider nonlinear relationships among climate, WBP, beetles, and seed dispersers. Pest management is included in the GYCC Whitebark Pine Strategy, largely aimed at protecting important individual trees such as those with high reproductive potential and genetic resistance to blister rust or stands within climate refugia [30]. Research on feasibility and effectiveness of pesticide treatments could improve understanding of the spatial scales at which such treatments could be applied.

Finally, mortality due to white pine blister rust can potentially be controlled by planting genetically resistant stock. Longer term studies of rust resistance would reduce uncertainty on this strategy. Analysis to determine the locations where the planted seedlings are most likely to survive under projected future climate conditions would also be informative.

5.2. Management and Policy Recommendations

5.2.1. Spatial Distribution of Treatments

Given the progress in developing strategic objectives and management treatments by the GYCC WBP Subcommittee [30], the key challenge to management involves how to distribute these treatments across the GYE landscape to be most effective under climate change. The challenge involves both where to place treatments and how large an area needs to be treated to meet goals related to WBP persistence and ecosystem function. Projected climate change will likely alter the strength of the interactions of the WBP system depicted in Figure 1 and the magnitude of change in strength will vary spatially across the biophysical gradients of the GYE. Thus, there is an opportunity to place management treatments so as to be most effective relative to climate suitability for WBP, competing tree species, mountain pine beetles, and fire regimes. We suggest a “screening” approach to placing treatments in the landscape that is based on changing climate suitability for these elements of the WBP system.

The first order screen is based on climate suitability for WBP. Hansen and Phillips [36] suggested that climate suitability is an appropriate starting point for climate adaptation planning because knowledge of climate suitability is a critical filter for deciding where to use management actions to protect, restore, or establish species populations under climate change. Plants seldom have viable populations where climate is outside of their tolerances. Bioclimate envelope modeling does not consider the many factors in addition to climate suitability that may influence actual species distributions such as soil type and texture, water balance, and changes in disturbance regimes, competitors and pests. Managers can manipulate many of these other factors, however, but cannot manipulate climate over large landscapes. Thus, climate suitability is a critical first filter for prioritizing management approaches.

We recognize three climate suitability zones [36]. “Core habitats” are locations where populations are currently present and habitat is projected to remain suitable in the future. “Future habitats” are currently unsuitable in climate but are projected to become suitable in the future. “Deteriorating habitats” are those that are currently suitable but are projected to become unsuitable. The distribution of these three zones in the GYE based on the analyses of Chang *et al.* [26] is depicted in Figure 5. As discussed above, those analyses should be revised after improved understanding of the climate tolerances of WBP and the distribution of microrefugia across the GYE become available. Nonetheless, the maps based on the current analyses are useful for illustrating the approach.

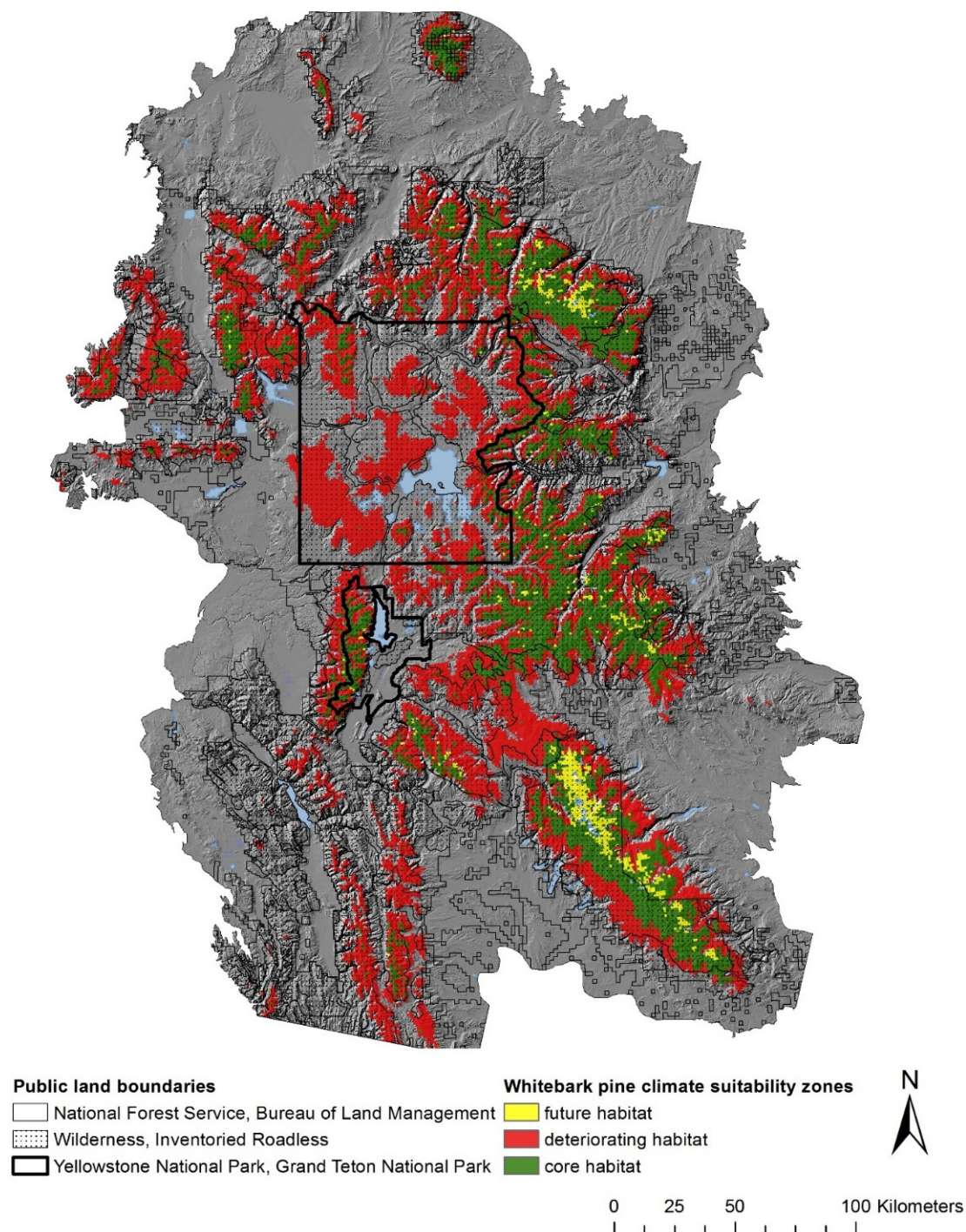


Figure 5. Distribution of projected deteriorating, core, and future habitat for WBP in the GYE under a moderate warming scenario for the period 2040–2070. These habitat projections are based on climate data from the CESM1-CAM5 global circulation model for the AR5 RCP 4.5 scenario [112]. WBP climate suitability is from [26]. Habitat types are defined in the text.

Core habitats for WBP in the GYE are largely in the current upper subalpine zone and represent 34% of the current WBP range (under the mid-range CESM1-CAM5 GCM for 2040–2070 for RCP 4.5). These habitats are of most ecological importance because populations within them have the highest chance of remaining viable in the future, given that climate is projected to remain suitable within them. The primary goal in these locations could be to maintain population viability (Table 4).

Additional goals include maximizing seed dispersal into adjacent future suitable habitats and obtaining blister rust-resistant seeds for growing and planting seedlings. Key management strategies in these settings include preventing stand-replacing fires that could kill large numbers of adult WBP, using prescribed fire, thinning, and pruning to reduce inter and intra specific competition, especially for early reproductive WBP individuals that are more resistant to mountain pine beetle, and use of insecticides to protect key older reproductive individuals. Particular focus could be placed on biophysical settings that may be microrefugia for WBP.

Table 4. A framework for managing WBP in the GYE based on projected future climate suitability.

Habitat Type	Goals	Objectives	Strategies
Core	Maintain currently viable populations	Reduce probability of stand replacing disturbances	Exclude stand replacing fires
		Maximize tree vigor to enhance survival and reproduction	Use prescribed fire and thinning to reduce competition
		Minimize beetle populations	Apply insecticides to reduce mortality due to beetles
	Maximize seed dispersal to future habitats	Maximize tree vigor to enhance survival and reproduction	Use prescribed fire and thinning to promote WBP cone production to swamp predation and maintain dispersers
	Produce seedlings for planting in future habitats	Grow rust-resistant and warm-tolerant stock	Collect seed from rust-resistant and/or warm tolerant WBP trees and rear in nurseries
Deteriorating	Retain WBP population functions as long as possible	Same objectives as in core habitat as resources allow	Same strategies as in core habitat as resources allow
Future	Encourage establishment of WBP	Create suitable sites for seedling establishment	Use prescribed fire and mechanical treatment to create suitable openings
		Establish new stands from nursery stock	Plant rust-resistant and/or warm tolerant WBP trees and rear in nurseries
	Encourage development of viable populations	Same objectives as in core habitat as resources allow	Same strategies as in core habitat as resources allow
All	Improve knowledge and management effectiveness	Refine management effectiveness	Research, monitoring, adaptive management

Most of the current range of WBP in GYE (66%) is projected to become deteriorating habitat by 2100. The goal in these habitats could be to maintain WBP population ecological functions as long as possible while populations build in future habitats. The strategies described above for core habitats could be used in deteriorating habitats as resources allow. Stands that are adjacent or connected to core or future habitats could be prioritized for treatments, in order to maximize the potential of natural colonization of areas which will be suitable for WBP in the future.

Future habitats for WBP in GYE are mostly alpine locations that are not currently forested (4% of the area of the current range). These areas represent opportunities for the species to expand to new locations under climate change. Management strategies to encourage such expansions include promoting high levels of seed immigration and or planting blister-rust resistant seedlings. The future habitats in the GYE are close to existing WBP stands (see Figure 5), thus the substantial ecological and philosophical issues associated with assisted migration [31,32] are less of a concern here. Planting experiments could be done to determine if soils are suitable for WBP in these locations and if seedlings sheltered from desiccating winds (which are not considered in the species distribution modeling) can survive and grow in these locations. As temperature warms in these locations in the coming decades,

sheltering may become less necessary. As these seedlings grow to sizes that are susceptible to mountain pine beetle attack, pest management could be used to reduce attack rates.

The locations of these treatments within each WBP climate suitability zone could be further refined based on screens relating to climate suitability for competing species e.g., [39], mountain pine beetles e.g., [73], and fire [113]. For example, thinning treatments would be most effective if focused on locations of increased suitability for competing tree species. Chemical treatments to protect WBP from mountain pine beetles may be most needed and effective in locations of intermediate beetle climate suitability where beetles are likely to be present but possibly at manageable densities. Fire protection strategies, such as reduction of ladder fuels, would be most needed in locations of increased suitability for stand-replacing fires.

As an example, we illustrate how just two climate suitability screens, WBP climate suitability zone and future fire risk, could be used to prioritize treatments (Table 5). Although these future climate suitability screens could be useful to prioritize general locations for different treatments, we recognize that implementation of specific treatments within these general areas will come down to site-specific decisions by managers acting at the stand or watershed level. Core habitats have the highest chance of maintaining viable WBP populations in the future, so all management options would be appropriate. The highest priorities would be focused on protecting existing stands from mountain pine beetle, promoting regeneration and establishment of WBP seedlings, and promoting wildland fire use to protect existing stands from high-severity fires and promote WBP cone production. Deteriorating habitats represent the majority of WBP in GYE, so the management options in these areas would be focused on maintaining WBP ecological functions as long as possible to allow for natural colonization of adjacent core and future habitats. The highest priority might be to allow wildland fire to promote landscape heterogeneity in areas where the risk of high-severity fire killing existing trees is low. Planting and protection from mountain pine beetle might be beneficial where future fire risk is low but not appropriate where high future fire risk decreases the likelihood of success. Future habitats represent opportunities for expansion of WBP into new locations, most of which are currently unforested, alpine areas. The primary goal in these habitats would be to promote natural colonization and the use of wildland fire in both low and high future fire risk categories to reduce fuels and promote conditions favorable to WBP establishment. In low future fire risk areas, where seedling survival is more likely, protection of newly established WBP from mountain pine beetle would be a priority.

The potential effectiveness of alternative landscape-scale management scenarios can perhaps best be evaluated by simulating them with mechanistic forest ecosystem models such as those mentioned above see [46,48]. The results of the mechanistic models can then be input into population viability models to evaluate likelihood of population persistence under each of the landscape management scenarios as a guide to the aerial extent of treatments necessary to meet population viability goals.

5.2.2. Adaptive Management

The high level of uncertainty on potential future climate and the direct and indirect effects on WBP viability necessitates that adaptive management be a central feature of a revised GYCC WBP Strategy. This involves three components: placing treatments across biophysical gradients; expanding monitoring efforts to gauge WBP response to these treatments; and using mechanistic and population viability models to project potential long-term outcome of the treatments.

Above, we suggested an approach for designing landscape-scale management scenarios based on current knowledge (Section 5.2.1). Under an adaptive management approach, the treatments could additionally be placed across gradients in climate, topography, and soils that span the edges of the climate suitability zones described above. The outcomes of these treatments would provide improved knowledge of the interactions of WBP, competing species, mountain pine beetles, and white pine blister rust as mediated by climate, topography, and soils. This knowledge can then be used to increasingly place treatments in the landscape settings where they are likely to be most effective.

Table 5. An example of placing treatments in the landscape based on future climate suitability for WBP and future fire risk. MPB refers to mountain pine beetle.

Climate Zone	Future Fire Risk	Treatment and Priority: 1-High, 2-Moderate, 3-Low, 4-not Appropriate				
		Planting	Thinning	MPB Protection	Prescribed Fire	Wildland Fire Use
Core	Low	1-plant to regenerate WBP stands following mortality from MPB or blister rust	2-reduce competition to increase vigor	1-protect rust-resistant individuals from MPB mortality	3-reduce competition to increase vigor	1-reduce fuels, increase vigor, and create landscape heterogeneity
	High	1-plant favorable burned areas with rust-resistant seedlings	2-reduce canopy and surface fuels to lower potential fire-caused mortality	1-protect rust-resistant individuals from MPB mortality	3-use prescribed fire to reduce competition and fuel loads	1-reduce fuels, increase vigor, and create landscape heterogeneity
Deteriorating	Low	3-plant rust-resistant seedlings to keep the species in historical lands to monitor for success	4-benefits will be minimal	3-protect rust-resistant individuals	3-reduce competition for rust-resistant individuals	2-promote landscape heterogeneity
	High	4-seedlings have a high risk of being burned	3-may promote growth of rust-resistant individuals	4-existing trees have a high risk of being killed by fire	3-reduce canopy and surface fuels to protect rust-resistant individuals	3-reduce fuels and promote landscape heterogeneity
Future	Low	3-plant burns with rust-resistant seedlings	4-most high elevation stands competition free	2-protect rust-resistant individuals	3-lower fuels to reduce fire risk to rust-resistant individuals	2-Promote landscape heterogeneity and reduce fuels
	High	3-plant to ensure future competitive advantage and mimic nutcracker dispersal	4-most high elevation stands competition free	3-Protect rust-resistant individuals	4-probably won't need additional fire	2-promote landscape heterogeneity, reduce fuels

The current monitoring program by the Greater Yellowstone Whitebark Pine Monitoring Working Group [67] was designed to detect trends in WBP demography under the influence of beetles, blister rust, and fire. The Forest Service conducts short-term monitoring post treatments. Either of these efforts could be supplemented to measure WBP response to management by adding monitoring plots at the locations where treatments are implemented and measure beyond shorter-term efforts underway. Metrics for effectiveness monitoring include WBP survival, growth, cone production, regeneration, beetle and blister rust prevalence, and the demography of competing species.

Given the slow growth rates of WBP, the success of treatments in increasing WBP viability will not be known for decades. Simulation modeling provides a means of projecting potential long-term outcomes of the treatments. As the adaptive management approach proceeds, results from the monitoring studies can be used to iteratively improve the parameterization of the models and reduce uncertainty in the long-term projections.

Through this combination of imposing treatments, monitoring short-term response, and simulating long-term outcomes, the management strategy can be revised to be increasingly effective.

5.2.3. Policy Evaluation for Restricted Federal Land Allocations

Active management of WBP in the GYE to date has focused on multiple-use federal lands, which comprise only 8% of the WBP stands (Table 1). This focuses attention on the need for re-evaluation of the legal and philosophical interpretations that currently constrain active management in restrictive federal lands.

The Wilderness Act of 1964 is considered among the most restrictive of U.S. natural resource laws. Thus debate on active management for climate adaptation centers on wilderness. Long and Biber [114] reviewed both legal interpretation on the question and federal agency policy. They concluded, “The vast majority of potential management actions for climate change adaptation, both active and passive, are possible under the Wilderness Act, provided that the right procedural steps are followed and the right substantive analyses are produced. Active management, even management that uses tools that are generally prohibited under the Act, is permissible if it can be shown to be necessary to achieve conservation purposes and if its impacts on other wilderness values are minimized.” Moreover, they cite federal agency policies and actions consistent with the conclusion above.

Philosophical views on active management in wilderness among both agency personnel and the public are varied. On the one hand, Stephenson and Millar [115] make a case that the Wilderness Act was written before there was widespread understanding that human activities could alter the state of the biosphere and consequently the act leads to a duality that will require tradeoffs. The duality is between “untrammeled quality” and “historical fidelity (primeval and natural character)”. They suggest in a global change world, retaining “primeval and natural character” will require increasing management intervention (trammeling). Alternatively, some national park managers are wary of their management actions doing more harm than good and advocate a “natural regulation” approach whenever possible [116]. For a rebuttal to this view, see Stephenson [117].

Regarding public views, a survey of visitors to Sequoia and Kings Canyon National Parks [118] found little support for strategies to make forests less vulnerable to climate change such as introducing new genetic material more resistant to drought or disease. Respondents showed mild to moderate support for management actions intended to restore natural conditions such as removing non-native species and reintroducing missing native species. A recent survey of residents in the three states surrounding the GYE found that respondents strongly supported active management for protection and restoration of WBP both on all federal public lands and within designated Wilderness Areas [119]. We agree with Stephenson and Millar [115] that climate adaptation planning “will require a broader engagement of wilderness stewards, policy makers, and the public to assess the implications of climatic changes for wilderness values and policy.”

Such engagement is increasingly crucial in the case of WBP in the GYE given that its current distribution lies largely in restricted federal lands and this is projected to be increasingly the case for habitat suitability under climate change (see also [7]).

6. Prognosis

The WBP is at the center of a complex web of interactions involving climate, competition, fire, and pests. Science is increasingly unravelling the one-way interactions within the WBP system, but the interactive effects and feedbacks within the system remain elusive. The population trajectory of adult WBP over the past decade in the GYE, however, is cause for alarm and speaks to the need for increased research and management. The majority of reproductive WBP trees in the ecosystem have died since 2000. Much of the vast subalpine forest across the GYE is covered with the grey cast of dead trees. The loss of ecosystem services associated with this die-off has not yet been quantified, but is certainly substantial. Climate warming, the ultimate factor driving the mortality, is projected to accelerate in the coming century and further favor competing species, pests, and severe fires that kill WBP.

This situation begs the question of if the WBP population in the GYE will remain viable in the coming century or will it be lost as climate change progresses. New perspectives on the complex WBP system have identified ecological mechanisms by which WBP may remain viable, particularly if aided by well-crafted management treatments. In the passages above we summarized the research questions and landscape-scale management approaches that show promise for better understanding and more effectively managing WBP across the GYE.

Our compilation of area treated to date by federal managers (Table 2), however, makes a strong case that the effort taken by the managers in the GYE is too little to be significant relative to the scale of the problem. Less than 1% of the aerial distribution of WBP has been treated by active management for protection and restoration. Above, we describe a landscape-scale adaptive management approach that has promise of meaningfully tackling the issue. Substantially more resources are required to enact this approach and treatments will need to be done much more widely across the GYE landscape to meaningfully influence the viability of WBP here and the ecosystem services they provide.

We hope that this paper further stimulates the conversation among federal managers in the GYE and at higher levels within agencies and the legislative branch on policy and commitment relative to managing the WBP and other natural resources under climate change. Beyond issues of funding and capacity, the discussion necessarily involves the question of appropriate levels of active management on restricted federal lands such as wilderness where many sensitive subalpine species are disproportionately located.

The challenges of WBP in GYE are typical of those for many species across the U.S. and globally. Other subalpine tree species showing direct and indirect responses to climate change include limber pine in the Rocky Mountains [120], red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) in the Appalachians [121], and Alaska yellowcedar (*Chamaecyparis nootkatensis*) in Southeast Alaska [122]. Within the European Alps, average range reductions of 44%–50% were projected for 150 high mountain plant species by 2100 and complete range loss was projected for 6%–8% of these species [6]. Many plants in mountains in the humid tropics are also sensitive to climate change because the relatively stable environment has led to narrow climate tolerances which are projected to be exceeded under projected climate change [123]. Other studies showing high vulnerability of subalpine species and montane ecosystems to climate change include [1–3,18,36,39,124–128].

The recommendations for WBP are likely relevant to many of these other vulnerable subalpine species. These include:

- Research to better understand the direct and indirect effects of climate change and mechanisms that may allow the species to remain viable under changing climate, especially if aided by management;
- Development of management strategies that are spatially and temporally organized in the context of future climate suitability for the target species and the organisms that influence that species;

- Adaptive management where treatments are arrayed across key biophysical gradients and monitored to quantify effectiveness and tailor future management to biophysical conditions;
- Use of demographic and mechanistic models to project treatments forward in time.
- Re-evaluation of legal and policy constraints regarding active management in high elevation locations; and
- Interagency collaboration to allow unified management approaches across the larger spatial scales relevant to managing these species under climate change.

Beyond improving viability of these subalpine species, application of these recommendations will provide a basis for managing the large number of tree and other plant species at lower elevations as climate change begins to exceed their limits of tolerance.

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Life-History Characteristics of Mule Deer: Effects of Nutrition in a Variable Environment

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(Top) Deer ID479 within a few hours of birth during the day of her initial capture on 20 June 2008. (Bottom) Deer ID479 and her mother ID256 in Round Valley, California, USA during autumn 2008. Deer ID256 was first captured on 20 November 2002, and remained in our study through the last capture event of our study in March 2009. During that time she resided on the east side of the Sierra crest during summer and was captured a total of 12 times. She failed to recruit young during 2005, but she was a successful mother and recruited a single young during 2006, 2007, and 2008, and twins during 2004. Our long-term, individual-based study revealed the importance of nutritional condition in understanding life-history characteristics and population regulation of large herbivores. Photos by Kevin L. Monteith



Life-History Characteristics of Mule Deer: Effects of Nutrition in a Variable Environment

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ABSTRACT Vital rates of large herbivores normally respond to increased resource limitation by following a progressive sequence of effects on life-history characteristics from survival of young, age at first reproduction, reproduction of adults, to adult survival. Expected changes in life-history characteristics, however, should operate through changes in nutritional condition, which is the integrator of nutritional intake and demands represented primarily by the deposition and catabolism of body fat. Elucidating seasonal patterns of nutritional condition and its relative influence on individual and population performance should improve our understanding of life-history strategies and population regulation of ungulates, provide insight into the capacity of available habitat to support population growth, and allow assessment of the underlying consequences of mortality on population dynamics. We acquired longitudinal data on individual female mule deer (*Odocoileus hemionus*), and linked those data with environmental and population characteristics. Our goal was to provide a nutritional basis for understanding life-history strategies of these large mammals, and to aid in the conservation and management of large herbivores in general. We studied a migratory population of mule deer that overwintered in Round Valley on the east side of the Sierra Nevada, California, USA, and was subject to a highly variable climate and predation from a suite of large carnivores. We intensively monitored nutritional and life-history characteristics of this population during 1997–2009 as it recovered from a population crash, which occurred during 1985–1991. Deer in Round Valley migrated to high-elevation summer ranges on both sides of the crest of the Sierra Nevada (Sierra crest), where a rain shadow resulted in a mesic and more forested range on the west side compared with xeric conditions east of the Sierra crest. Average survival of neonatal mule deer to 140 days of age during 2006–2008 was 0.33 (SE = 0.091), but was lower for neonates on the west side (0.13, SE = 0.092) compared with those on the east side (0.44, SE = 0.11) of the Sierra crest. Birth mass and nutritional condition of mothers had a positive effect on survival of young; however, those effects were evident only for neonates born east of the crest where predation pressure was less intense compared with the west side. Black bear (*Ursus americanus*) predation was the main cause of mortality for west-side young (mortality rate = 0.63, SE = 0.97) compared with canid and felid predation for east-side young (0.29, SE = 0.076). Mean autumn recruitment of young during 1997–2008 was lower for females on the west side (0.42, SE = 0.037) than for females on the east side (0.70, SE = 0.041) of the crest, and was affected positively by March ingesta-free body fat (IFBFat) of individual females. At the level of the population, ratios of young-to-adult females (1991–2009) were highly variable and strongly related to March IFBFat of adult females during the current and preceding year. Reproduction by yearling females was sensitive to per capita availability of forage during summer (as 1-yr-old individuals), thereby influencing whether a sufficient body mass for ovulation was obtained. Litter size remained high (1.69, SE = 0.027) during the study, but was influenced positively by forage availability, negatively by summer temperature, and was greater for females that resided on the west side of the Sierra crest during summer than those on the east side. In contrast, pregnancy rates remained unchanged across years of study (0.98, SE = 0.005). Survival of prime-age (2- to 9-yr-old) females was 0.90 (SE = 0.021) in summer, 0.94 (SE = 0.012) in winter, and 0.87 (SE = 0.025) annually. Although relatively stable across years, both winter and summer survival

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were influenced positively by the preceding April snowpack relative to the density of the population. Mean IFBFat of adult females was 7.2% (SE = 0.077) in March 1997–2009 and 9.7% (SE = 0.23) in November 2002–2008. Nutritional condition offered a mechanistic link between factors that influence resource limitation and population performance, because condition of adult females in autumn and late winter was sensitive to the nutritional history of individual animals as related to forage growth, population density, migratory tactic, reproductive costs, and nutritional carryover. Nutritional condition of adult females in March also was the most parsimonious predictor of finite rate of population growth (λ) during the forthcoming year. The relative magnitude of effect of nutritional condition on survival and reproduction was mostly in accordance with the predicted changes of vital rates in response to resource limitation for populations of large herbivores. Our results indicate that management and conservation of large herbivore populations could be improved by integrating indices of nutritional condition into current monitoring and research programs. We offer a method to estimate the proximity of a population to nutritional carrying capacity (NCC) that is based on nutritional status of the population relative to population performance (termed animal-indicated NCC). The proximity of the population to animal-indicated NCC represents the short-term capacity of the environment to support population growth. A nutritional approach to monitor and manage populations offers a direct link to the capacity of the habitat, and reduces the need to estimate population abundance or set goals according to population size. We also propose that the consequences of mortality (degree of additive or compensatory mortality) on population dynamics can be assessed by comparing the estimated nutritional capacity for survival and recruitment of young to that measured empirically, because more young are produced than what the habitat can support when nutrition is limiting. Our approach is useful for quantifying effects of predation, and provides a basis for determining the efficacy of predator control to enhance ungulate populations. © 2014 The Wildlife Society.

KEY WORDS additive mortality, California, carrying capacity, compensatory mortality, density dependence, environmental stochasticity, migration, nutritional condition, *Odocoileus hemionus*, predation, Sierra Nevada.

Características de Historia de Vida del Ciervo Mulo: el Efecto de la Nutrición en Presencia de un Medio Ambiente Variable

RESUMEN Normalmente, la respuesta de las estadísticas vitales de los grandes herbívoros a una mayor restricción de recursos es una secuencia progresiva de efectos en las características de la historia de vida, que van desde la supervivencia de los juveniles y la edad de la primera reproducción, hasta la reproducción de los adultos y la supervivencia de estos. Los cambios previstos en las características de la historia de vida, sin embargo, deben experimentarse a través de cambios en el estado de nutrición (niveles de grasa corporal), constituido por la ingesta y las necesidades alimenticias, representadas principalmente por la deposición y el catabolismo de la grasa corporal. El esclarecimiento de los patrones estacionales del estado de nutrición y su influencia relativa, tanto en el desempeño individual como en el de la población, debe mejorar la comprensión de las estrategias de historia de vida y de la regulación de las poblaciones de ungulados, así como también, dar una idea de la capacidad del hábitat disponible para sustentar el crecimiento de la población y permitir la evaluación de las consecuencias subyacentes que tiene la mortalidad en la dinámica demográfica. Adquirimos datos longitudinales sobre individuos de ciervo mulo (*Odocoileus hemionus*), y vinculamos estos datos con las características ambientales y demográficas. Nuestro objetivo era ofrecer una base nutricional para la comprensión de las estrategias de historia de vida de estos grandes mamíferos y ayudar en la conservación y gestión de los grandes herbívoros en general. Se estudió una población migratoria de ciervo mulo que habitó, por un período que sobrepasó el invierno, en Round Valley, al este de la Sierra Nevada en California, EE.UU., la cual estuvo sujeta a un clima muy variable y a la depredación de un conjunto de grandes carnívoros. Monitoreamos intensamente las características nutricionales y de historia de vida de esta población durante el período 1997–2009, período durante el cual, dicha población se recuperaba del drástico descenso experimentado durante el período 1985–1991. En el verano, los ciervos emigraron de Round Valley a las cordilleras de gran altitud a ambos lados de la cima de la Sierra Nevada (cima de la Sierra), en cuya parte oeste, como resultado de una sombra pluviométrica, se desarrolló una cordillera mesofítica y más boscosa, si se la compara con las condiciones xerófilas al este de la cima de la Sierra. Durante el período de 2006–2008 la supervivencia promedio del ciervo mulo neonatal hasta los 140 días de edad fue de 0,33 (ES = 0,091), sin embargo; la supervivencia de los recién nacidos en el lado oeste fue menor (0,13, ES = 0,092), en comparación con los del lado este de la cima de la Sierra (0,44, ES = 0,11). La masa corporal al nacimiento y el estado de nutrición de la madre afectaron positivamente la

supervivencia de los jóvenes, sin embargo; estos efectos sólo se evidenciaron en los neonatos nacidos al este de la cima, donde estuvieron expuestos a una depredación menos intensa en comparación con los del lado oeste. La actividad depredadora del oso negro (*Ursus americanus*) fue la principal causa de mortalidad en los juveniles en el lado oeste (tasa de mortalidad = 0,63, ES = 0.97) si se la compara con la actividad depredadora de los cánidos y félidos en el lado este (0,29, ES = 0.076). El nivel de agregación medio de los juveniles para el otoño durante el período 1997–2008 fue menor para las hembras en el lado oeste de la cima (0,42, ES = 0.037) que para las hembras en el lado este (0,70, ES = 0.041), y se vio afectada positivamente por la medida, para marzo, de la grasa corporal con exclusión de sustancias ingeridas (siglas en inglés, IFBFat), de las hembras. A nivel de la población, la proporción de juveniles por hembra adulto (1991–2009) fue muy variable y estuvo fuertemente relacionada con el IFBFat para marzo de las hembras adulto durante el año en curso y los años anteriores. La reproducción de las hembras juveniles (de un año de edad) fue susceptible a la disponibilidad de forraje per cápita durante el verano (en su condición de individuo de 1 año de edad), influyendo, en consecuencia, en el logro o no de masa corporal suficiente para la ovulación. Durante el estudio, el tamaño de las crías se mantuvo alto (1.69, ES = 0.027), pero se vio afectado positivamente por la disponibilidad de forraje, negativamente, por la temperatura durante el verano, y fue mayor para las hembras que residían en el lado oeste de la cima de la Sierra durante el verano, que para las del lado este. Por el contrario, la tasa de preñez se mantuvo relativamente estable durante años de estudio (0,98, ES = 0.005). La supervivencia de las hembras de edad óptima (2–9 años), fue 0,90 (ET = 0,021) en el verano, 0,94 (ES = 0,012) en el invierno, y 0,87 (ES = 0,025) al año. Aunque la supervivencia lo largo de los años ha sido relativamente estable, tanto en invierno como en verano, esta fue afectada positivamente por la nieve acumulada del abril precedente, en relación con la densidad de la población. El IFBFat medio para marzo de las hembras adulto fue de 7,2% (ES = 0,077) de 1997 a 2009, y de 9,7% (ES = 0.23) de noviembre de 2002 a 2008. El estado de nutrición permitió una relación mecánica entre los factores que influyen en la limitación de los recursos y el desempeño de la población, debido a que la condición de las hembras adulto en el otoño y a finales del invierno fue susceptible tanto a la historia nutricional de los individuos en relación con el crecimiento del forraje, como a la densidad de la población, la táctica migratoria, el costo de reproducción y el remanente nutricional. El estado de nutrición para marzo de las hembras adultas también fue la explicación más prudente para la tasa finita de crecimiento poblacional (λ) durante el año siguiente. La magnitud relativa del efecto que tiene el estado nutricional sobre la supervivencia y la reproducción estuvo generalmente conforme con los cambios previstos en la estadística vital de las poblaciones de grandes herbívoro, resultantes la restricción de recursos. Nuestros resultados indican que la gestión y la conservación de grandes poblaciones de herbívoros podrían mejorarse mediante la integración de los índices de estado de nutrición en los programas de investigación y supervisión en curso. Ofrecemos un método para estimar la inminencia de una población a alcanzar la capacidad de aporte nutricional (singla en inglés, NCC) con base en el estado nutricional de la población en relación con el desempeño de la población (denominado NCC de indicación animal). La proximidad de la población a la NCC de indicación animal representa la capacidad a corto plazo del medio ambiente para sustentar el crecimiento de la población. Un enfoque nutricional para el monitoreo y administración de las poblaciones ofrece un nexo directo con la capacidad del hábitat, y reduce la necesidad de estimar la abundancia de la población o establecer metas de acuerdo con el número de habitantes. También proponemos que las consecuencias de la mortalidad (grado de mortalidad agregado o compensatorio) sobre la dinámica demográfica pueden calcularse mediante la comparación de la estimación de la capacidad nutricional necesaria para la supervivencia y la agregación de juveniles, con aquellas calculadas empíricamente, debido a que se producen más juveniles de los que el hábitat puede sustentar cuando la nutrición es una limitante. Nuestro enfoque es útil para efectos de la cuantificación de la depredación, y proporciona una base para determinar la eficacia del control de la depredación en el aumento de las poblaciones de ungulados.

Traits Biodémographiques chez le Cerf Mulet: Effets de la Nutrition dans un Environnement Variable

RÉSUMÉ Les taux démographiques des grands herbivores répondent habituellement à une limitation croissante des ressources et cela, selon une séquence progressive d'effets sur les traits biodémographiques en débutant par des effets sur la survie des juvéniles, puis sur l'âge à la première reproduction, la reproduction des adultes et enfin, la survie des adultes. Les changements attendus des traits biodémographiques devraient toutefois se produire en fonction des changements dans la condition physique qui intègre l'apport et les besoins nutritionnels qui se traduisent principalement par l'accumulation et le catabolisme des réserves de gras corporel. L'étude des tendances saisonnières de la condition physique et de leur influence relative sur la performance individuelle et populationnelle

pourrait améliorer notre compréhension des stratégies d'histoire de vie et de la régulation des populations d'ongulés et cela, tout en déterminant la capacité des habitats disponibles à supporter la croissance de la population et en évaluant les conséquences sous-jacentes de la mortalité sur la dynamique de population. Nous avons acquis des données longitudinales sur des individus de cerfs muets (*Odocoileus hemionus*), et avons relié ces données à des caractéristiques environnementales et populationnelles. Notre objectif était de fournir une base nutritionnelle pour comprendre les stratégies d'histoire de vie de ces grands mammifères et pour aider à la conservation et la gestion des grands herbivores en général. Nous avons étudié une population migratrice de cerfs muets qui hiverne dans la Round Valley, dans la partie est du Sierra Nevada, Californie, USA. Cette population est sujette à des conditions climatiques très variables et à de la prédation par une large guildes de carnivores. Entre 1997 à 2009, nous avons suivi intensivement les caractéristiques nutritionnelles et les traits biodémographiques de cette population, alors qu'elle récupérait d'un déclin marqué s'étant produit entre 1985 et 1991. Les cerfs de la Round Valley ont migré vers les aires estivales situées à des élévations élevées sur les deux côtés de la crête de la Sierra Nevada (crête de la Sierra). Sur le côté ouest de la crête, la pluie et l'ombrage ont résulté en une aire mésique présentant un couvert forestier plus important comparativement aux conditions xériques retrouvées sur le côté est de la crête de la Sierra. La survie moyenne des faons de la naissance à l'âge de 140 jours était, entre 2006 et 2008, de 0,33 (SE = 0,091), mais était plus faible pour les faons sur le côté ouest (0,13, SE = 0,092) que sur le côté est (0,44, SE = 0,11) de la crête de la Sierra. La masse à la naissance et la condition physique maternelle avaient un effet positif sur la survie des jeunes; toutefois, ces effets étaient évidents seulement pour les faons nés sur le côté est de la crête où la pression de prédation était plus faible que sur le côté ouest. La prédation par l'ours noir (*Ursus americanus*) était la principale cause de mortalité des faons sur le côté ouest (taux de mortalité = 0,63, SE = 0,97) comparativement à la prédation par les canidés et les félinés pour les jeunes nés sur le côté est de la crête de la Sierra (0,29, SE = 0,076). Entre 1997 et 2008, le recrutement moyen des jeunes à l'automne était plus faible pour les femelles sur le côté ouest (0,42, SE = 0,037) que pour les femelles sur le côté est (0,70, SE = 0,041) de la crête, et était positivement influencé par le niveau de gras corporel en mars mesuré à partir de la masse éviscérée des femelles (IFBFat). À l'échelle de la population, le ratio de jeunes par rapport aux femelles adultes (1991–2009) était très variable et fortement relié à l'IFBFat en mars des femelles adultes pour l'année en cours et l'année précédente. La reproduction des femelles d'un an était sensible à la disponibilité de la nourriture *per capita* pendant l'été (en tant qu'individus d'un an) qui influençait ainsi l'atteinte d'une masse corporelle suffisante pour permettre l'ovulation. La taille de la portée est demeurée élevée (1,69, SE = 0,027) au cours de l'étude. Elle était positivement influencée par la disponibilité de la nourriture, mais négativement par la température estivale, et était plus élevée pour les femelles résidant sur le côté ouest de la crête de la Sierra pendant l'été que pour celles résidant du côté est. À l'opposé, le taux de gestation est demeuré relativement stable au cours de l'étude (0,98, SE = 0,005). La survie des femelles matures (2 à 9 ans) était de 0,90 (SE = 0,021) en été, de 0,94 (SE = 0,012) en hiver, et de 0,87 (SE = 0,025) pour l'année entière. Malgré une relative stabilité entre les années, la survie estivale et la survie hivernale étaient positivement influencées le rapport entre le couvert de neige en avril de l'année précédente et la densité de la population. La valeur moyenne de IFBFat des femelles adultes était de 7,2% (SE = 0,077) en mars 1997–2009 et de 9,7% (SE = 0,23) en novembre 2002–2008. La condition physique représente un lien mécanistique entre les facteurs influençant la disponibilité et la qualité ressources et la performance d'une population, puisque la condition des femelles adultes à l'automne et à la fin de l'hiver est sensible à l'histoire nutritionnelle individuelle qui est liée à la croissance de la végétation, à la densité de population, aux tactiques de migration, aux coûts de la reproduction et aux effets nutritionnels différés. La condition physique des femelles adultes en mars est la variable la plus parcimonieuse permettant d'expliquer le taux de croissance de la population (λ) au cours de l'année à venir. L'ampleur relative de l'effet de la condition physique sur la survie et la reproduction était généralement en accord avec les changements prédits des taux démographiques en réponse à une limitation des ressources chez les populations de grands herbivores. Nos résultats indiquent que la gestion et la conservation des populations de grands herbivores pourraient être améliorées en intégrant des indices permettant de mesurer la condition physique individuelle dans les programmes de suivis et de recherche actuels. Nous proposons une méthode permettant d'estimer la proximité d'une population à sa capacité de support nutritionnel (NCC) qui est basé sur le statut nutritionnel de la population par rapport à la performance de la population (nommé indice-animal NCC). La proximité de la population à l'indice-animal NCC représente la capacité à court terme de l'environnement à soutenir la croissance de la population. Une approche nutritionnelle pour suivre et gérer les populations propose ainsi un lien direct avec la capacité de support de l'habitat tout en réduisant la nécessité d'estimer l'abondance de la population ou d'établir des objectifs en fonction de la taille de la population. Nous suggérons également que les effets de la mortalité (niveau de mortalité additive ou compensatoire) sur la dynamique de population peuvent être évalués en comparant la capacité nutritionnelle estimée pour la survie et le recrutement aux données empiriques mesurées, puisqu'on s'attend à ce que le nombre de jeunes produits soit plus important que ce que peut supporter l'habitat lorsque la nutrition est limitante. Notre approche est utile pour quantifier les effets de la prédation et fournit une base permettant de déterminer l'efficacité du contrôle des prédateurs sur les populations d'ongulés.

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INTRODUCTION

Nutritional ecology, the science relating an animal to its environment through nutritional interactions (Parker et al. 2009), holds implications for understanding behavior, life-history strategies, and effects of climate and predation on demographics (Raubenheimer and Boggs 2009). Despite advances in the understanding of nutritional ecology of numerous large herbivores (Parker et al. 2009), the complex interactions between predation, climate, and density dependence on population dynamics continue to hamper identification of factors ultimately responsible for regulating population growth (Skogland 1991, Coulson et al. 2001, Sinclair and Krebs 2002, Sinclair et al. 2003). Concepts such as carrying capacity (K ; McCullough 1979, McLeod 1997), additive and compensatory mortality (Errington 1946, 1967), and top-down or bottom-up forcing (Bowyer et al. 2005, Pierce et al. 2012) are all aspects known to affect population dynamics and life-history characteristics of large mammals, but often are of greater heuristic than practical value because those characteristics are difficult to quantify.

Vital rates of large herbivores generally respond to resource limitation in a predictable sequence, starting with decreased survival and recruitment of young, increased age of first reproduction, decreased reproduction by adults and, finally, decreased survival of adults (Gaillard et al. 1998, 2000; Eberhardt 2002). Reproduction demands resources above those necessary for maintenance (Monteith et al. 2014) and life-history theory predicts that when those resources are limited, long-lived, iteroparous mammals should favor their own survival over successful reproduction (Stearns 1992). In addition, young animals have fewer nutritional reserves, and thereby have a lower

tolerance for unfavorable conditions (Barboza et al. 2009). The sequential changes in reproduction and survival, therefore, are underpinned largely by nutrition (Cameron and Verhoef 1994, Testa and Adams 1998, Keech et al. 2000, Cook et al. 2004, Stewart et al. 2005, Bender et al. 2007), and the resources required to support each life-history component.

A better understanding of seasonal patterns of nutritional condition and its relative influence on population dynamics would improve our knowledge of life-history strategies and population regulation of ungulates (Stephenson et al. 2002, Cook et al. 2004, Parker et al. 2009, Monteith et al. 2013). Making inferences concerning effects of climate, density, or predation on vital rates and mortality factors without knowledge of seasonal deficiencies or surpluses in nutrition can be difficult (Bowyer et al. 2005, Brown et al. 2007). Nutritional condition integrates the balance of nutritional intake and expenditure, and is represented primarily by the deposition and catabolism of body fat (Parker et al. 2009). As a result, nutritional condition (i.e., percent body fat) ultimately should function as the mechanism through which intraspecific competition for resources is mediated, and should provide the most direct and sensitive measure of habitat quality and resource limitation.

Temperate and arctic herbivores follow seasonal cycles in nutrient intake according to seasonal changes in quality and quantity of food resources, activity levels, reproductive effort, and metabolic rate (Moen 1978, Parker et al. 1993, Taillon and Côté 2006, Barboza et al. 2009), with declines in all processes occurring during winter. Research typically has focused on nutrition during winter, likely because of the conspicuous effects of malnutrition during that season (Kucera 1997, Parker et al. 2005, Page and Underwood 2006). In contrast, forage

quality and quantity are highest during the growing season, and fat and protein deposition, thus, typically are greatest during spring and summer, and are thought to prepare animals for the food-limited winter (Moen 1978, Cook et al. 2013). Carryover of nutritional condition from one season to the next, however, underscores the importance of not considering a particular season in isolation (Monteith et al. 2013). For example, gestation and lactation are nutritionally taxing for large herbivores (Moen 1978, Pekins et al. 1998, Monteith et al. 2014). As a result, range conditions and reproductive status during summer directly influence nutritional condition of individuals entering winter (Chan-McLeod et al. 1999; Cook et al. 2004, 2013; Couturier et al. 2009).

Several investigators have identified proximate factors affecting survival and reproduction of large herbivores, but few have characterized the underlying mechanisms that influence vulnerability to mortality, or the ability to produce and successfully rear young (Pettorelli et al. 2011). The relative influence of nutrition (bottom-up) and predation (top-down) on the regulation of populations remains a common theme in ecological studies (Hairston et al. 1960, Skogland 1991, Estes et al. 2011, Pierce et al. 2012). Indeed, the reintroduction and expanding populations of large carnivores have fueled, and likely will continue to promote, the controversy behind the ecological consequences of their presence (Bangs et al. 1998, Pyare et al. 2004, Carroll et al. 2006, Kauffman et al. 2010, Smith et al. 2010). In systems where ungulates co-occur with large carnivores, predation is commonly the leading proximal cause of mortality among young ungulates (Linnell et al. 1995, Singer et al. 1997, Bowyer et al. 1998b, Ballard et al. 2001), but simply identifying cause of death is of little value without characterizing the implications or underlying basis of those mortalities (Bleich and Taylor 1998, Ballard et al. 2001, Bowyer et al. 2005). Errington (1967:235) forewarned against confusing “the *fact* of predation with the *effect* of predation.” Understanding the nutritional basis for survival and reproduction has potential to reveal the compensatory or additive effects of mortality, and thereby the relative role of large carnivores in the population dynamics of their ungulate prey.

Studies at the population level have provided the basis for our understanding of the regulation of animal abundance (Lack 1954); most studies of large herbivores have focused on population-level phenomena because of the logistical challenges associated with acquiring sufficient data for individuals (McCullough 1979, Stewart et al. 2005, Clutton-Brock and Sheldon 2010). Data collection and analyses at the level of the individual are complementary to those at the population level, but provide greater insights into the mechanisms of population change and selection for particular life-history strategies (Stearns 1992, Lindström 1999, Testa 2004, Benton et al. 2006). Although few such investigations have been conducted for cervids in North America, individual-based studies have been the cornerstone for recent advances in understanding population ecology (Clutton-Brock and Sheldon 2010). Moreover, carryover of nutritional deficiencies or incomes can confound interpretation of dynamics at the population level (Testa 2004), and can only be elucidated by long-term, individual-based studies (Clutton-Brock and Sheldon 2010, Harrison et al. 2011).

Populations of mule deer have experienced periodic declines over the latter part of the last century; causes of those declines remain speculative and controversial (deVos et al. 2003, Connelly et al. 2012). Potential sources of declines include loss or fragmentation of habitat because of development, altered forage quality, competition with other ungulates, predation, disease, increased hunting mortality, poaching, severe winter weather, and droughts (deVos et al. 2003, Bishop et al. 2009, Hurley et al. 2011). Given high and consistent rates of pregnancy and fecundity (Andelt et al. 2004, Bishop et al. 2009), however, reduced survival of neonates during their first year-of-life is the most likely explanation for population declines (Gill et al. 2001, Andelt et al. 2004, Wasley 2004). Although predation is routinely identified as the proximate cause of mortality for neonatal mule deer, survival and recruitment of young mule deer also are sensitive to maternal nutritional condition and forage condition (Lomas and Bender 2007, Tollefson et al. 2011). Habitat quality is believed to have declined across most of the western United States because of successional changes in vegetation caused by altered fire regimes, noxious weeds, overgrazing, energy development, and habitat loss (Lutz et al. 2003, Bishop et al. 2009). Furthermore, alterations in temperature, snowpack, and hydrologic regimes as a result of recent changes in climate (Knowles et al. 2006, Barnett et al. 2008, Shuman 2011) likely are affecting the phenological patterns of forage growth and abundance. Failure to identify specific factors that regulate populations, however, has precluded the detection of the underlying causes, because habitat condition, weather, and predation interact with density dependence to affect population processes (Kie et al. 2003). Detailed and long-term investigations are needed to identify factors regulating populations of mule deer and to improve their conservation and management (Caughley 1977, deVos et al. 2003, Bleich et al. 2006, Connelly et al. 2012, Pierce et al. 2012). Results of 2 recent and comprehensive studies on mule deer in Colorado (Bishop et al. 2009) and Idaho (Hurley et al. 2011), USA, underscored the effects of nutrition and climate on dynamics of mule deer populations. Our research is an extension of those studies and melds population ecology with longitudinal data on nutrition and life history of individual mule deer in a variable environment.

We studied a population of mule deer that overwintered in Round Valley, located on the east side of the Sierra Nevada, California, USA. This population of mule deer has been subjected to a highly variable climate and receives predation pressure from a suite of large carnivores (Kucera 1988; Pierce et al. 2000, 2004). We intensively monitored the population of mule deer in Round Valley from 1997 to 2009, as it recovered from a population low in 1991 (Pierce et al. 2012). Deer that overwintered in Round Valley migrated to high-elevation summer ranges on both sides of the crest of the Sierra Nevada (hereafter Sierra crest), where a rainshadow caused by the Sierra Nevada results in a more xeric range on the east side of the crest compared with the mesic west side (Pierce et al. 1999, Storer et al. 2004, Bleich et al. 2006, Monteith et al. 2011).

The divergent migratory pattern of mule deer that overwintered in Round Valley afforded a unique opportunity to evaluate influences of summer range on factors influencing their recruitment and survival. Differential fitness between migratory

strategies may permit the coexistence of 2 strategies, but advantages of each tactic are sensitive to changes in reproductive success and survival (Kaitala et al. 1993). In 1987, Kucera (1988) determined that 87% of the population of mule deer in Round Valley migrated to the west side of the Sierra crest during summer. The mesic west side presumably offered better foraging opportunities for mule deer during summer, which likely supported high recruitment and survival favoring that migratory tactic.

Our objectives were to examine life-history characteristics of individual mule deer, including migratory tactic, to better understand interactions of those characteristics with nutritional ecology. We evaluated the influence of nutritional condition on survival and reproduction of female mule deer, factors that influenced nutritional condition, and the seasonal carryover of their nutritional state. We hypothesized that nutritional condition would serve as a sensitive metric of resource limitation, and function as the underlying mechanism of those life-history patterns in mule deer, thereby providing insights into population dynamics (Fig. 1). Accordingly, we predicted that nutritional condition would influence vital rates of mule deer in the same order proposed by their sensitivity to resource limitation (Eberhardt 2002), and that those vital rates would be influenced by seasonal patterns of climate, forage abundance, and animal density (Fig. 1). We also hypothesized that the migratory tactic employed by an individual would interact with other life-history components to determine patterns of nutritional condition and fitness within the population (Hebblewhite and Merrill 2009).

We expected nutritional condition of individuals to be sensitive to environmental factors including precipitation and growth of forage relative to population density, migratory tactic, season, and reproductive status (Fig. 1). We also assessed the degree of carryover effects on seasonal levels of nutritional condition and their influence on population characteristics (Fig. 1). Our overarching goal was to integrate nutrition with life-history theory in a free-ranging large mammal to provide a nutritional basis for understanding life-history strategies, and aid in the conservation and management of large herbivores.

STUDY AREA

The Sierra Nevada is a mountain range oriented northwest to southeast that extends about 250 km from the shore of Lake Almanor in the north, to Tehachapi Pass, east of Bakersfield (Storer et al. 2004), and lies entirely within California, USA, except for the Carson Range, which extends eastward into Nevada. This mountain range is a massive granitic block that tilts to the west with a gradual slope of 2–6%, extending 75–100 km from the crest to the San Joaquin or Sacramento valleys. Conversely, the precipitous east side of the Sierra crest is characterized by steep slopes rising abruptly from the bordering valleys that merge with the western edge of the Great Basin. The Owens Valley, extending from the Sherwin Grade north of the town of Bishop and southward about 120 km, is demarcated by elevations of 4,200 m at the mountain summits to 1,220 m at the

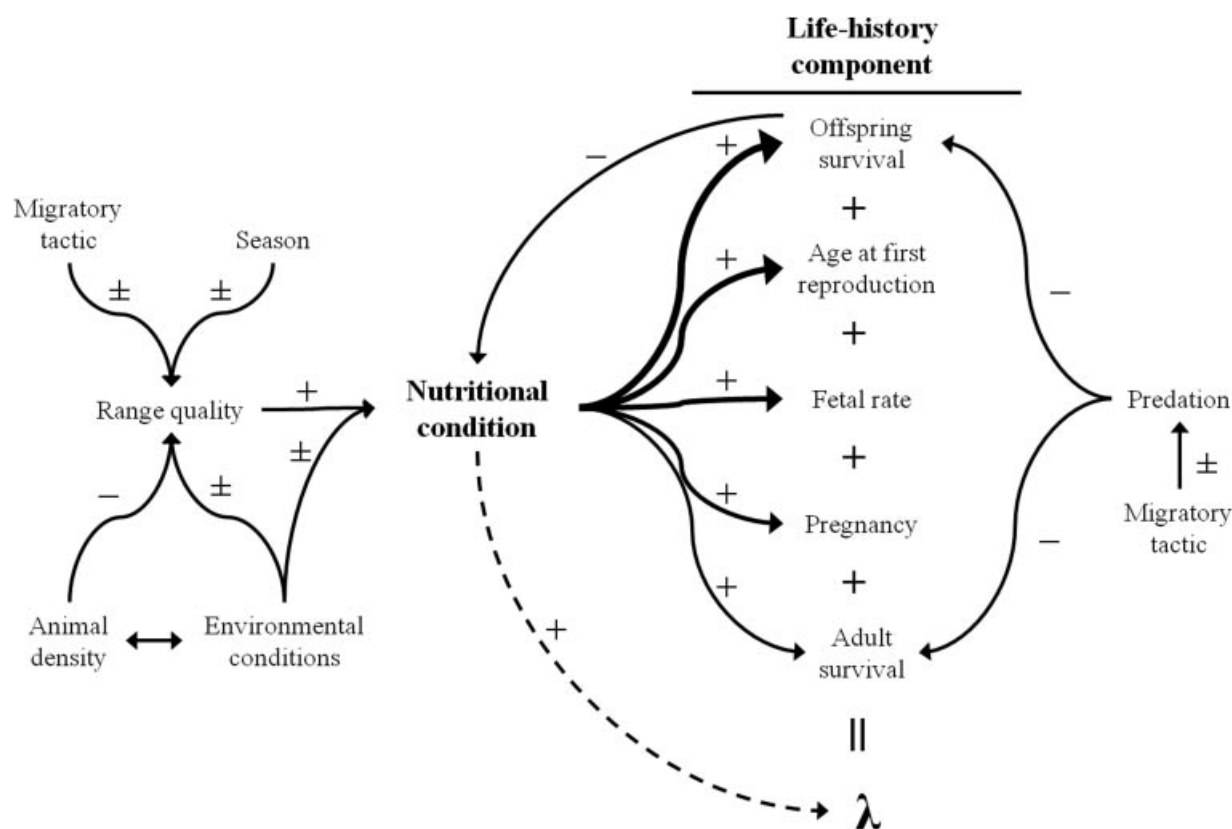


Figure 1. Conceptual model illustrating the predicted association between nutritional condition and life history, and the factors expected to influence nutritional condition. Weight of the arrows between nutritional condition and life-history component represent the expected sensitivity of each life-history component to resource limitation. Expected direction of relationships (i.e., positive, negative, or both) are indicated with each connection. Season refers to winter versus summer conditions and the feedback from offspring survival to nutritional condition refers to the cost of reproduction on autumn nutritional condition.

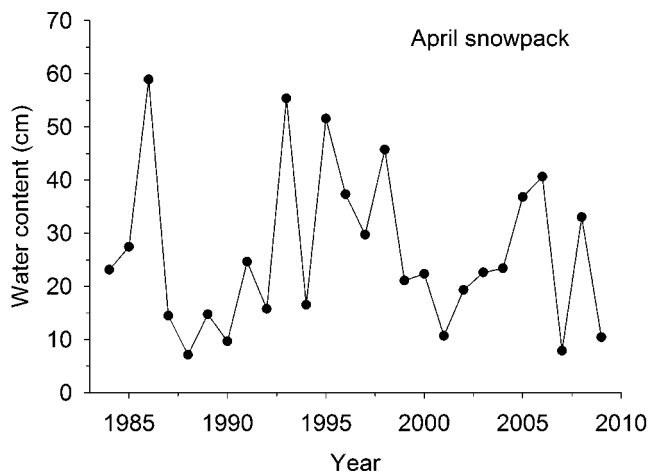


Figure 2. Water content (cm) of the snowpack during April in the Rock Creek drainage adjacent to Round Valley, Bishop, California, USA, 1984–2008 (Station ID: RC2, California Department of Water Resources).

valley floor over horizontal distances of <10 km (Kucera 1988). Few passes allow vehicular traffic over the Sierra crest; thus, most passes are accessible to humans only by foot or on horseback.

The Sierra Nevada is typified by dry, hot summers (Jun–Sep), short, mild autumns (Oct), and long, cool winters, with most annual precipitation accumulating as snow (Nov–Apr; Monteith et al. 2011). Within the region, 75% of the precipitation, including rain or snow, accumulates between November and March (Monteith et al. 2011). Snow accumulation measured by water content of the April snowpack in a drainage adjacent to Round Valley (Station ID: RC2, California Department of Water Resources) was highly variable during 1984–2009, and ranged from 7.1 cm to 58.9 cm (Fig. 2). The Sierra crest, which sharply delineates the western slope from the eastern slope of that range, causes a rain-shadow that results in >3× greater deposition of moisture on the west side and produces an arid landscape on the eastern slope, where the Great Basin Desert begins.

Mule deer inhabited approximately 90 km² of Round Valley (37°24', 118°34'W) during November–April (Fig. 3), but the size of the area used was dependent on snow depth in any particular year (Kucera 1988). Most of these mule deer migrated northward and westward to high-elevation ranges in summer (Kucera 1992, Pierce et al. 1999); some migrated over passes to the west side of the Sierra crest, whereas others remained on the east side (Monteith et al. 2011).

Round Valley is bounded to the west by the eastern escarpment of the Sierra Nevada. Vegetation in Round Valley was characteristic of the western Great Basin and the sagebrush belt (Storer et al. 2004). Typical vegetation that characterized habitats used by mule deer in Round Valley included bitterbrush (*Purshia glandulosa*), sagebrush (*Artemesia tridentata*), blackbrush (*Coleogyne ramosissima*), desert peach (*Prunus andersonii*), rabbitbrush (*Chrysothamnus nauseosus*), and Mormon tea (*Ephedra nevadensis*). Riparian areas consisted of willow (*Salix* spp.), rose (*Rosa* spp.), and water birch (*Betula occidentalis*); forbs and graminoids were uncommon in Round Valley during winter (Kucera 1988, Pierce et al. 2004). Open pastureland comprised

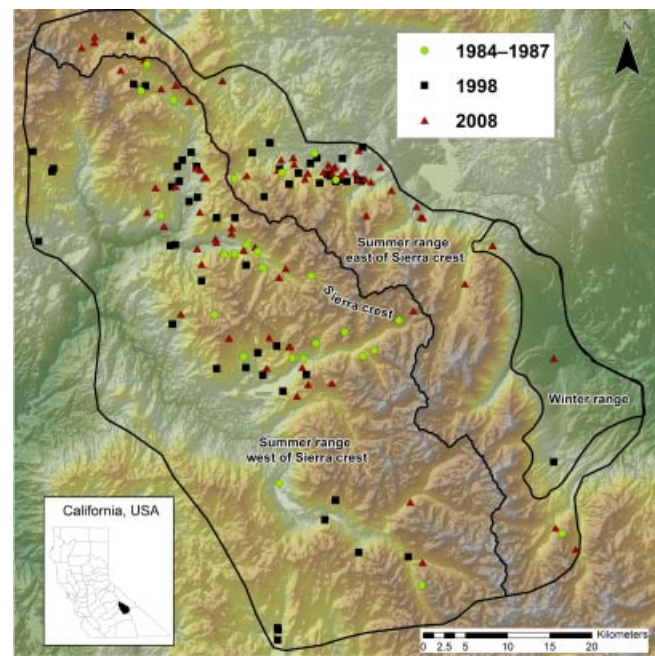


Figure 3. Range occupied by migratory mule deer that share a common winter range in Round Valley and migrate to distinct summer ranges on both sides of the crest of the Sierra Nevada, California, USA with summer range locations of adult female mule deer monitored during 1984–1987 (Kucera 1988), 1998, and 2008.

parts (18.3 km²) of the eastern portion of the valley; however, deer used pastures only when heavy snows forced them from higher elevation areas dominated by bitterbrush, which was a primary winter forage for mule deer (Pierce et al. 2004, 2012).

Deer overwintering in Round Valley migrated in spring to summer ranges on both sides of the Sierra crest at elevations ranging from 2,200 m to >3,600 m (Monteith et al. 2011). The western slope of summer range for mule deer was dominated by the upper-montane and mixed-conifer vegetation zones (Storer et al. 2004) consisting of conifer stands with little understory, including red fir (*Abies magnifica*), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), Jeffery pine (*Pinus jeffreyi*), and quaking aspen (*Populus tremuloides*). Montane chaparral, composed of dense stands of manzanita (*Arctostaphylos* spp.), ceanothus (*Ceanothus* spp.), and bush chinquapin (*Chrysolepis sempervirens*), occurred at lower elevations within drainages on the western slope (Storer et al. 2004). The relatively common and dense pine-fir (*Pinus-Abies* spp.) stands and rivers on the west side contrast with the sparse forests (*Pinus* spp.) transitioning to sagebrush (*Artemesia* spp.) steppe on the east side. The eastern slope of the Sierra was characterized largely by the sagebrush vegetation zone (Storer et al. 2004). This zone was dominated by sagebrush, but also included other shrub species such as bitterbrush, ceanothus, manzanita, rabbitbrush, and mountain mahogany (*Cercocarpus betuloides*), and supported pure stands of Jeffrey pine in some areas (Storer et al. 2004).

Mule deer inhabiting winter range in Round Valley have been subjected to the vagaries of climate, coupled with influences of density dependence (Kucera 1988), and have exhibited marked variation in population size during the past quarter century. Coincident with a likely overshoot of *K* and a severe drought

during 1987–1990, when water content of winter snowpack was 27% of the long-term mean (Pierce et al. 2012), total numbers (based on minimum counts) declined from 5,978 (66 deer/km²) animals in 1985 (Kucera 1988) to a low of 939 (10 deer/km²) in 1991 (Pierce et al. 2012). During the population decline, pregnancy rates, fetal rates, fetal sizes, adult weights, and kidney fat varied with precipitation and forage growth on winter range (Kucera 1988, Pierce et al. 2012). Following the prolonged drought and population nadir in 1991, deer numbers increased to approximately 1,900 in 1997 (Pierce et al. 2012), when we initiated our research. With the exception of winter 1984, when an antlerless hunt removed 200 female mule deer (approx. 3.3% of the total population at that time) on the northern portion of the study area as part of a research project (Kucera 1988), only limited hunting of male mule deer occurred during autumn in all years of our study. Hunting opportunity on winter range in Round Valley resulted in the harvest of approximately 15 males per year, but the harvest of male mule deer on summer range was difficult to estimate because deer from Round Valley mingle with deer from other populations. Nevertheless, limited harvest of males would have had a negligible influence on population dynamics of deer (McCullough 1979, 2001; Kie et al. 2003).

Areas occupied by migratory mule deer include a full complement of other predators on both winter and summer ranges, including cougars (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*; Pierce et al. 2000, Villepique et al. 2011). Black bears (*Ursus americanus*) were abundant on summer ranges west of the Sierra crest, but were less common in the eastern Sierra Nevada. Grizzly bears (*Ursus arctos*) formerly existed west of the Sierra crest, but were extirpated by 1922 (Storer and Tevis 1955).

METHODS

Animal Capture and Handling

Adult females.—During March 1997–2009 and November 2002–2008, we captured adult (>1 yr old) female mule deer on winter range in Round Valley using a hand-held net gun fired from a helicopter (Barrett et al. 1982, Krausman et al. 1985). We hobbled and blindfolded each animal before transporting it via helicopter to a central processing station. We removed 1 incisiform canine using techniques described by Swift et al. (2002) to allow age estimation by cementum annuli (Matson's Laboratory, Milltown, MT). This procedure had no effect on body mass, percent body fat, pregnancy rate, or fetal rate in mule deer (Bleich et al. 2003). We measured body mass with an electronic scale (± 1 kg). We fitted each animal with a standard very high frequency (VHF) radiocollar (Telonics, Inc., Mesa, AZ; Advanced Telemetry Systems, Isanti, MN) equipped with mortality sensor, and covered with orange tape or orange plastic to enhance visibility during mark-resight surveys. To obtain longitudinal data on individual females, we attempted to capture every radiocollared female in March and >50% of the radiocollared females during November. We captured new, unmarked females in an effort to maintain a sample of ≥ 75 adult females for the duration of the study. Our sample included 347 individual adult females, which we captured an average of 3.6 times each

(range = 1–20 times) on winter range in Round Valley during 1997–2009.

We conducted ultrasonography (Aloka 210 with 5-MHz transducer, Aloka, Inc., Wallingford, CT) to determine nutritional condition of captured animals using standard protocols developed for mule deer. We measured maximum thickness (to the nearest 0.1 cm) of subcutaneous fat at the thickest point cranial to the cranial process of the tuber ischium (Stephenson et al. 2002). We accompanied ultrasonography with palpation to achieve a body-condition score validated for mule deer (Cook et al. 2007) to aid in estimating nutritional condition of animals that had catabolized subcutaneous fat reserves (<5.6% ingesta-free body fat; IFBFat). We then combined body mass, body-condition score, and maximum thickness of rump fat to estimate percent IFBFat according to relationships ($r^2 = 0.81$, $P < 0.001$) and equations provided by Cook et al. (2010). When body mass was not available, we used measurements of chest girth to estimate body mass ($r^2 = 0.74$) for calculations of IFBFat (Cook et al. 2010). We also converted kidney-fat indices collected during 1985–1996 (Kucera 1988, Pierce et al. 2012) using standard equations (Cook et al. 2007) to obtain estimates of IFBFat during that period ($r^2 = 0.84$), which provided a long-term trend in nutritional condition of deer.

We also used ultrasonography during March to determine pregnancy and fetal rates of captured females (Stephenson et al. 1995). We shaved the left-caudal abdomen behind the last rib and applied lubricant to facilitate transabdominal scanning using a 3-MHz transducer. Upon completion of ultrasonography, we fitted numerous (approx. 60/yr) pregnant females with vaginal implant transmitters (VITs) during 2006–2008; we used VITs (M3930, Advanced Telemetry Systems) to facilitate locating and capturing neonatal mule deer. We inserted VITs using a technique similar to that described by Bishop et al. (2007). We placed VITs approximately 20 cm into the vaginal canal, or until the silicone wings of the VIT were pressed firmly against the cervix. We used a temperature-sensitive switch that increased pulse rate of transmissions from 40 pulses to 80 pulses per minute when the temperature decreased below 32° C, which was representative of the VIT being expelled by the deer and the subsequent birth of young. Vaginal implant transmitters have been employed without reproductive problems or effects on female survival, and are a practical technique for locating birth sites and neonates (Carstensen et al. 2003, Johnstone-Yellin et al. 2006, Bishop et al. 2007).

Neonates.—During 2006–2008, we located and captured 119 neonatal mule deer from 15 June to 20 July by searching for and observing females that exhibited postpartum behavior and by locating expelled VITs. We located radiocollared females and monitored VITs for evidence of parturition at first light each day during the period of parturition (i.e., 15 Jun–31 Jul) using a Cessna 180 fixed-wing aircraft (Cessna Aircraft Company, Wichita, KS) fitted with 2, 2-element H-antennas, and used ground-based telemetry to locate the VIT and radiocollared female as quickly as possible. We used the location of the VIT and the location and behavior of the female to identify search areas.

When our ground searches failed to produce neonates, we evaluated whether the location of the VIT was an actual birth

site, and confirmed that supposition by observing the pregnancy status and behavior of the radiocollared female. If the female appeared to have undergone parturition and personnel were available, we attempted to observe the female from a distance (≥ 300 m, depending upon terrain and cover) sufficient to avoid disturbance, and used postpartum behavior of the female to locate fawns (Monteith et al. 2007). In addition to radiocollared females with VITs, we opportunistically observed random females at first light with binoculars ($6\text{--}15\times$) or spotting scopes ($20\text{--}50\times$), and located neonates by focusing on adults that exhibited maternal behavior (Huegel et al. 1985, Carstensen et al. 2003). When we located a neonate, we hiked to the area where the neonate bedded, and conducted ground searches to locate and capture young mule deer.

We captured neonatal deer by hand and placed them in a cloth bag containing sagebrush to minimize scent transfer, although that likely would have had little influence on potential abandonment (Bowyer et al. 1998a, Carstensen et al. 2003). We determined sex of each neonate and acquired a measurement of new hoof growth using dial calipers (Robinette et al. 1973, Brinkman et al. 2004). We determined the body mass of each neonate within the cloth bag to the nearest 0.1 kg using a hand-held spring scale. We recorded the geographic coordinates of each capture site using a global positioning system (GPS) device, and processed all neonates quickly to minimize the potential for abandonment or attraction of predators (Livezey 1990). We fit all neonatal deer with an expandable radiocollar (Advanced Telemetry Systems, Inc.; Telemetry Solutions, Walnut Creek, CA) with a 4-hour mortality delay. Methods of research and animal capture were approved by an independent Institutional Animal Care and Use Committee at Idaho State University (protocol: 650-0410), were in accordance with guidelines for research on wild mammals adopted by the American Society of Mammalogists (Gannon et al. 2007), and followed protocols of California Department of Fish and Game for restraint of ungulates.

Deer Monitoring and Cause-Specific Mortality

We endeavored to monitor all radiocollared mule deer with ground telemetry on winter range ≥ 3 days per week from October to April to determine survival and cause-specific mortality. During summer, we attempted to monitor radiocollared neonates daily from a fixed-wing aircraft and ground-based radiotelemetry from their time of capture until at least 31 August, when risk of mortality was greatest (Bishop et al. 2009); we monitored young deer approximately 3 days per week thereafter. The near absence of roads in the 2,800-km² summer range precluded frequent monitoring of most adult females on summer range. Therefore, we often did not detect mortality of adults during summer for ≥ 1 week, reducing the likelihood of ascertaining cause of death. We attempted to locate each animal at least once during 15 June–30 September to determine summer occupancy and migratory status. We grouped animals based on their summer residency, which we defined by their use of summer range on the east or west side of the Sierra crest. To illustrate the relative changes in density of individuals that migrated to the east versus west side of the Sierra crest, we developed a metric of relative change in density between decades using summer

locations of radiocollared females (i.e., single location per female each summer) obtained using aerial telemetry for summers of 1984–1987 (Kucera 1988), 1998, and 2008. With those summer locations, we calculated the Euclidian distance to the nearest female for each 30-m pixel within our study area. We then developed a map where the shading per pixel was based on the relative change in density, which we determined by subtracting the Euclidian distance for each pixel between 1998 and 1984–1987, and 2008 and 1998.

Frequent monitoring of animals on winter range and of neonates during summer typically allowed us to detect mortality early enough to determine proximate cause of death. When mortalities were detected, we used ground telemetry to locate carcasses as quickly as possible (< 8 hr). We examined carcasses to estimate date of death based on decomposition and condition of the animal. We evaluated and recorded the location and arrangement of the carcass, presence and position of tooth marks, ante- and post-mortem bleeding or bruising, fractures, and remaining organs when present. We identified other physical evidence of predation including tracks and feces (Elbroch 2003), and collected hair for confirmation of the predator responsible (Moore et al. 1997). When we could not ascertain cause of death, we transported the carcass to the laboratory to be necropsied; we performed field necropsies when distance or a precarious location hindered transport of the carcass from the field.

We classified proximate causes of death as 1) predation; 2) malnutrition, which included small and emaciated neonates where the carcass remained intact with no signs of predation and adults with $< 25\%$ femur marrow fat; 3) other natural causes if the carcass was intact, did not show signs of predation, malnutrition, or trauma, and post-mortem examination indicated potential infection or disease; 4) accident if a carcass was located mainly intact with broken bones or other premortem physical trauma, which included deer-vehicle collisions; or 5) undetermined if cause of death could not be placed in 1 of the aforementioned categories, or lack of evidence otherwise precluded determination of cause of death. For predation-related mortalities, we attempted to identify the predator responsible for the death.

For neonates, we included abandonment as a proximate cause of death if the neonate was apparently healthy and post-mortem necropsy revealed an abomasum that was empty or contained soil and vegetation rather than milk, an indication of the absence of nursing (Church 1988). When available, we collected femurs from mortalities and evaluated femur marrow from its appearance and texture; we also estimated femur-marrow fat based on percent dry weight (Neiland 1970). We considered the proximate cause of mortality as the ultimate cause except for those adult animals that had a visual score of 1 (marrow was red and fluid) and femur-marrow fat $< 25\%$ (Neiland 1970). Femur-marrow fat $< 25\%$ is indicative of malnutrition and depletion of the last remaining fat reserves (Mech 2008); we considered the cause of mortality to be malnutrition in those instances, regardless of proximate indicators of death (Ratcliffe 1980, Depperschmidt et al. 1987).

We defined recruitment status of radiocollared females by the number of young-at-heel identified each autumn, which we determined as females arrived on winter range in late-October through November, when mother–infant bonds were still intact

(Bonenfant et al. 2005). We located each radiocollared female and stalked to within ocular range (<200 m) aided by ground-based telemetry. We observed each female using binoculars or spotting scopes until we could determine the number of young-at-heel confidently, which we identified by observing nursing and other maternal behaviors (Monteith et al. 2011).

Population Surveys

We conducted 2 helicopter surveys during each January to estimate the number of deer wintering in Round Valley and the proportion of adult females, adult males, and young in the population. We conducted surveys in a Bell Jet Ranger 206 BIII (Bell Helicopter, Hurst, TX) with 3 observers; we removed the doors to improve visibility (Clancy 1999). Aerial transects overlapped the entire winter range to an elevation at which deer tracks were no longer evident in snow. We established the location of the initial transect randomly, but subsequent transects were parallel to the initial transect, and spaced at intervals of approximately 0.4 km. We also calibrated reference points on the door jambs of the helicopter to allow observers to estimate distances from the centerline out to 200 m.

For population-composition surveys, we flew aerial transects with 3 observers and classified deer as we encountered them. For each group or individual encountered, we identified the size and composition of each group, which included adult males, adult females, and young (<1 yr old). Visibility bias among sex and age classes were likely kept to a minimum (Bonenfant et al. 2005), because we collected our herd composition data with helicopter surveys on winter range, in open sagebrush-steppe habitat in January. Sample sizes were typically >1/3 of the population estimate. We calculated age ratios and their standard errors according to Bowden et al. (1984), which assumed sampling without replacement.

We obtained population size from a total count of deer before 1994 (Pierce et al. 2012), for which no measure of variance existed because these were censuses. Subsequently, we estimated population size using the marked deer in Round Valley (Chao and Huggins 2005). During those mark-resight surveys, we noted the number of marked female deer in each group, but did not classify deer with respect to age class or sex, thereby alleviating the need for the pilot to deviate from, and then attempt to return to, the transect line. The pilot tried to maintain an elevation of 25 m above ground level (AGL) and an air speed of approximately 75 km/hour.

We used the Chapman (1951) modification of the Lincoln-Petersen estimator to calculate unbiased estimates and the associated variance of population size for mule deer from the mark-resight data collected during the annual helicopter surveys. We assumed that marked animals had sightabilities similar to unmarked animals (White and Shenk 2001), and that the population was geographically and demographically closed during the survey period, based on aerial or ground-based telemetry immediately before each aerial survey to confirm the number of marked deer available within the survey area. We did not identify individually marked animals during the survey; therefore, we assumed homogeneity in sighting probability per individual. We recognize that if heterogeneity in sighting probabilities for individuals existed, our error estimates could be

biased. Any bias caused by differences in sightability among individuals likely was minimal, however, because of the open habitat on winter range in Round Valley.

Statistical Analyses

Modeling approach.—We modeled neonatal and adult survival, cause-specific mortality, reproductive rates, nutritional condition, sex and age ratios, and the finite rate of population growth (λ) for mule deer as a function of predictor variables that were representative of 3 different levels: population, individual, and maternal. Population-level covariates were environmental factors or variables that corresponded to the entire population, or a large proportion of the population. Individual-level covariates were unique attributes of individuals, and maternal variables were characteristics of the mother of a particular neonate. We first evaluated effects of covariates at the population level and retained those variables identified as being influential in this first stage of analysis (Arnold 2010, Monteith et al. 2011, Grovenburg et al. 2012a), and used them for the same analysis with incorporation of variables at the individual level, and then at the maternal level when relevant. Therefore, we modeled response variables in 1–3 stages according to the aforementioned levels. We conducted our analyses in that 2- or 3-stage approach because covariates at the individual or maternal level were not available for every animal, and population-level and individual-level factors can affect life-history characteristics differently (Monteith et al. 2011, 2013). We also conducted an additional analysis that included only data from 2002 to 2008 to assess relationships related to life-history characteristics of females in autumn, because capture efforts in November occurred only during those years.

We used an information-theoretic approach to assess variable importance. In each stage of the analysis, we evaluated all possible combinations of predictor variables that we hypothesized to influence the response variable (Whittingham et al. 2006, Arnold 2010, Doherty et al. 2010). For each model, we calculated Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weight (w_i ; Burnham and Anderson 2002). We then calculated model-averaged parameter estimates and the associated 90% confidence intervals, based on unconditional standard errors. Model averaging minimized effects of uninformative parameters, and thereby provided a conservative assessment of variable importance (Whittingham et al. 2006, Arnold 2010, Doherty et al. 2010). We determined if model-averaged parameter estimates differed from zero based on whether their 90% confidence intervals overlapped zero. We used importance weights, calculated as the sum of w_i across all models that contained that particular variable (Burnham and Anderson 2002, Arnold 2010, Doherty et al. 2010, Monteith et al. 2011), to evaluate the relative ranking of each predictor variable. We retained variables from the previous stage of an analysis if the parameter estimate differed from zero (i.e., 90% CI did not overlap 0) or had an importance weight >0.50 (Arnold 2010, Monteith et al. 2011). To best depict relationships between a specific predictor variable and a response variable in figures, we used the top model ($\Delta AIC_c = 0$) of all possible combinations of variables, and modeled expected effects (y -axis) of the variable of interest (x -axis) within the observed range,

while holding all other variables constant at their mean (or other values as specified).

We evaluated biologically meaningful interactions between predictor variables using the global model in each stage of the analysis based on whether confidence intervals of the parameter estimate for the interaction overlapped 0 and if the inclusion of the interaction term resulted in an improvement of model fit ($<2 \Delta AIC_c$). We removed all interaction terms with confidence intervals that overlapped zero and did not result in an improvement of model fit from analyses because inclusion of those interaction terms can alter model-averaged estimates of the independent counterpart of those terms. In addition, for age-specific patterns, we evaluated both the inclusion of the quadratic effect of age (age^2) and a threshold model of age ($\ln[age]$), because demographic and morphometric relationships with age may take many forms (Nussey et al. 2011). We retained age^2 or $\ln(age)$ if its inclusion resulted in improved model fit.

Predictor variables.—For each level of analysis, we developed a set of variables a priori based on the literature and that we expected would influence or be related to the response variable, with the overarching goal of assessing effects of nutrition on life-history characteristics of mule deer (see Appendices A–O for complete list of variables). Predictor variables at the population level (Table 1) included environmental variables such as weather, categorical variables that applied to a large portion of the population (e.g., summer residency), and annual metrics of the condition or performance of the mule deer population (e.g., mean Mar IFBFat). At the individual level, variables included life-history characteristics that corresponded to each individual (e.g., age, recruitment status, IFBFat; Table 2), and variables at the maternal level were characteristics of the mother of a specific neonate (e.g., age, IFBFat; Table 2). We evaluated multicollinearity among all predictor variables in each stage of analysis, and did not allow variables that were correlated ($r > |0.50|$) enter the same model.

Growth of bitterbrush, the primary winter forage for mule deer in the Sierra Nevada (Kucera 1997, Pierce et al. 2004), was influenced largely ($r^2 = 0.65$, $P = 0.001$) by the water content of

the snowpack from the preceding April (Fig. 2; Pierce et al. 2012). Accordingly, seasonal nutrition was influenced by snowfall from the preceding year; however, per capita availability of forage was determined by the relationship of snowpack and number of individuals present in the subsequent year (Pierce et al. 2012, Monteith et al. 2013). Therefore, we calculated a density-dependent proxy to forage availability based on the quotient of the water content of the snowpack during the preceding April, and the estimated number of females for that year (per capita snowpack; cm/female). This variable integrated factors that affected growth of forage and population density to yield a density-dependent index to forage availability. Our per capita snowpack metric was similar to relationships established for African ungulates, where plant growth was strongly associated with rainfall, but the influence on demography depends on the current relative abundance of herbivores (i.e., animals per kg green grass; Sinclair et al. 1985). We included estimated number of females rather than a population estimate because males and females partition use of resources throughout much of the year (McCullough 1979; Bowyer 1984, 2004; Kie and Bowyer 1999). We assessed the relative importance of including either per capita snowpack, or snowpack and number of females, or their interaction based on ΔAIC_c for each separate analysis, and then included the most influential variable(s) in the remainder of model sets.

We also included location of summer residency as a predictor variable, because deer that overwinter in Round Valley reside on disparate ranges on opposite sides of the Sierra crest, and life-history patterns may differ between females residing in different areas (Monteith et al. 2011). We coded females occurring on the west side as 0 and females residing on the east side of the Sierra crest as 1 (Table 1).

Survival.—We used the known-fate model in Program MARK (White and Burnham 1999), which accommodated staggered entry and exit of radiocollared animals (Kaplan and Meier 1958, Pollock et al. 1989), to estimate survival and determine factors that influenced seasonal survival of adult (>1 yr) female mule deer. We first estimated winter (Nov–Apr) and summer (May–Oct) survival for prime-aged females (2- to 9-yr-

Table 1. Definitions of predictor variables used to assess factors that influence life-history characteristics of mule deer at the population level.

Level	Predictor	Units	Definition
Population	Summer residency	East or west	Side of the Sierra crest occupied during summer (east = 1; west = 0)
	Spring precipitation	cm	Total precipitation during May–June
	Spring temperature	°C	Mean temperature during May–June
	Summer precipitation	cm	Total precipitation during July–October
	Summer temperature	°C	Mean temperature during July–October
	Monthly precipitation	cm	Total monthly precipitation
	Monthly temperature	°C	Mean of daily temperature per month
	Snowpack	cm	Water content of snowpack during the previous April
	Number females	Estimate	Number of females on winter range
	Per capita snowpack	cm/female	Water content of the previous April snowpack divided by the estimated number of females in the population
	Mean litter size	Number/female	Mean number of fetuses per adult female in March
	Mean Mar IFBFat	%	Mean ingesta-free body fat (IFBFat) of adult females during March
	Mean Nov IFBFat	%	Mean IFBFat of adult females during November
	Stage	Category	Stage-specific variable allowing survival of neonates to vary during the first 4 weeks, with constant survival thereafter
	Month	Category	Nuisance parameter allowing response variable to vary as a function of month
	Year	Category	Nuisance parameter allowing response variable to vary as a function of year

Table 2. Definitions of predictor variables used to assess factors that influence life-history characteristics of mule deer at individual and maternal levels.

Level	Predictor	Units	Definition
Individual	Age and age ²	yrs	Age of individual females
	Mar IFBFat	%	Ingesta-free body fat (IFBFat) of individual females during March
	Nov IFBFat	%	IFBFat of individual females during November
	Mar body mass	kg	Body mass of individual females during March
	Nov body mass	kg	Body mass of individual females during November
	Litter size	Number	Number of fetuses as determined during neonate capture or March ultrasonography for individual females
	Recruitment status	Number	Number of young-at-heel in autumn for individual females
	Sex	Category	Male or female
	Julian birth	Julian date	Estimated date of birth via vaginal implants or hoof growth of neonate
	Deviation from mean birth	Days	Number of days prior to or post mean birth dates per year
	Birth mass	kg	Estimated body mass of neonates at birth
	Age at death	Days	Age at death based on estimated date of birth for neonates
	Age and age ²	yrs	Age of dam
	Mar IFBFat	%	IFBFat of dam the preceding March
Maternal	Mar body mass	kg	Body mass of dam the preceding March

old), without the addition of covariates, by allowing survival to vary monthly during each season and thereby estimate survival without heterogeneity introduced by different survivability of young or senescent females. We estimated annual survival as the product of summer and winter survival within years and used the delta method to calculate associated variances (Seber 1982). Thereafter, we modeled factors that affected survival during winter and summer separately for all females >1 year old. We expected environmental and individual factors to affect survival differently on seasonal ranges, because of differences in life-history patterns of deer between seasons. Therefore, we modeled monthly survival separately during 2 periods of 6 months as a function of environmental and individual-based covariates using the aforementioned modeling approach. We censored adult females that died within 14 days of capture to avoid underestimating survival for individuals that perished as a result of capture-related causes.

We determined date of birth for each neonate from a combination of hoof, umbilicus, and behavioral characteristics (Haugen and Speake 1958, Brinkman et al. 2004, Haskell et al. 2007). We considered all neonates that we captured with wet pelage, wet umbilicus, or with the aid of an expelled VIT to be 0 or 1 day old, after assessing those characteristics. For all others, we estimated age for neonatal mule deer based on new-hoof growth with the equation of Robinette et al. (1973), where age (days) = mean hoof growth (mm) \times 2.55–6.3. More recently, Haskell et al. (2007) provided an additional equation for estimating age of neonatal mule deer; however, we chose not to use their equation, because negative hoof growth is required for a neonate to be <5 days old. We assumed mass of neonates at capture was the birth mass for neonates \leq 1 day old at capture. For older neonates, we back-calculated birth mass from the slope of the regression between body mass and age at capture for all neonates in our study (mass [kg] = 2.76 + age \times 0.27; r^2 = 0.67, P < 0.001); growth rates were similar between sexes ($F_{1,110}$ = 1.39, P = 0.24). We multiplied age of the neonate (based on new-hoof growth) by the slope from the previous equation, and subtracted the product from body mass at time of capture. We recognize that our estimates of birth mass for neonates >1 day old could be affected by low precision in hoof-growth equations or by differences in growth rate among

individual neonates (Haskell et al. 2007). Nevertheless, 76% of neonates in our sample were \leq 2 days old and estimates of birth mass were nearly identical for neonates captured at birth (\bar{x} = 2.76 kg, SE = 0.089, range: 1.0–4.0) compared with older neonates for which we back-calculated birth mass (\bar{x} = 2.75 kg, SE = 0.075, range: 1.86–4.1). Consequently, estimating age at capture and birth mass should have a limited effect on our analyses.

We used the known-fate model in Program MARK (White and Burnham 1999) to estimate survival and determine factors that influenced survival of neonatal mule deer at population, individual, and maternal levels. We estimated preweaning survival of young mule deer weekly from birth until 20 weeks of age (140 days; approx. Jul–Oct), at which time we considered young mule deer to be weaned (Sadleir 1980). For encounter histories in the known-fate model, we placed all events, including capture, survival monitoring, mortality, and censors into 1-week intervals. Neonates that were \leq 1 week old when captured entered the survival analysis in the first interval; neonates >1 week old and \leq 2 weeks old when captured entered the analysis during the second interval, and so forth. We right-censored all animals that prematurely shed collars (n = 4), because censoring likely was independent of the fate of the neonate.

We first modeled summer survival of neonates through 20 weeks of age with a time-dependent model that allowed survival to vary randomly by week and plotted the resulting weekly estimates of survival to identify periods of time with consistent survival (Barber-Meyer et al. 2008). Survival varied during the first 4 weeks of life, but remained relatively constant thereafter, which was expected because of changing patterns of vulnerability of young to predation, activity of young deer, and degree of association with the dam (Haskell et al. 2010). Accordingly, we developed a model that was life-stage specific and allowed survival to vary during the first 4 weeks of life, with constant survival for the remaining 16 weeks. We selected that stage-specific model from among other models (i.e., constant survival and different survival each week) using AIC_c, because no other candidate models were within 2 Δ AIC_c. Subsequently, we used that stage-specific model, and added factors that we predicted to influence survival of neonates at the population (n = 119), individual (n = 113), or maternal (n = 73) levels using

the same modeling approach described previously to evaluate variable importance.

We hypothesized that effects of birth mass and maternal condition on neonatal survival would be age-dependent. We predicted that birth mass would be most influential during the first few weeks of life, because birth mass affects viability of neonates (Verme 1962, Sams et al. 1996, Keech et al. 2000, Carstensen et al. 2009), whereas effects of maternal condition on offspring development and survival should be stronger when maternal provisioning and the energetic costs of lactation rise (Sadleir 1982, Taillon et al. 2012). Therefore, we evaluated models that incorporated an age-dependent effect of birth mass by adding the covariate birth mass starting with only week 1, and then incrementally added weeks up to week 4, and compared those models against a model with an effect of birth mass from 1 week to 20 weeks of age. Similarly, at the maternal level, we incorporated an age-dependent effect of maternal nutritional condition from 1 week to 20 weeks of age, and then incrementally removed weeks from 1 to 4. Doing so allowed us to evaluate our hypothesis directly by developing models that included effects of birth mass within the first few weeks of life that transitioned to an effect of maternal condition as neonates grew older. We selected from among the differing structures for age-dependent parameterization of birth mass and maternal condition using AIC_c and included that structure in all subsequent models where the covariates birth mass or maternal condition were included.

Our data on survival for neonates probably were not fully independent (i.e., were overdispersed), because siblings share maternal resources and occupy similar environments in both space and time (Bishop et al. 2008); our sample contained 2 sets of triplets, 31 sets of twins, and 51 singletons. We used data-bootstrap analysis in Program MARK to estimate overdispersion by generating 10,000 replicate datasets by resampling our data with replacement (White and Burnham 1999, Bishop et al. 2008). We resampled within litters of adult females; thus, the number of samples within each replicate equaled the number of adult females with litters ($n=84$) rather than the number of neonates ($n=119$) in the original dataset. We used a time-dependent global model (year \times week) for bootstrap analyses to avoid misinterpreting poor model fit as overdispersion (Burnham and Anderson 2002). We estimated overdispersion by dividing the theoretical variance estimates with empirical variance estimates calculated from the bootstrap analysis (Bishop et al. 2008). The estimate of overdispersion in our survival analysis for neonates was 1.18, which indicated only modest overdispersion, and was similar to that reported for mule deer in Colorado (1.25; Bishop et al. 2008). Therefore, for all neonatal survival analyses, we set the variance inflation factor (\hat{c}) to 1.18.

Cause-specific mortality.—We modeled causes of mortality for neonates (i.e., up to 20 weeks of age) during summer and winter as a function of population and individual factors predicted to influence cause of death using multinomial logistic regression (Bishop et al. 2009), and the same multi-stage modeling approach that we outlined previously with covariates at the population, individual, and maternal levels. For this analysis, we included only mortalities, because we were interested in evaluating factors that influenced cause of mortality and how those causes contributed to total observed mortality. We excluded

all mortalities for which cause was undetermined, because those samples provided no information regarding cause of death and may simply be a combination of various sources of mortality (Bishop et al. 2009). We were unable to determine cause of mortality for 11% of all neonate mortalities. We only conducted the analyses on cause-specific mortality for neonates, because proportion of unknown mortalities for adults was high (41% of mortalities during winter and 55% during summer).

For multinomial models, we grouped response variables of cause-specific mortality into separate categories that were easily distinguishable to yield sufficient sample sizes. We assessed 4 categories of neonate mortality: bear predation ($n=23$), malnutrition ($n=9$), other predation ($n=19$; composed mostly canid and felid predation), and other natural causes ($n=12$; comprised of accident, injury, drowning, or undetermined disease). Following the analysis of cause-specific mortality, we calculated rates of mortality for neonates and adult females by combining those results with our survival analyses. We estimated rates of cause-specific mortality for neonates based on the product of the probabilities of each mortality cause and the overall mortality rate from our survival analyses, which we calculated from $1 - \hat{S}$ (estimated survival rate). We used the delta method to estimate variances of rates of cause-specific mortality for each analysis (Seber 1982).

Reproduction and nutritional condition.—We modeled birth mass, timing of birth, pregnancy status, litter size, recruitment rate, March IFBFat, March body mass, November IFBFat, and November body mass of adult female mule deer as a function of population and individual-level covariates using the approach described previously (see Appendices C–O). We used linear mixed models (PROC MIXED, SAS Institute, Cary, NC) with a repeated-measures structure to avoid inflating degrees of freedom and account for potential autocorrelation from repeatedly sampling individual deer. For each analysis, we used AIC_c to select the best-fitting covariance structure for repeated measures (Ferron et al. 2002) from those deemed biologically appropriate (Verbeke and Molenberghs 2000, Yoccoz et al. 2001), and used the best covariance structure in subsequent models for a particular analysis. We considered models with covariance structures of variance components, compound symmetry, spatial power, spatial exponential, spatial Gaussian, and heterogeneous autoregressive (Littell et al. 1996).

We conducted separate analyses for pregnancy status of yearlings (1.5-yr-old), and pregnancy status and litter sizes of females ≥ 2.5 years old to avoid having low or more variable reproduction by yearling females unduly influence models of age-specific reproduction (Gaillard et al. 2000, Bonenfant et al. 2009). We modeled pregnancy status of yearling females using logistic regression (PROC LOGISTIC in SAS). For adult females ≥ 2.5 years old, we also modeled pregnancy status using logistic regression (PROC GLIMMIX in SAS), but with a Poisson distribution, because non-pregnant females were rare (McDonald and White 2010), and used a random effect with the RESIDUAL option to specify an R-side covariance structure (which is similar to repeated measures in PROC MIXED). We removed 2 adult females that were ≥ 2.5 years old because they were barren during every year of monitoring (>4 yrs) and, thus, may have confounded analyses on factors that influenced patterns

of fecundity. One was incapable of becoming pregnant because of the awkward position and abnormally small size of the vulva; the absence of pregnancy in the other deer occurred for unknown reasons.

Age ratios and population growth rate.—For population-level analyses of age ratios and lambda, we combined our data with those of Pierce et al. (2012) to lengthen our dataset and strengthen our statistical power for detecting relationships at the population level. We did not include data from Kucera (1988) for this set of models, with the exception of an additional post hoc analysis of lambda, because sample sizes were small and estimates of variance were not always available. Furthermore, data collection by Kucera (1988) occurred during a population crash; demographic patterns can be misleading during different trajectories of population growth when they are combined (Pierce et al. 2012). We estimated λ based on annual population estimates where: $\lambda_t = N_{(t+1)}/N_t$. We used general linear models (PROC GLM, SAS Institute) to determine population-level factors that influenced age ratios and λ . We weighted models based on the inverse of the variance around each annual metric to account for uncertainty in those estimates (Neter et al. 1996).

Consequences of mortality on population dynamics differ depending upon the proximity of a population to its food supply (nutritional carrying capacity; NCC) and, thus, the degree of density dependence (i.e., nutritional limitation) within a population determines the level of compensatory or additive effects of mortality (McCullough 1979, Boyce et al. 1999, Bowyer et al. 2005). The residuals of the relationship between the nutritional capacity for recruitment (i.e., model-based predictions) and actual recruitment should indicate the degree to which mortality is additive or compensatory, because the nutritional potential for survival determines the consequences of mortality for a population (Bartmann et al. 1992, Tveraa et al. 2003). More specifically, nutritional potential for recruitment reflects the point at which mortality transitions from being compensatory to additive with increasing rates of mortality (Fig. 4).

We employed this approach using 2 datasets from our long-term research in the Sierra Nevada: ratios of young-to-adult females and autumn recruitment of young (number of young at heel per radiocollared female). For each analysis, we incorporated variables that reflected the nutritional ability to support young (i.e., habitat and nutritional condition) and that were identified as being influential in previous analyses, and removed effects of variables that accounted for other external factors not related to nutrition. We estimated the nutritional capacity for recruitment (Fig. 4) of young mule deer using the same mixed models with repeated measures for recruitment rate, and mixed models weighted by the inverse of the variance in each estimate for age ratios. We then used the residuals between model-based predictions of the nutritional potential for recruitment and empirically measured recruitment to infer the relative consequences of mortality (i.e., amount of additive and compensatory mortality). Negative residuals reflect the amount of mortality that was additive because the nutritional potential for recruitment was greater than what was realized (Fig. 4). Conversely, residuals near zero or slightly positive would be indicative of recruitment equal to or greater than what was expected on a nutritional basis; thus, observed mortality was compensatory.

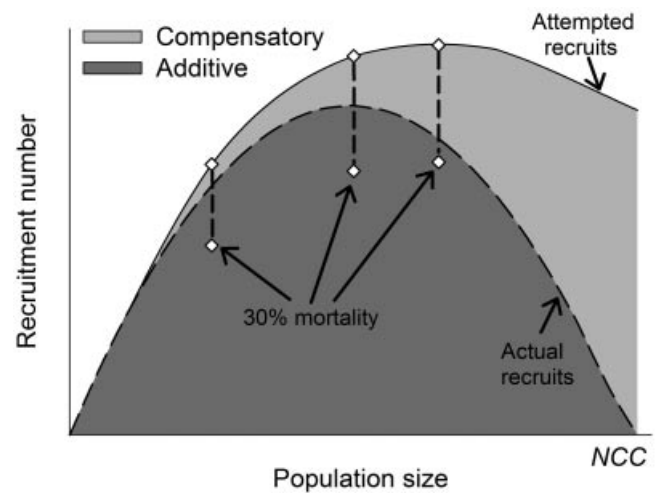


Figure 4. Changes in number of attempted recruits (number of young born) and actual recruits limited by density-dependent feedbacks relative to size of an ungulate population increasing towards its food supply (nutritional carrying capacity; NCC) in the absence of other external mortality factors (i.e., predation). Actual recruits represent the number of young that can be recruited given current habitat limitation via density-dependent feedback (i.e., nutritional potential for recruitment). The difference between the number of attempted and actual recruits therefore represents the component of mortality that is compensatory. Note that the position of the population relative to NCC and thus, the nutritional potential for recruiting young, determines the degree of compensatory or additive mortality even when mortality rates remain unchanged (0.30). Adapted from McCullough (1979) and Kie et al. (2003).

RESULTS

Mean size of the population of mule deer overwintering in Round Valley between 1985 and 2009 was 2,428 animals (range: 939–5978), but was highly variable (CV = 50%; Fig. 5). Winter precipitation also was highly variable; the coefficient of variation of water content of the April snowpack was 57% (Fig. 2). Mean

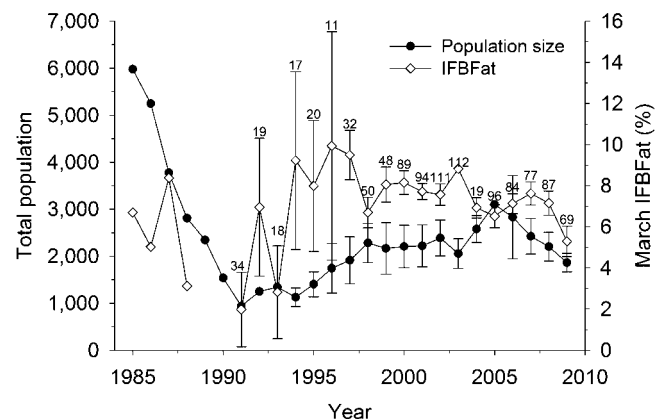


Figure 5. Annual population estimates (solid circles \pm 95% CI) of mule deer in January and ingesta-free body fat (hollow diamonds \pm 95% CI) of adult female mule deer in March on a winter range in Round Valley, Inyo County, California, USA. We determined population estimates from total counts before 1994 and from mark-resight surveys thereafter. We measured ingesta-free body fat (IFBFat) via kidney fat indices before 1997 and ultrasonography thereafter. We obtained data before 1997 from Kucera 1988 and Pierce et al. (2012), and estimates since 1997 are estimates from this study. Sample sizes for IFBFat are displayed above means.

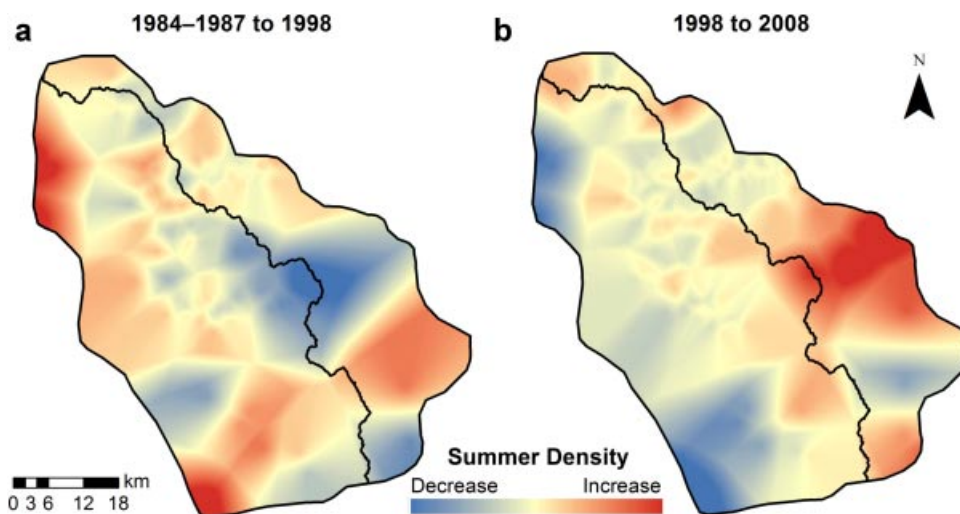


Figure 6. Relative change in density during summer from 1984–1987 to 1998 (a), and from 1998 to 2008 (b), with warm colors indicating increases in density and cool colors indicating declines in density of mule deer that migrate to summer ranges on both sides of the crest of the Sierra Nevada, California, USA. Relative change in density was measured as the change in distance to the nearest location of a female mule deer during summer between the aforementioned years.

nutritional condition (IFBFat) of adult females in March ranged from 2.0% to 9.9% with a coefficient of variation of 33%. Despite that variation in population size and nutritional condition, pregnancy (0.98; CV = 4.4%) and fetal rates (1.69; CV = 10.4%) of adult females remained high, with markedly less variation. The proportion of the population that migrated to the west side of the Sierra crest declined from 87% in 1985 to 58% when our study began in 1998, and was followed by further reductions to <50% of our marked sample of adult females by 2005 (Fig. 6). This shift in proportion of west-side migrants in the population occurred despite high fidelity to summer ranges, indicating the shift was caused by demographics rather than behavior. Of the 251 adult females that we monitored for >1 summer, females never switched summer ranges to the opposite side of the Sierra crest, and none of the young that we

monitored in subsequent years ($n = 26$) switched sides from where they were born.

Survival of Neonates

The stage-specific pattern of neonatal survival indicated low, but generally increasing survival during the first 4 weeks of age ($\bar{x} \pm \text{SE}$; week 1 = 0.75 ± 0.047 ; week 2 = 0.88 ± 0.039 ; week 3 = 0.96 ± 0.026 ; week 4 = 0.90 ± 0.041), and relatively constant survival from 5 weeks to 20 weeks of age (0.97 ± 0.007 weekly). Average survival of neonatal mule deer to 140 days of age during 2006–2008 was 0.33 (SE = 0.091). Survival of young was influenced by the side of the Sierra crest on which a neonate was born (Table 3); survival of west-side neonates averaged 0.13 (SE = 0.092), whereas east-side neonates averaged 0.44 (SE = 0.11). At the individual level, we evaluated the hypothesis that

Table 3. Model-averaged parameter estimates, confidence interval, and Akaike importance weights of factors that influenced survival of neonatal mule deer to 20 weeks of age conducted at the population ($n = 119$), individual ($n = 113$), and maternal ($n = 73$) levels, Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendix A.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	0.98*	0.49	1.47	1.00
	Stage ^a				1.00
Individual	Summer residency	0.33	−0.45	1.10	1.00
	Stage ^a				1.00
	Deviation from mean birth	0.039	-2.8×10^{-3}	0.081	0.68
	Birth mass ^b	0.73*	0.19	1.27	1.00
Maternal	Summer residency \times birth mass ^b	1.19*	0.61	1.78	1.00
	Summer residency	−2.19	−4.64	0.24	1.00
	Stage ^a				1.00
	Birth mass ^b	0.25	−0.34	0.85	1.00
	Summer residency \times birth mass ^b	1.82*	0.84	2.80	1.00
	Mar IFBFat ^c	−0.068	−0.46	0.32	1.00
	Summer residency \times Mar IFBFat ^c	0.39*	0.089	0.68	1.00

^a Stage-specific variable that allowed survival to vary during the first 4 weeks, with constant survival the remaining 16 weeks.

^b Age-specific effect of birth mass on survival during the first 3 weeks of life.

^c Age-specific effect of March ingesta-free body fat (IFBFat) of the mother on survival during 4–20 weeks old.

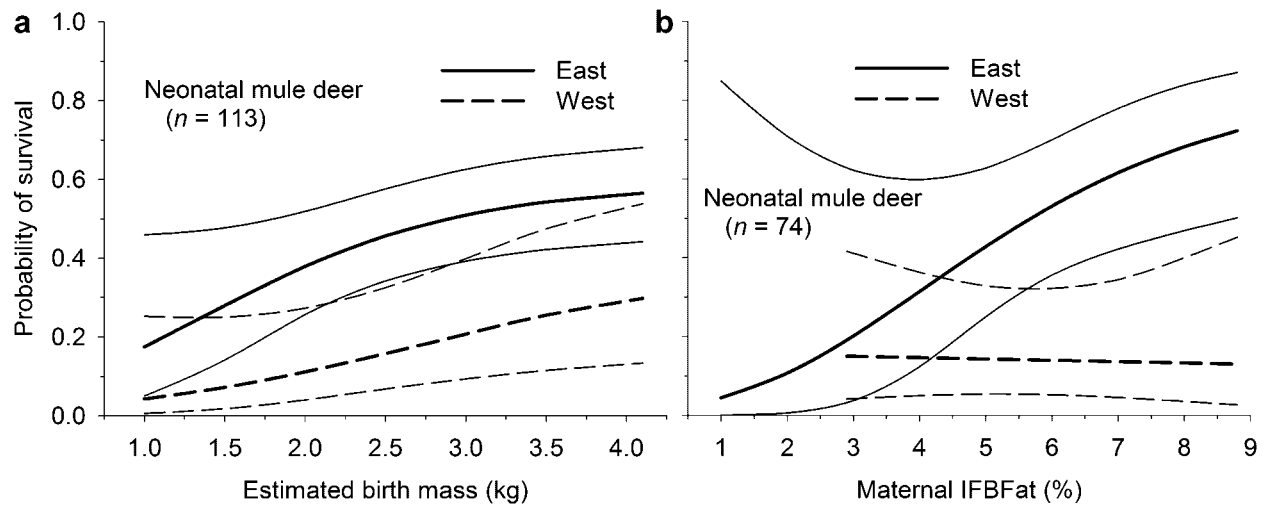


Figure 7. Estimated probability ($\pm 95\%$ CI) of survival of neonatal mule deer from birth to 20 weeks of age during 2006–2008 as a function of estimated birth weight (a), and ingesta-free body fat of the mother in March (b), Sierra Nevada, California, USA. Results are based on best model at the individual level with stage, summer residency, deviation from mean birth, birth mass, and summer residency \times birth mass (a), and at the maternal level with stage, summer residency (east or west), birth mass, summer residency \times birth mass, maternal IFBFat, and summer residency \times maternal March IFBFat (b). We constrained effects of birth mass to weeks 1–3, and effects of maternal IFBFat to weeks 4–20. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

effects of birth mass and nutritional condition of mothers on neonatal survival were age-dependent, with effects of birth mass on survival occurring early in life (<1 month old), and effects of maternal condition being most prominent when lactation demands increase (≥ 4 weeks old). By incrementally adjusting the temporal effect of each covariate and assessing model fit, we determined that birth mass was most influential during the first 3 weeks of life, whereas nutritional condition of the mother (IFBFat) affected survival from 4 weeks to 20 weeks. Nevertheless, the expected positive effect of birth mass and maternal IFBFat was evident only for young mule deer born on the east side of the Sierra crest (as evidenced by significant interactions of summer residency with birth mass and maternal IFBFat; Table 3). For east-side young, individuals that were large at birth and with mothers in good nutritional condition had a greater probability of survival during summer than those born small to mothers in poor nutritional condition (Fig. 7). Those effects were muted (birth mass) or non-existent (maternal IFBFat) for offspring born on the west side of the crest.

Distribution of cause-specific mortality for neonatal mule deer contrasted between the side of the Sierra crest on which an individual was born (Table 4). Neonates born on the west side of the Sierra crest were >6 times more likely to die of predation by black bears (0.72, $SE = 0.093$) than any other cause (Fig. 8). In contrast, the primary cause of mortality for neonates inhabiting the east side was predation by canids and felids (Fig. 8), with low probability of bear predation. At the individual level, the distribution of cause-specific mortality was influenced by birth mass (Table 4); small neonates (<2.0 kg) were most likely to succumb to malnutrition, whereas large neonates (>3.0 kg) had a low probability of dying from malnutrition, while being equally likely to die from either predation or other natural sources of mortality (Fig. 9a). Cause of mortality for neonatal mule deer also changed modestly as individuals grew older (Table 4), albeit the model-averaged parameter estimates overlapped 0. Deaths of neonates from malnutrition and bear predation were most likely to occur within the first 2 weeks of life (Fig. 9b). Conversely, probability of mortality of young caused by other sources of

Table 4. Model-averaged parameter estimates and Akaike importance weights for factors that influence cause of mortality of neonatal mule deer evaluated at the population ($n = 62$), individual ($n = 57$), and maternal levels ($n = 47$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendix B.

Level	Parameter	Cause of mortality ^a			Importance weight
		Bear	Other natural	Other predation	
Population	Summer residency	−2.39*	0.50	1.47	1.00
Individual	Summer residency	−2.67	1.91	2.86	1.00
	Age at death	0.26	0.25	0.25	0.64
	Birth mass	2.21*	3.16*	3.30*	1.00
Maternal	Birth mass	1.96*	2.47*	2.44*	0.98
	Age	3.0×10^{-3}	−0.063	0.21	0.61

^a Multinomial logistic regression included malnutrition as the reference category thus, parameter estimates represent the relative likelihood of dying from a particular cause compared with malnutrition.

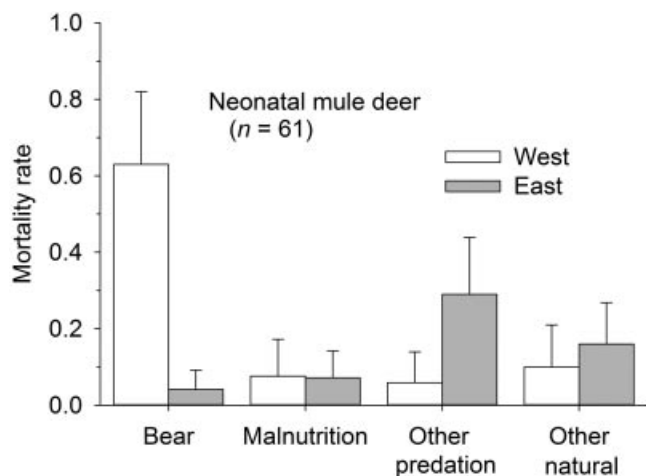


Figure 8. Estimated probability ($\pm 95\%$ CI) of mortality caused by black bear, malnutrition, other forms of predation (canid and felid), and other natural causes (e.g., physical injury, potential disease, drowning) for neonatal mule deer ≤ 20 weeks of age as a function of the side of the Sierra crest occupied in the Sierra Nevada, California, USA, 2006–2008. Results are based on the best model at the population level, which included summer residency as the only influential predictor variable.

predation (mostly canids or felids) increased from birth to 140 days-of-age relative to other causes (Fig. 9b).

Mean estimated birth mass was 2.8 kg ($SE = 0.061$), and ranged from 1.0 kg to 4.1 kg; mass at birth was influenced primarily by litter size (Table 5), and was not influenced strongly by sex (Table 5). From a maternal standpoint, larger litters had lower individual birth mass (Fig. 10a), but greater total litter mass (Fig. 10a). Date of parturition was highly synchronous (based on SD) during 2006 ($SD = 8.0$ days), 2007 ($SD = 8.1$ days), and 2008 ($SD = 6.5$ days), and was 6 days earlier for east-side females (178.6, $SE = 1.18$ days; 28 June) than for females on the west side (184.7, $SE = 1.62$ days; 4 July; Fig. 10). In addition, females with

larger litters gave birth later than those with smaller litters (Fig. 10b; Table 5), and females of larger body mass gave birth earlier than smaller-bodied females (Fig. 11).

Recruitment and Ratios of Young-to-Adult Females

At the population level, autumn recruitment of young mule deer was influenced by summer residency and nutritional condition of adult females in March (Table 6). Recruitment of young was consistently higher for females that summered on the east side ($\bar{x} = 0.70$, $SE = 0.043$) of the Sierra crest than for females on the west side ($\bar{x} = 0.42$, $SE = 0.034$; Fig. 12a). Annual variation in recruitment was influenced positively by mean IFBFat (%) of adult females in March (Fig. 12b). IFBFat (Fig. 13a) and litter size (Fig. 13b) of individual females positively affected autumn recruitment of young (Table 6), indicating that females in better nutritional condition with larger litter sizes yielded more recruits (Table 6). After accounting for the influence of nutritional condition on recruitment, effects of summer residency remained (Table 6), with lower recruitment for west-side compared with east-side females (Fig. 13).

Ratios of young-to-adult females collected in January surveys from 1985 to 2009 were highly variable ($CV = 30.2\%$), averaged 37.9 ($SE = 2.31$), and ranged from 19.3 to 63.0 (Fig. 14a). Percent IFBFat of females in the current March and that of the preceding March were positively related to age ratios at the end of the calendar year (Fig. 14b). Mean IFBFat of females in the current March ($\beta = 3.2$) had a stronger positive effect than mean IFBFat from the preceding year ($\beta = 2.3$), although their parameter estimates were not significantly different (Table 6). Predicted ratios of young-to-adult females dropped below the 24-year average of 37.9 when mean IFBFat of females in March was $< 5.7\%$ (95% CI: 3.5–6.5%), and mean March IFBFat of the preceding year was held constant at the long-term average. Notably, correlation of mean March IFBFat between successive years was low ($r = 0.29$).

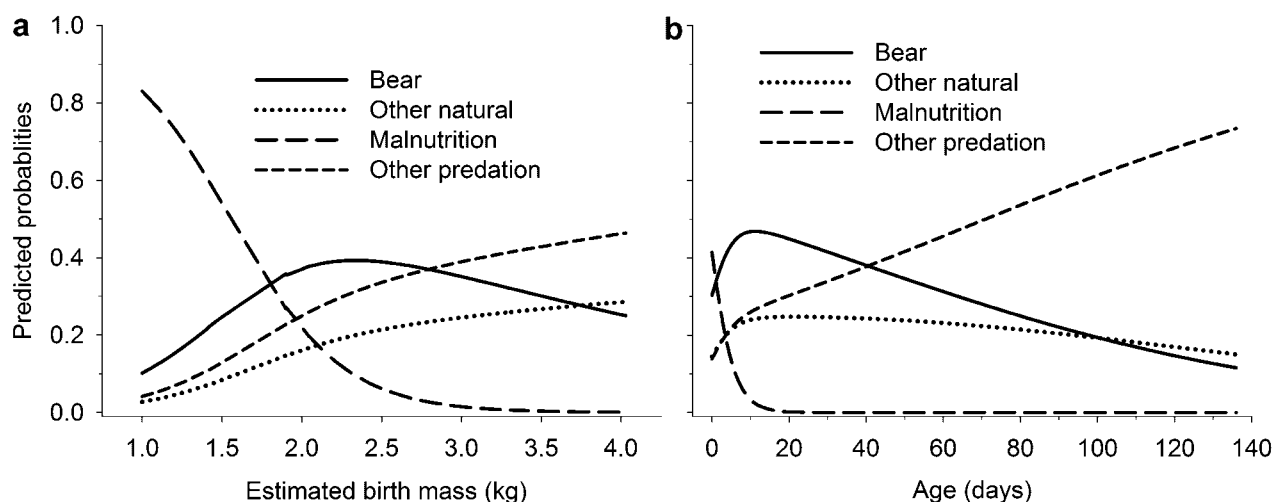


Figure 9. Estimated probability of mortality caused by black bear, malnutrition, other forms of predation (canid and felid), and other natural causes (e.g., physical injury, potential disease, drowning) for neonatal mule deer ≤ 20 weeks of age as a function of estimated birth weight (a) and age (b) in the Sierra Nevada, California, USA, 2006–2008. Predicted probabilities of mortality represent the relative likelihood of a neonate dying from a particular cause given that the deer dies. Results are based on the best model at the individual level, which included summer residency, age at death, and birth weight. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean. We removed confidence intervals for ease of interpretation.

Table 5. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced birth characteristics of adult (>1 yr) female mule deer at the population and maternal levels, Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices C and D.

Response	Level	Parameter	Estimate	90% CI		Importance weight
				Lower	Upper	
Birth mass	Individual	Litter size	−0.21*	−0.37	−0.055	0.82
	Maternal	Litter size	−0.37*	−0.60	−0.14	0.93
		Mar IFBFat	−0.051	−0.01	6.0×10^{-4}	0.56
Julian birth	Population	Summer residency	−4.08*	−7.22	−0.94	0.98
		Mean Mar IFBFat	−0.82	−2.27	0.63	0.51
		Litter size	2.93*	0.74	5.12	0.97
	Maternal	Summer residency	−5.48*	−8.45	−2.52	1.00
		Mean Mar IFBFat	−1.53	−3.83	0.77	0.88
		Litter size	5.86*	3.10	8.63	1.00
		Age	0.20	−0.15	0.56	0.58
		Mar IFBFat	−0.13	−0.56	0.30	0.56
		Mar body mass	−0.36*	−0.65	−0.073	0.99

IFBFat, ingesta-free body fat.

Pregnancy and Fetal Rate

Thirty-two percent of yearling females (1.5-yr-old) that we monitored failed to attain pregnancy at 1.5 years of age, but all that survived became pregnant the following autumn. Although

our sample size for yearling females was small ($n = 22$), probability of primiparity as a yearling was influenced positively by per capita snowpack during their second summer of growth before rut in autumn (Table 7, Fig. 15a). Unfortunately, logistical constraints precluded us from directly assessing the effect of body mass during November when young females potentially were bred. For adult females (≥ 2 -yr-old), body mass in March was related ($r^2 = 0.35$, $F_{1,252} = 136.0$, $P < 0.001$) to November body mass; body mass of yearling females in March likely provided a surrogate for their body mass in November. At the individual level, March body mass was the most parsimonious explanation for probability of pregnancy for yearling females (Table 7). Yearling females that were >41 kg in March had a >0.90 (95% CL: 0.50–0.99) probability of having conceived the previous autumn (Fig. 15b).

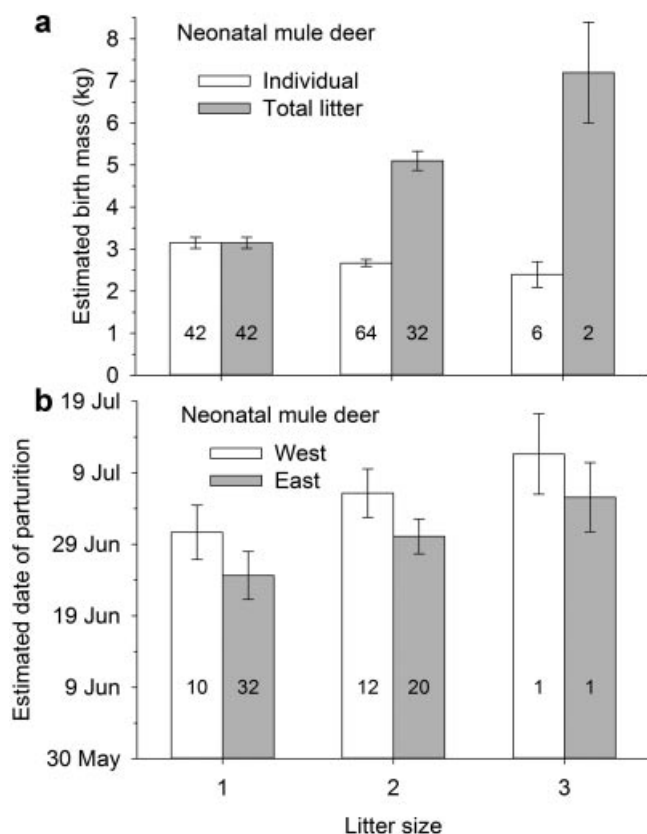


Figure 10. Average individual birth mass and total litter mass relative to litter size (a) and estimated effect ($\pm 95\%$ CI) of litter size on estimated date of parturition (b) for adult (>1 yr) female mule deer, Sierra Nevada, California, USA, 2006–2009. Results are based on the best model at the population level, which included summer residency (east or west), per capita snowpack, mean March ingesta-free body fat (IFBFat), and litter size for date of parturition (b). Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean. Numbers within bars represent sample sizes for each group.

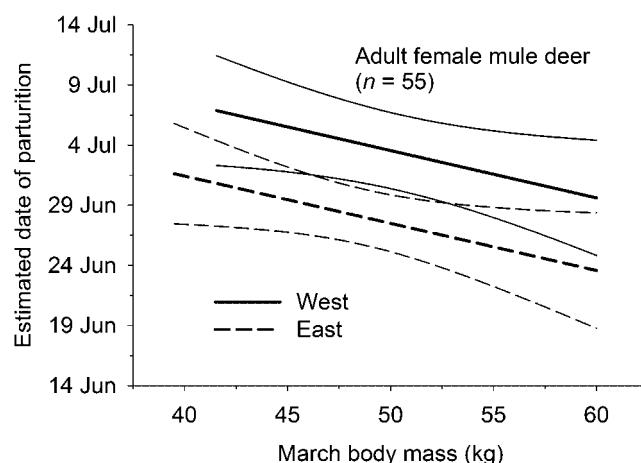


Figure 11. Estimated effect ($\pm 95\%$ CI) of March body mass of adult (>1 yr) female mule deer relative to side of the Sierra crest occupied during summer on estimated date of parturition, Sierra Nevada, California, USA, 2006–2009. Results are based on the best model at the maternal level, which included summer residency, mean March ingesta-free body fat (IFBFat), litter size, age, March IFBFat, and March body mass. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

Table 6. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced age ratios and individual recruitment of young for mule deer, Sierra Nevada, California, USA, 1991–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices E and F.

Response	Level	Parameter	Estimate	90% CI		Importance weight
				Lower	Upper	
Recruitment	Population	Summer residency	0.27*	0.18	0.36	1.00
		Per capita snowpack	5.44	−1.22	12.10	0.96
		Mean Mar IFBFat	0.090*	0.032	0.15	0.84
	Individual	Summer residency	0.35*	0.25	0.45	1.00
		Per capita snowpack	2.30	−3.66	8.27	0.88
		Mar IFBFat	0.025*	3.9×10^{-3}	0.046	0.83
		Litter size	0.12*	9.3×10^{-3}	0.23	0.94
		Mar weight	7.3×10^{-3}	-3.3×10^{-3}	0.018	0.92
Age ratio	Population	Mean Mar IFBFat _{t-1}	2.28*	1.12	3.53	0.99
		Mean Mar IFBFat _t	3.21*	1.89	4.50	1.00
		Mean Mar body mass	−0.41	−1.52	0.70	0.72
		Mean litter size	2.89	−27.43	33.22	0.99
		Per capita snowpack	44.61	−132.33	221.58	0.78
		Summer precipitation	0.29	−1.20	1.78	0.75
		Summer temperature	−5.58	−11.41	0.24	0.97

IFBFat, ingesta-free body fat.

Fetal rate of females ≥ 2.5 years old during 1997–2009 was 1.69 (SE = 0.027), and ranged from 1.57 (SE = 0.065) in 2001 to 1.91 (SE = 0.053) in 1999 (Fig. 16). In addition, litter size varied as a function of per capita snowpack and summer temperature (Table 7). Per capita snowpack had a positive effect on litter size (Fig. 17), whereas summer temperature had a negative influence. At the individual level, litter size was not related to age, November body mass, or nutritional condition (Appendix H). Nonetheless, females residing on the west side (1.72, SE = 0.026) had larger litter sizes than females that summered on the east side of the Sierra crest (1.59, SE = 0.031; Table 7). Notably, inclusion of yearlings in the sample for litter size resulted in a significant effect of age and November body mass, which were not influential when only females ≥ 2.5 years old were considered.

Pregnancy of females ≥ 2.5 years old during 1997–2009 was relatively constant at 0.98 (SE = 0.006; Fig. 16), despite

substantial variation in nutritional condition during those years (Fig. 5). Initial models that included yearlings indicated pregnancy varied as a curvilinear function of age; however, that pattern was dictated by variable pregnancy among yearlings. After removing yearlings from the analysis we considered summer residency, per capita snowpack, summer precipitation, summer temperature, mean November IFBFat, and year at the population level, and age, age², November IFBFat, and November body mass at the individual level. No single variable at the population or individual levels influenced probability of pregnancy for females ≥ 2.5 years old, despite an adequate sample size ($n = 803$; Table 7).

Seasonal Survival of Adult Females

We conducted a separate survival analysis that included only prime-aged females (2–9 yrs old) before evaluating factors that

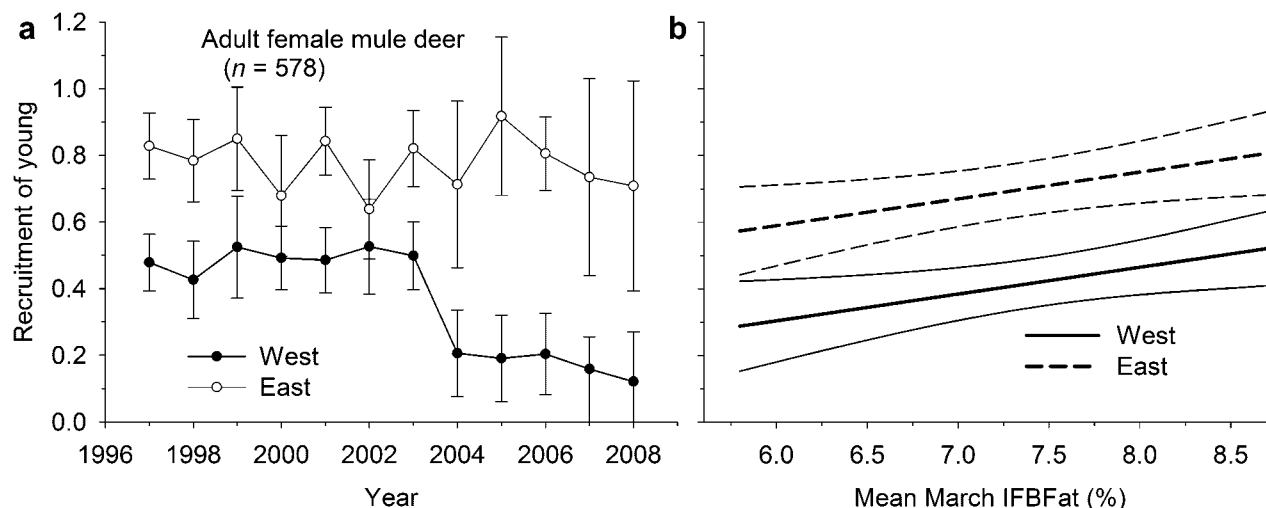


Figure 12. Annual average (\pm SE) recruitment of young in autumn (a) and predicted effect (\pm 95% CI) of mean ingesta-free body fat (IFBFat) of female mule deer in March on number of young recruited in autumn (b) by adult (>1 yr) female mule deer relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Effect of mean IFBFat is based on the best model at the population level, which included summer residency, per capita snowpack, and mean March IFBFat.

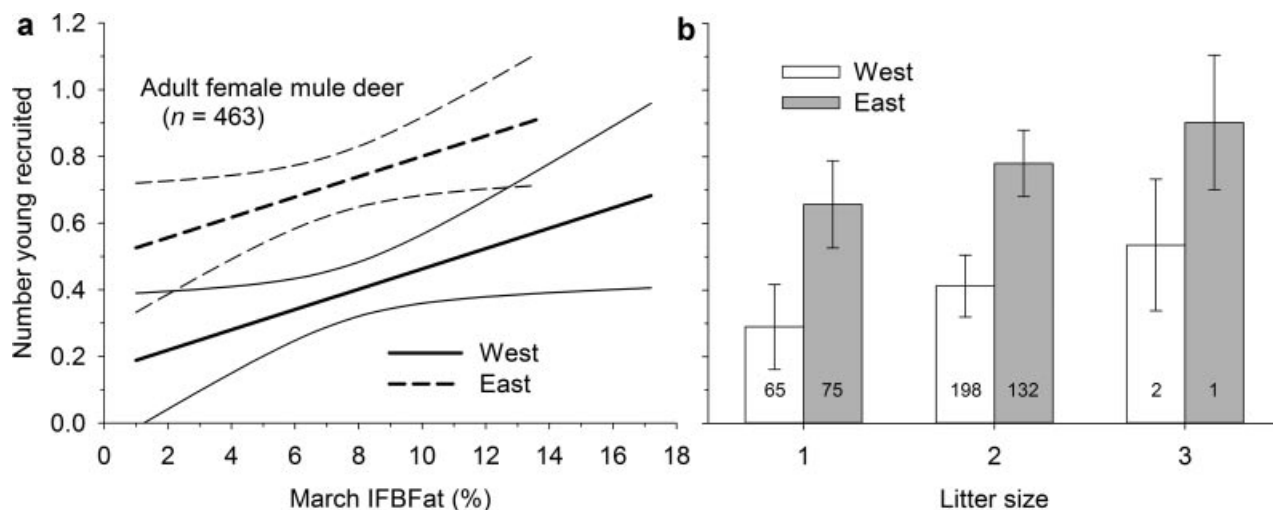


Figure 13. Estimated effect ($\pm 95\%$ CI) of percent ingesta-free body fat (IFBFat) of individual females in March (a) and number of young in utero in March (b) on number of young recruited in autumn by adult (>1 yr) female mule deer relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the maternal level, which included summer residency, per capita snowpack, litter size, March body mass, and March IFBFat. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean. Numbers within bars represent sample sizes for each group.

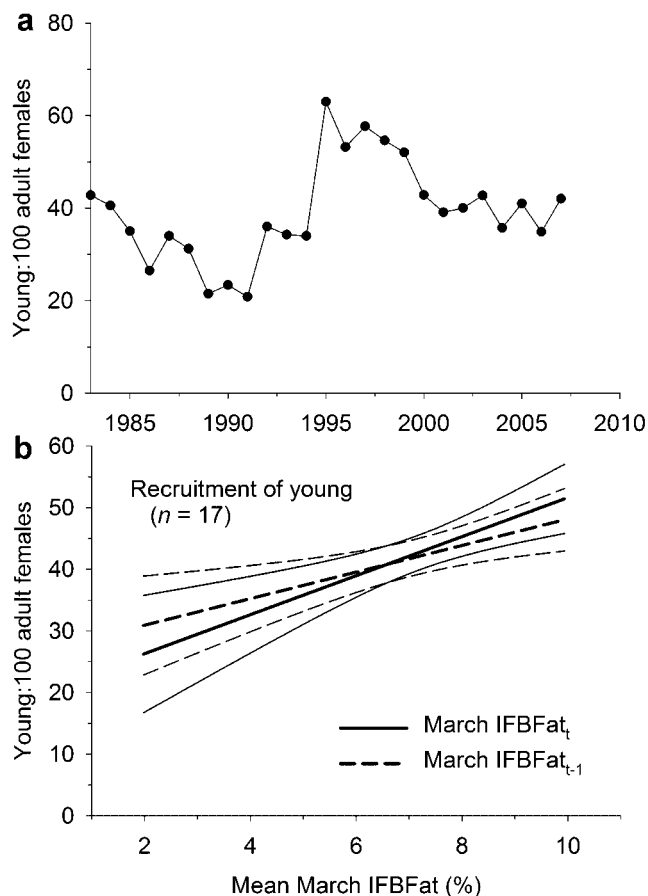


Figure 14. Annual estimates of recruitment of young from surveys conducted in January (a) and estimated effect ($\pm 95\%$ CI) of mean ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer during the current (t) and preceding ($t-1$) March on annual herd composition of young (<1 yr):100 adult females the following January (b), Sierra Nevada, California, USA, 1991–2008. Results for recruitment of young are based on the best model, which included per capita snowpack, mean March IFBFat_t, mean March IFBFat_{t-1}, mean litter size, mean March body mass, summer precipitation, and summer temperature. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

affected seasonal survival to obtain seasonal and annual estimates of survival during 1998–2008. Estimates of summer survival for prime-age females ranged between 0.76 and 1.0, with a mean of 0.90 ($SE = 0.021$; Fig. 18a). Overwinter survival of prime-age females averaged 0.94 ($SE = 0.012$) and ranged between 0.87 and 1.0 (Fig. 18b). Mean annual survival of prime-age females was 0.87 ($SE = 0.025$) with minor variation among years ($CV = 9.6\%$; Fig. 18c).

Summer survival among years for adult females was related to the previous April snowpack and the number of females estimated in the population (Table 8). Models of survival for adult females during summer that included April snowpack and estimated number of females as separate variables performed better ($\Delta AIC_c > 2$) than combining the 2 variables into per capita snowpack; the relationships, however, remained in the expected direction (Fig. 19). Estimated number of females in the population had a stronger negative effect on summer survival, compared with the positive effect of winter snowpack (Fig. 19). Mean IFBFat of adult females in March was positively related to annual patterns of survival in summer for adult females, and was significant for analyses at the individual level (Table 8). In contrast, summer residency had no effect on summer survival of adult females (Appendix I).

Winter survival of adult females varied by month, and interannual patterns varied as a function of per capita snowpack (Table 8). Probability of overwinter survival increased with per capita snowpack (Fig. 20a), but was not affected by previous summer residency (Appendix J). At the individual level, body mass in November had a positive effect on overwinter survival, with heavier females having a greater probability of surviving winter than lighter ones (Fig. 20b). Levels of IFBFat for individual females in March or November did not influence survival in summer or winter significantly (Appendices I and J).

Probability of survival during summer and winter declined with age (Table 8). Adult females were progressively less likely to survive winter as they grew older (Fig. 21b). Probability of

Table 7. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced reproduction of yearling (1.5 yr) and adult female (≥ 2.5 yr) mule deer at the population and individual levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices G, and H.

Response	Level	Parameter	Estimate	90% CI		Importance weight
				Lower	Upper	
Yearling primiparity	Population	Per capita snowpack	92.86*	3.58	182.12	0.64
	Individual	Mar body mass _{<i>t-1</i>} ^a	0.51*	0.044	0.98	0.91
Litter size	Population	Summer residency	-0.11*	-0.17	-0.043	0.88
		Per capita snowpack	2.95*	0.96	4.95	1.00
		Summer temperature	-0.042	-0.058	-8.1×10^{-3}	0.68
	Individual	Summer residency	-0.11*	-0.18	-0.050	0.92
		Per capita snowpack	4.12*	1.98	6.13	0.93
		Summer temperature	-0.031*	-0.062	-1.2×10^{-4}	0.63
Pregnancy		None				

^a We used March body mass of the previous year ($t-1$) because sample size ($n=7$) was insufficient for November body mass.

surviving an average winter for females 9.5 years old was 0.89 (Fig. 21b), declining to approximately 0.60 at 15.5 years of age. Although survival of females during summer also declined with age, the parameter estimate for age² was positive, indicating the additional mortality with each year of age declined as females grew older (Fig. 21a). On an annual basis, probability of survival declined as a curvilinear function of age (Fig. 21c).

For adult females during summer, mortalities for which we could determine cause of death included cougar predation ($n=13$), canid or ursid predation ($n=11$), accidents ($n=15$; comprised of deer-vehicle collisions, illegal harvest, dystocia, and drowning), and malnutrition ($n=3$). During winter, causes of mortality included cougar predation ($n=32$), coyote predation ($n=12$), malnutrition ($n=7$), and accidents ($n=7$; comprised of deer-vehicle collisions and poaching). Small sample sizes and a large proportion of undetermined causes of death precluded a rigorous analysis of cause-specific mortality; however, during summer the most common cause of mortality for females on the east side of the Sierra crest was accidents (0.52; mostly deer vehicle collisions) compared with cougar predation (0.45) for west-side females. During winter, the most common source of

mortality for both east-side (0.53) and west-side (0.43) females was cougar predation, followed by malnutrition (east = 0.27, west = 0.21).

Nutritional Condition, Body Mass, and Life-History Characteristics

Mean IFBFat of adult female mule deer in March during 1997–2009 was 7.22% (SE = 0.077), and ranged from 4.98% (SE = 0.27) in 2009 to 8.74% (SE = 0.27) in 1999 (Fig. 5). For individual females, IFBFat ranged from 1.0% to 17.1%. At the population level, March IFBFat varied as a function of summer residency, per capita snowpack, mean IFBFat the previous March, and winter precipitation (Table 9). Per capita snowpack had a positive influence on IFBFat of adult females in March (Fig. 22a). Females that summered on the west side of the Sierra crest (7.46%, SE = 0.10) maintained higher levels of IFBFat through winter compared with females that summered on the east side (6.92%, SE = 0.11). Mean IFBFat of adult females during March of the previous year exhibited a strong, positive relationship with IFBFat of females the following year (Fig. 22b). In contrast, at the individual level, IFBFat of a female

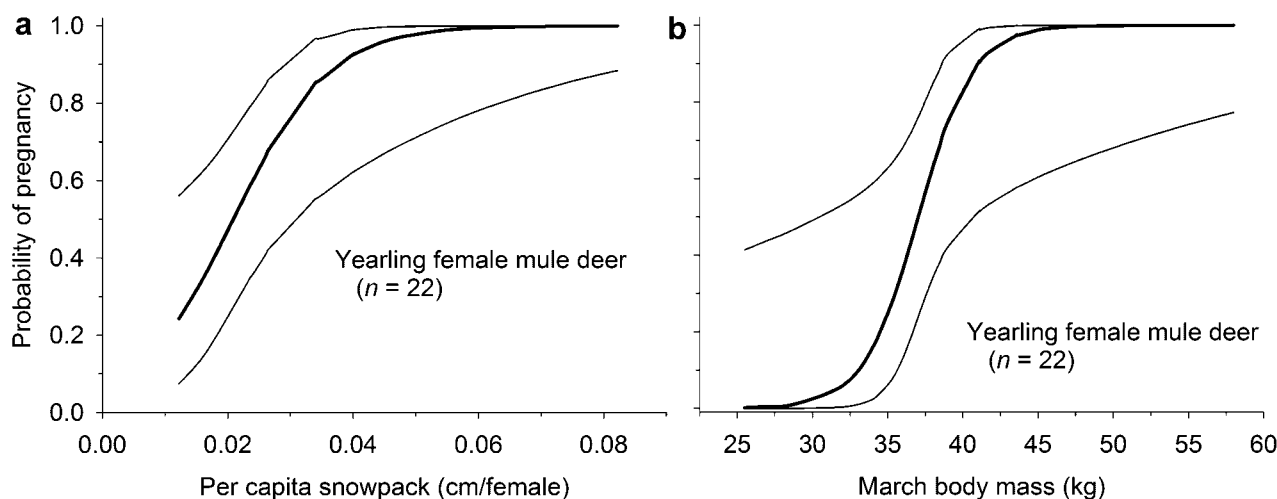


Figure 15. Estimated probability ($\pm 95\%$ CI) of pregnancy for yearling (1.5 yr) female mule deer as a function of per capita snowpack (a) and March body mass (b) in the Sierra Nevada, California, USA, 1997–2009. Results are based on the best model, which included per capita snowpack at the population level (a), and body mass at the individual level (b).

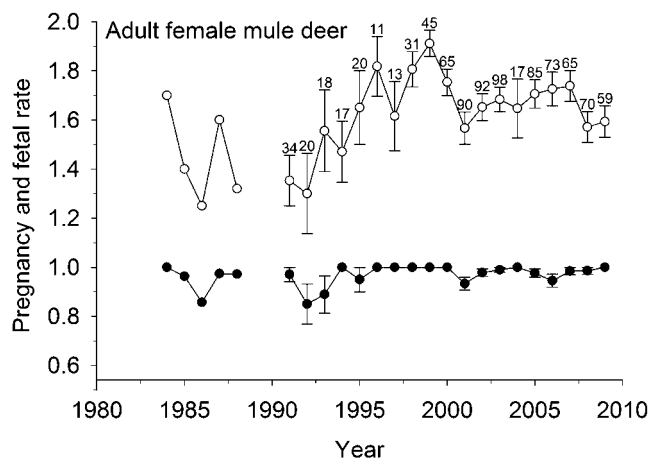


Figure 16. Annual pregnancy (solid circles \pm SE) and fetal rate (hollow circles \pm SE) of adult female mule deer in March on a winter range in Round Valley, Inyo County, California, USA. We determined reproductive variables by deer collections before 1997 and ultrasonography thereafter. We obtained point estimates before 1997 from Kucera 1992 and Pierce et al. (2012), and those following 1997 were from adult females (≥ 2.5 yr) monitored in this study. Sample sizes for fetal rates are displayed above means.

in March had little effect on her IFBFat in March the following year (Appendix K). Percent IFBFat of an individual female in November, however, carried over winter and had a positive effect on her IFBFat in March (Fig. 23a). Litter size was positively related to IFBFat of individual female deer in March (Table 9), indicating that females with larger litters had higher fat levels. In addition, March IFBFat declined linearly with age (Fig. 23b).

Annual variation in body mass of adult female deer (CV = 2.97%) was markedly less than for IFBFat (CV = 15.03%) during March 1997–2009. Body mass during March averaged 48.5 kg (SE = 0.18) and ranged from 47.1 kg (SE = 0.51) in 2000

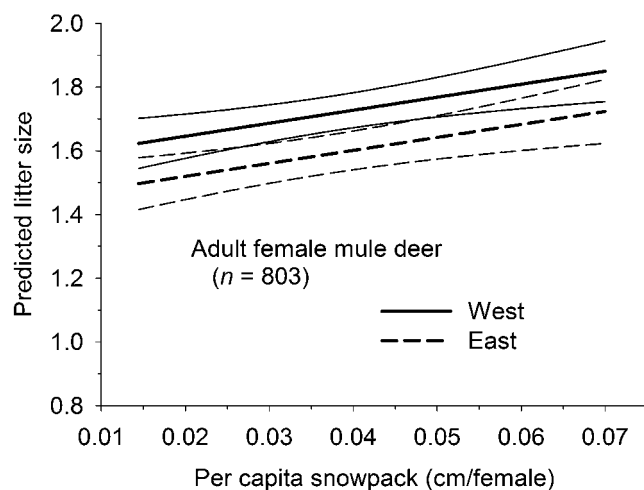


Figure 17. Estimated litter size ($\pm 95\%$ CI) for adult (≥ 2.5 yrs) female mule deer as a function of per capita snowpack relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2009. Results are based on the best model, which included summer residency (east or west), per capita snowpack, and summer temperature at the population level. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

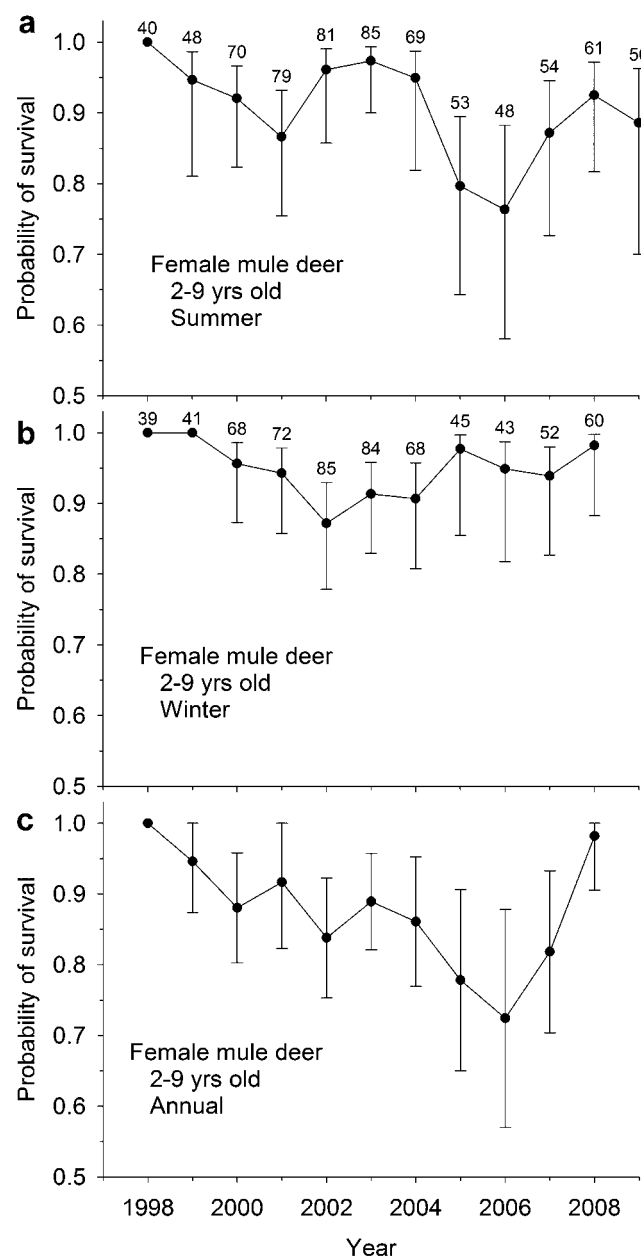


Figure 18. Estimates ($\pm 95\%$ CI) of summer (a; May–Oct), winter (b; Nov–Apr), and annual (c; May–Apr) survival of prime-aged (2–9 yr) female mule deer in the Sierra Nevada, California, USA. Seasonal sample sizes are displayed above estimates.

to 50.4 kg (SE = 0.61) in 2006. Among individual adult females, body mass in March ranged from 25.5 kg to 68.9 kg. At the population level, body mass of adult females varied as a function of summer residency and positively with winter temperature (Table 9). On average, females that summered on the west side (49.0 kg, SE = 0.23) of the Sierra crest during summer were heavier than east-side females (47.9 kg, SE = 0.21 kg). Individual females exhibited a curvilinear pattern of body mass with respect to age in March (Table 9), with middle-aged (6- to 12-yr) females being heaviest (Fig. 24b). In addition, IFBFat of individual female deer in March had a positive effect on body mass (Table 9), indicating that after accounting for effects of

Table 8. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced summer (Apr–Oct) and winter (Nov–Mar) survival of adult (>1 yr) female mule deer at the population ($n = 944$ and 1037, respectively) and individual ($n = 830$ and 574, respectively) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices I and J.

Response	Level	Parameter	Estimate	90% CI		Importance weight
				Lower	Upper	
Adult summer	Population	Snowpack	0.011*	1.2×10^{-3}	0.020	0.72
		Number female	-2.7×10^{-3} *	-3.9×10^{-3}	-1.5×10^{-3}	0.94
		Mean Mar IFBFat	0.18	-6.9×10^{-4}	0.361	0.66
	Individual	Snowpack	0.014*	2.4×10^{-3}	0.025	0.80
		Number female	-2.3×10^{-3} *	-3.7×10^{-3}	-8.5×10^{-4}	0.98
		Mean Mar IFBFat	0.26*	0.036	0.49	0.79
		Age	-0.60*	-1.10	-0.11	1.00
		Age ²	0.023	-4.7×10^{-3}	0.052	1.00
Adult winter	Population	Per capita snowpack	50.72*	21.37	80.12	1.00
		Month				0.97
	Individual	Per capita snowpack	31.54*	1.89	61.08	0.74
		Month				1.00
		Age	-0.24*	-0.345	-0.15	1.00
		Nov body mass ^a	0.064*	0.015	0.11	0.86

IFBFat, ingesta-free body fat.

^a Results obtained from a separate set of models using a subset of data ($n = 334$) during 2002–2008.

summer residency and age on body mass, females in better nutritional condition were generally heavier (Fig. 24a).

Mean IFBFat of adult female mule deer in November during 2002–2008 was 9.7% (SE = 0.23), and ranged from 8.4% (SE = 0.57) in 2007 to 11.0% (SE = 0.68) in 2005, whereas IFBFat of individual females in November ranged from 1.0% to 24.3%. At the population level, November IFBFat varied as a function of summer residency, per capita snowpack, and summer precipitation (Table 10). West-side females (11.10%, SE = 0.30) had greater IFBFat in autumn (Table 10, Fig. 25a) compared with east-side females (8.32%, SE = 0.30). Total summer precipitation and per capita snowpack had similar, positive influences on IFBFat of adult females in November (Fig. 25). Mean IFBFat the preceding March had a positive influence on IFBFat in November at the individual level after we accounted

for variation of IFBFat in November explained by other individual covariates (Table 10). Percent IFBFat of individual females in March was less influential than mean IFBFat (Table 10), likely because individual recruitment status in November had an overriding influence on nutritional condition of females in autumn (Table 10). Number of young recruited had a strong negative effect on IFBFat of adult females in November (Fig. 26); however, the effect of summer residency remained significant (Table 10). Adult females summering on the east side of the Sierra crest had lower IFBFat in November with respect to number of young recruited compared with females summering on the west side of the Sierra crest (Fig. 26a).

Mean body mass of adult females in November was 52.2 kg (SE = 0.36), and ranged from 49.2 kg (SE = 0.93) in 2007 to 55.7 kg (SE = 0.89) in 2005, whereas body mass of individual

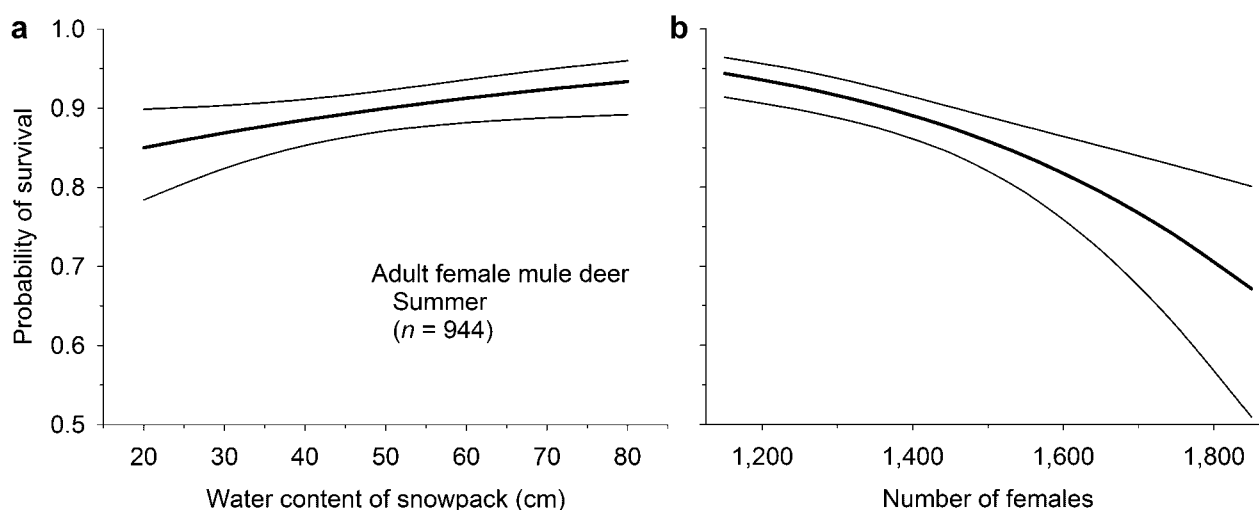


Figure 19. Estimated probability ($\pm 95\%$ CI) of summer survival of adult (>1 yr) female mule deer as a function of the water content of the April snowpack (a), and the estimated number of adult females in the population during January (b), Sierra Nevada, California, USA. Results are based on the best model at the population level, which included April snowpack, number females, and mean March ingesta-free body fat (IFBFat).

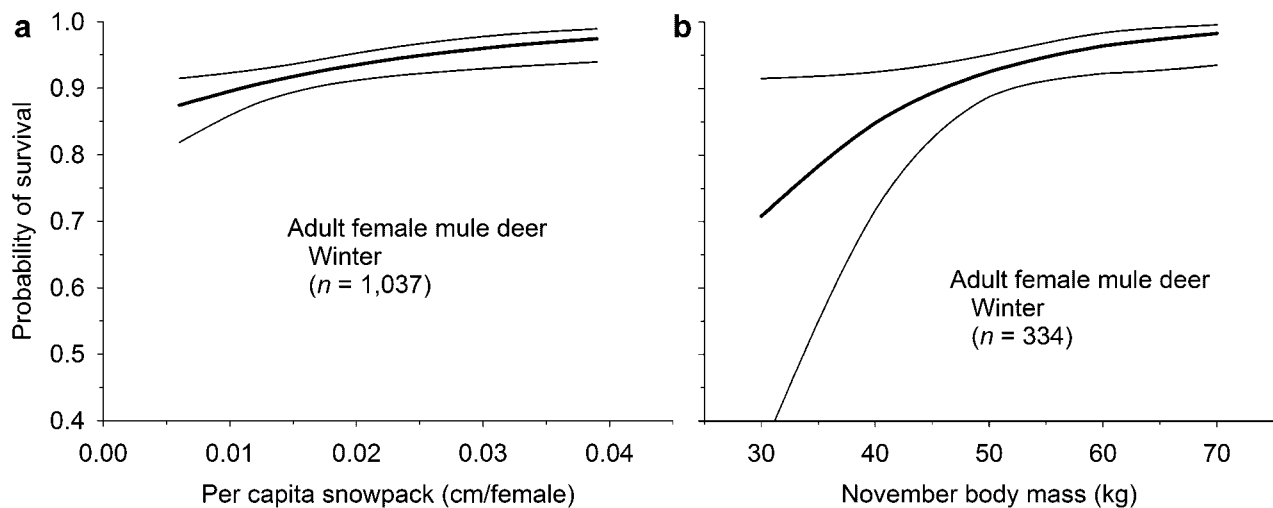


Figure 20. Estimated probability ($\pm 95\%$ CI) of winter survival of adult (>1 yr) female mule deer as a function of per capita snowpack at the population level (a), and November body mass at the individual level (b), 1998–2008, Round Valley, Inyo County, California, USA. Results are based on the best model at the population level, which included per capita snowpack, monthly temperature, and Month (a), and at the individual level, which included per capita snowpack, month, age, and November body mass (b). Predictions represent expected effects of the variable of interest (x-axis) within the range we observed, while holding all other variables constant at their mean.

adult (>1 yr old) females ranged from 20.8 kg to 70.2 kg. Females that resided on the west side of the crest during summer (54.2 kg, $SE=0.40$) were heavier than east-side females (50.0 kg, $SE=0.52$; Table 10). Summer precipitation had a positive effect on November body mass, whereas summer temperature had a negative effect on November mass (Table 10). At the individual level, November body mass of adult females varied as a function of age, IFBFat, and recruitment status. Females that had higher levels of IFBFat in November were generally heavier than those with lower IFBFat after accounting for age-specific patterns (Fig. 24c). Similar to March body mass, November body mass exhibited a curvilinear relationship with age (Fig. 24d); however, the senescent pattern of declining body mass was not as pronounced in autumn compared with late winter (Fig. 24b). In addition, albeit not significant, recruitment status was related negatively (importance weight = 1.0) to body mass of females in November (Table 10).

Finite Rate of Increase

The most parsimonious explanation for annual population growth of mule deer (λ) was a single variable that represented nutritional condition of adult females in March of the current year (importance weight = 0.79). Therefore, we conducted an additional analysis using simple linear regression, which supported a positive relationship between March IFBFat and λ ($\lambda = 0.63 + 0.055 \times \text{IFBFat}$; $r^2 = 0.32$, $P = 0.018$). Increasing mean IFBFat of adult females in March above 6.7% (95% CI: 3.6–8.6%) resulted in a predicted increase in total population size of mule deer in Round Valley during the following year (Fig. 27). Predicted λ ranged from 0.74 (95% CI: 0.49–0.99) at 2.0% IFBFat, to 1.18 (95% CI: 1.04–1.31) at 9.4% IFBFat, based on the range in IFBFat that we observed during 1991–2009. One data point in 1993, when the population had low IFBFat and experienced a decline ($\lambda = 0.84$; Fig. 27), potentially had a strong influence on those results (leverage = 0.59). Removing that datapoint, however, had little influence

on the relationship ($\lambda = 0.51 + 0.07 \times \text{IFBFat}$; $r^2 = 0.26$, $n = 16$, $P = 0.045$) or the point at which $\lambda = 1$ (IFBFat = 7.0%). Because our post-1991 dataset was somewhat sparse with IFBFat values $<7\%$ (Fig. 27), we also included data on IFBFat and λ during the population crash (1985–1991) to further examine this relationship. The relationship remained positive and significant ($\lambda = 0.62 + 0.052 \times \text{IFBFat}$; $r^2 = 0.30$, $n = 21$, $P = 0.011$), with a slight adjustment in the IFBFat level when $\lambda = 1.0$ (IFBFat = 7.3%); both analyses support the robustness of the relationship.

Nutritional Potential for Recruitment

To estimate the nutritional potential for recruitment (Fig. 4), we included mean March IFBFat during the current and preceding year, mean litter size, per capita snowpack, summer precipitation, and summer temperature for age ratios, because those variables potentially reflected the nutritional capacity to support allocation of resources to provisioning offspring (Table 6). For individual recruitment models, we included mean March IFBFat and summer residency; however, we removed the effects of summer residency ($\beta = -0.28$) on females residing on the west side of the Sierra crest (by subtracting out its effect), because that variable largely reflected increased predation (i.e., a negative effect) on young born on the west side rather than a positive effect from better nutrition available to west-side females.

Annual variation in patterns of ratios of young-to-adult females was similar to that predicted based on the nutritional state of the population. Residuals indicated that during 1992–2009, overall mortality of young at the level of the population was largely compensatory (Fig. 28), except during the early 2000s, when mortality of young was likely beginning to have an additive effect on population growth, as evidenced by young-to-female ratios that were less than the predicted nutritional capacity for females to recruit young (Fig. 28). A slightly different pattern emerged when we considered the influence of migratory tactic on patterns of recruitment. Observed recruitment for females summering on the east side was similar to that predicted based on nutritional

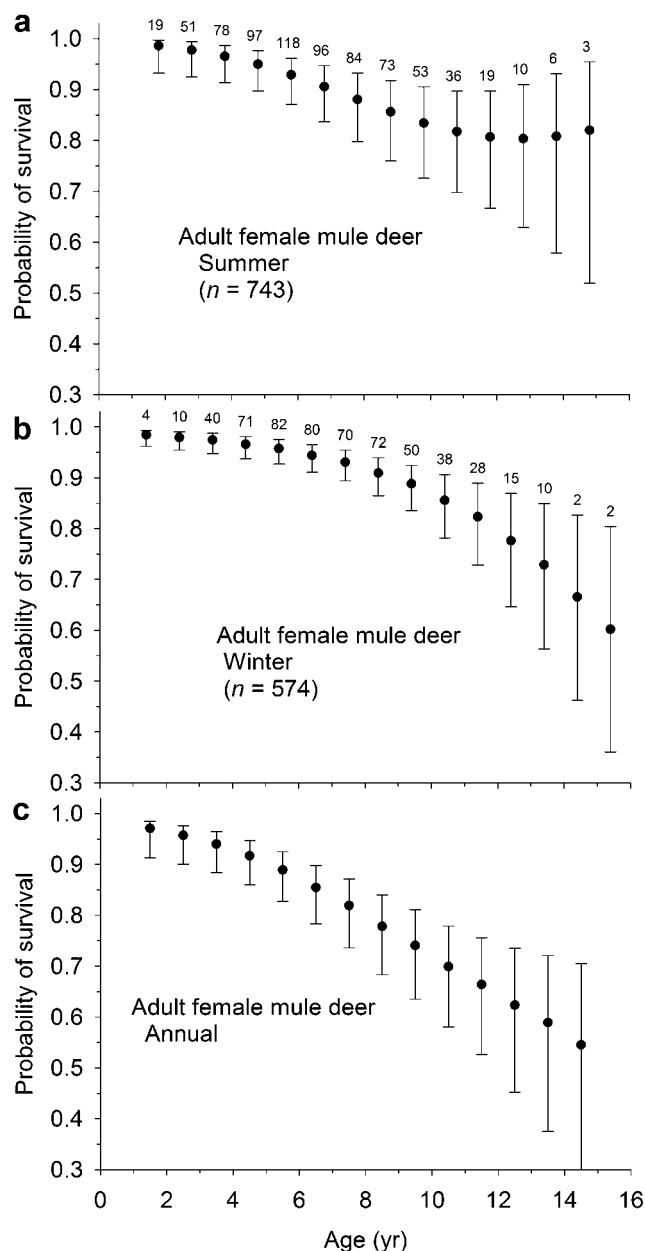


Figure 21. Estimated probability ($\pm 95\%$ CI) of summer (a), winter (b), and annual (c) survival of adult (>1 yr) female mule deer as a function of age in the Sierra Nevada, California, USA. Results are based on the best model at the individual level, which included snowpack, number females, mean March ingesta-free body fat (IFBFat), age, and age² for summer (a); per capita snowpack, age, month, and November body mass for winter (b); and the product of summer and winter survival within age classes using the delta method for annual survival (c). Predictions represent expected effects of the variable of interest (*x*-axis) within the range we observed, while holding all other variables constant at their mean. Sample sizes are indicated above error bars.

capacity; thus, mortality was largely compensatory (Fig. 29a). Conversely, for west-side females, recruitment residuals often were lower than nutritionally based predictions, indicating that at least some mortality was additive (Fig. 29b). The difference between the nutritional potential and realized recruitment for west-side females (Fig. 29b) indicated that average amount of additive mortality during 1997–2008 was 0.30 young per female per year.

DISCUSSION

Our long-term, longitudinal investigation of individual mule deer in the central Sierra Nevada revealed that nutritional condition at the population, individual, and maternal levels provided the necessary framework for understanding factors regulating population growth. Nutritional condition of female mule deer was sensitive to environmental stochasticity and density-dependent processes. The influence of nutritional condition on fitness components of mule deer mostly supported the paradigm of sensitivity to resource limitation expected for large herbivores (Fig. 1; Table 11), indicating that nutrition serves as an underlying foundation for life-history characteristics in large herbivores.

The carryover of nutritional relationships from previous seasons and years, which also may interact with migratory status, presents a difficult obstacle to overcome for research and monitoring programs that focus solely on demography and mortality factors to address population status. Demographic relationships, even when accompanied with information on cause-specific mortality, can be deceptive when nutritional status is unknown, because observed patterns may reflect previous, rather than current, environmental conditions (Testa 2004, Monteith et al. 2009). Nutritional condition at the level of the population provided a metric for assessing habitat adequacy relative to population density, and was related to finite rate of population growth. At the individual level, nutritional condition had implications for fitness and tradeoffs in life-history strategies that, in turn, determined the nutritional state of an individual transitioning between seasons. Along with a growing body of literature (Franzmann 1985; Cook et al. 2004, 2013; Bowyer et al. 2005; Parker et al. 2009; Pierce et al. 2012), our results provide additional support for the notion that nutritional condition, when considered in concert with other life-history and population characteristics, is an ecological indicator of critical importance for research, conservation, and management of large herbivores.

Long-term studies are essential to understanding natural processes that develop slowly and are highly variable and complex, and for evaluating ecological concepts and theoretical hypotheses, especially for long-lived, iteroparous mammals (Lindström 1999, Gaillard et al. 2000, Bleich et al. 2006, Clutton-Brock and Sheldon 2010). Short-term studies can be misleading and yield entirely different conclusions compared with more lengthy research (McCullough 1990, Kie et al. 2003, Monteith et al. 2009, Pierce et al. 2012). Long-term study (>20 yr) of a population of mule deer in the Sierra Nevada allowed us to capture variation in fitness components during disparate trajectories of population growth and intensities of predation (Kucera 1991, 1997; Bowyer et al. 2005; Pierce et al. 2012).

Conducting long-term research presents other challenges including the integration of new technology and improved techniques with older methodologies. In our study area before 1997, data on nutritional condition of adult females were obtained via culling and estimating body fat from kidney-fat indices. Beginning in 1997, we employed ultrasonography, which allowed in vivo estimation of IFBFat, and longitudinal monitoring of individual deer. We estimated IFBFat from

Table 9. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced ingesta-free body fat (IFBFat) and body mass of adult (>1 yr) female mule deer in March at the population ($n = 842$ and 828 , respectively) and individual ($n = 531$ and 517 , respectively) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices K and L.

Response	Level	Parameter	Estimate	90% CI		Importance weight
				Lower	Upper	
Mar IFBFat	Population	Summer residency	−0.50*	−0.73	−0.26	1.00
		Per capita snowpack	45.23*	30.69	59.77	1.00
		Mean Mar IFBFat _{<i>t</i>−1}	0.51*	0.36	0.66	1.00
		Winter precipitation	−0.28*	−0.35	−0.21	1.00
	Individual	Mean Mar IFBFat _{<i>t</i>−1}	33.07	−2.54	68.67	0.99
		Per capita snowpack	0.74*	0.26	1.26	0.95
		Winter precipitation	−0.15*	−0.27	−0.018	0.71
		Age	−0.16*	−0.24	−0.079	0.96
		Litter size	0.56*	0.17	0.96	1.00
		Nov IFBFat _{<i>t</i>−1} ^a	0.14*	0.088	0.20	1.00
Mar body mass	Population	Summer residency	−1.00*	−1.81	−0.19	0.92
		Winter temperature	0.67*	0.37	0.96	0.99
	Individual	Summer residency	−1.11*	−1.87	−0.35	0.96
		Winter temperature	0.24*	0.018	0.47	0.74
		Age	2.70*	2.22	3.19	1.00
		Age ²	−0.15*	−0.18	−0.11	1.00
		Mar IFBFat	0.30*	0.19	0.40	1.00

^a Results obtained from a separate set of models using a subset of data ($n = 215$) during 2002–2008.

kidney-fat indices for all deer before 1997 to provide a comparable estimate; however, kidney-fat indices are less sensitive to IFBFat at high levels of nutritional condition (Stephenson et al. 1998, Cook et al. 2007, Pierce et al. 2012). The bulk of our detailed analyses included only those data collected since 1997, which we collected with consistent methodology using ultrasonography. Nonetheless, we incorporated data from 1991 to 1996 for analyses of population-level metrics to increase sample size and obtain a wider range of population densities. Although those analyses may have been biased slightly because we calculated IFBFat from kidney fat or from smaller sample sizes during that time (Fig. 5), we weighted each sample by the

inverse of the variance, which apportioned less weight to estimates with greater uncertainty. Sample size (often >100) was adequate for most analyses, but logistical challenges resulted in reduced sample size for neonatal survival, pregnancy of yearlings, and for characterizing cause-specific mortality of both neonates and adults. Consequently, evaluation of some covariates was not possible.

Effects of Nutritional Condition on Vital Rates

Survival and recruitment of young.—Because of the influence of survival and recruitment of young on the population dynamics of large ungulates (Gaillard et al. 1998, 2000; Raithel et al. 2007),

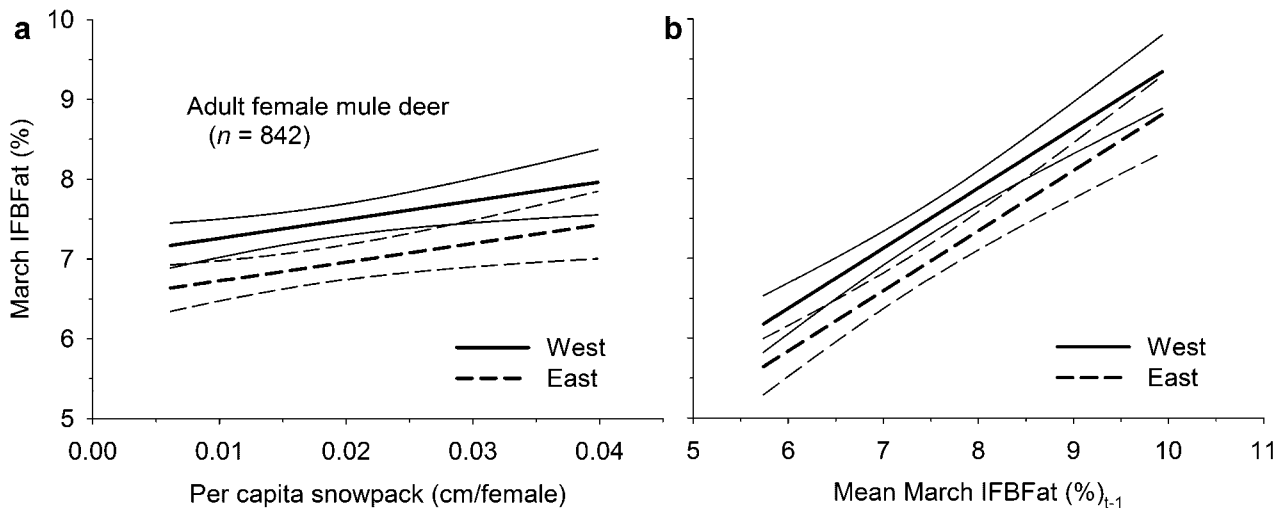


Figure 22. Estimated population-level effects ($\pm 95\%$ CI) of per capita snowpack (a) and mean March ingesta-free body fat (IFBFat; b) on IFBFat of individual adult (>1 yr) female mule deer the subsequent March relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the population level, which included summer residency (east or west), per capita snowpack, winter precipitation, and mean March IFBFat the previous year ($t - 1$). Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

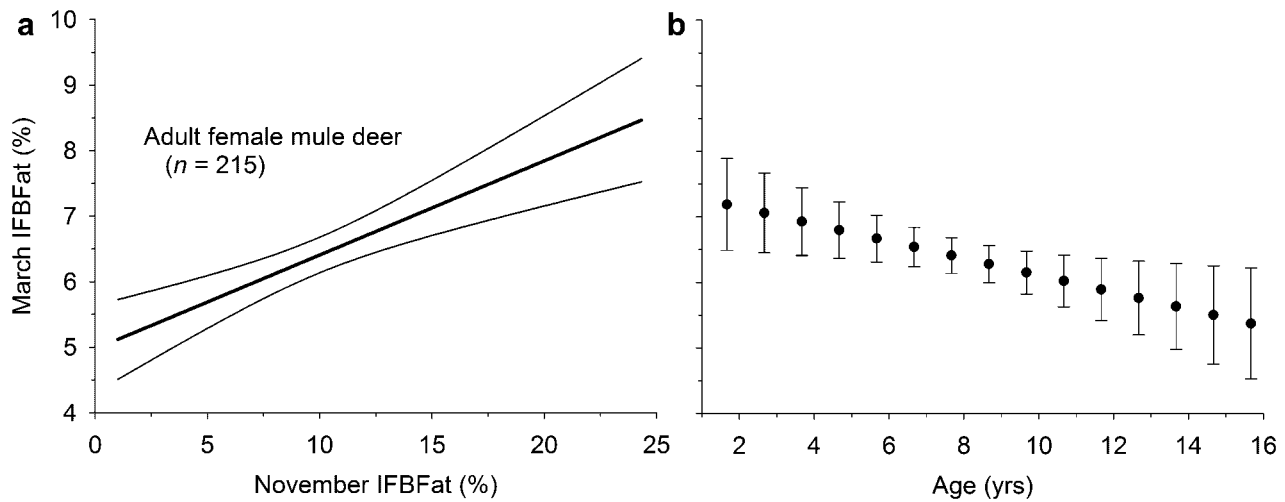


Figure 23. Estimated effect ($\pm 95\%$ CI) of percent ingesta-free body fat (IFBFat) of individual females in November (a) and age (b) on IFBFat of adult (>1 yr) female mule deer in March, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the individual level, which included per capita snowpack, mean March IFBFat the previous year ($t-1$), winter precipitation, age, litter size, and November IFBFat _{$t-1$} . Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

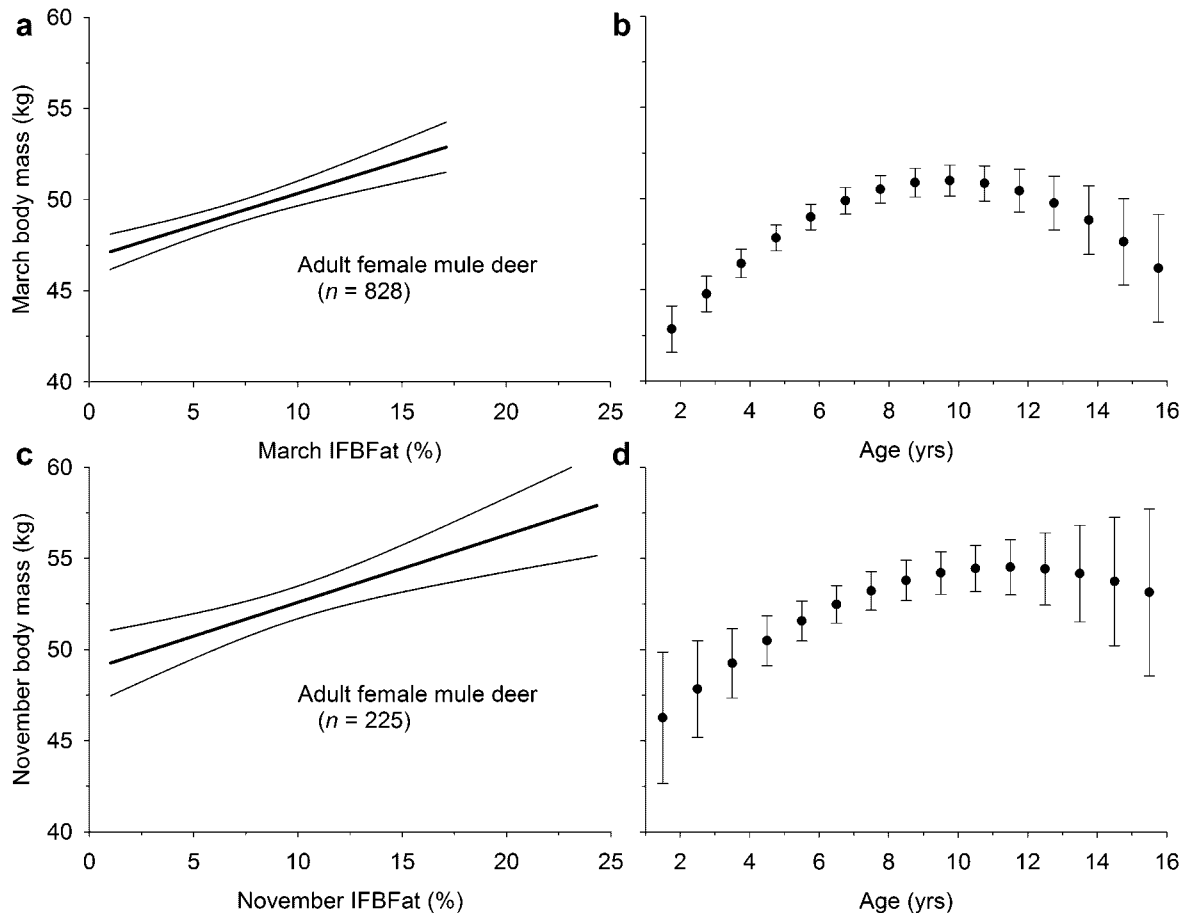


Figure 24. Estimated effect ($\pm 95\%$ CI) of percent ingesta-free body fat (IFBFat) of individual females in March (a) and November (c), and age (b and d) on body mass of adult (>1 yr) female mule deer in March and November, respectively, Sierra Nevada, California, USA, 1997–2009. Results are based on the best model at the individual level, which included summer residency (east or west), winter temperature, age, age², and March IFBFat for March body mass (a and b), and included summer residency, summer precipitation, summer temperature, mean March IFBFat, age, age², November IFBFat, and recruitment status for November body mass (c and d). Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

Table 10. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights of factors that influenced ingesta-free body fat (IFBFat) and body mass of adult (>1 yr) female mule deer in November at the population ($n=359$ and 330 , respectively) and individual ($n=249$ and 253 , respectively) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence intervals do not overlap zero. A full list of predictor variables considered are provided in Appendices M and N.

Response	Level	Parameter	Estimate	90% CI		Importance weight
				Lower	Upper	
Nov IFBFat	Population	Summer residency	−2.35*	−3.22	−1.48	1.00
		Per capita snowpack	78.53*	14.16	142.89	1.00
		Summer precipitation	0.087*	0.012	0.16	0.69
		Mean Mar IFBFat	0.27	−0.12	0.65	0.64
	Individual	Summer residency	−1.97*	−2.84	−1.11	1.00
		Per capita snowpack	132.38*	71.54	193.22	1.00
		Mean Mar IFBFat	0.89*	0.28	1.50	0.94
		Age	−0.030	−0.18	0.13	1.00
		Mar IFBFat	0.10	−0.027	0.23	0.51
		Litter size	−0.24	−0.93	0.45	1.00
		Recruitment status	−2.81*	−3.43	−2.20	1.00
		Summer residency	−2.75*	−4.15	−1.33	1.00
		Summer precipitation	0.37*	0.27	0.47	1.00
Nov body mass	Population	Summer temperature	−0.61*	−1.11	−0.12	0.88
		Mean Mar IFBFat	−0.55	−1.13	0.039	0.79
	Individual	Summer residency	−2.72*	−4.27	−1.16	1.00
		Summer precipitation	0.27*	0.15	0.39	0.99
		Summer temperature	−0.36	−0.86	0.14	0.69
		Mean Mar IFBFat	0.13	−0.11	0.37	1.00
		Age	1.93*	0.80	3.06	1.00
		Age ²	−0.084*	−0.15	−0.016	1.00
		Nov IFBFat	0.37*	0.22	0.52	1.00
		Recruitment status	−0.81	−1.71	0.079	1.00

identifying factors that limit those life-history components is critically important. Survival of neonatal mule deer up to 20 weeks of age in the Sierra Nevada was relatively low compared with other populations of mule deer (Hamlin et al. 1984, Pojar and Bowden 2004, Bishop et al. 2009, Johnstone-Yellin et al. 2009), but similar to those experiencing nutritional limitation (Lomas and Bender 2007) or other large herbivores experiencing high predation (Barber-Meyer et al. 2008). Al-

though comparing mortality rates is common among studies of neonatal survival, a simple comparison of rates of survival among populations reveals little information as to the underlying consequences of mortality, and their effect on population dynamics. Indeed, we observed distinct differences in factors affecting mortality of neonates within a single population during 2006–2008. Nutrition was the dominant factor affecting survival of young on the east side of the Sierra crest (Fig. 7), whereas

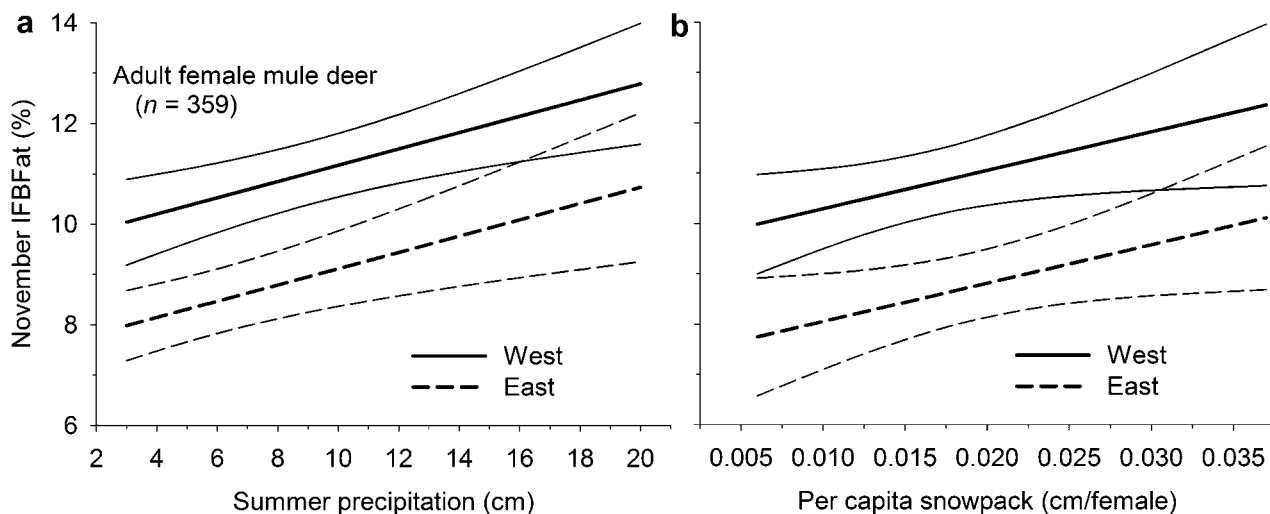


Figure 25. Estimated effect ($\pm 95\%$ CI) of total summer precipitation (a) and per capita snowpack (b) on percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in November relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2009. Results are based on the best model at the population level, which included summer residency (east or west), per capita snowpack, mean March IFBFat, and summer precipitation. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

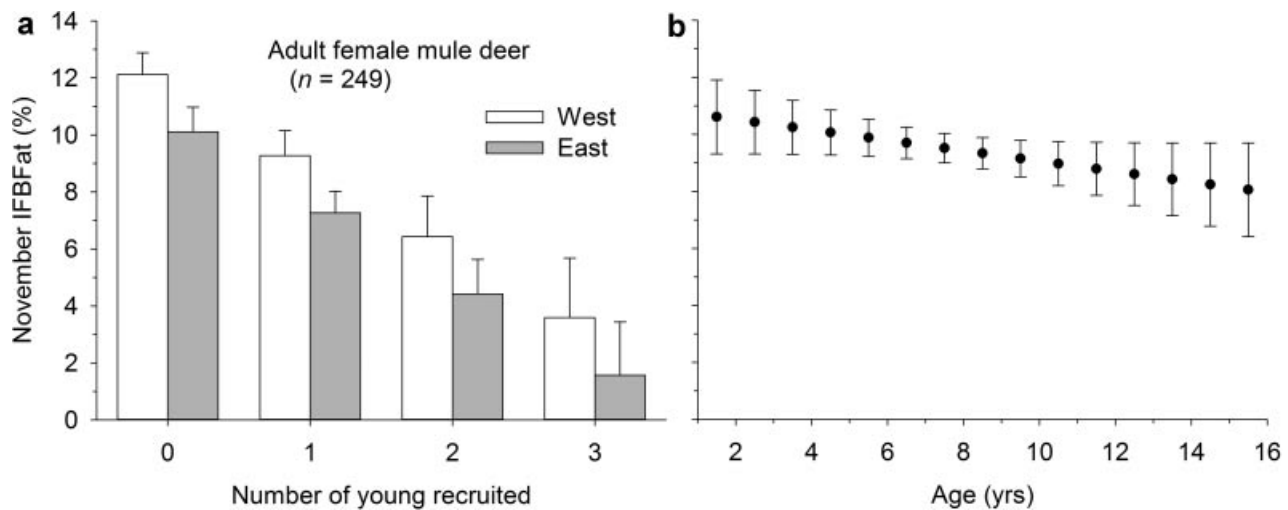


Figure 26. Estimated effect ($\pm 95\%$ CI) of number of young recruited in autumn (a) and age (b) on percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in November relative to side of the Sierra crest occupied during summer, Sierra Nevada, California, USA, 1997–2008. Results are based on the best model at the individual level, which included summer residency, per capita snowpack, mean March IFBFat, age, March IFBFat, litter size, and recruitment status. Predictions represent expected effects of the variable of interest (x -axis) within the range we observed, while holding all other variables constant at their mean.

survival of young born on the west side was affected mostly by predation (Fig. 8).

Birth mass of young is a widely recognized life-history trait that can have life-lasting consequences (Albon et al. 1987, Monteith et al. 2009), and often has a marked influence on survival of neonatal ungulates (Clutton-Brock et al. 1987, Keech et al. 2000, Tveraa et al. 2003, Lomas and Bender 2007, Carstensen et al. 2009, Johnstone-Yellin et al. 2009). Nevertheless, when predation is high and has an additive effect on mortality rates, effects of birth mass on viability and survival of young can be negligible and washed out by condition-independent predation (Fig. 7a; Barber-Meyer et al. 2008). On the east side of the Sierra crest, smaller neonates had a lower probability of survival (Fig. 7a), with those <2.0 kg at birth having $<35\%$ chance of survival and being most likely to succumb to malnutrition

(Fig. 9a), which is in accordance with poor survival of neonatal white-tailed deer ≤ 1.9 kg (*Odocoileus virginianus*; Verme 1962). Neonates dying of malnutrition are likely to die immediately after birth (Ozoga and Clute 1988, Carstensen et al. 2009), which also was evident in our study (Fig. 9b). Low birth mass is often attributed to poor maternal nutrition (Verme 1965, 1969; Robinette et al. 1973; Cook et al. 2004; Adams 2005; Lomas and Bender 2007), but birth mass in our study was not influenced strongly by any maternal characteristic that we measured

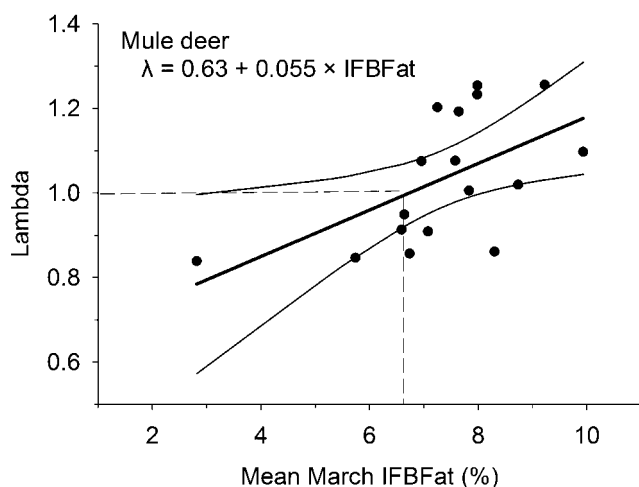


Figure 27. Estimated effect ($\pm 95\%$ CI) of mean ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in March on population growth (lambda) during the current year, Sierra Nevada, California, USA, 1991–2008. Results are based on the best model, which included only mean March IFBFat.

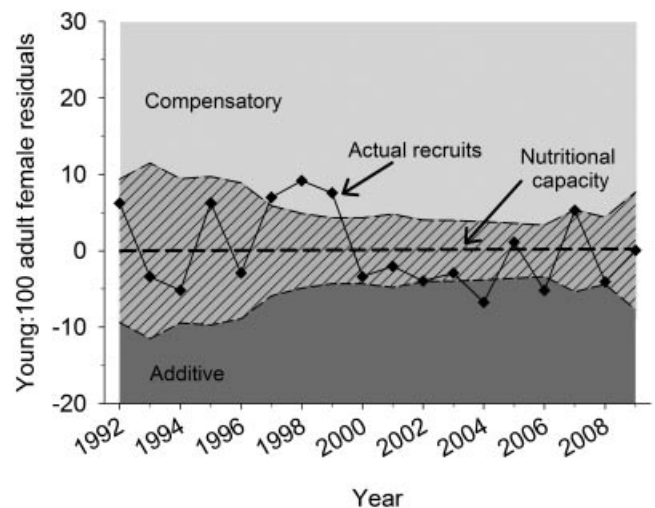


Figure 28. Residuals of the model used to predict the nutritional capacity of female mule deer to recruit young, relative to that attempted (based on fetal rates) and observed (based on ratios of young-to-adult females). Residuals in ratios of young-to-adult females above that predicted (dashed line) indicate the level of mortality that was compensatory (light gray), whereas ratios below that expected dictate the amount of mortality that was additive (dark gray) with respect to the nutritional capacity for recruitment of young. Hashed area around model predictions are 95% confidence intervals. The population level model included mean March ingesta-free body fat (IFBFat) of the current year (t), mean March IFBFat of the previous year ($t - 1$), mean March body mass, mean litter size, per capita snowpack, summer precipitation, and summer temperature.

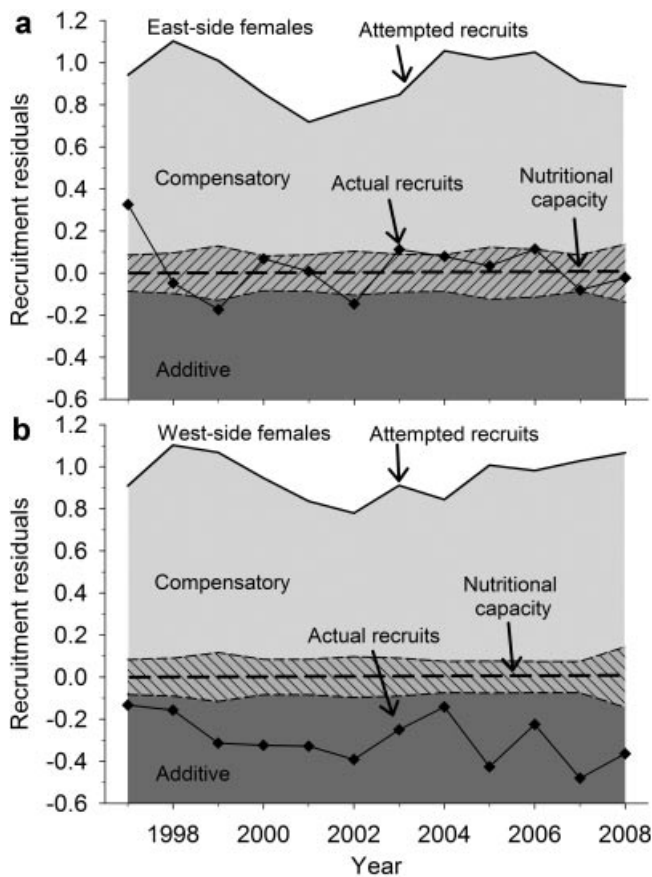


Figure 29. Residuals of the model used to predict the nutritional capacity of adult (>1 yr) female mule deer to recruit young (dashed line), relative to that attempted (based on fetal rates) and observed (based on recruitment rates) for east-side (a) and west-side (b) females. Residuals in recruitment above that predicted (dashed line) indicate the level of mortality that was compensatory (light gray), whereas recruitment below that expected dictate the amount of mortality that was additive (dark gray) with respect to the nutritional capacity for recruitment of young. Hashed area around model predictions are 95% confidence intervals. Model included summer residency and mean March ingesta-free body fat (IFBFat), with the effects of summer residency removed because it largely reflected increased predation pressure for west-side females.

(Appendix C). Birth mass of mule deer was related primarily to litter size, with larger litters resulting in lower birth mass among littermates (Fig. 10a). In contrast, timing of birth was related to maternal characteristics, which may have reflected an attempt by females to compensate for poor maternal nutrition,

thereby enhancing growth and survival of young (Monteith et al. 2009).

Gestation length is a plastic life-history trait that may be lengthened to compensate for retarded fetal development caused by nutritional deprivation (Verme 1965, Rachlow and Bowyer 1991, Berger 1992, Flydal and Reimers 2002, Clements et al. 2011), or shortened to coincide with resource availability if females are nutritionally capable (Berger 1992, Mysterud et al. 2009, Rowell and Shipka 2009). Heavier females in good nutritional condition may have conceived earlier in the autumn, resulting in earlier parturition dates (Robinette et al. 1973, Garel et al. 2009, Mysterud et al. 2009, Clements et al. 2011); however, conception date is often related negatively to gestation length (Scott et al. 2008, Mysterud et al. 2009, Clements et al. 2011). We postulate that females with larger litter sizes, or possibly low body mass, lengthened gestation to boost fetal growth and enhance birth mass of young, because larger litter size resulted in delayed birth dates (Fig. 10a) and low birth mass was selected against (Fig. 7a). Females also may have increased allocation of maternal resources to compensate for late birth dates and enhance neonatal growth (Rachlow and Bowyer 1994, Andersen and Linnell 1997), although this may not always occur (Asher et al. 2005, Whiting et al. 2009). Red deer (*Cervus elaphus*) maintained on varying levels of nutrition gave birth to similar-sized young; gestation length varied widely, however, with females on poor-quality diets lengthening gestation (Asher et al. 2005). In contrast, large-bodied females may have the potential to enhance fetal growth and give birth earlier than smaller females (Fig. 11). Timing of birth occurred earlier for caribou (*Rangifer tarandus*) that were heavier in summer (Cameron et al. 1993), Alaskan moose (*Alces alces*) with greater rump fat (Keech et al. 2000), and during years of lower population density for North American elk (*Cervus elaphus*; Singer et al. 1997). Similarly, date of parturition occurred earlier, and offspring were heavier at birth, following a mild winter compared with a harsh winter for reindeer (*Rangifer tarandus*) in Norway (Tveraa et al. 2003).

Varying gestation length to compensate for poor fetal growth may be possible only under moderate levels of nutrition (Albon et al. 1983a, Asher et al. 2005). Although limited peritoneal space probably constrained birth mass potential for females with larger litters (Fig. 10; Robinette et al. 1973), selective pressures likely favored reproductive strategies to maximize birth mass of young within morphological limits, because birth mass is one of the

Table 11. Relative magnitude of the influence of density-dependent (DD) availability of forage, mean nutritional condition (population level), individual nutritional condition, and migratory tactic on life history of mule deer in the central Sierra Nevada, California, USA, 1997–2009.

Life-history component	Population level		Individual level	
	DD forage availability	Nutritional status	Nutritional status	Migratory tactic
Neonate survival	Minimal	Minimal	Strong	Strong
Recruitment of young	Minimal	Moderate	Strong	Strong
Young:adult female	Moderate	Strong		
Age at first reproduction	Strong	Minor	Strong	None
Litter size	Strong	Minimal	None	Strong
Pregnancy	None	None	None	None
Adult summer survival	Moderate	Moderate	Minimal	None
Adult winter survival	Strong	Minimal	Strong	None
Population growth	None	Strong		

most influential factors affecting survival of young. Strategies of extending gestation may not be favorable, however, for species that depend on parturition to coincide with a flush of nutrients in spring to support lactational costs (Côté and Festa-Bianchet 2001, Post et al. 2008) and provide sufficient time for growth and accruing body reserves to survive winter (Rachlow and Bowyer 1991, Bowyer et al. 1998b, Cook et al. 2004, Bishop et al. 2005, Hurley et al. 2011).

Date of birth often influences survival, with neonates born early or during the peak of birthing enjoying greater survival rates (Testa 2002, Landete-Castillejos et al. 2003, Whiting et al. 2011). Timing of nutritional needs to support late-born young may be mismatched with peak resource availability in spring, with young being underweight and experiencing poor survival (Clutton-Brock et al. 1987, Rachlow and Bowyer 1994). Other studies have shown that young born outside the peak of parturition may be subjected to increased predation pressure (Testa 2002, Barber-Meyer et al. 2008). Conversely, timing of parturition had no effect on survival in other studies (Bowyer et al. 1998b, Feder et al. 2008, Musante et al. 2010) or for neonates in the Sierra Nevada (Appendix A). Despite substantial predation experienced by young within the first few weeks of life, no effect of timing of birth on probability of survival led us to reject the potential for a dilution effect on predation.

Lactation is the most energetically demanding event (up to 4× baseline metabolism) in the life-history of an ungulate (Moen 1978, Monteith et al. 2014), and forage demands increase from 130% of summer maintenance when supporting 1 young during peak lactation to 170% for 2 young during peak lactation (Sadleir 1982). Provisioning of young following birth was influenced positively by the nutritional condition of the dam, but that effect was most evident with the onset of peak lactation (4 weeks post-parturition; Monteith et al. 2014), and was diluted by high predation pressure on young born on the west side of the Sierra crest (Fig. 7b). During early life, growth and development of young depend on the amount and quality of milk produced by the dam (Robbins and Robbins 1979; Cook et al. 2004; Tollefson et al. 2010, 2011), which may be dependent upon her nutritional state or foraging conditions (Sadleir 1982, Landete-Castillejos et al. 2003, Tollefson et al. 2011).

Ungulates are generally thought to be capital breeders because they rely on stored energy for reproduction (Jönsson 1997); however, small ungulates such as mule deer and European roe deer (*Capreolus capreolus*) may function more like an income breeder, because they rely on energy acquired during reproduction to support provisioning of young (Andersen et al. 2000, Tollefson et al. 2010). The relationship between nutritional condition and probability of survival of young for females summering on the east side of the Sierra crest, and the evident costs of reproduction on nutritional condition in autumn, indicate that mule deer also are reliant on current capital to support reproductive allocation (Stearns 1992, Jönsson 1997, Stephens et al. 2009). Similar relationships between nutritional capital, as measured by body mass or fat reserves, and survival of young have been reported for numerous large herbivores including North American elk (Cook et al. 2004), red deer (Landete-Castillejos et al. 2003), moose (Keech et al. 2000), bighorn sheep (*Ovis canadensis*; Festa-Bianchet 1998, Festa-Bianchet and Jorgenson 1998), caribou

(Bårdsen et al. 2010), and mule deer (Lomas and Bender 2007, Johnstone-Yellin et al. 2009, this study).

The young-to-adult female ratio is a composite measure of several demographic processes including survival of adult females, fertility, fecundity, and survival of young (Bonenfant et al. 2005). Although the use of ratio data for inferring population dynamics has been criticized (Caughley 1974, McCullough 1994), others have used these data for characterizing demographics of ungulate populations (Raithel et al. 2007; Harris et al. 2008; Hegel et al. 2010a, b). If reproductive rates and survival of adult females remain high with little variation, age ratios can provide a reliable index to relative changes in λ , because variation in survival of young drives interannual changes in that metric (Gaillard et al. 1998, 2000; Raithel et al. 2007; Harris et al. 2008).

The young-to-female ratio for mule deer in the Sierra Nevada was highly variable (Fig. 14a), and was influenced primarily by nutritional condition of adult females in March. Density-dependent effects on age ratios were evident in a number of studies reviewed by Bonenfant et al. (2009). Nutritional condition in March provided an integrative measure of range conditions as affected by precipitation and density-dependent processes; nutritional condition reflected reproductive potential for females the following summer, and was a reference of carryover of range conditions and nutritional limitation from the previous year (Fig. 14b).

Age at first reproduction.—The age at which young females first reproduce is of considerable theoretical interest for understanding life-history strategies (Stearns 1992, Proaktor et al. 2008), and can have a profound effect on population dynamics (Cole 1954). Age at first reproduction is expected to follow recruitment of young in sensitivity to resource limitation (Eberhardt 2002). In support of that prediction, probability of pregnancy for yearling female mule deer in the Sierra Nevada was determined mostly by an index of density-dependent availability of forage, which likely influenced growth of young females before the mating season (Fig. 15).

Age of primiparity for most species of large ungulates is associated with attaining a threshold in body mass before mating (Langvatn et al. 1996, Sand and Cederlund 1996, Adams and Dale 1998, Swihart et al. 1998, DelGiudice et al. 2007), which is sensitive to resource limitation and may delay age at first reproduction for 1–3 years depending on the severity of such limitation (Jorgenson et al. 1993, Festa-Bianchet et al. 1995, Bonenfant et al. 2002, Strickland et al. 2008). Although our data on body mass were collected during March, the threshold of ≥ 41 kg for a high (0.90) probability of pregnancy among yearling mule deer was comparable to that reported previously for 6-month-old and yearling mule deer (41–45 kg; Robinette et al. 1973) and white-tailed deer (55.1 kg; DelGiudice et al. 2007). In contrast, probability of pregnancy for females ≥ 2.5 years old was unrelated to age, nutritional condition, or body mass, even though body mass of pregnant females ranged as low as 34 kg in November and 30 kg in March—body-mass levels that represented a probability of pregnancy of almost zero for yearlings (Fig. 15b). Likewise, young female moose required greater body mass to ovulate compared with older females (Schwartz and Hundertmark 1993, Garel et al. 2009). We hypothesize that the strong effect of body mass on age of

primiparity when compared with the absence of such a relationship in older females may represent a tradeoff between early maturation and future growth (Green and Rothstein 1991, Stearns 1992, Sand 1996). Furthermore, nutrition experienced by dams during the year of birth holds the potential to influence age of primiparity (Pettorelli et al. 2003, McLoughlin et al. 2008), which may be manifested through its influence on birth mass and growth of offspring (Monteith et al. 2009).

Fetal rate.—Mean litter size during 1997–2009 (1.69 young/adult female) was comparable to that reported for other populations of mule deer in California (1.72; Salwasser et al. 1978) and Colorado (1.70; Andelt et al. 2004), was less than in a captive herd in Colorado (1.82; Robinette et al. 1973), and a free-ranging population in Colorado (1.81; Bishop et al. 2009), but was greater than that observed (1.40) during the population crash in Round Valley in the late 1980s (Kucera 1988). Litter size of female mule deer ≥ 2.5 years old was sensitive to summer climate, per capita snowpack, and summer residency. We hypothesize that summers with warmer temperatures resulted in accelerated drying and senescence of forage, thereby reducing its nutritional quality (Marshall et al. 2005a, b). Winters with greater snowpack relative to population density, however, probably helped sustain forage quality further into the summer, which may moderate effects of summer weather (Table 7).

Effects of nutritional condition on fertility rates have been reported for numerous species of ungulates (Adamczewski et al. 1997, Cook et al. 2004, Stewart et al. 2005), including mule deer (Johnstone-Yellin et al. 2009, Tollefson et al. 2010). Our results, however, indicated that age, nutritional condition, and body mass did not influence fertility patterns for female mule deer ≥ 2.5 years old. In other studies, patterns of fertility were related either to body mass or nutritional condition (Cameron et al. 1993, Adams and Dale 1998, Stewart et al. 2005, Tollefson et al. 2010); however, forage resources available immediately before or during estrus have the potential to override effects of current nutritional state (Verme 1969, Bowyer 1991, Tollefson et al. 2010).

Maintaining high fertility may be possible for migratory ungulates that are capable of following phenological gradients (Monteith et al. 2011, Sawyer and Kauffman 2011) and relocating to ranges that have experienced negligible browsing pressure during the preceding season (Skogland 1985, Andelt et al. 2004). Mule deer in the Sierra Nevada migrate to winter range before rut in autumn, where browsing intensity has been relaxed during the entire growing season (Monteith et al. 2011), which may offer a diet sufficient in digestible energy and protein to enhance probability of pregnancy and litter size, and may partially explain the absence of an effect of nutritional condition on those reproductive parameters. Large litter size among females that summer on the west side of the Sierra crest, however, may be explained partially by their longer residence on summer ranges supporting greater plant diversity and quality of forage than females summering on the east side (Monteith et al. 2011).

Reproductive senescence in fertility or fecundity did not occur for mule deer up to 15.5 years old in the Sierra Nevada despite lower body mass (Fig. 24d) and nutritional condition (Fig. 26b) of old-aged females in autumn. Pregnancy and litter size

remained largely unaffected by age for females ≥ 2.5 years old. These data are consistent with the absence of a strong relationship between fertility and body mass or nutritional condition. Verme and Ullrey (1984) suggested that reproductive senescence occurs in white-tailed deer >7 years old; however, most empirical evidence indicates an absence of senescence in fertility or fecundity for *Odocoileus* (McCullough 1979, Nelson and Mech 1990, Strickland et al. 2008), including up to 15.5 years old in white-tailed deer in midwestern North America (DelGiudice et al. 2007). Despite actuarial senescence for mule deer occurring at about 10 years old (Fig. 21), particularly during winter, reproductive senescence was not evident.

Increases in occurrence of reproductive pauses and declines in fecundity have been reported for other female ungulates at advanced ages (generally >12 yr), or within a few years of actuarial senescence (Festa-Bianchet et al. 1994, Adams and Dale 1998, Bérubé et al. 1999, Ericsson et al. 2001, Festa-Bianchet and King 2007). We suspect reproductive senescence is unlikely to be evident in deer populations experiencing hunter harvest or predation by large carnivores, especially when senescence in survival begins as early as 10 years of age. Litter sizes remained high and were inconsistent with individual nutritional status, which limits their value for evaluating interannual variation in degree of resource limitation for populations of *Odocoileus*.

Pregnancy in adults.—Patterns of pregnancy for large herbivores vary markedly among species and populations, with reproductive pauses commonly occurring in some taxa (Julander et al. 1961, Testa and Adams 1998, Cook et al. 2004, Stewart et al. 2005), compared with high and consistent patterns of pregnancy that appear insensitive to resource limitation in others (Skogland 1985, DelGiudice et al. 2007, Bishop et al. 2009). Although low rates have been documented under extreme levels of population density and range deterioration (Julander et al. 1961, Bowyer 1991), high levels of pregnancy across a wide range of environmental variation, and nutritional limitation seems to be the norm for *Odocoileus* (Andelt et al. 2004, DelGiudice et al. 2007, Strickland et al. 2008). Those patterns support pregnancy of adult females as being one of the last factors to be influenced by inadequate nutrition (Fig. 1; Eberhardt 2002), and indicate that monitoring of pregnancy rates will provide limited insight into variation of nutritional limitation within or among populations (Andelt et al. 2004), except under extreme nutritional deprivation. In contrast, patterns of pregnancy in moose are sensitive to nutritional condition with 9% and 13% IFBFat in autumn equating to 50% and 100% pregnancy rates, respectively (Testa and Adams 1998).

Reproductive pauses and variable pregnancy rates do occur in polytocous species (Julander et al. 1961, Hamel et al. 2010, Pierce et al. 2012), but are much more common in species that typically give birth to a single offspring such as red deer and North American elk (Albon et al. 1983b, Cook et al. 2004, Stewart et al. 2005), and caribou (Cameron 1994, Adams and Dale 1998), where an adjustment from 1 to 0 young is normally the only possibility. High rates of pregnancy and litter sizes >1 are typical for *Odocoileus*, which are more likely to adjust resource allocation to reproduction according to nutritional conditions during gestation or at onset of post-natal care, rather than during

ovulation (Johnstone-Yellin et al. 2009, Monteith et al. 2009). Prenatal mortality among *Odocoileus* has been documented, but mostly occurs early in gestation and is rare (Robinette and Gashwiler 1950, Kie and White 1985, Bishop et al. 2008).

Adult female survival.—Survival of adult female ungulates generally exhibits a consistent pattern of high (>85%) survival with a strong resilience to climatic or density-dependent factors (Barrett 1982; van Vuren and Bray 1986; Gaillard et al. 1993, 2000; Loison and Langvatn 1998; Unsworth et al. 1999; Hamel et al. 2010). We documented positive effects of snowpack relative to animal density on both summer and winter survival of adult females, after accounting for age structure (Festa-Bianchet et al. 2003). Despite those interannual relationships with density and forage growth, mean annual survival was 0.87 and seasonal survival was almost always >0.90, albeit with some variation among years. High adult survival (Fig. 18) within a variable environment supports the stability in survival of adult females for large herbivores (Fig. 1), especially when compared with the variation in weather, predation, and nutrition we observed. Adult survival may be strongly influenced, however, in overshoots of *K* coupled with extreme drought (Pierce et al. 2012).

Besides age, the only individual characteristic that was related to seasonal survival of adult female mule deer was November body mass, which increased the probability of overwinter survival (Fig. 20b). Diets of mule deer in Round Valley progressively shift from bitterbrush to sagebrush as winter browsing depletes the availability of bitterbrush (Pierce et al. 2004). Sagebrush is high in protein, but can contain an abundance of toxic phenolics (Bray et al. 1991), and is consumed primarily when alternative forage sources are unavailable in Round Valley (Kucera 1997; Pierce et al. 2004, 2012). Overwinter survival may have been related to body mass rather than IFBFat, because body mass integrates both body protein and fat, and may represent total endogenous reserves available to buffer against depletion in forage protein and digestible energy as winter progresses (Barboza and Parker 2008). Loss of body mass over winter is substantial for most ungulates and, as fat reserves are depleted, mobilization of muscle mass accelerates to satisfy energy and nitrogen requirements for maintenance (Torbit et al. 1985, Parker et al. 1993, Monteith et al. 2013). Therefore, maintaining sufficient muscle mass for individuals experiencing poor range conditions may be critical to their survival (Torbit et al. 1985, Bender et al. 2008).

Nutritional condition of adult females can influence their survival (Lawrence et al. 2004, Bender et al. 2007), but rare events of extreme weather or nutritional deprivation may be necessary for relationships between nutrition and adult survival to become evident (*sensu* Gaillard et al. 2000, Bishop et al. 2005). During a 3-year study coincident with a drought in north-central New Mexico, nutritional condition of individuals had a significant influence on survival of female mule deer (Bender et al. 2007). Likewise, the population of mule deer in Round Valley crashed from roughly 6,000 animals in 1985 to <1,000 by 1991 in response to severe drought conditions with declines in adult survival caused by nutritional deprivation (Kucera 1988, Pierce et al. 2012). Alternatively, nutritional enhancement of winter range increased annual adult survival by 0.05 (Bishop et al. 2009). Although our study overlapped a 12-year period with highly variable precipitation, deer were not subjected to extremes in

climatic conditions or density that would be expected to dramatically affect a life-history characteristic that can be buffered against moderate environmental variation (Gaillard et al. 1998, 2000). The resistance in adult survival to nutritional limitation may be accounted for by the number of behavioral and reproductive strategies available to females to preserve their own survival in light of other decisions that increase risk of mortality (Festa-Bianchet and Jorgenson 1998; Bårdsen et al. 2010; Monteith et al. 2011, 2013).

Actuarial senescence (Nussey et al. 2008), or suppressed survival with increasing age, occurred during both winter and summer, but is likely to be most apparent during seasons or years of nutritional limitation (Gaillard et al. 1993, Garrott et al. 2003, Nussey et al. 2008). Although survival declined as females progressed in age during summer, predicted survival of females >10 years old declined at a reduced rate and remained >80% in older age classes (Fig. 21a). This moderate decline contrasted with the increasing rate of mortality with age for females during winter (Fig. 21b), as is typical for large ungulates (Loison et al. 1999; Nussey et al. 2007, 2008). Summer, for many temperate ungulates, represents the season of forage abundance (Parker et al. 2009), which may have lowered the nutritional suppression associated with old age and tooth wear (Loe et al. 2006, Nussey et al. 2008). In contrast, the nutritional bottleneck of winter offers aged females fewer options to reduce energy expenditure or increase forage gain (Monteith et al. 2013), especially when they are generally in poorer nutritional condition by March than are prime-aged females (Fig. 23b).

Sensitivity of Nutritional Condition

Our results were in general accordance with the hypothesized sensitivity of life-history traits to nutritional limitation (Gaillard et al. 2000, Eberhardt 2002) with the exception of pregnancy rates, which were less variable and also affected to a lesser extent by nutritional limitation than was survival of adult females (Fig. 1). We hypothesized that nutritional condition would offer the most sensitive and direct measure of resource limitation. In support of that hypothesis, nutritional condition was more variable than other life-history traits and the influence of nutritional condition on life-history characteristics followed those same predictions (Fig. 1).

Numerous life-history traits, including nutritional condition, reflected a lag of population-level (mean) nutritional condition from previous years. Nutritional condition at the population level, particularly post-winter, likely reflected a metric of habitat condition from the previous year that would carry over between seasons (McCullough 1979, Fryxell 1991, Singer et al. 1997, Cook et al. 2013, Monteith et al. 2013). Direct and lagged effects of density dependence have been documented in numerous populations of large mammals across an array of habitats (Singer et al. 1997, Beckerman et al. 2002, Pettorelli et al. 2002, Månsson et al. 2007), which likely caused lagged effects of age structure, delayed effects of nutritional carryover at the individual level, and residual effects of habitat conditions relative to density from the previous season. If nutritional condition represents the relative position of the population with respect to *K* (Piasecke and Bender 2009), then that position would be expected to be partially reflected in the following year. Time lags and carryover

effects in response to resource limitation are becoming increasingly recognized as influential factors in the regulation of ungulate populations (Fryxell 1991, Gilbert and Raedeke 2004, Keyser et al. 2005, Monteith et al. 2009, Harrison et al. 2011), and stress the importance of not considering a particular season or year in isolation (Kie et al. 2003, Monteith et al. 2013).

Nutritional condition represents a direct measure of energy acquisition and debt experienced by an individual; hence, nutritional condition is sensitive to minor changes in resource quality and availability (Cook et al. 2004, Parker et al. 2009). Accordingly, changes in habitat quality and animal density will be reflected by nutritional condition before demographic effects are observed, because demographic effects are mediated largely through nutrition (Bender et al. 2008, Parker et al. 2009). Moreover, because long-lived, iteroparous ungulates favor a conservative life-history strategy (Gaillard and Yoccoz 2003), some vital rates are insensitive to habitat changes or are only affected once a threshold is reached, thereby offering incomplete information across a wide range of resource limitation.

Nutritional condition (i.e., percent body fat) is more sensitive to habitat factors experienced by an individual than is body mass. Patterns of body mass can reflect resource limitation and environmental variation, but interpreting patterns of body mass as a reference to nutritional limitation can be plagued by long-term cohort and maternal effects (Albon et al. 1987, Post et al. 1997, Sams et al. 1998, Hamel et al. 2009, Monteith et al. 2009). For example, individuals may be in good nutritional condition after habitat conditions have improved, yet body mass remains low because of intergenerational and cohort effects acting through maternal nutrition (Monteith et al. 2009). Furthermore, fat reserves provide a different form of energetic currency compared with protein reserves, which is what body mass primarily reflects (Monteith et al. 2013). Protein reserves, and thus body mass, function mostly as insurance against winter malnutrition, whereas fat reserves provide a universal source of energy for both survival and reproduction (Monteith et al. 2013). Despite marked changes in nutritional condition for mule deer in Round Valley during 1997–2009, patterns of body mass were nearly invariable ($CV = 3\%$) and were influenced primarily by age and summer residency, with females residing on the west side of the crest being larger than east-side females. The higher plane of nutrition on the west side of the Sierra crest, and greater potential for pre- and post-natal allocation by mothers summering on the west side likely explains the disparity in body mass between females occupying opposite sides of the Sierra crest. We hypothesize that nutritional limitation on the east side has resulted in life-long negative effects on adult body mass for young born to mothers on the east side, because body mass can reflect maternal condition from previous generations (Mech et al. 1991, Monteith et al. 2009), rather than current habitat conditions.

Variation in access to resources and how individuals allocate those resources during a particular season has implications for inclusive fitness, particularly for animals that partially rely on current capital for survival and reproduction (Stearns 1992, Jönsson 1997, Stephens et al. 2009). Such residual effects from previous seasons are defined as carryover effects, wherein life-history events and ecological processes evident in one season

result in individuals transitioning between seasons having different nutritional states, and thereby affecting individual performance in the subsequent season (Harrison et al. 2011, Monteith et al. 2013). Downstream consequences of current nutritional and reproductive state on future fitness have important implications for the evolution of life-history strategies and the dynamics of populations when individual effects are scaled up to the population level (Testa and Adams 1998, Norris 2005). Despite their importance, carryover effects are difficult to document, because they occur at the individual level and, thus, require longitudinal data on individuals throughout the annual cycle (Clutton-Brock and Sheldon 2010, Harrison et al. 2011).

The relative magnitude of the effect of current nutritional state of individual mule deer on life-history components during the following season were in accordance with life-history theory for large herbivores (Stearns 1992, Eberhardt 2002). Furthermore, individuals made transitions between seasons at different nutritional states depending upon previous forage availability, migratory status, and reproductive output. The most evident carryover effect on reproductive success was mediated through the winter environment, where foraging opportunities on winter range along with nutritional condition during November determined late-winter nutritional condition (Figs. 22 and 23), which in turn influenced survival and recruitment of young the following summer (Figs. 7b, 13a, and 14b). Similarly, nutritional state of individuals transitioning from summer to winter was largely determined by migratory tactic and reproductive expenditure (Figs. 25 and 26). Substantial carryover of nutritional condition reinforces the notion that K is a year-round phenomenon (Kie et al. 2003), and nutritional contributions from seasonal ranges are not independent (Monteith et al. 2013).

Nutritional Cost of Reproduction

A central question in life-history theory is the degree to which individuals allocate resources to support current reproduction versus securing their own survival (Stearns 1992). Species with long life spans that have the opportunity to reproduce repeatedly are expected to employ a conservative strategy regarding reproductive allocation that favors maternal survival over reproductive output (Martin and Festa-Bianchet 2010). This bet-hedging strategy has been termed risk-sensitive reproductive allocation (Bårdsen et al. 2008), and is the primary reason why survival of young is more variable and more sensitive to resource limitation than adult survival (Gaillard et al. 1998, 2000). Indeed, individual females may rely on body reserves to fuel periods of low energy intake or high reproductive output (Monteith et al. 2013). Although spring and summer represent the season of forage abundance in many ecosystems, mothers incur substantial energetic costs to support late gestation and lactation (Moen 1978, Pekins et al. 1998, Monteith et al. 2014), which may result in a tradeoff if current reproductive allocation affects nutritional reserves that are insurance against nutritional deprivation during winter (Bender et al. 2007).

Nutritional condition in late winter had a positive effect on reproductive success of female mule deer the following summer; however, reproductive effort, in turn, influenced autumn

nutritional condition (Fig. 26a). The lactational costs incurred by mothers during the summer, along with their summer residency, were the most influential factors determining nutritional reserves of females before the onset of winter (Fig. 26a). Although IFBFat of individual females did not affect probability of overwinter survival, heavier females were more likely to survive winter (Table 8). Body mass for adult females in autumn was positively influenced by their fat reserves, which was determined primarily by their reproductive status in autumn (Table 10). Furthermore, nutritional condition of females in autumn had a positive influence on nutritional condition in March, which in turn, affected reproductive success the following summer (Fig. 13a). Therefore, mule deer incurred a fitness cost by trading-off current reproductive allocation against accumulation of somatic reserves to survive winter and support reproduction the following summer.

Large herbivores undergo seasonal rhythms in nutritional condition, with poor condition often occurring following winter, and summer forage offering support for reproduction and fat accretion (Parker et al. 2009). In accordance with that pattern, mean nutritional condition of females in autumn (9.7% IFBFat) was greater than in late winter (7.2%). Nonetheless, for reproductive individuals, seasonal dynamics of body mass and nutritional condition did not follow the expected pattern, because of the considerable somatic costs incurred from successful reproduction. For example, we observed a measurable cost of reproduction on nutritional condition for female mule deer during autumn based on the number of young recruited, which likely reflected a reduction in the autumn threshold of nutritional condition among females that successfully recruited young (Monteith et al. 2013). Negative effects of reproduction on fat stores was moderated by per capita snowpack and summer precipitation (Fig. 25), which likely influenced forage quality and availability on seasonal ranges (Sinclair et al. 1985; Marshal et al. 2005a, b). Regardless of summer residency or climatic variation, females that recruited 1 young were still in poorer condition in autumn than those that failed to recruit young.

The substantial immediate cost of reproduction to nutritional condition and the influence of range quality in summer indicated that mule deer rely on nutritional reserves (i.e., capital) and available forage (i.e., income) to subsidize reproductive allocation (Stephens et al. 2009). Although other investigators have suggested that mule deer might function like other small ungulates (Andersen et al. 2000) by relying on nutritional income (Johnstone-Yellin et al. 2009, Tollefson et al. 2010), our results indicate that they reside somewhere in the middle of the capital-income continuum. Furthermore, that current capital is used to finance reproductive allocation attests to the value of nutritional condition for interpreting or predicting population dynamics.

Selective Pressures on Migratory Tactics

Patterns of migration within populations affect subsequent life-history characteristics and, thus, selective pressures that determine the balance between migratory segments of a population (Kaitala et al. 1993). Coexistence of divergent migratory tactics within a single population indicates that animals are following a mixed evolutionary stable strategy, wherein various strategies may occur at some relatively equal benefit, but at different times

(Sinclair 1983). Differential mortality among migratory segments may permit the coexistence of the 2 tactics, but advantages of each will be sensitive to changes in reproductive success and survival (Kaitala et al. 1993). Poor recruitment and survival resulting from a particular migratory tactic, given natal and adult fidelity to a particular seasonal range, will inherently reduce the proportion of individuals in the population employing the more costly tactic. Indeed, we documented differences in litter size, survival and recruitment of young, and seasonal fat levels between females that shared a common winter range but exhibited divergent migratory tactics relative to occupancy of summer ranges on opposite sides of the Sierra crest (Fig. 3).

Migration to the west side of the Sierra crest was the most common migratory tactic for mule deer wintering in Round Valley before 1985, because deer migrating to the west side of the Sierra crest composed most (87%) of the population (Kucera 1988); by 2005, however, that proportion had declined to <50% and continued to decline through the remainder of our study (Appendix P). During 1997–2009, we documented high fidelity to summer range, with an absence of switching summer residency between sides of the Sierra crest for adult females ($n=251$) and young ($n=26$). Given high fidelity to seasonal range, which is common among mule deer (McClure et al. 2005), dispersal was not responsible for the shifting trends in migratory segments of the population.

Habitats and annual moisture regimes differed considerably between sides of the Sierra crest (Storer et al. 2004, Bleich et al. 2006). The more mesic environment and lower deer densities on the west side of the Sierra crest probably resulted in better foraging conditions for mule deer (Monteith et al. 2013). Accordingly, females that summered on the west side of the Sierra crest were larger than east-side females, which likely represents long-term differences in summer nutrition and growth of young (Monteith et al. 2009). Similar relationships with body size were documented for caribou occupying disparate summer ranges (Crête and Huot 1993). Furthermore, females that summered on the west side of the Sierra crest were consistently in better nutritional condition in autumn after controlling for lactational costs (Fig. 26a), and remained in better nutritional condition through March (Fig. 22). Despite those nutritional benefits, survival of young on the west side of the Sierra crest during 2006–2008 was <30% that of young born on the east side. In addition, autumn recruitment of young during 1997–2008 for west-side females was only 60% that of east-side females. Long-term suppression in recruitment of young in the absence of a difference in adult survival between females occupying summer ranges on opposite sides of the Sierra crest, in conjunction with high fidelity to their summer ranges, indicates that disparity in recruitment of young was the life-history component responsible for the shift in migratory segments of the population. Examples of natural selection bringing about demographic changes in large mammals are rare.

Selective pressures for mule deer overwintering in Round Valley have shifted during the most recent decades to favor animals that reside on the east side of the Sierra crest during summer, ostensibly the result of greater predation on the west side. Populations of black bears throughout California and other western states have increased dramatically in recent decades

(Brown et al. 2009). Abundance estimates of black bears in California have increased nearly 5-fold in the last 3 decades (California Department of Fish and Game 2010), the same period that the proportion of deer migrating to the west side of the Sierra crest declined from nearly >80% to <50%. The proliferation of black bears in the Sierra Nevada may have resulted from expansion of the urban–wildlife interface (Beckmann and Berger 2003) or competitive release associated with elimination of the California grizzly bear in 1922 (Storer and Tevis 1955, Brown et al. 2009). The poor recruitment of young despite greater nutritional potential on the west side of the Sierra crest indicates that high mortality of young caused by bear predation is limiting that migratory segment of the population.

Although migration generally is presumed to be a favorable strategy (Fryxell et al. 1988), the interplay between intensity of predation and nutritional gain can determine trajectories for different migratory segments of a population (Kaitala et al. 1993, McClure et al. 2005, Middleton et al. 2013a). For example, North American elk obtained forage of 6.5% greater digestibility by migrating to higher elevation during summer than resident elk (Hebblewhite et al. 2008), which resulted in greater pregnancy rates and increased body mass of offspring during midwinter (Hebblewhite and Merrill 2011). Despite the increase in forage quality obtained by migrants, predation risk from gray wolves (*Canis lupus*) during migration was 1.7 times higher than that observed for resident elk. Lower survival of adult females and reduced recruitment of young by migratory elk resulted in a decline in the migratory segment of the population (Hebblewhite and Merrill 2007, 2009). High rates of predation for particular migratory segments of populations that have a greater nutritional potential imply that some mortality is additive if their migratory counterpart is capable of successfully recruiting disproportionately more young while on an inferior nutritional plane.

Carrying Capacity

Carrying capacity (K) in wildlife management is usually defined by the number of animals a range supports at equilibrium (i.e., long-term mean of population abundance; McCullough 1979, Macnab 1985, Kie et al. 2003). In stochastic environments, herbivore populations may rarely, if ever, be at equilibrium with their highly variable food supply (McCullough 1999), which may undermine density-related estimates of K (Macnab 1985, McLeod 1997, Kie et al. 2003), and complicate detection and interpretation of density dependence (Marshall et al. 2009). The absence of a relationship with density does not always imply an absence of density dependence, but may merely be a consequence of a fluctuating food supply. In arid environments, quality and abundance of forage is sensitive to precipitation (Sinclair et al. 1985; Marshall et al. 2005a, b; Pierce et al. 2012) and annual food supply varies markedly relative to the density of the population. Consequently, the position of the population with respect to their food supply varies not by animal density alone, but by the interaction between forage production (a consequence of environmental conditions) and population density (Sinclair et al. 1985, McCullough 1999).

Although many methods have been proposed to estimate K (or other derivations thereof) for large herbivore populations, including Ricker-like models (McCullough 1979), food-based

models (Hobbs et al. 1982, Hobbs and Swift 1985, DeYoung et al. 2000, Beck et al. 2006), and time-series models (Boyce 1989, Sæther et al. 2002, Forsyth and Caley 2006, Kaeuffer et al. 2009), all have experienced only limited application to research or management scenarios (Macnab 1985). For most approaches, data collection can be difficult and labor intensive (DeYoung et al. 2000), models are sensitive to precision of population estimates and require long-term estimates of population size (Freckleton et al. 2006, Clark et al. 2010, Knape and de Valpine 2011), and generally perform poorly in variable environments. A method of determining the capacity of habitat to support large herbivores that integrates both animal density and variation in food availability caused by environmental variation, and that is logistically feasible and tangible, is warranted. Such an approach would further our understanding of the interaction between density dependence and environmental variation (Caughley and Gunn 1993), and would be more likely to be applied in research and management of large herbivores.

Piasecke and Bender (2009) presented a new approach for estimating K for North American elk, based on the difference in autumn nutritional condition of lactating versus nonlactating elk, whereby the relative difference indicates the proximity of the population to K . Application of this technique may be limited to some monotocous species, such as elk, in which lactating females can acquire similar fat levels by autumn compared with nonreproductive females when under an adequate nutritional regime (Cook et al. 2004). For polytocous species, reproductive costs can be markedly greater (Sadleir 1982, Tollefson et al. 2010), and timing of mortality of young alters reproductive costs for the nonlactating individuals, thereby affecting the baseline reference of comparisons when determining proximity to K . Nonetheless, the use of nutritional condition is an insightful advance in identifying the proximity of a population to K .

Animal-indicated nutritional carrying capacity.—Because nutritional condition is an integrated measure of previous energetic gains and expenditures experienced by individuals (Parker et al. 2009), forage quality and quantity relative to the density of the population (density dependence) for large herbivores is inherent within that metric. Nutritional condition of a population should signify the relative position of that population to its current food supply, with the food supply being representative of nutritional carrying capacity (NCC). We propose that the relative position of a population to its annual food supply is reflected by, and thus can be determined by, the seasonal patterns of nutritional condition and population performance. We term our approach animal-indicated NCC because nutritional condition is a product of an animal's environment (animal-indicator concept; Franzmann 1985), which is determined by a population's food supply (NCC). We parameterized animal-indicated NCC based upon the nutritional condition of the population when $\lambda = 1$, which is in keeping with the classic definition of K when the population is at (or near) equilibrium with its environment (Caughley 1979). Poor nutritional condition relative to that threshold implies proximity to, or above, NCC when compared with good nutritional condition, which is typical of a population below

NCC, and is indicative of habitat conditions that support population growth.

Nutritional condition during the current March explained 32% of the variation in λ for mule deer in the Sierra Nevada (Fig. 27). An absolute increase in IFBFat of 1 percentage point yielded a predicted increase in λ of 0.06 and the predicted point of animal-indicated NCC ($\lambda = 1$) occurred at 6.7% IFBFat. Because nutritional condition is sensitive to forage growth, competition for forage, and carryover from the previous year (Fig. 22), the actual number of individuals that can be supported at animal-indicated NCC during a particular year may vary. This approach does not require the herbivore population to be at equilibrium with its environment and, therefore, should be of value for estimating NCC in stochastic systems.

We admonish that animal-indicated NCC does not represent a long-term equilibrium density that may be referred to as K but, instead, represents the short-term capacity of the environment to support population growth as a function of resource availability and animal density. For example, we observed a mean IFBFat in March near 6.7% when estimated population size was 1,250 animals in 1992 and 2,281 animals in 1998. Water content of snowpack the preceding April was markedly lower for 1992 (15.7 cm), and higher for 1998 (45.7 cm) than the 24-year average (26.3 cm). Differences in habitat conditions as a function of snowpack and browsing pressure the preceding year likely were responsible for the differences in the number of animals the habitat could support at a nutritional level of 6.7% IFBFat, and determined the expected population performance the following year. Carryover effects of life history and nutrition from the previous season affect populations (Harrison et al. 2011), both of which are inherent in estimates of animal-indicated NCC (Fig. 23). Nutritional status at one point in time provides a reference point of nutritional history and nutritional carryover to the following season (Monteith et al. 2013).

Using the long-term mean or historical highs in population size to estimate K can be deceptive when true changes in K have occurred as a result of habitat alteration or changing climate. For example, in Round Valley an alfalfa ranch (approx. 0.36 km²) that was frequented by hundreds of deer on a daily basis during winter was enclosed in the late-1980s. In addition, in June 1995, a fire burned 22 km² (approx. 24%) of primary winter range in an area dominated by bitterbrush and sagebrush in Round Valley. Because of the intensity of the fire, little regrowth of bitterbrush occurred in subsequent years, and the burned area has become dominated by desert peach and cheat grass (*Bromus tectorum*), both of which offer little forage value to deer (Pierce et al. 2004). Based on the nutritional limitation and leveling of the population size that we observed between 1991 and 2009 as the population recovered from the crash in the late 1980s, habitat in Round Valley can no longer support the abundance of deer present in the 1980s (Fig. 5)—a conclusion that would have been far less certain or more speculative without data on nutritional condition. Patterns of nutritional condition were indicative of increased nutritional limitation as the population approached 3,000 animals, indicating that animal-indicated NCC was reached well below the nearly 6,000 animals in 1985 (Fig. 5), and that K has decreased to <2,500 animals. This outcome illustrates the importance of avoiding the use of historical levels of ungulates to

estimate K , and that concluding habitat is not limiting because animal densities are lower than previously documented is poorly justified. These complications reinforce the use of animal-indicated NCC, because that metric directly accounts for changes, whether by habitat alteration or climate, in the nutritional capacity of the habitat.

Predation risk may affect habitat use and foraging efficiency for large herbivores (Bleich et al. 1997, Bleich 1999, Creel and Winnie 2005, Schroeder et al. 2010); however, the links of those non-consumptive effects of predation with prey demography and how non-consumptive effects scale up to influence the ability for large herbivores to make use of available habitats remain uncertain (Lima 2002, Christianson and Creel 2008, Creel and Christianson 2008, White et al. 2011, Middleton et al. 2013b). If predation risk limits the ability of individuals to make complete use of available habitats and reduces foraging efficiency and energetic gain, then nutritional interactions between large herbivores and their habitat may be modified because of the distribution of forage and risky habitat in the presence of large carnivores (Creel and Christianson 2008) or other novel disturbances (Sawyer et al. 2009, Wasser et al. 2011). Regardless, those non-consumptive effects are inherently incorporated in estimates of animal-indicated NCC. We postulate that experiments incorporating in vivo measures of nutritional condition with changes in use of space will provide the best means to directly test risk-effect hypotheses, because the physiological costs can be quantified (White et al. 2011, Middleton et al. 2013b), and models can be developed to account for state-dependent behavior (Monteith et al. 2011, Lendrum et al. 2013) and use of habitat (Morales et al. 2010).

Despite many advantages, an approach incorporating nutritional condition to estimate animal-indicated NCC may be of less value for populations of large herbivores that are maintained at low density by predation or other sources of mortality. Nutrition in those populations is not a major limiting factor; females are in good nutritional condition and population growth is regulated by predation rather than nutrition (Gasaway et al. 1992, Bowyer et al. 2005, Boertje et al. 2007)—much like females residing on the west side of the Sierra crest that experienced heavy and additive predation by black bears (Figs. 9 and 29b). Nutritional condition, however, would reflect potential top-down forcing by predators and the lack of bottom-up forcing, indicating that habitat was not a major limiting factor (Bowyer et al. 2005).

Another potential weakness in the use of nutritional condition to calibrate animal-indicated NCC is the confounding effect of pathogens or other diseases on nutritional condition; prevalence of specific pathogens, parasites, or diseases can have a negative influence on nutritional condition. For example, tick infestations were attributed to nutritional deprivation and eventual death for moose in New Hampshire (Musante et al. 2010). Infections and nutritional status may be interactive because malnutrition can lead to immunosuppression and greater parasitism and disease, whereas pathogens cause tissue damage and have a negative effect on energy balance, resulting in greater nutritional suppression (Gulland 1992, Holmes 1995, Sams et al. 1995, Gunn and Irvine 2003). Knowledge of the nutritional status of the population or individuals relative to other mortality factors

related to disease could provide the inference necessary to disentangle pathological and nutritional limitation, or their synergistic effects, just as it can for patterns of mortality.

Consequences of Mortality

The ultimate causes and consequences of mortality are fundamental questions in population ecology, management, and evolutionary biology (Messier 1994, Metcalf and Pavard 2007, Griffin et al. 2011, Pettorelli et al. 2011, Connelly et al. 2012). In particular, the influence of predation by large carnivores on population dynamics of ungulates has been hotly debated (Ballard et al. 1991, 2001; Boutin 1992; Powell 2001), and remains a controversial topic (Bowyer et al. 2005, 2013; Griffin et al. 2011). Interpreting predator–prey relationships are difficult considering the myriad of factors that influence their dynamics including climate, diversity and abundance of predators and prey, habitat conditions, and nutrition (Van Ballenberghe and Ballard 1994, Linnell et al. 1995, Lima 2002, Sinclair et al. 2003, Griffin et al. 2011, Grovenburg et al. 2012b).

The relative influence of mortality on limiting a prey population is characterized by its additive or compensatory effects on population growth. The concepts underlying the consequences of mortality for prey populations originally were formulated by Errington (1946) based on his observations that prey populations contain a surplus of individuals that are doomed to face mortality each year, which he coined the “doomed surplus.” Predation that cuts only into the doomed surplus has no net effect on prey population growth (compensatory mortality), whereas predation taking more than the doomed surplus (additive mortality) results in a prey population maintained at a lower level than would have occurred in the absence of such predation (Errington 1956). Therefore, compensatory mortality operates under the fluxes of density dependence, where a decrease in population density with respect to NCC lessens intraspecific competition for resources resulting in decreased natural mortality rates and, subsequently, the potential for increased survival and reproduction (Boyce et al. 1999). Indeed, differentiating between the proximate and ultimate causes (Mayr 1961) of mortality is necessary to understand the population dynamics of ungulate populations. The killing of an individual results in a numerical change in the population and is thus limiting (Sinclair 1991), but this alone is not very informative and its relative consequence is inextricably linked to the level of density dependence (i.e., nutritional limitation) within the population (Van Ballenberghe and Ballard 1994, Pierce et al. 2012). Nevertheless, the interaction between mortality because of predation or malnutrition is difficult to disentangle without manipulative experiments or other means of assessment (Boutin 1992).

Numerous investigators have confronted the challenge of identifying the relative effects of predation on prey populations by comparing rates of predation or malnutrition, population density, and winter severity among populations or years (Ballard et al. 2001, Barber-Meyer et al. 2008, Boertje et al. 2009, Garrott et al. 2009, White et al. 2010). In these instances, authors often were faced with the challenge of interpreting the consequences of mortality without direct knowledge of the nutritional status of the population. The conclusion that mortality is additive because mortality rates were high compared with other populations or

during another time, or because predation rates remained constant through time without sufficient evidence describing the nutritional status of the population, is potentially erroneous. Interannual variability in environmental conditions, density, carryover effects from previous seasons, and potential changes in NCC, make temporal and between-population comparisons of mortality rates and their consequences tenuous (Kie et al. 2003).

Another approach used to distinguish additive versus compensatory mortality that has experienced increased use in recent years (Griffin et al. 2011, Brodie et al. 2013, Johnson et al. 2013) is to regress rates of mortality caused by predation against overall survival rates. Predation rates that correlate negatively with survival rates are assumed to be additive (Anderson and Burnham 1976, Schaub and Lebreton 2004); but when predation is compensatory, no relationship is expected between predation and survival. Although this method is novel and seemingly intuitive, the basis for distinguishing differences in the consequences of specific mortality causes is circular, because survival rate is inherently an artifact of mortality (i.e., predation) rate and, thus, may be of value only for demonstrating which proximate mortality factors are driving survival rate. Furthermore, vulnerability to predation is influenced by individual variability in the vitality and size of prey, and prowess and size of the predator (Fitzgibbon and Fanshawe 1989, Kunkel et al. 1999, Husseman et al. 2003, Sinclair et al. 2003, Barber-Meyer et al. 2008), which may dictate the likelihood that a specific predator could have an additive effect on a prey population, but does not imply that predation was additive (Errington 1946, 1956, 1967).

Some advances have been made in elucidating the relative influence of these ecological processes (Burnham and Anderson 1984, Bowyer et al. 2005, Servanty et al. 2010), but little progress has been made regarding a quantitative approach to characterize compensatory versus additive mortality for large ungulates. Failure to recognize the underlying mechanism dictating the population-level consequences of mortality likely has hampered progress in this field, yet that underlying mechanism has been identified in experimental studies.

Bartmann et al. (1992) evaluated effects of coyote predation on survival of young mule deer by manipulating the presence of predators. The proportion of animals lost to predation simply replaced those lost to malnutrition when predators were absent. The study emphasized that the number of individuals lost to malnutrition (often used to reference compensatory mortality) was not a good reference to the consequences of mortality, which is a common fallacy in predator–prey studies. Malnutrition is an obvious consequence of nutritional limitation in the absence of predators; however, in the presence of large carnivores, losses to malnutrition can be replaced by predation, thereby clouding interpretation of the underlying effects of mortality. Tveraa et al. (2003) monitored survival of neonatal reindeer after being released at approximately 5 weeks of age from a predator-free enclosure following mild and severe winters. High losses of young to predators occurred following the severe winter when females were food limited. In contrast, after the mild winter, when females were in markedly better physical condition, no loss to predation occurred (Tveraa et al. 2003). Loss of young to predation in both studies was

conditional upon nutrition—the underlying factor dictating the consequences of mortality.

We propose that the consequences of mortality, regardless of the cause, can be determined based on an assessment of the nutritional capacity for survival and reproduction. In predation-regulated systems, the nutritional capacity for survival or recruitment is greater than what is observed (Fig. 4), compared with resource-regulated systems where nutritional capacity for survival or recruitment is similar to that observed. As populations approach NCC, females attempt to produce more young than the habitat can support (McCullough 1979); that is, the nutritional capacity to recruit young is less than what females attempt to recruit (Fig. 4). The difference between those values indicates the amount of mortality that is potentially compensatory. Mortality that reduces recruitment to the nutritional potential in any 1 year is compensatory, with greater mortality transitioning toward having an additive effect on recruitment (Fig. 4). Resource availability and density are inherently linked to determine nutritional condition, and dictate the nutritional capacity for adults to survive and for females to produce and rear young. Therefore, estimating the nutritional capacity for survival or recruitment should provide a reference for the degree to which mortality is compensatory or additive relative to observed survival and recruitment. Indeed, studies have demonstrated positive effects of predator removal for ungulate populations that were not resource-limited (i.e., those in which predation had an additive effect; Gasaway et al. 1983, Kie and White 1985, Gasaway et al. 1992, Hegel et al. 2010a, White et al. 2010), compared with those that were resource-limited when predator removal had little effect (i.e., those in which predation was compensatory; Bartmann et al. 1992, Ballard et al. 2001, White et al. 2010, Hurley et al. 2011).

Adult survival.—Life-history theory and empirical evidence for long-lived ungulates indicate that females should favor their own survival over reproductive allocation, which results in adult survival being relatively insensitive to resource limitation (Unsworth et al. 1999, Eberhardt 2002, Bonenfant et al. 2009). Nonetheless, during rare conditions such as extreme drought (Bender et al. 2007, Pierce et al. 2012) or severe winter conditions (DeGiudice et al. 2006), adult mortality may be constrained by nutritional deprivation as a result of reductions in NCC. During the severe drought in Round Valley in the late 1980s, estimated adult survival of female mule deer was the demographic largely responsible for the population crash (Pierce et al. 2012); however, that change in vital rate was underpinned by severe nutritional deprivation likely caused by an overshoot of NCC. Therefore, mortality of adult females during the population crash was largely compensatory, because fewer animals could be supported following the reduction in food supply (Pierce et al. 2012). Following the population crash, adult survival was high and relatively consistent with modest influences of forage availability on survival (Table 8).

Survival of young.—Survival and recruitment of young are typically highly variable, and sensitive to nutritional limitation and the maternal capacity to support reproduction (Gaillard et al. 1998, 2000; Eberhardt 2002). Because female ungulates rely on nutritional capital and income to support reproductive allocation (which influences survival of young), accounting for

variation attributable to nutrition while removing other external factors not related to nutrition in predictive models should yield the nutritional potential for recruitment of young. Interannual patterns in the young-to-adult female ratio in the Sierra Nevada closely mirrored that expected based on the nutritional state of the population, indicating that from 1992 to 2009, mortality of young at the level of the population was mostly compensatory (Fig. 28). Contrasting patterns of autumn recruitment of young emerged when we compared the 2 migratory segments within the mule deer population wintering in Round Valley. Observed recruitment was mostly compensatory for females that summered on the east side of the Sierra crest, whereas recruitment of young by west-side females often was less than what should have been possible based on their nutritional capacity to provision young (Fig. 29). Mortality of young that had a large additive component (0.30 young per female per year) for females that occupied the west side of the Sierra crest supports the hypothesis that changes in predation, mostly by black bears, were responsible for the shift in the proportion of migratory segments within the population of mule deer wintering in Round Valley in recent decades (Fig. 3).

The influence of bear predation on survival of neonatal ungulates has been emphasized in a number of recent studies (Linnell et al. 1995, Bowyer et al. 1998a, Zager and Beecham 2006, Barber-Meyer et al. 2008, Griffin et al. 2011, Middleton et al. 2013c). Bears specialize on neonates during the period of greatest vulnerability within the first few weeks of life (Fig. 9b; White et al. 2010, Griffin et al. 2011). Consequently, among large carnivores, bears have been proposed to have the greatest potential to affect dynamics of ungulate populations, because vulnerability of neonates may not strongly reflect nutrition at that age (Barber-Meyer et al. 2008, White et al. 2010). Although greater nutritional limitation within a population will inherently result in an increase in the proportion of prey predisposed to mortality, viewing compensatory versus additive mortality as a function of the vulnerability of individual prey—especially neonates—is misleading because the true consequences of mortality are based on the nutritional capacity of the habitat. Documenting that predation by a particular predator seems to be unaffected by the condition of prey indicates the potential for that predator to have an additive effect, but does not imply that all deaths because of predation were additive. Mortality of neonates on one side of the Sierra crest was partially additive (Fig. 29b), whereas mortality of neonates on the other side was largely compensatory (Fig. 29a).

Our approach for assessing the consequences of mortality on a population provides a simple, yet sensitive, measure for determining whether recruitment patterns of young are limited purely by nutrition (i.e., mortality is compensatory), or if other extrinsic factors such as predation are having a partially additive effect on mortality. We recognize that model predictions were determined from field data and, thus, may not reflect the true nutritional capacity to support young when predation or other extrinsic factors interact to influence the potential for survival and reproduction (Fischhoff et al. 2007, Christianson and Creel 2010, Hegel et al. 2010b). Placing individuals on an identical nutritional regime in captivity would likely yield higher recruitment, because young exhibiting poor growth and vigor may survive in captivity, but be predisposed to predation where

predators occur. Nonetheless, the interaction among nutrition, weather, and predation in a natural system should reveal the nutritional capacity to recruit young in light of other competing risks, and should provide a conservative and realistic estimate of the nutritional ability of females to recruit young.

We caution that attempts to conclude whether mortality is purely additive or purely compensatory are likely misguided. Purely additive mortality would only occur when the population is in superb nutritional condition (i.e., density well below NCC), and mortality would be purely compensatory only when nutrition is limiting and mortality rates do not exceed the nutritional potential for survival and reproduction (e.g., east-side females; Fig. 29a). Between those 2 endpoints, however, mortality up to a certain point (depending on the proximity to NCC) is compensatory, with higher levels of mortality becoming increasingly additive (Fig. 4). For mule deer in Round Valley during 1997–2008, in no single year was all mortality additive given the nutritional limitation that we observed (Fig. 29) but, instead, was compensatory to a specific level of mortality and transitioned to being additive when levels of mortality forced recruitment below what was nutritionally achievable. This pattern of compensatory versus additive mortality is in accordance with that proposed in conceptual models by others (McCullough 1979, Kie et al. 2003, Bowyer et al. 2005), and indicates that compensatory and additive mortality should be viewed as more of a continuum rather than as a dichotomy, because both processes can occur within a single year and population.

We recognize that patterns of recruitment of young may not be as sensitive to nutritional condition for all species or systems. The approach proposed herein should work well for species that rely heavily on current capital to support reproduction such as bighorn sheep (Festa-Bianchet 1998), moose (Testa and Adams 1998, Keech et al. 2000), or North American elk and red deer (Landete-Castillejos et al. 2003, Cook et al. 2004). Nevertheless, for more income-based breeders, incorporating variables that describe the nutritional capacity of females to support reproduction such as timing and rate of spring green up (Pettorelli et al. 2007, Post et al. 2008), population density (Andersen et al. 2000), spring and summer precipitation (Marshall et al. 2005a, b; Lomas and Bender 2007; Tollefson et al. 2011), or other climatic factors (Albon et al. 1983a) may provide the information necessary to explain the variation in recruitment patterns caused by nutrition. Moreover, factors such as density or winter severity could be incorporated into models for overwinter survival of young, and be used to explain variation caused by interactions of forage availability with severe weather (Bartmann et al. 1992, White and Bartmann 1998, Hurley et al. 2011). Additionally, an absence of a relationship between nutritional condition and patterns of recruitment for a capital breeder could be indicative of strong top-down forcing. Such forcing should result in ungulate populations held well below NCC. Therefore, nutritional condition would be high and not strongly related to recruitment, because high rates of predation, despite good nutrition, would limit annual recruitment.

MANAGEMENT IMPLICATIONS

Monitoring programs for large herbivores often seek to determine population trajectory, or total population size to

interpret effects of harvest, predation, and other factors that might be limiting or regulating populations, because animal abundance is usually considered the minimal information necessary for management. Nonetheless, estimating population size of large herbivores that occupy broad geographic regions with reasonable precision and accuracy is difficult and often cost-prohibitive (Jachmann 2002, Morellet et al. 2007). Attempts frequently are made to interpret time-series data of population size; however, pattern-oriented analyses of those data are limited in their ability to detect factors underlying population dynamics (Coulson et al. 2000). Moreover, estimates of population density alone provide no inference about the relationship between population and habitat (i.e., proximity to NCC), yet understanding that relationship is critically important to informed management of large herbivores. Management of large herbivores may be improved if resources invested in monitoring programs are aimed at variables of greater ecological relevance than simple estimates of abundance (Morellet et al. 2007).

Empirical estimates of vital rates that underpin population trajectories provide important information regarding the dynamics of ungulate populations, but are difficult and costly to obtain, and require monitoring for multiple years (Lebreton et al. 1992, White and Lubow 2002, Johnson et al. 2010). Much like abundance estimates, data on vital rates also lack a mechanistic foundation. Morellet et al. (2007) called for the use of appropriate ecological indicators to assess the response of animals to their habitat, thereby providing a quantitative basis for management decisions. Dale and Beyeler (2001) noted that useful ecological indicators should be measured easily, be sensitive to factors affecting the system, respond in a predictable manner, be anticipatory, predict changes that can direct management actions, be integrative, and have a consistent response to system changes. We propose that nutritional condition is the most insightful ecological indicator for research, management, and understanding population dynamics of large herbivores. Nutritional condition can be accurately quantified by both in vivo and post-mortem measures (Stephenson et al. 1998, 2002; Cook et al. 2010); is sensitive to and responds in a predictable manner to density-dependent availability of forage, habitat conditions, and individual life-history traits; holds predictive value for future performance (including λ) in populations regulated by bottom-up factors; is an integrative measure of the current nutritional state of the population when viewed at the population level; and incorporates previous nutritional gains and debts relative to life history at the individual level (Table 11).

Combining data on nutritional condition with routine monitoring data such as recruitment patterns of young and occasional abundance estimates should provide greater insight to interpret factors underpinning population growth and, thus, allow for empirically driven management. Using a nutritional approach to monitor and manage populations reduces the need to estimate population abundance or set goals according to population size. Alternatively, management goals can be set according to measures of nutritional condition and the proximity of a population to animal-indicated NCC.

We recommend monitoring nutritional condition and population density over a period of years, depending upon the

fluctuations in population size and conditions, to uniquely define the relationship between λ , population size, and nutritional condition. When funds to cover such an expense are unavailable, animal condition could be determined from harvested females (as long as seasonality is recognized) or with small capture efforts each year or every few years. Implementing special antlerless hunts, with required examination of harvested animals for data acquisition, would provide valuable data on nutritional condition at minimal cost, while simultaneously allowing increased recreational opportunity and the opportunity for stakeholders to be involved with data collection. Those data could be used to understand the nutritional status of the population relative to relationships or expectations that have been established in other studies for that species and, at a minimum, should indicate the potential degree of bottom-up forcing within the population (Bowyer et al. 2005). Those few data also would yield expectations for population growth in subsequent years, and anticipated effects of management strategies.

Because nutritional condition indicates the position of a population relative to animal-indicated NCC, harvest criteria can be based on a desired nutritional level as indexed by measures of nutritional condition. For example, a realistic goal with respect to incorporating female harvest for mule deer in Round Valley could be one of reducing density to lower competition for resources and maintain a mean IFBFat level of approximately 7%, which was near animal-indicated NCC for mule deer in that population (Fig. 27). Reducing density with respect to NCC would result in improved nutritional condition and increased recruitment of young, especially for females summering on the east side of the Sierra crest. Improved nutritional condition also could result in less variable population dynamics because the population would potentially be better buffered against environmental perturbations (Kie et al. 2003).

We caution that immediately adjusting harvest in response to changing nutritional status in a stochastic environment may be problematic, because animal-indicated NCC represents the short-term capacity of the habitat and is thus, sensitive to environmental variation. An emphasis on more long-term goals of the proximity to animal-indicated NCC is a more reasonable strategy for density-dependent species, where the harvest determines the surplus because of feedbacks of enhanced nutrition and younger age structure with reduced population size relative to NCC (Leopold 1933, McCullough 1979, Boyce et al. 1999). The position of a population relative to animal-indicated NCC can fluctuate from year to year in response to environmental variation, which is beyond the control of managers unless densities are reduced in an attempt to improve nutritional condition and reduce the influence of massive fluctuations in food supply. We recommend parameterizing where the population is with respect to animal-indicated NCC, and examining how the proximity of the population to animal-indicated NCC responds to various levels of harvest.

Evidence of additive mortality often is used as a justification for predator control to increase ungulate populations (Ballard et al. 2001), which highlights the need to interpret the consequences of mortality correctly. We offer a new approach for quantifying the influence of predation on large ungulate populations by assessing the degree of compensatory or additive

mortality based on the nutritional capacity to produce and provision young. From a management perspective, if nearly all mortality is compensatory, and thus is a function of interannual patterns of nutrition, then predator control would yield little change in population performance (Ballard et al. 2001, Hurley et al. 2011). In those situations, management efforts should focus on strategies to enhance nutrition, such as habitat improvements or density reductions (McCullough 1979, Bishop et al. 2009).

The combined effects of anthropogenic and climate-induced changes in habitat for mule deer may have reduced K of mule deer range throughout western North America, thereby affecting population trends through nutritionally mediated reductions in recruitment of young. We suggest that incorporating indices of nutritional condition (i.e., estimates of body fat) into current monitoring and research programs holds the greatest potential for disentangling the relative effects of habitat alteration, climate, and predation on the population dynamics of mule deer and other large herbivores. Moreover, linking habitat use and selection with change in nutritional condition and fitness among seasons will provide a means to quantify the net benefits of particular habitat assemblages or habitat treatments.

SUMMARY

- Our goal was to evaluate the nutritional basis of life-history strategies and population ecology of free-ranging mule deer to aid in the management of large herbivores.
- We obtained longitudinal data on 347 individual females in a population of mule deer in the Sierra Nevada, California, USA, during 1997–2009 as it recovered from a population crash during 1985–1991.
- Survival and recruitment of young was highly variable, and was strongly influenced by nutritional condition at the population level. Maternal nutritional condition had a strong influence on survival and recruitment of young except under intense predation, mostly by black bears, wherein nutritional relationships with probability of survival of young were diluted.
- Summer residency of females affected probability of recruiting young; females that summered on the west side of the Sierra crest recruited fewer young than females summering on the east side, despite better nutrition on the west side. Primary proximate cause of mortality for neonates on the west side was predation by black bears (cause-specific mortality = 0.63), compared with low bear predation on neonates born on the east side of the Sierra crest (0.041).
- Reproduction by yearling females was sensitive to foraging conditions during summer as a function of per capita snowpack (a density-dependent index to annual forage growth) that determined whether yearling females reached sufficient body mass (>41 kg in Mar) to conceive.
- Litter size of adult females ≥ 2.5 years old was less variable and less sensitive to resource limitation when compared to yearling females, but was influenced moderately by per capita snowpack and summer temperatures, which influenced forage availability.
- Pregnancy of adult females ≥ 2.5 years old was high and constant (0.98) throughout our study. Adult females failed to exhibit senescent effects on fecundity up to 15.5 years of age.

- Seasonal survival of adult females exhibited minor variation among years with only modest effects of resource limitation. Females exhibited actuarial senescence at >9.5 years of age, but that decline in survival with age was most prominent during winter.
- Nutritional condition of adult females during both winter and summer was sensitive to the nutritional history of individual animals, including forage growth, population density, migratory tactic, reproductive allocation, and nutritional carryover. Nutritional condition of adult females in March also was the most parsimonious predictor for λ during the forthcoming year.
- Nutritional status of a population can provide inferences about the proximity of a population to NCC (termed animal-indicated NCC), even in stochastic environments.
- Partially additive predation, mostly by black bears, was the likely explanation for shifting selective pressures on migratory tactic as individuals migrating to the west side of the Sierra crest declined from 87% of the population in 1985 to <50% by 2005.
- We offer a new approach to assess the consequences of mortality on population dynamics that is based on the nutritional capacity to recruit young. Our approach provides a mechanistic basis for gauging the effectiveness of predator-management programs.
- Our results indicate that management and conservation of large herbivores would be improved by integrating indices of nutritional condition into current monitoring and research programs.

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Appendix A. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis of survival of neonatal mule deer from birth to 20 weeks of age evaluated at the population ($n = 119$), individual ($n = 113$), and maternal levels ($n = 73$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero and results were based on $\hat{c} = 1.18$.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	0.98*	0.49	1.47	1.00
	Spring precipitation	0.097	−4.09	4.29	0.28
	Spring temperature	0.023	−5.19	5.24	0.31
	Summer precipitation	−0.033	−4.89	4.82	0.33
	Summer temperature	−0.065	−4.35	4.22	0.33
	Snowpack	2.7×10^{-3}	−0.16	0.17	0.24
	Number female	9.5×10^{-5}	−0.014	0.014	0.26
	Mean March IFBFat	0.013	−2.34	2.37	0.18
	Stage ^a				1.00
	Year				0.02
Individual	Summer residency	0.33	−0.45	1.10	1.00
	Stage ^a				1.00
	Age at capture	0.035	−0.017	0.086	0.49
	Sex	0.062	−0.087	0.21	0.29
	Litter size	2.8×10^{-3}	−0.092	0.087	0.21
	Julian birth	1.7×10^{-3}	-9.1×10^{-3}	5.7×10^{-3}	0.22
	Deviation from mean birth	0.039	-2.8×10^{-3}	0.081	0.68
	Birth mass ^b	0.73*	0.19	1.27	1.00
	Summer residency \times birth mass ^b	1.19*	0.61	1.78	1.00
	Summer residency	−2.19	−4.64	0.24	1.00
Maternal	Stage ^a				1.00
	Birth mass ^b	0.25	−0.34	0.85	1.00
	Summer residency \times birth mass ^b	1.82*	0.84	2.80	1.00
	Deviation from mean birth	0.024	−0.013	0.061	0.46
	Mar IFBFat ^c	−0.068	−0.46	0.32	1.00
	Summer residency \times Mar IFBFat ^c	0.39*	0.089	0.68	1.00
	Age	2.9×10^{-3}	−0.033	0.027	0.27
	Mar body mass	5.1×10^{-3}	−0.012	0.022	0.29

^a Stage-specific variable that allowed survival to vary during the first 4 weeks, with constant survival the remaining 16 weeks.

^b Age-specific effect of birth mass on survival during the first 3 weeks of life.

^c Age-specific effect of March ingesta-free body fat (IFBFat) on survival during 4–20 weeks old.

Appendix B. Model-averaged parameter estimates and Akaike importance weights from an analysis to determine the factors that influence cause of mortality of neonatal mule deer evaluated at the population ($n = 62$), individual ($n = 57$), and maternal levels ($n = 47$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Cause of mortality ^a			Importance weight
		Bear	Other natural	Other predation	
Population	Summer residency	−2.39*	0.50	1.47	1.00
	Per capita snowpack	−37.32	−16.67	7.29	0.47
	Mean Mar IFBFat	0.35	0.042	−0.13	0.24
	Year				0.04
Individual	Summer residency	−2.67	1.91	2.86	1.00
	Litter size	−0.15	−0.011	−0.072	0.10
	Julian birth	0.082	0.11	0.11	0.34
	Sex	0.56	1.35	1.36	0.39
	Age at death	0.26	0.25	0.25	0.64
	Birth mass	2.21*	3.16*	3.30*	1.00
	Summer residency	−0.041	3.3×10^{-3}	9.0×10^{-3}	0.02
Maternal	Age at death	0.19	0.19	0.19	0.45
	Birth mass	1.96*	2.47*	2.44*	0.98
	Age	3.0×10^{-3}	−0.063	0.21	0.61
	Mar IFBFat	−0.41	−0.19	−0.44	0.43
	Mar body mass	0.015	0.017	0.024	0.28

IFBFat, ingesta-free body fat.

^a Multinomial logistic regression included malnutrition as the reference category thus, parameter estimates represent the relative likelihood of dying from a particular cause compared with malnutrition.

Appendix C. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence birth mass (kg) of neonatal mule deer evaluated at the population ($n=113$), individual ($n=113$), and maternal levels ($n=55$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	0.066	−0.050	0.18	0.40
	Per capita snowpack	−0.13	−0.44	0.70	0.07
	Spring precipitation	1.6×10^{-4}	-8.7×10^{-4}	5.5×10^{-4}	0.01
	Spring temperature	−0.037	−0.11	0.040	0.31
	Mean Mar IFBFat	−0.010	−0.028	8.2×10^{-3}	0.05
	Year				0.00
Individual	Julian birth	1.1×10^{-4}	-4.8×10^{-4}	2.7×10^{-4}	0.02
	Sex	0.083	−0.037	0.20	0.46
	Litter size	−0.21*	−0.37	−0.055	0.82
Maternal	Litter size	−0.37*	−0.60	−0.14	0.93
	Age	-1.3×10^{-3}	-5.5×10^{-3}	2.8×10^{-3}	0.08
	Mar IFBFat	−0.051	−0.010	6.0×10^{-4}	0.56
	Mar body mass	-5.6×10^{-3}	−0.016	3.9×10^{-3}	0.27

IFBFat, ingesta-free body fat.

Appendix D. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence date of parturition of mule deer evaluated at the population ($n=88$), and maternal levels ($n=55$), Sierra Nevada, California, USA, 2006–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−4.08*	−7.22	−0.94	0.98
	Per capita snowpack	−31.71	−91.79	28.37	0.47
	Spring precipitation	−0.18	−0.51	0.16	0.35
	Spring temperature	−0.58	−1.80	0.65	0.42
	Mean Mar IFBFat	−0.82	−2.27	0.63	0.51
	Litter size	2.93*	0.74	5.12	0.97
	Year				0.10
Maternal	Summer residency	−5.48*	−8.45	−2.52	1.00
	Mean Mar IFBFat	−1.53	−3.83	0.77	0.88
	Litter size	5.86*	3.10	8.63	1.00
	Age	0.20	−0.15	0.56	0.58
	Mar IFBFat	−0.13	−0.56	0.30	0.56
	Mar body mass	−0.36*	−0.65	−0.073	0.99

IFBFat, ingesta-free body fat.

Appendix E. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence annual age ratios ($n=17$) evaluated at the population level, Sierra Nevada, California, USA, 1991–2009. Herd composition and population estimates from 1991 to 1996 were obtained from Pierce et al. (2012). We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Parameter	Estimate	90% CI		Importance weight
		Lower	Upper	
Mean Mar IFBFat _{<i>t</i>−1}	2.28*	1.12	3.53	0.99
Mean Mar IFBFat _{<i>t</i>}	3.21*	1.89	4.50	1.00
Mean Mar body mass	−0.41	−1.52	0.70	0.72
Mean litter size	2.89	−27.43	33.22	0.99
Per capita snowpack	44.61	−132.33	221.58	0.78
Summer precipitation	0.29	−1.20	1.78	0.75
Summer temperature	−5.58	−11.41	0.24	0.97

IFBFat, ingesta-free body fat; $t-1$, previous year; t , current year.

Appendix F. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence autumn recruitment of young for adult (>1 yr) female mule deer evaluated at the population ($n = 578$) and individual levels ($n = 484$), Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	0.27*	0.18	0.36	1.00
	Per capita snowpack	5.44	−1.22	12.1	0.96
	Summer precipitation				0.00
	Summer temperature	6.2×10^{-3}	-6.7×10^{-3}	0.019	0.15
	Mean Mar IFBFat	0.090*	0.032	0.15	0.84
Individual	Year				0.00
	Summer residency	0.35*	0.25	0.45	1.00
	Per capita snowpack	2.30	−3.66	8.27	0.88
	Mean Mar IFBFat	0.17	-8.9×10^{-3}	0.043	0.17
	Age	1.2×10^{-3}	-2.5×10^{-3}	4.8×10^{-3}	0.15
	Mar IFBFat	0.025*	3.9×10^{-3}	0.046	0.83
	Litter size	0.12*	9.3×10^{-3}	0.23	0.94
	Mar body mass	7.3×10^{-3}	-3.3×10^{-3}	0.018	0.92

IFBFat, ingesta-free body fat.

Appendix G. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence primiparity of yearling (1.5 yr) female mule deer evaluated at the population ($n = 22$) and individual ($n = 22$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−0.54	−6.85	5.77	0.47
	Per capita snowpack	92.86*	3.58	182.12	0.64
	Summer precipitation	0.86	−3.32	5.05	0.32
	Summer temperature	−0.77	−1.99	0.45	0.43
	Mean Mar IFBFat _{<i>t</i>−1} ^a	−1.76	−13.86	10.34	0.19
	Mean Mar IFBFat _{<i>t</i>−2} ^a	1.31	−8.33	10.95	0.22
Individual	Year				0.00
	Per capita snowpack	11.96	−7.98	31.90	0.09
	Mar IFBFat _{<i>t</i>−1} ^a	3.9×10^{-2}	−0.26	0.18	0.30
	Mar body mass _{<i>t</i>−1} ^a	0.51*	0.044	0.98	0.91

^a We used March ingesta-free body fat (IFBFat) and body mass because sample size ($n = 7$) for November was insufficient; $t - 1$, previous year; $t - 2$, 2 years prior.

Appendix H. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence litter size of adult (≥ 2 yr) female mule deer evaluated at the population ($n = 803$) and individual ($n = 803$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50 . Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−0.11*	−0.17	−0.043	0.88
	Per capita snowpack	2.95*	0.96	4.95	1.00
	Summer precipitation	2.6×10^{-5}	-5.8×10^{-5}	1.0×10^{-4}	0.02
	Summer temperature	−0.042	−0.058	-8.1×10^{-3}	0.68
	Mean Nov IFBFat ^a	1.5×10^{-3}	-1.2×10^{-3}	4.3×10^{-3}	0.02
	Year				0.05
Individual	Summer residency	−0.11*	−0.18	-5.0×10^{-2}	0.92
	Per capita snowpack	4.12*	1.98	6.13	0.93
	Summer temperature	−0.031*	−0.062	-1.2×10^{-4}	0.63
	Age	-1.9×10^{-4}	-3.3×10^{-4}	7.1×10^{-4}	0.02
	Age ²	-1.0×10^{-5}	-2.9×10^{-5}	8.8×10^{-5}	0.02
	Nov IFBFat ^a	1.0×10^{-4}	-5.1×10^{-4}	7.2×10^{-4}	0.05
	Nov body mass ^a	1.5×10^{-4}	-3.1×10^{-4}	6.1×10^{-4}	0.04

^a We obtained results for November ingesta-free body fat (IFBFat) and body mass from a separate set of models using a subset of data ($n = 268$) during 2002–2008.

Appendix I. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis of summer (Apr–Oct) survival of adult (>1 yr) female mule deer evaluated at the population ($n=944$) and individual ($n=830$) levels, Sierra Nevada, California, USA, 1998–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	0.070	−0.086	0.23	0.33
	Montly precipitation	-6.6×10^{-3}	−0.028	0.014	0.19
	Monthly temperature	−0.30	−0.65	.060	0.44
	Snowpack	0.011*	1.2×10^{-3}	0.020	0.72
	Number female	-2.7×10^{-3} *	-3.9×10^{-3}	-1.5×10^{-3}	0.94
	Mean Mar IFBFat	0.18	-6.9×10^{-4}	0.36	0.66
	Month				0.42
Individual	Year				0.06
	Snowpack	0.014*	2.4×10^{-3}	0.025	0.80
	Number female	-2.3×10^{-3} *	-3.7×10^{-3}	-8.5×10^{-4}	0.98
	Mean Mar IFBFat	0.26*	0.036	0.49	0.79
	Age	−0.60*	−1.10	−0.11	1.00
	Age ²	0.023	-4.7×10^{-3}	0.052	1.00
	Mar IFBFat	9.7×10^{-3}	−0.025	0.045	0.29
	Mar body mass	0.043	−0.099	0.19	0.28
	Litter size	−0.046	−0.18	0.092	0.29

IFBFat, ingesta-free body fat.

Appendix J. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis of winter (Nov–Mar) survival of adult (>1 yr) female mule deer evaluated at the population ($n=1,037$) and individual level ($n=574$), Sierra Nevada, California, USA, 1998–2008. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	5.4×10^{-3}	−0.10	0.12	0.27
	Monthly precipitation	0.031	−0.025	0.087	0.43
	Monthly temperature	0.10	−0.011	0.21	0.47
	Per capita snowpack	50.72*	21.37	80.12	1.00
	Mean Nov IFBFat ^a	0.083	−0.080	0.25	0.41
	Month				0.97
	Year				0.01
Individual	Per capita snowpack	31.54*	1.89	61.08	0.74
	Age	−0.24*	−0.34	−0.15	1.00
	Nov IFBFat ^a	3.4×10^{-3}	−0.016	0.022	0.19
	Nov body mass ^a	0.064*	0.015	0.11	0.86
	Recruitment status ^a	−0.041	−0.16	0.077	0.31
	Month				1.00

^a We obtained results for November ingesta-free body fat (IFBFat), November body mass, and recruitment status from a separate set of models using a subset of data ($n=334$) during 2002–2008.

Appendix K. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in March evaluated at the population ($n = 842$) and individual ($n = 531$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−0.50*	−0.73	−0.26	1.00
	Per capita snowpack	45.23*	30.69	59.77	1.00
	Winter temperature	0.050	−0.013	0.030	0.29
	Mean Mar IFBFat _{<i>t</i>−1}	0.51*	0.36	0.66	1.00
	Winter precipitation	−0.28*	−0.35	−0.21	1.00
Individual	Year				0.00
	Summer residency	−0.018	−0.24	0.20	0.43
	Per capita snowpack	33.07	−2.54	68.67	0.99
	Mean Mar IFBFat _{<i>t</i>−1}	0.74*	0.26	1.26	0.95
	Winter precipitation	−0.15*	−0.27	−0.018	0.71
	Age	−0.16*	−0.24	−0.079	0.96
	Litter size	0.56*	0.17	0.96	1.00
	Mar IFBFat _{<i>t</i>−1}	0.033	−0.017	0.081	0.28
	Nov IFBFat _{<i>t</i>−1} ^a	0.14*	0.088	0.20	1.00

^a We obtained results for November IFBFat of the previous year from a separate set of models using a subset of data ($n = 215$) during 2002–2008.

Appendix L. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence body mass (kg) of adult (>1 yr) female mule deer in March evaluated at the population ($n = 828$) and individual ($n = 517$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−1.00*	−1.81	−0.19	0.92
	Per capita snowpack	2.19	−7.48	11.87	0.32
	Winter temperature	0.67*	0.37	0.96	0.99
	Mean Mar IFBFat _{<i>t</i>−1}	0.011	−0.094	0.12	0.33
	Year				0.00
Individual	Summer residency	−1.11*	−1.87	−0.35	0.96
	Winter temperature	0.24*	0.018	0.47	0.74
	Age	2.70*	2.22	3.19	1.00
	Age ²	−0.15*	−0.18	−0.11	1.00
	Mar IFBFat	0.30*	0.19	0.40	1.00

IFBFat, ingesta-free body fat, $t - 1$, previous year.

Appendix M. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence percent ingesta-free body fat (IFBFat) of adult (>1 yr) female mule deer in November evaluated at the population ($n = 359$) and individual ($n = 249$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−2.35*	−3.22	−1.48	1.00
	Per capita snowpack	78.53*	14.16	142.89	1.00
	Summer precipitation	0.087*	0.012	0.16	0.69
	Summer temperature	−0.030	−0.23	0.16	0.42
	Mean Mar IFBFat	0.27	−0.12	0.65	0.64
	Year				0.00
Individual	Summer residency	−1.97*	−2.84	−1.11	1.00
	Per capita snowpack	132.38*	71.54	193.22	1.00
	Summer precipitation	0.037	−0.016	0.092	0.37
	Mean Mar IFBFat	0.89*	0.28	1.5	0.94
	Age	−0.030	−0.18	0.13	1.00
	Mar IFBFat	0.10	−0.027	0.23	0.51
	Litter size	−0.24	−0.93	0.45	1.00
	Recruitment status	−2.81*	−3.43	−2.20	1.00

Appendix N. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence body mass (kg) of adult (>1 yr) female mule deer in November evaluated at the population ($n = 330$) and individual ($n = 253$) levels, Sierra Nevada, California, USA, 1997–2009. We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Level	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Population	Summer residency	−2.75*	−4.15	−1.33	1.00
	Per capita snowpack	6.98	−30.61	44.57	0.49
	Summer precipitation	0.37*	0.27	0.47	1.00
	Summer temperature	−0.61*	−1.11	−0.12	0.88
	Mean Mar IFFat	−0.55	−1.13	0.039	0.79
	Year				0.00
Individual	Summer residency	−2.72*	−4.27	−1.16	1.00
	Summer precipitation	0.27*	0.15	0.39	0.99
	Summer temperature	−0.36	−0.86	0.14	0.69
	Mean Mar IFFat	0.13	−0.11	0.37	1.00
	Age	1.93*	0.80	3.06	1.00
	Age ²	−0.084*	−0.15	−0.016	1.00
	Nov IFFat	0.37*	0.22	0.52	1.00
	Recruitment status	−0.81	−1.71	0.079	1.00

IFFat, ingesta-free body fat.

Appendix O. Model-averaged parameter estimates, confidence intervals, and Akaike importance weights from an analysis to determine the factors that influence population growth (λ ; $n = 17$) evaluated at the population level, Sierra Nevada, California, USA, 1991–2009. Herd composition and population estimates from 1991 to 1996 were obtained from Pierce et al. (2012). We included variables we identified as being influential in lower levels of analyses. We considered variables to be influential if their 90% confidence interval did not overlap zero or if their importance weight was >0.50. Asterisks adjacent to parameter estimates indicate 90% confidence do not overlap zero.

Response	Parameter	Estimate	90% CI		Importance weight
			Lower	Upper	
Lambda	Mean Mar IFFat _{$t-1$}	1.4×10^{-4}	-2.0×10^{-4}	2.2×10^{-3}	0.07
	Mean Mar IFFat _{t}	0.043*	0.013	0.075	0.79
	Mean Mar mass	5.5×10^{-4}	-1.7×10^{-3}	2.8×10^{-3}	0.07
	Per capita snowpack				0.00
	Summer precipitation	1.3×10^{-3}	-2.9×10^{-3}	5.6×10^{-3}	0.10
	Summer temperature	-5.9×10^{-4}	−0.016	0.015	0.18
	Young ratio	1.7×10^{-4}	-1.9×10^{-4}	5.3×10^{-4}	0.03

IFFat, ingesta-free body fat; $t - 1$, previous year; t , current year.



Photograph looking south on winter range for mule deer (*Odocoileus hemionus*) in Round Valley with Mount Tom in the distance demarking the western edge of Round Valley and the eastern edge of the Sierra Nevada, California, USA, where the Great Basin Desert begins. Note the fire lines evident at the base of Mount Tom from a fire that burned approximately 24% of the winter range in June 1995. Photo by Kevin L. Monteith.



A biologist processes twin mule deer (*Odocoileus hemionus*) recently born to a radiocollared adult female in the Sierra Nevada, California, USA. Photo by Ryan A. Long.



Biologists conduct aerial telemetry for radiocollared mule deer (*Odocoileus hemionus*) along the east side of the Sierra crest in November 2008 after a recent snowstorm. Note the Sierra crest at the horizon line and the notable rainshadow caused by the Sierra Nevada. Photo by Kevin L. Monteith.



Female mule deer (*Odocoileus hemionus*) being transported to a central staging area for processing in Round Valley, California, USA. Photo by Tim Glenner.



Mule deer (*Odocoileus hemionus*) on winter range in Round Valley, California, USA. Photo by Thomas R. Stephenson.



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Resilience and Conservation of Large Carnivores in the Rocky Mountains

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Abstract: Large carnivores evolved behaviors and life-history traits that conferred resilience to environmental disturbances at various temporal and spatial scales. We synthesize empirical information for each large carnivore species in the Rocky Mountains regarding three basic mechanisms of resilience at different hierarchical levels: (1) behavioral plasticity in foraging behavior that ameliorates flux in food availability, (2) demographic compensation that mitigates increased exploitation, and (3) dispersal that provides functional connectivity among fragmented populations. With their high annual productivity and dispersal capabilities, wolves (*Canis lupus*) possess resiliency to modest levels of human disturbance of habitat and populations. Cougars (*Puma concolor*) appear to have slightly less resiliency because of more specific requirements for stalking habitat and lower biennial productivity. Grizzly bears (*Ursus arctos horribilis*) possess much less resiliency because of their need for quality forage in spring and fall, their low triennial productivity, and the strong philopatry of female offspring to maternal home ranges. Based upon limited information, wolverines (*Gulo gulo*) appear more susceptible to natural fluctuations in scavenging opportunities and may have lower lifetime productivity than even grizzly bears. By accelerating the rate and expanding the scope of disturbance, humans have undermined the resiliency mechanisms of large carnivores and have caused widespread declines. Both the resiliency profiles and the historical record attest to the need for some form of refugia for large carnivores. With their productivity and dispersal capability, wolves and cougars might respond adequately to refugia that are well distributed in several units across the landscape at distances scaled to successful dispersal (e.g., less than five home range diameters). With their lower productivity and dispersal capability, grizzly bears and wolverines might fare better in a landscape dominated by larger or more contiguous refugia. Refugia must encompass the full array of seasonal habitats needed by large carnivores and should be connected to other refugia through landscape linkages.

Resistencia y Conservación de Carnívoros Mayores en las Montañas Rocallosas

Resumen: La evolución del comportamiento y de características de la historia natural de los carnívoros mayores les ha conferido resistencia a perturbaciones ambientales en varias escalas temporales y espaciales. En este trabajo sintetizamos información empírica sobre cada especie de carnívoro mayor en las Montañas Rocallosas en relación con tres mecanismos básicos de resistencia en distintos niveles jerárquicos: (1) plasticidad conductual en la conducta del forrajeo que mejora el flujo de disponibilidad de alimento, (2) compensación demográfica que atenúa el incremento de la explotación y (3) dispersión que proporciona conectividad funcional a las poblaciones fragmentadas. Los lobos (*Canis lupus*) son resistentes a niveles moderados de perturbación humana de su hábitat y poblaciones debido a su elevada productividad anual y sus capacidades de dispersión. Los pumas (*Puma concolor*) aparentan ser ligeramente menos resistentes debido a que tienen requerimientos de hábitat para acechar y una productividad bianual menor. Los osos pardos (*Ursus arctos horribilis*) son mucho menos resistentes debido a su necesidad de forraje de calidad en la primavera y el otoño, su baja productividad trianual y la marcada filopatria de las hembras de la progenie por los rangos de hogar materno. Con base en información limitada, los cárcayús (*Gulo gulo*) son aparentemente más sus-

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ceptible a las fluctuaciones naturales en las oportunidades de búsqueda de alimento y podrían tener una productividad a lo largo de su vida aún menor a la de los osos pardos (*Ursus arctos horribilis*). Los humanos han minado los mecanismos de resistencia de los carnívoros mayores y provocado su declinación al acelerar y expandir el alcance de las perturbaciones. Tanto los perfiles de resistencia, como el registro histórico dan testimonio de la necesidad de establecer algún tipo de refugios para carnívoros mayores. Por su productividad y capacidad de dispersión, los lobos y pumas pueden responder adecuadamente en refugios bien distribuidos en varias unidades a lo largo del paisaje, espaciados para una dispersión exitosa (e.g. <5 diámetros del rango de hogar). Debido a su menor productividad y capacidad de dispersión, los osos pardos y los carcajús podrían estar mejor en un paisaje dominado por refugios más grandes o contiguos. Los refugios deben abarcar toda la serie de hábitats estacionales que requieran los carnívoros mayores y deben estar conectados con otros refugios mediante corredores en el paisaje.

Introduction

Larger carnivore species—wolves (*Canis lupus*), cougars (also called mountain lions, panthers, or pumas; *Puma concolor*), wolverines (*Gulo gulo*), and grizzly bears (*Ursus arctos horribilis*)—once occurred throughout much of North America. These carnivores evolved in ecological milieus that included prevailing disturbance regimes with certain characteristics and boundary conditions. Disturbances varied in frequency, duration, extent, and intensity, thereby resulting in different spatio-temporal patterns of change (Pickett & White 1985). Behaviors and life-history traits conferred a resilience that enabled carnivore populations to absorb these indigenous disturbances and still persist (Karr & Freemark 1985).

Following the arrival of Europeans, however, distribution and abundance of large carnivores decreased dramatically in the wake of spreading human enterprise (Paquet & Hackman 1995). With technological innovations, *Homo sapiens* became a “supra” keystone species by accelerating the rate and expanding the scope of disturbance. Modern human activities presented new regimes of disturbance that could be considered “exotic” because they were qualitatively novel or quantitatively atypical (Denslow 1985). Systematic loss of habitat and excessive killing caused reductions in population size, distribution, and connectivity and clearly precipitated regional extirpations (Caughley 1994), even if stochastic factors may have played a role in the demise of the last individuals (Gilpin & Soulé 1986).

Successful conservation strategies for large carnivores in the Rocky Mountains will have to incorporate scientific knowledge of how these species persist in the face of different disturbances. We (1) examine the ecological concept of resiliency, (2) develop resiliency profiles of these large carnivore species, and (3) consider implications for conservation. The central role of humans in the decline of large carnivores compels researchers and managers to incorporate the human dimension explicitly in defining the problem and devising pragmatic conservation strategies (Paquet & Hackman 1995; Clark et al., this issue).

Ecological Concept of Resilience

Resilience has been defined as the “ability of systems to absorb disturbance and still maintain the same relationships between populations or state variables” (Holling 1973:14) and “the degree to which an entity can be changed without altering its minimal structure” (Pickett et al. 1989:133). Resilience is the property of the system, and persistence is the outcome. Species can be considered as nested hierarchies of individuals, populations, and metapopulations in which the higher levels provide context for mechanisms at lower levels. Persistence is accomplished laterally by “spreading the risk” (den Boer 1968) or vertically as a higher level in the hierarchy incorporates or absorbs disturbance at a lower level (O'Neill et al. 1986). Because disturbances occur at different spatial and temporal scales, no single level of organization can respond adequately to all disturbances. The nested structure increases resilience by linking the system across hierarchical levels (Pickett et al. 1989).

We examine one basic mechanism at each of three hierarchical levels: (1) individual—behavioral plasticity in food acquisition; (2) population—demographic compensation, and (3) metapopulation—dispersal. In reference to human disturbance, behavioral plasticity addresses the problem of habitat loss; demographic compensation, the problem of overexploitation; and dispersal, habitat fragmentation at a landscape scale.

Behavioral plasticity in food acquisition refers to the capacity of individuals to substitute one resource for another in the face of environmental disturbance, thereby ameliorating flux in food availability. The home ranges of adult female carnivores integrate the space necessary to meet energetic requirements for reproductive success (Lindstedt et al. 1986), and population density in solitary carnivores is strongly and inversely correlated with the size of adult female home ranges (Sandell 1989). Thus, it is particularly important to consider foraging behavior by adult females.

Demographic compensation refers to the capacity of animals to respond to increased rates of juvenile and adult mortality with increased reproduction and/or sur-

vival, thereby mitigating demographic fluctuations. Gittleman (1993) reanalyzed carnivore life histories in light of new theory, statistical models, and comparative empirical data. He found that many temporal life-history variables (e.g., age at maturity, interbirth interval) were significantly and negatively correlated with variations in age-specific mortality rates. The implication is that reproductive traits evolved in some long-term dynamic relationship to certain patterns and rates of mortality. In particular, high survival and longevity of adult females appears critical to the continued well-being of most carnivore populations.

Dispersal refers to movements by juvenile animals when leaving their natal range after reaching the age of independence (philopatry here refers to nondispersal or limited dispersal that includes portions of the maternal range). Effective dispersal—the number of home ranges an animal moves through before settling to breed—scales movement to the species and its environment (Shields 1987). Dispersal is successful if the individual survives, establishes a new home range, finds a mate and reproduces. Movements per se—no matter how far—do not constitute successful dispersal. In landscapes fragmented by human disturbance, successful dispersal is the mechanism by which vanishing local populations are rescued from extirpation (Brown & Kodric-Brown 1977) and functional connectivity of metapopulations is established (Hansson 1991).

Resiliency Profiles of Large Carnivores

It is in the natural history of a species that we discover clues about the relative efficacy of these mechanisms. Accordingly, we have examined the literature for empirical information to sketch resiliency profiles for each of these large carnivore species. We have emphasized data from the Rocky Mountains as available.

Gray Wolf

BEHAVIORAL PLASTICITY IN FOOD ACQUISITION

With their extensive geographic and ecological range across North America, gray wolves exhibit a high degree of plasticity in using different prey and habitats (Mech 1991). For wolves living amidst the high ungulate diversity (6–7 species) of the Rocky Mountains, Weaver (1994) reanalyzed predation data from several studies (Cowan 1947; Carbyn 1974; Schmidt & Gunson 1985; Huggard 1993a; Boyd et al. 1994). In summer wolves preyed principally upon deer (*Odocoileus hemionus* and *O. virginianus*; 53% of individuals represented in scats) and elk (*Cervus elaphus*; 34%) and to a lesser extent upon moose (*Alces alces*; 8%) and bighorn sheep (*Ovis canadensis*; 5%). Elk, however, contributed most of the

ungulate biomass (53%) to the wolves' diet, followed by deer (24%), moose (21%), and bighorn sheep (2%). Based upon the relative abundance of *groups* of ungulates in summer, wolves selected elk (especially calves) significantly more than expected and bighorn sheep significantly less so ($p < 0.05$). During winter wolves preyed mainly upon deer (45% of kills) and elk (39%) and to a lesser extent upon moose (11%) and bighorn sheep (5%). Again, elk contributed most of the biomass (54%) to the wolves' diet, followed by moose (24%), deer (20%), and bighorn sheep (2%). Based upon relative abundance of ungulate groups in winter, wolves selected elk more than expected and moose significantly less ($p < 0.05$).

In the context of multi-prey species in the Rocky Mountains, wolves may be viewed as “expanding specialists” that specialize on vulnerable individuals of large prey (elk and moose) yet readily generalize to common prey (usually deer). In snow-tracking wolves amidst diverse prey during winter, field researchers have found much plasticity by individual packs in killing prey of different species in sequence. Herd size, terrain, snow depth, and forest cover influence prey vulnerability and wolf predation among areas and years (Huggard 1993a, 1993b, 1993c; Weaver 1994).

Fuller (1989), following up on earlier work by Keith (1983), reported a strong ($r^2 = 0.72$), positive relationship between ungulate biomass and wolf density. Composition of the prey base, though, does have consequences for wolf density. In six areas of North America where the ungulate biomass index averaged 196 ± 21 (SE), composed of $\geq 85\%$ deer and $\leq 15\%$ moose, wolf density averaged $3.5 \pm 0.3/100 \text{ km}^2$ (calculated from Fuller 1989). In contrast, in eight areas where the ungulate biomass index averaged 290 ± 60 , composed of $\geq 65\%$ moose and/or dall sheep (*O. dalli*), wolf density averaged $0.8 \pm 0.1/100 \text{ km}^2$.

DEMOGRAPHIC COMPENSATION

Wild wolves become capable of reproducing at 2 years of age. Due to the dominance hierarchy of wolf-pack social structure, however, some young wolves may not necessarily breed when sexually mature. Age of female wolves at first parturition may vary according to the impact of human exploitation on pack structure, but it usually averages about 3 years (range: 2–5) (Mech 1991). Litter size averages about 5.4 (range of averages between studies: 4.0 to 7.0; see Fuller 1989). Once a female attains dominant status, she will usually whelp litters every year. Assuming that 20% of mature females do not breed because of their subordinate status within a pack, annual productivity rate averages about 4.2 pups per adult female (range: 2.2–5.3). Age at reproductive senescence has not been well documented, but few female wolves survive to reproduce past the age of 9 years

(Mech 1988). Assuming these average parameters and an annual survivorship of 0.70, the average female wolf might have a lifetime productivity of 6 female pups.

At very low levels of ungulate biomass per wolf, the reproductive potential of wolves may be diminished (Boertje & Stephenson 1992). Human exploitation of wolf populations increases the amount of ungulate biomass per wolf, which may increase fecundity or survival. The number of pups surviving to autumn or early winter appears more strongly related ($r^2 = 0.77$) to the amount of ungulate biomass per wolf than does litter size ($r^2 = 0.14$) (Fuller 1989). In southcentral Alaska Ballard et al. (1987) found that about 10% of packs had multiple litters and suggested that this constituted a form of compensatory natality in heavily exploited wolf populations.

Fuller (1989) estimated that established wolf populations could sustain an overwinter mortality rate of 35% and a human kill of 28%. Such values would vary with the level of nutrition, pack size, and age and sex structure of the population and of the kill. In areas with lower pup survivorship resulting from lower ungulate biomass, sustainable harvest rates may be closer to 20% (Gasaway et al. 1983). Of course, small packs composed primarily of the breeding pair would be most susceptible to reproductive failure if one of the pair was killed (Ballard et al. 1987; Hayes 1995).

DISPERSAL

Various aspects of dispersal have been documented for wolves in Alaska (Peterson et al. 1984; Ballard et al. 1987), Minnesota (Fritts & Mech 1981; Mech 1987; Fuller 1989; Gese & Mech 1991), Yukon (Hayes 1995), and in the Rocky Mountains of Montana, Alberta, and British Columbia (Boyd et al. 1995). Wolves typically disperse from natal packs at 2 years of age (range: 1–5); older animals are most likely pack subordinates. The overall sex ratio of dispersers has been 57 male to 43 female. In several studies young wolves, mostly females, established territories within the edge of or adjacent to their natal territory. Dispersal distance averaged 85 km overall (91 km male; 83 km female). This is a minimum figure because numerous individuals moved out of the monitoring range of the telemetry study or were killed before settling. Although males tend to disperse farther (732 km for a pair of males [Ballard et al. 1983]; 917 km for a single male [Fritts 1983]), a young female wolf moved 840 km from Glacier National Park, Montana, to Dawson Creek, British Columbia (Boyd et al. 1995). Nonetheless, most dispersals (not necessarily successful) have been out to an effective distance of about five home-range diameters (HRD) (Approximately 196 km).

Typically, dispersers suffer substantially higher mortality (from vehicular collisions, shooting, and trapping) than do resident wolves (Peterson et al. 1984). Dispersal

success has averaged 48% among North American studies (range: 27–85%). Up to about 10 HRDs (X), dispersal success (Y) decreased with increasing distance ($Y = -5.5 \times + 74.7$; $df = 4$ studies, $r^2 = 0.63$, $p = 0.11$). Nonetheless, in Minnesota four of eight wolves dispersing beyond 10 HRDs were successful in settling in a new territory (Gese & Mech 1991) (Approximately 391 km). The consistently high proportion of eventual dispersers in these studies (26% of radio-collared samples; range: 17–35%) indicates that a pool of animals usually exists for ready colonization. Plasticity in dispersal strategies enables wolves to colonize successfully under a variety of social and environmental conditions. Little information has been published, though, on specific use of the landscape by dispersing wolves, especially across fragmented landscapes.

BEHAVIORAL AND DEMOGRAPHIC RESPONSE TO HUMAN DISTURBANCE

Most field researchers have found that wolves tend to avoid human settlements, to exhibit slight aversion within about 1 km of open roads, and to use gated and unplowed roads readily (Thurber et al. 1994). They appear to avoid exploiting prey near clusters of human habitation and developments, especially in narrow river valleys (Paquet 1993). Wolves are sensitive to human disturbance near active den sites from mid-April to July.

Humans are directly responsible for most mortality of adult wolves. In Alaska and Minnesota 80–85% of wolf deaths were attributed to human-caused mortality (shooting, trapping, vehicular collisions) and 15–20% to natural causes (intraspecific strife, disease, and starvation) (Peterson et al. 1984; Ballard et al. 1987; Fuller 1989). In the Rocky Mountains between Banff and Glacier National Parks (US), 91% of 57 deaths of radio-collared wolves in recent years were caused by humans (Boyd et al. 1995).

In Minnesota approximately 75% of wolf packs occur where the density of open roads passable by two-wheel-drive vehicles is $< 0.6 \text{ km/km}^2$ and human density is 0–4 persons/ km^2 (Mech et al. 1988; Fuller et al. 1992). Adjacent and inclusive areas in Minnesota with open-road densities of 0.8–0.9 km/km^2 do not harbor wolf packs (Mech et al. 1988). Wolves recolonizing Wisconsin have been selecting those areas with low road density ($< 0.45 \text{ km/km}^2$; Mladenoff et al. 1995). The relationship between road density (open and total) and wolf survivorship or density has not been determined for the more open landscapes of the Rocky Mountains.

Following experimental killing by humans, wolf populations have demonstrated an ability to recover through immigration and reproduction. In Alaska, where wolf reduction created a lacuna or gap approximately 90 km wide (or 2.3 HRDs), wolf densities recovered to 81% of pre-control levels within 1 year (Ballard et al. 1987). Fol-

lowing a wolf-reduction program in the Yukon, wolves recovered to 60% of the original population size in 2 years and to 96% in 4 years (Hayes 1995). Recolonization by dispersing animals from outside the study area filled in the gap with breeding pairs during early recovery, followed by increases in pack size from reproduction. Interestingly, the initial locus of recolonization in Wisconsin along the Minnesota border was about 90 km or 6 HRDs straight-line distance from the nearest edge of occupied wolf habitat in Minnesota (calculated from Mladenoff et al. 1995). In the Rocky Mountains during the 1980s, wolves most likely from southeast British Columbia or southwest Alberta recolonized northwest Montana (Ream et al. 1991).

Cougar

BEHAVIORAL PLASTICITY IN FOOD ACQUISITION

With their extensive geographic and ecological range in North and South America, cougars have demonstrated a high degree of plasticity in using different habitats and prey (Anderson 1983). In the western mountains of North America cougars prey primarily upon cervids: deer, elk, and (regionally) moose (Hornocker 1970; Spalding & Lesowski 1971; Anderson 1983; Murphy 1983; Ackerman et al. 1984; Spreadbury 1988; Jalkotzy et al. 1992; Williams et al. 1995). In a cervid population in central Idaho with an estimated composition of 37% elk and 63% mule deer in winter, cougars selected elk (53% of kills, 76% of diet biomass) more than deer (46% of kills, 24% of diet biomass) (Hornocker 1970). In Alberta male cougars exploited moose (68% of kills, 84% of diet biomass), whereas female cougars preyed on deer (53% of kills, 40% of diet biomass) and elk (19% of kills, 39% of diet biomass) more than moose (8% of kills, 15% of diet biomass) (Jalkotzy et al. 1992). Other large carnivores, especially wolves, may usurp ungulate kills from cougars (I. Ross, personal communication).

Scant information has been reported on prey populations in these studies from which a relationship between cervid biomass and cougar density could be determined (as Fuller [1989] did for wolves). In central Idaho there were an estimated 197 elk, 331 mule deer, and 2.9 cougars per 100 km² (Hornocker 1970). In southern Utah there were about 4 elk, 107 mule deer, and 0.5 cougars per 100 km² (Ackerman et al. 1984; Lindzey et al. 1994). The 7.7-fold difference in the ungulate biomass index between these areas compares to a 6-fold difference in the density of adult female cougars. In central Idaho density of adult female cougars increased with increasing density of prey (Quigley et al. 1989). In four areas density of adult female cougars was inversely related to the average size of their home range ($r^2 = 0.91$, $df = 3$, $p = 0.05$), and total density of resident cougars was directly related to that of resident adult females ($r^2 = 0.79$, $df =$

23, $p < 0.001$; calculated from data in Seidensticker et al. 1973; Logan et al. 1986; Ross & Jalkotzy 1992; Lindzey et al. 1994). Thus, limited data suggest that cougar density is related positively to the abundance of cervids in habitats with stalking cover. Interestingly, cougar density was about 18% lower in Idaho and 36% lower in Utah than Fuller's (1989) equation would have predicted for wolves.

DEMOGRAPHIC COMPENSATION

Demographic parameters have been documented for several cougar populations in the mountain West (Hornocker 1970; Seidensticker et al. 1973; Anderson 1983; Murphy 1983; Logan et al. 1986; Lindzey et al. 1988; Ross & Jalkotzy 1992; Lindzey et al. 1994). Age of female cougars at first parturition averaged about 3.0 years (range of averages between studies: 2.5–4.0). Mean litter size at 4–8 months of age was 2.5 (range: 2.2–2.8), and the interval between litters averaged 1.7 years (range: 1.3–2.0). Mean annual productivity was about 1.5 kittens per adult female (range: 1.3–2.1). Age at reproductive senescence has not been well documented for wild cougars, but few females likely survive to reproduce past the age of 10–12 years (Beier 1993). Assuming these average parameters and an annual survivorship of 0.85 for adult females, the average female cougar would have a lifetime production of 3–4 female young.

Survivorship in an increasing cougar population in Alberta averaged 0.89 (range in annual survivorship: 0.86–0.97) over a 5-year period (adult male 0.77, adult female 0.95, juvenile male 0.95, juvenile female 0.85; calculated from data in Jalkotzy et al. 1992; Ross & Jalkotzy 1992). Survivorship in a stable population in western Montana averaged 0.80 (range in annual survivorship: 0.72–1.00) over a 3-year period (adult male 0.75, adult female 0.83, juvenile 0.80; calculated from data in Murphy 1983), whereas survivorship in a stable to slightly decreasing population in central Idaho averaged 0.78 (range in annual survivorship: 0.54–0.88) over a 4-year period (adult male 0.87, adult female 0.85, juvenile male and female 0.68; calculated from data in Hornocker 1970). Natural mortality from intraspecific killings, starvation, and fatal injuries sustained during prey capture have averaged about 0.04 per year (range: 0.03–0.05; Hornocker 1970; Logan et al. 1986; Lindzey et al. 1988; Ross & Jalkotzy 1992). Hunting mortality may not be fully compensated by a reduction in other sources of mortality; rather, it likely will be partly additive (Lindzey et al. 1988). Cougar populations can sustain an overall mortality rate of about 15%, of which 5% will be from natural causes (Jalkotzy et al. 1992). Wide-scale loss of breeding females can be crucial because it reduces the number of female progeny available for replacement (Lindzey et al. 1992).

DISPERSAL

Important information regarding dispersal has been collected in several areas (Hornocker 1970; Seidensticker et al. 1973; Logan et al. 1986; Ross & Jalkotzy 1992; Laing & Lindzey 1993; Lindzey et al. 1994). Young cougars disperse between the ages of 10 and 22 months, with an average of about 16 months. Nearly all male offspring disperse from their maternal home range. Replacement is principally by young males immigrating from other areas. Young female cougars exhibit a wider range of dispersal strategies, including a higher level of philopatry. In central Idaho nearly all young females dispersed, even though some maternal ranges were vacant (Seidensticker et al. 1973). In Alberta, however, 7 juvenile female cougars established home ranges adjacent to or slightly overlapping with their mother's home range (Ross & Jalkotzy 1992). In an unhunted cougar population in Utah, 7 of 10 resident females were replaced by either one of their own independent daughters or a daughter of a neighboring resident female (Laing & Lindzey 1993). Dispersal distances have averaged 85 km (range: 6–274 km), for an effective distance of about 5–7 HRDs. Although young male cougars have accounted for the longest dispersal distances, young females have moved up to 366 km (I. Ross, personal communication).

Little information has been published on the spatio-temporal patterns of dispersal by juvenile cougars or on their specific use of the landscape in the Rocky Mountains, especially across fragmented landscapes. In a particularly useful study, Beier (1995) found that dispersing cougars (eight males, one female) in southern California used a series of small, transient home ranges along an urban-wildland interface. Five of the nine dispersers discovered and successfully used corridors 1.5–6 km long during nighttime. These corridors were located along natural travel routes with ample woody cover, had less than one dwelling unit per 16 ha, and lacked artificial outdoor lighting. Ultimately, though, seven of the nine dispersers died before establishing a home range; three deaths were due to vehicle collisions.

BEHAVIORAL AND DEMOGRAPHIC RESPONSE TO HUMAN DISTURBANCE

Limited scientific data have been published on cougar tolerance of human activities. In Arizona and Utah, resident cougars and successful dispersers selected home ranges with road densities lower than average for the study area and with few or no sites of human residence (Van Dyke et al. 1986). Some cougars will travel or hunt near human developments, mostly at night (Van Dyke et al. 1986; Beier 1995).

Most (75%) of the adult cougar mortality recorded in the various studies has been caused by humans. Favorable snowtracking conditions can facilitate hunters locating cougars in winter, and hounds are usually quite

successful in treeing the cats (Murphy 1983; Jalkotzy et al. 1992). Houndsmen in western Montana located and killed disproportionately more cougars along the main road up a drainage than along secondary roads in tributaries (Murphy 1983).

The resilience of cougar populations to hunting likely depends on the rate of male immigration to the population and the availability of recruitment-age female progeny (Lindzey et al. 1992). Dispersal plays a crucial role because replacement of nearly all males as well as some females in a local population occurs mainly by immigration of juveniles from nearby sources rather than by *in situ* replacement. Based upon simulation modeling, Beier (1993) reported that, for any combination of demographic parameters, minimum habitat area for > 98% likelihood of persistence over 100 years was 200–600 km² smaller with immigration of 1–4 cougars per decade than without immigration.

Wolverine

BEHAVIORAL PLASTICITY IN FOOD ACQUISITION

Wolverines remain the least studied of the larger carnivores: only five field studies have been completed and published in North America (Hornocker & Hash 1981; Gardner 1985; Magoun 1985; Banci 1987; Copeland 1996). Weaver (1993) and Banci (1994) have summarized the meager base of knowledge for this species.

Wolverines use a wide variety of foods, particularly in summer when they feed on ground squirrels and marmots, ungulate carrion, microtines, birds, and berries. For the remainder of the year wolverines seem to subsist largely on ungulate carrion (Banci 1994). In northwest Montana elk and deer carrion were important winter food sources (Hornocker & Hash 1981). Banci (1994) surmised that the larger predators, especially wolves, may be important providers of ungulate carcasses for wolverines to scavenge. She also suggested that diversity of habitats and foods per se may be more important than any single resource for this predominant scavenger.

Home ranges (minimum convex polygon) of 13 adult female wolverines in northwest Montana averaged 344 km² (Hornocker & Hash 1981). In central Idaho home ranges averaged 280 km² for five adult females and 1525 km² for four adult males (Copeland 1996). Estimated densities of wolverines based in part on telemetry have ranged from 0.5/100 km² in Idaho (Copeland 1996) to 1.5/100 km² in Montana (Hornocker & Hash 1981). No relationship between habitat or prey and wolverine abundance has been determined.

DEMOGRAPHIC COMPENSATION

Wolverines appear to have a very low realized natality (Rausch & Pearson 1972; Liskop et al. 1981; Magoun

1985; Banci & Harestad 1988). Age of females at first parturition is 2 years, with an average of 63% of females (range of averages: 50–85%) having fetuses at this age. Litter size in utero has averaged 2.9 (range of averages: 2.2 in Montana to 3.5 in Alaska), but litter sizes less than 2.0 observed after den abandonment suggest some pre- or post-partum mortality (Banci & Harestad 1988). Percentage of adult (≥ 2 years) female wolverines pregnant in any year has varied from more than 50% in northwest Montana (Hornocker & Hash 1981) to 74% in western Canada (Liskop et al. 1981; Banci 1987) to 92% in Alaska (Rausch & Pearson 1972). The annual proportion of adult females successful in reproduction has been as low as 25–50% because some females have not borne live young for 3 years in a row (Hornocker & Hash 1981; Magoun 1985; Banci 1987). Thus, the interval between litters for the average adult female wolverine is greater than 1 year and likely 2 years or more. The net result is low production, ranging from an optimistic rate of 1.0 offspring per adult female per year (assuming litter size of two and a 2-year average interval) down to a documented rate of 0.6–0.7 offspring per adult female per year (Magoun 1985). Such low reproductive output probably reflects the tenuous nutritional regime for this scavenger. Reproductive success may be keyed to the availability of ungulate carrion in winter and spring, when blastocysts implant and kits are born (Magoun 1985; Banci 1987). Age at reproductive senescence has not been well documented for wild wolverines, but few females likely survive to reproduce past the age of 8 years (Rausch & Pearson 1972; Hash 1987). Assuming these average parameters and an annual survivorship of 0.85 for adult females, the average female wolverine would have a lifetime production of two female offspring.

For an estimated population of 20 wolverines in northwest Montana that was considered stable, survivorship was about 0.81 (calculated from data in Hornocker & Hash 1981). In the Yukon study survivorship of resident adults was approximately 0.89 (calculated from data in Banci 1987).

DISPERSAL

Data on dispersal by wolverines are limited. The longest involved a 378-km movement by a 2-year-old male from Alaska to the Yukon (Gardner et al. 1986). Magoun (1985) reported a 300-km trip by one yearling female, whereas another female was still in her natal range at 28 months of age. These dispersals were terminated by trapping of the animals. In an unexploited wolverine population in central Idaho, two independent subadult females established home ranges that overlapped with their mother's, whereas two 2-year-old males dispersed more than 200 km (Copeland 1996). That at least some dispersers can be successful is suggested by the appar-

ent recolonization of former ranges in Montana (Newby & McDougal 1964; Hash 1987) and Wyoming (Hoak et al. 1982). The initial source of such dispersers decades ago may have been southern British Columbia, especially the Kootenay region (see Hatler 1989).

BEHAVIORAL AND DEMOGRAPHIC RESPONSE TO HUMAN DISTURBANCE

Wolverines appear to avoid human settlements (Banci 1994) and may be particularly sensitive to human disturbance during denning periods (J. Copeland, personal communication). The incidence of known mortality for radio-collared wolverines in field studies has been 30% (24 of 80), but the fate of many dispersing juveniles has not been well documented. Trapping and hunting accounted for 58% of recorded mortalities. Many of these occurred when animals left study areas that were closed to harvest. Wolverines appear susceptible to trapping around baits, particularly in years when carrion availability is low because of mild winters or other factors. In the Montana study, Hornocker and Hash (1981) reported that trapping caused 15 of 18 (83%) recorded mortalities and noted that many of the captured wolverines exhibited missing toes and broken teeth attributable to previous encounters with leg-hold traps. In the various field studies, four wolverines (17%) starved, two died from disease or infection (8%), and predators killed two others (8%). Thus, nonhuman causes accounted for 33% of recorded mortality. Using data from Alaska and the Yukon, Gardner et al. (1993) estimated that the wolverine population they modeled could sustain an annual harvest of 7–8% of the fall population.

Grizzly Bear

BEHAVIORAL PLASTICITY IN FOOD ACQUISITION

Numerous studies have documented grizzly bear diets throughout the Rocky Mountains, including the Greater Yellowstone Ecosystem (Mattson et al. 1991; Craighead et al. 1995), northwest Montana (Craighead et al. 1982; Mace & Jonkel 1986; Aune & Kasworm 1989), and the Canadian Rockies (Russell et al. 1979; Hamer & Herrero 1983; Hamer et al. 1985; Wielgus 1986; Raine & Riddell 1991). Grizzly bears are the most omnivorous of the four larger carnivores. Although grizzly bears use a wide variety of foods, four main groups compose most of their diet: grasses and sedges; forbs and forb roots; berries and pine seeds; and mammals, including ungulates and rodents.

In spring (April–May) grizzly bears scavenge on ungulate carrion where available, graze succulent grasses and sedges, or dig roots (e.g., *Hedysarum* spp.). In early summer some bears prey on elk calves for 2–3 weeks in June, whereas others feed on rodents, grasses, or forbs. During midsummer grizzlies forage on horsetail (*Equiset-*

tum) and a variety of forbs (*Heracleum*, *Angelica*) and insects. During late summer and fall (August-October) they feed on berries (especially *Vaccinium* and *Shepherdia*) or the seeds of whitebark pine (*Pinus albicaulis*) cached in middens by tree squirrels (*Tamiasciurus hudsonicus*), with occasional predation on male ungulates in rut. Foraging patterns, habitat use, and movements may vary among bears and among locales of the Rocky Mountains, depending on the temporal and spatial availability of key resources and perhaps learned behavior.

Adequate weight gain and fat deposition appears crucial to successful hibernation and reproduction in bears (Rogers 1987a). In late summer and fall, grizzly bears forage voraciously (hyperphagia). During years of poor production of berries and pine seeds, bears respond by substituting lower-quality foods (e.g., roots of *Hedysarum* or *Lomatium*). Unlike true ruminants, however, grizzly bears cannot adequately assimilate nutrients from coarse vegetation that is high in cellulose (Mealey 1975). In the face of a shortfall in nutritious foods, bears move widely in search of food, which may bring them into contact with humans (Blanchard & Knight 1991; Mattson et al. 1992). This substantially increases the risk of direct human-caused mortality or leads to management capture and translocation with problematic success (Riley et al. 1994; Blanchard & Knight 1995; Mattson et al., this issue).

Annual home-range sizes for adult female grizzlies in eight locales of the Rocky Mountains averaged 230 km² (range of averages among studies: 119–413 km²). Relationships between grizzly bear abundance and variables of habitat or key food resources have not yet been determined (Boyce 1995). Estimated densities of grizzly bears in the Rocky Mountains have ranged from 0.6 bears/100 km² along the eastern front in Montana (Aune & Kasworm 1989) to a very high 6.2 bears/100 km² in south-east British Columbia (McLellan 1989a).

DEMOGRAPHIC COMPENSATION

Several published studies have documented the reproductive parameters of grizzly bear populations at various places in the Rocky Mountains (Martinka 1974; Russell et al. 1979; Aune & Kasworm 1989; McLellan 1989c; Wielgus & Bunnell 1993; Eberhardt et al. 1994; Aune et al. 1994; Craighead et al. 1995). Age of female grizzly bears at first parturition averaged 5.7 years (range of averages between studies: 5.0–6.2). Mean litter size after emergence from winter dens was 2.1 (range: 1.7–2.3), with an average interval between litters of 3.1 years (range: 2.7–3.4). Annual production averaged about 0.7 cubs per adult female (range: 0.6–0.8), with females most productive between the ages of 10 and 20 years. Assuming these average parameters and an annual survivorship of 0.94 for adult females from ages 6 to 20, the

average female grizzly bear would have a lifetime production of 3–4 female cubs. Productivity appears to be positively related to increased body mass of adult females which, in turn, may reflect the quantity and quality of key foods (Stringham 1990; McLellan 1994, but see Craighead et al. 1995). A survivorship of higher than 0.92 for adult female grizzly bears has characterized all Rocky Mountain populations estimated to be stable or increasing (McLellan 1989b; Wielgus & Bunnell 1993; Eberhardt et al. 1994).

DISPERSAL

Aspects of dispersal by grizzly bears have not been well documented. Subadult females often establish a range encompassing a portion of their mother's home range, whereas subadult males tend to move much farther away from the maternal home range (Blanchard & Knight 1991). Such a pattern is common in mammals with polygynous mating systems, including black bears (*Ursus americanus*; Rogers 1987b). In the Greater Yellowstone Ecosystem four male grizzlies weaned as 2-year-olds moved an average of 70 km (straight-line distance) from their maternal range, or about 2 HRDs. Another weaned male, however, was captured as a 5-year-old within his maternal home range and killed the following year only 15 km west of that range (Blanchard & Knight 1991). None of the more than 460 grizzly bears radio-tracked in the American West over the past 25 years has been documented to move from one grizzly bear ecosystem to another where inter-ecosystem distances vary from 60 to 384 km (C. Servheen, personal communication).

BEHAVIORAL AND DEMOGRAPHIC RESPONSE TO HUMAN DISTURBANCE

Human traffic along open roads displaces most grizzly bears from 100 to 900 m (Mattson et al. 1987; McLellan & Shackleton 1988; Aune & Kasworm 1989; Kasworm & Manley 1990; Mace et al. 1996). Because adult female grizzly bears are security-conscious in the presence of adult males, they may use areas adjacent to roads and human settlements that the males avoid (Mattson 1990). These adult females, however, may then become habituated to humans and eventually become nuisance animals that are either relocated, removed to zoos, or destroyed (Mattson et al. 1987). Limited evidence suggests that some bears use the cover of darkness to exploit areas that are disturbed during the day (Aune & Kasworm 1989).

In the Greater Yellowstone Ecosystem during 1973–1985, illegal kills accounted for 41% (29% hunters) of 101 known grizzly bear deaths; management control actions, 35%; and road kills, 6% (Knight et al. 1988). As of 1995, humans were responsible for 91% of the 53 recorded mortalities of adult females (R. Knight, personal

communication). Shooting has accounted for 86% (38% illegal kills) of 56 known mortalities in other Rocky Mountain ecosystems, with natural mortality occurring in 12% of cases (Knick & Kasworm 1989; McLellan 1989b; Mace et al., 1996).

There is no conclusive evidence of a sharp reproductive response or increased survivorship of young by grizzlies to compensate for increased mortality (McLellan 1994; Craighead et al. 1995). Simulation modeling consistently shows that high adult female survivorship is critical to the persistence of grizzly bear populations (Bunnell & Tait 1981; Eberhardt 1990). Grizzly bear populations cannot sustain known, human-caused mortality rates exceeding about 5% annually (Bunnell & Tait 1981). Recent grizzly bear management programs have established upper limits of about 4–5% known mortality from human causes, with female deaths not to exceed 30–35% of that level (Dood et al. 1986; Nagy & Gunson 1990).

Security from human disturbance facilitates survivorship and reproduction of adult females. In the Flathead River region of northwest Montana, road density was lower (0.6 km/km²) within the composite home range of adult female bears than outside (1.1 km/km²) (Mace et al., 1996). Approximately 56% of the composite home range was unroaded, compared to 30% outside. More than 80% of bear locations occurred in blocks of undisturbed habitat 9 km² or more in size, or about 7% of the average home range. For grizzly bears in the Yellowstone Ecosystem, D. Mattson (personal communication) recommends security blocks 28 km² in size, or about 10% of an average adult female's home range.

Implications for Conservation

Over millennia, large carnivores persisted by a variety of mechanisms that buffered environmental disturbance at various temporal and spatial scales: (1) plasticity in foraging behavior, (2) relatively high survivorship of adult females, enabling replacement over a full lifetime, and (3) recolonization of vacant habitats by dispersal. This resiliency, though, had definite limits. As human activities accelerated rates of disturbance across a greater portion of the landscape (Turner et al. 1989, 1993), the combination of speed and simplification undermined the resiliency mechanisms of the species and rendered their populations more fragile. Cumulative impacts accrued that threaten their persistence (Weaver et al. 1986).

For large carnivores to persist, human disturbance must be constrained within the bounds of the species' resilience. Obtaining reliable information about population status and trends of these low-density and secretive animals, however, is difficult, expensive, and problem-

atic (Mattson et al., this issue). Moreover, each species is vulnerable to overexploitation from illegal or incidental mortality that can be difficult to detect and control.

A common strategy of managers facing similar uncertainty in other arenas is to minimize exposure to risk by providing safe havens or refugia. Indeed, the powerful role of refugia in population persistence has emerged as one of the most robust concepts of modern ecology (Fahrig 1988). Conceptually, refugia can be identified and managed as population sources (Pulliam & Danielson 1991) by (1) maximizing natality through enhancement of habitat productivity or (2) minimizing mortality through reduced access or curtailment of harvest. In the broader sense, therefore, refugia are safety nets from habitat loss and overexploitation. Both the resiliency profiles and the historical record attest to the need for some form of refugia for large carnivores.

The type, size, and distribution of refugia needed across the landscape likely will vary by the degree of disturbance in the intervening matrix and by species. For example, Knick (1990) found that the necessary size of refugia for bobcats (*F. rufus*) varied with the intensity of harvest in the areas between refuges. His model predicted that refugia must be large enough to completely enclose 3–5 territories, for a total of 12–16 contiguous territories. Based upon simulation modeling, Joshi and Gadgil (1991) reported that if multiple refugia were adequately dispersed across a landscape to ensure complete mixing of the protected and exploited populations, harvest was sustainable while minimizing the risk of extirpation. The key was a tight feedback loop so that increases in harvesting effort were accompanied by increases in the number or size of refugia.

With their high annual productivity and dispersal capabilities, wolves possess resiliency to modest levels of human disturbance of habitat and populations. Cougars appear to have slightly less resiliency because of more specific requirements for stalking habitat, less competitive ability in multi-carnivore communities, and lower biennial productivity. With their productivity and dispersal capability, wolves and cougars might respond sufficiently to refugia that are well distributed in several units across the landscape at distances scaled to successful dispersal (e.g., < 5 HRDs; Beier 1995; Mech 1995).

Grizzly bears fall much lower on the resiliency scale and appear extremely vulnerable to anthropogenic disturbance (Mattson et al., this issue). The need of grizzly bears for quality forage in spring and fall, their low triennial productivity, and the strong philopatry of female offspring to maternal home ranges does not provide much resiliency in human-dominated landscapes. Based on limited information, wolverines seem more susceptible to natural fluctuations in scavenging opportunities, are vulnerable to traps set near baits, and may have lower lifetime productivity than even grizzly bears. With their lower productivity and dispersal capability, grizzly

bears and wolverines might fare better in a landscape dominated by larger or more contiguous refugia.

Both ecological theory and simulation modeling underscore the importance of functional connectivity in facilitating population persistence (Hansson 1991; Harrison 1991). Thus, refugia must encompass the full array of seasonal habitats needed by large carnivores and should be connected to other refugia through landscape linkages. Empirical data for large carnivores confirms the capability of these animals to move long distances, yet most successful dispersal occurs within five HRDs. Efforts to identify and secure key linkage zones are crucial before options are lost.

The resilience framework does not require a precise capacity to predict the future, but only a qualitative capacity to devise systems that can absorb and accommodate future events in whatever unexpected form they may take (Holling 1973). We believe that populations of large carnivores will persist longer with well-designed networks of refugia.

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Sport Hunting, Predator Control and Conservation of Large Carnivores

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Abstract

Sport hunting has provided important economic incentives for conserving large predators since the early 1970's, but wildlife managers also face substantial pressure to reduce depredation. Sport hunting is an inherently risky strategy for controlling predators as carnivore populations are difficult to monitor and some species show a propensity for infanticide that is exacerbated by removing adult males. Simulation models predict population declines from even moderate levels of hunting in infanticidal species, and harvest data suggest that African countries and U.S. states with the highest intensity of sport hunting have shown the steepest population declines in African lions and cougars over the past 25 yrs. Similar effects in African leopards may have been masked by mesopredator release owing to declines in sympatric lion populations, whereas there is no evidence of overhunting in non-infanticidal populations of American black bears. Effective conservation of these animals will require new harvest strategies and improved monitoring to counter demands for predator control by livestock producers and local communities.

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Introduction

Management agencies typically skew harvests toward males in order to protect adult females. However, in species with extensive paternal investment such as African lions (*Panthera leo*), trophy hunting can increase the rate of male replacement (and associated infanticide) to the point of reducing population size unless off-takes are restricted to males old enough to have reared their first cohort of dependent offspring (≥ 5 –6 yrs of age) [1–3]. Solitary felids have none of the “safety nets” provided by the cooperative cub rearing strategies of African lions [4–5], and Fig. 1ab illustrates the greater vulnerability of solitary species by examining the effects of trophy hunting on a hypothetical population of “solitary lions” while leaving other demographic parameters from ref. [1] unchanged (Supporting Information Table S1, also see ref. [6]). Leopards (*Panthera pardus*) may be more sensitive to sport hunting than solitary lions (with a safe minimum age of 6–7 yrs of age, Fig. 1c), whereas cougar (*Felis concolor*) males can be safely harvested as young as 4 yrs of age (Fig. 1d).

We tested whether infanticidal species are vulnerable to over-hunting by focusing on four large carnivore species with sizable markets for sport-hunted trophies, comparing three infanticidal felids (lions, cougars and leopards) to American black bears (*Ursus americanus*). We used black bears as a control case because males do not kill cubs in order to increase mating opportunities (sexually-selected infanticide – SSI), so rates of infanticide are not increased

by male-biased trophy hunting; in fact, among ursids, SSI has been documented in only one population of European brown bears (*U. arctos*) [7–9].

We extracted data from the UNEP World Conservation Monitoring Centre (WCMC) CITES trade database (See Materials and Methods). Data on total trophy harvests of lions and leopards are not available, so we used CITES-reported exports, which in cougars and black bears were highly correlated with domestic sport-hunting totals (Supporting Information Fig. S1); likewise CITES-reported trade in Tanzania's lion trophies showed a close match between imports and exports. Given sustained market demand, harvest trends should provide a reasonable proxy of population trends since sport hunters use intensive methods such as baits and hounds to locate these animals, and quotas on annual off-takes are either too high to limit harvests or (for black bears) reflect the management agency's perception of population trend [10].

Results

Fig. 2 shows the annual CITES exports for lions and leopards and US off-takes of cougars and black bears (See Materials and Methods). The reported number of trophies increased rapidly across all four species as markets grew during the 1980's and 1990's [11–12]. Off-takes have continued to increase for black bears, reflecting the sustained growth of bear populations

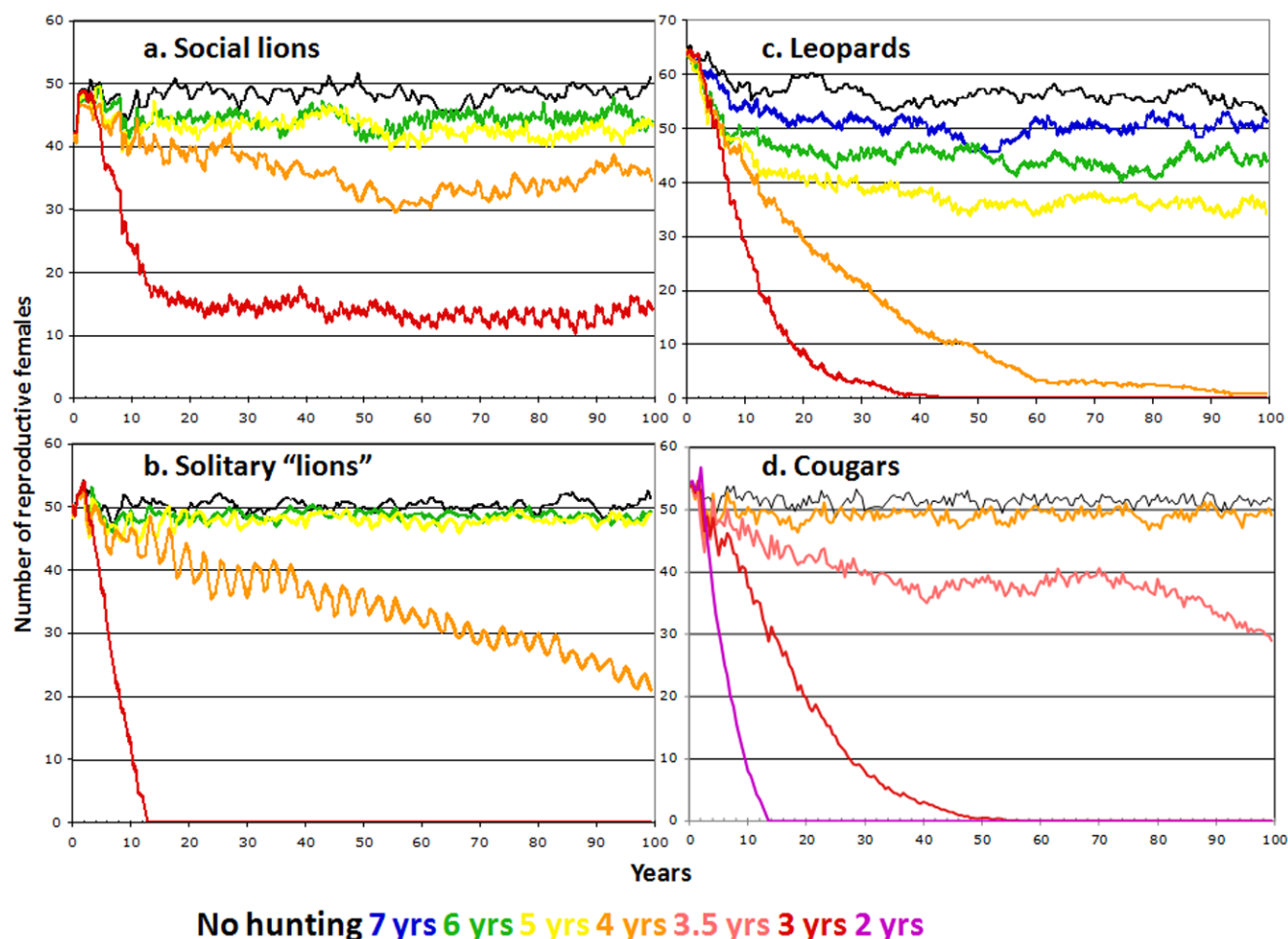


Figure 1. Average number of adult females in population simulations where all eligible males are removed during a 6-mo hunting season each year for 100 yrs. Colors indicate outcomes for different age minima for trophy males; each line indicates average from 20 runs. **A.** Population changes for “social lions” follow the assumptions and demographic variables in ref. [1] except to restrict hunting to 6-mo seasons and to incorporate additional details of dispersal, survival and reproduction [44–46]. **B.** Population changes for a hypothetical lion population where males and females are solitary and each territorial male controls one female. **C.** Population changes for leopards based on long-term data from Phinda Private Game Reserve [33,47] and other sources [37,48]. **D.** Population changes for cougars based on demographic data from refs. [27,49–53]. doi:10.1371/journal.pone.0005941.g001

throughout North America [13]. Leopard offtakes reached an asymptote in most countries, except for declines in Zambia in the 1980’s and Zimbabwe in the 1990’s and a recent CITES-granted increase to Namibia. In contrast, lion offtakes peaked then fell sharply in the 1980’s and 1990’s in Botswana, Central African Republic, Namibia, Tanzania, Zambia and Zimbabwe. Cougar offtakes showed similar peaks and declines in the 1990’s in Arizona, Colorado, Idaho, Montana and Utah (Fig. 2).

The downward harvest trends for lions and cougars (highlighted in Supporting Information Fig. S2) most likely reflected declining population sizes: success rates (as measured by harvest/quota) have fallen for both cougars and lions (Supporting Information Fig. S3). Demand for lion trophies (as measured by total imports from across Africa) has grown in the US and held stable in the EU since the mid-1990s, sustained in recent years by imports of trophies of captive lions from South Africa [12,14] (Supporting Information Fig. S3). Several countries instituted temporary bans on lion trophy hunting (Botswana in 2001–2004, Zambia in 2000–2001 and western Zimbabwe in 2005–2008) or banned female lions from quota (Zimbabwe, starting in 2005), but these measures were implemented well after the major decline in lion offtake in

each country. The harvest trends are also consistent with recent surveys suggesting a 30% continent-wide population decline in African lions [15] and declining cougar populations in several US states [16–17]. Conversely, black bear populations appear to be increasing across their range [13], even in states where cougar populations have declined (Fig. 2). Although not apparent from most hunting offtakes, leopards have undergone an estimated range decline of 35% in Africa [18] and were recently listed as Near Threatened by IUCN due to habitat loss, prey depletion, illegal skin trade and problem animal conflicts [19].

Trophy hunting is likely to have contributed to the declines in lion and cougar populations in many areas. Over the past 25 yrs, the steepest declines in cougar and lion harvests occurred in jurisdictions with the highest harvest intensities (Fig. 3a). Similarly, hunting blocks with the highest lion offtakes per 1000 km² in Tanzania’s Selous Game Reserve showed the steepest declines between 1996 and 2008 ($r^2 = 0.26$, $n = 45$ blocks, $P = 0.0004$). The Selous is the largest uninhabited hunting area in Africa (55,000 km²) and has long been the premier destination for lion trophies. Across jurisdictions, declining harvests were unrelated to habitat loss for either lions or cougars (Fig. 3b) or to snow

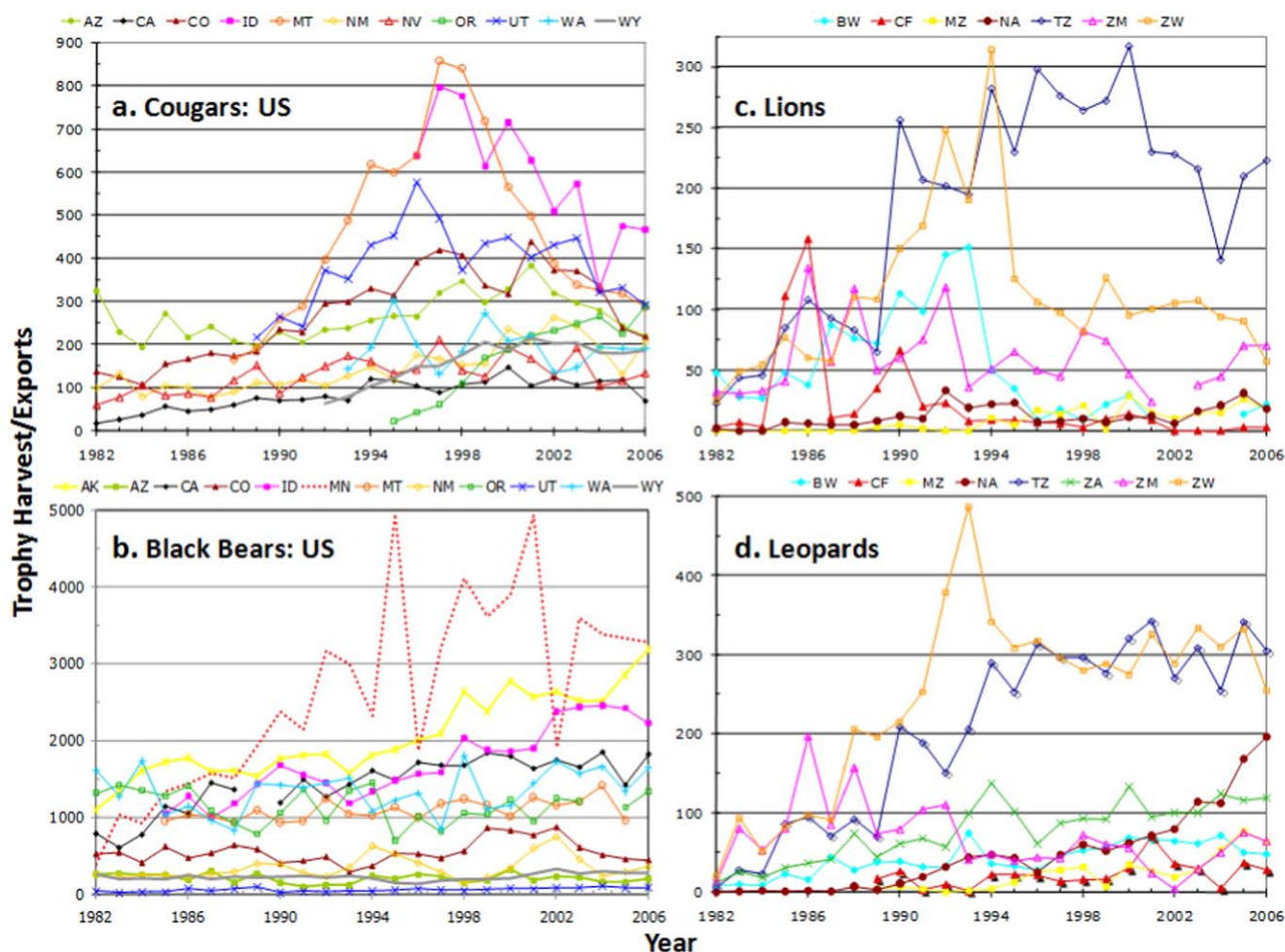


Figure 2. Domestic offtakes of a) cougars and b) black bears and CITES-reported trophy exports of c) lions and d) leopards. For US states: AK=Alaska, AZ=Arizona, CA=California, CO=Colorado, ID=Idaho, MN=Minnesota, MT=Montana, NM=New Mexico, NV=Nevada, OR=Oregon, UT=Utah, WA=Washington, WY=Wyoming. For CITES data: BW=Botswana, CF=Central African Republic, MZ=Mozambique, NA=Namibia, TZ=Tanzania, ZM=Zambia, ZW=Zimbabwe. doi:10.1371/journal.pone.0005941.g002

conditions for cougars. We modified our population simulation models to estimate impacts of sport hunting in a changing environment and found that habitat loss only imposes an additive effect on the impact of trophy hunting (Supporting Information Fig. S4). Note that habitat loss in many African nations has been so extensive (Fig. 3b) that lion offtakes have failed to recover for 10–20 yrs following the peak harvest years except in Namibia.

Although trophy hunting of lions and cougars is often portrayed as an economic strategy for increasing support for carnivore conservation, local communities often seek extirpation of problem animals [15,20–22]. Thus, sport hunting quotas may sometimes reflect pressures to control carnivores rather than to conserve them. Across Africa, countries with the highest intensity of lion offtake also had the highest number of livestock units per million hectares of arable land ($P = 0.047$, $n = 7$). In the US, Oregon announced plans in 2006 to reduce its cougar population by 40% to decrease depredation on livestock, pets and game mammals [23], Washington altered its cougar quotas in response to human-wildlife conflicts in the 1990s–2000s, and recent offtakes have exceeded government-sanctioned eradication programs in several states. For example, Utah's sport-hunting cougar harvests averaged 500/yr in 1995–7

compared to peak culls of 150/yr in 1946–1949 [24], and Montana sport hunters harvested 800/yr in 1997–1999 vs. 140/yr in the peak “bounty” years of 1908–11 [25]. Likewise, South Africa exported 120 leopard trophies per year in 2004–2006, similar to the cull of 133 leopards per year in Cape Province (which covered most of the country) during 1920–1922 [26].

Fig. 4 shows the potential consequences of coupling a 40% cull of cougars with intensive sport hunting if the control program only targets males (reflecting traditional trophy hunting), removes males and females in proportion to their abundance, or only removes adult females. Fig. 4adg show population trends for the maximum fixed offtakes that never resulted in population extinctions during 20 simulations, whereas Fig. 4beh show the minimum fixed harvests that caused extinction in all 20 runs (often within 10 yrs of an initial decline). Fig. 4cfi show the consequences of applying the maximum “safe” offtakes if the population were inadvertently culled by 50% because of inaccurate population estimates. Consistent with population viability analyses [27–28], a female-only harvest comes closest to maintaining a persistent population reduction; a mixed male-female strategy allows the largest number of trophies to be harvested; a male-only harvest never maintains a

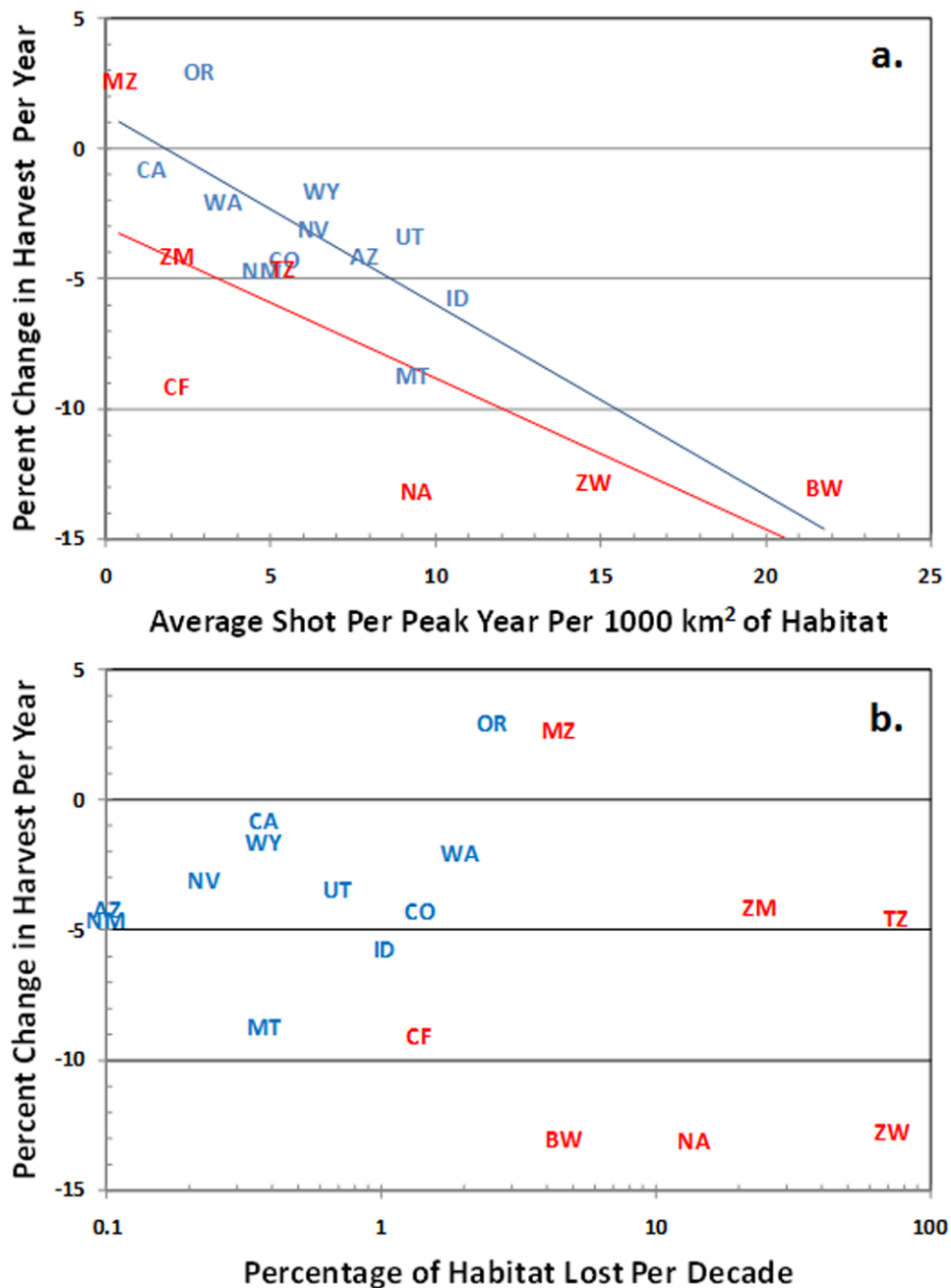


Figure 3. Recent trends in cougar off-takes (blue) and lion off-takes (red) as functions of a) harvest intensity and b) habitat loss. Jurisdictions with the highest harvest intensity showed the greatest decline in cougar off-takes ($r^2 = 0.5151$, $P = 0.0129$) and lion off-takes ($r^2 = 0.5796$, $P = 0.0468$). Habitat loss is plotted on a log scale to allow comparison between the African countries and the US states. doi:10.1371/journal.pone.0005941.g003

40% reduction in population size and has the smallest margin of error (male-only harvests can have catastrophic effects even in non-infanticidal species [29]).

These simulations assume a fixed harvest whereas many wildlife agencies reduce their quotas in response to lowered off-takes (Supporting Information Fig. S3 also see ref. [30]). However, off-takes may often be maintained at constant levels through compensatory increases in hunting effort, running the risk of an “anthropogenic Allee effect” [31–32]. Hunters in Zambia, Zimbabwe and Tanzania maintain their lion harvests by shooting males as young as 2 yrs of age (Fig. 5). In Zimbabwe, high lion off-takes were sustained from 1995 until 2005 by allowing females

on quota [3], and the duration of lion safaris increased by nearly 18% from 1997 to 2001 (Supporting Information Fig. S3). Similarly, hounds have been used to hunt leopards in Zimbabwe since 2001, potentially masking a continued population decline.

Discussion

Mortality from state-sanctioned and illegal predator control likely contributed to the overall population declines of cougars and lions; while leopards are also killed as pests, the leopard’s CITES Appendix I status requires international approval for national export quotas, potentially providing safeguards against overhar-

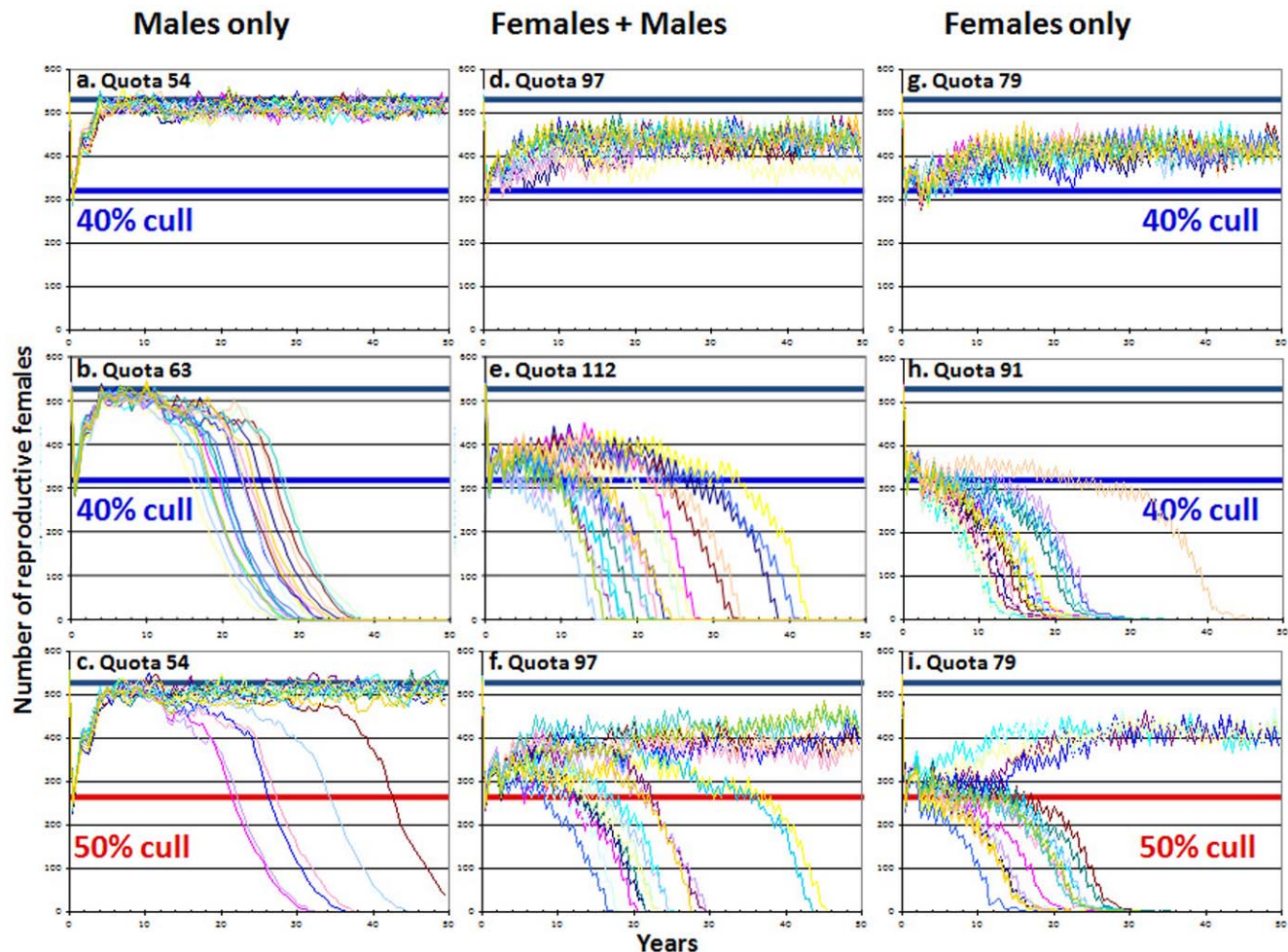


Figure 4. Simulated cougar populations subjected to an initial cull followed by fixed offtakes for 50 yrs. The initial cull is either 40% (top and middle rows) or 50% (bottom row), and the subsequent harvests are either the maximum offtake that incurred no extinctions in 20 runs following a 40% cull (top and bottom rows) or the minimum that produced 20 extinctions in 20 runs following a 40% cull (middle row). In the absence of sport hunting, the stable population size in these simulations is 527 reproductive females (indicated by the heavy black line in each graph); a 40% reduction in population size is indicated by blue lines, a 50% reduction by red lines. Each column represents a different harvest strategy: male only (left column), males and females (middle) and female only (right). Demographic parameters are set as in Fig. 1; quotas allow offtake of animals as young as 2 yrs; each graph shows outputs from 20 runs.
doi:10.1371/journal.pone.0005941.g004

vest. However, leopard exports have declined in some countries, quotas have risen in others, and concerns have been raised over the level of problem animal offtakes and the management of leopard hunting practices [33–35]. Further, leopard populations in many areas may have been “released” [36] by large scale declines in lion numbers: lions inflict considerable mortality on leopards [37]; consequently, hunting blocks in Tanzania’s Selous Game Reserve with the highest lion harvest intensities showed the largest increases in leopard harvests ($P=0.0059$ after controlling for declines in lion offtakes, $n=45$ blocks). Thus the full impact of current trophy hunting practices on leopards may not be fully apparent for several more years.

Harvest policies for infanticidal species such as lions, cougars and leopards that relied on “constant proportion” or “fixed escapement” could help protect populations but require accurate information on population size and recruitment rates, which are virtually impossible to collect; a harvest strategy of “constant effort” can more easily be achieved by measuring catch rates and regulating client days [38–40]. Hunting efficiency could be reduced by banning or limiting the use of baits and hounds, but

the absence of direct oversight in remote hunting areas would make enforcement difficult. Alternatively, the age-minimum harvest strategies illustrated in Fig. 1 could be implemented without risk of over-hunting, assuming that ages can be reliably estimated before the animals are shot [41] rather than afterwards [42]. Unsustainable levels of trophy hunting of lions and cougars appear to be driven by conflicts with humans and livestock: the intensity of lion hunting was highest in countries with the most intensive cattle production, and wildlife managers are under similar pressure from US ranchers to raise cougar offtakes. Thus an even more fundamental challenge for carnivore conservation will be to build community tolerance for predators by reducing the need for retaliatory predator control and by improving benefit sharing from well managed trophy hunting [15].

Materials and Methods

We analyzed trophy exports (<http://www.unep-wcmc.org/citestrade/>) by using the term “trophy” and restricting the analysis to countries that exported at least 25 trophies of a particular



Figure 5. Sample of under-aged male African lions shot by sport hunters in various countries from 2004–2008.
doi:10.1371/journal.pone.0005941.g005

species for at least 2 yrs from 1982 to 2006 (excluding captive-bred lion trophies from South Africa). Other types of exports (skins) were also analyzed for lions, since non-standard terms are sometimes used by reporting countries [43], but these did not alter overall export trends. Data on Tanzanian hunting quotas were provided by the CITES office at the Division of Wildlife headquarters in Dar es Salaam; data on duration of hunting safaris in Zimbabwe were from the head office of Parks and Wildlife Management Authority in Harare.

Offtake data for black bears and cougars were provided by the Alaska Dept. of Fish & Game, Arizona Game & Fish Dept., California Dept. of Fish & Game, Colorado Division of Wildlife, Idaho Fish & Game, Minnesota Dept. of Natural Resources, Montana Fish, Wildlife & Parks, New Mexico Game & Fish, Nevada Dept. of Wildlife, Oregon Dept. of Fish & Wildlife, Utah Division of Wildlife Resources, Washington Dept. of Fish & Wildlife, and Wyoming Game & Fish. Note that all cougar offtakes in California are due to predator control.

“Harvest intensity” is the average harvest of the three peak offtake years divided by the extent of habitat in that state/country. Regression coefficients were calculated across the time period beginning with the earliest of the three peak harvests and ending in 2006 for cougars or the last of the three lowest subsequent harvest years for lions (Supporting Information Fig. S3); percent change is the regression coefficient divided by the peak harvest. Limited lion and leopard offtake data were available from 1996–2008 in Tanzania’s hunting blocks; trends were only calculated for blocks reporting ≥ 5 yrs of activity.

Cougar habitat is forest cover taken from the National Land Cover Database (NLCD) www.mrlc.gov/changeproduct.php; lion habitat is the extent of GLOBCOVER land classification categories 42, 50, 60, 70, 90, 100, 110, 120, 130, 134, 135, 136, 160, 161, 162, 170, 180, 182, 183, 185, 186 and 187 in each country, see <http://postel.mediasfrance.org/en/DOWNLOAD/Biogeophysical-Products/>. Habitat loss is based on change in forest cover in the US 1990–2000 and in woodland/forest habitat in Africa 1990–2005 from FAO Global Forest Resources Assessment 2005, <http://www.fao.org/forestry/32185/en/>. Snow conditions for cougars are taken from <http://www.wrcc.dri.edu/Climsum.html> and African livestock production is taken from http://www.fao.org/es/ess/yearbook/vol_1_1/pdf/b02.pdf, using production levels from years of peak lion offtake in each country.

Supporting Information

Figure S1 The number of CITES-reported exports of a) cougar trophies and b) black bear trophies from the US were highest in years when the most animals were harvested domestically in the western states ($P < 0.001$ for each species).

Found at: doi:10.1371/journal.pone.0005941.s001 (0.69 MB EPS)

Figure S2 Trendlines for the population declines of a) cougars and b) lions. Individual states with statistically significant declines in cougar offtakes: MT, ID, AZ, UT and CO; individual countries with significant declines in lion offtakes: BW, TZ and ZW.

Found at: doi:10.1371/journal.pone.0005941.s002 (1.08 MB EPS)

Figure S3 Quotas, offtakes and catch rates each year since the peak harvests for cougars in Colorado, Montana and Utah and lions in Tanzania and Botswana; duration of lion hunts in

Zimbabwe. Catch rates are (offtakes/quotas). Catch rates have generally declined because offtakes have fallen more quickly than quotas. Catch rates briefly improved in Utah and Botswana when quotas were adjusted downwards, but subsequently resumed an overall decline; Montana’s adjustments in quotas are too recent to evaluate. For Zimbabwe, vertical lines indicate standard errors; numbers are sample sizes; duration of lion hunts became significantly longer between 1997 and 2001 ($P < 0.01$). No other data are available on quotas or hunt durations from these or other countries/states. The bottom graphs show that declines in lion trophy exports are unlikely to reflect declining market demand; imports of lion trophies have increased, especially in recent years for captive-bred or “canned” lion trophies for South Africa. The declines in trophy exports are also unlikely to be caused by irregular reporting; adding additional exports of skins from Botswana, Tanzania and Zimbabwe would not significantly change the pattern of decline.

Found at: doi:10.1371/journal.pone.0005941.s003 (1.38 MB EPS)

Figure S4 Simulated impacts of trophy hunting in cougars for varying degrees of habitat loss. Solid lines are the same as in Fig. 1: all available males above the age minimum are harvested each year and available habitat remains unchanged over 100 yrs. Dashed lines show population sizes with the same harvest strategies but with 20% habitat loss in 100 yrs; dotted lines represent outputs with 40% habitat loss.

Found at: doi:10.1371/journal.pone.0005941.s004 (1.49 MB EPS)

Table S1

Found at: doi:10.1371/journal.pone.0005941.s005 (0.03 MB DOC)

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Author Contributions

Conceived and designed the experiments: CP MK KN. Performed the experiments: MK. Analyzed the data: CP MK HB LP KN. Contributed reagents/materials/analysis tools: MK HC HB LP DLG GP MS AS GB LH KN. Wrote the paper: CP DLG KN.

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Idiosyncratic responses of grizzly bear habitat to climate change based on projected food resource changes

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Abstract. Climate change vulnerability assessments for species of conservation concern often use species distribution and ecological niche modeling to project changes in habitat. One of many assumptions of these approaches is that food web dependencies are consistent in time and environmental space. Species at higher trophic levels that rely on the availability of species at lower trophic levels as food may be sensitive to extinction cascades initiated by changes in the habitat of key food resources. Here we assess climate change vulnerability for *Ursus arctos* (grizzly bears) in the southern Canadian Rocky Mountains using projected changes to 17 of the most commonly consumed plant food items. We used presence-absence information from 7088 field plots to estimate ecological niches and to project changes in future distributions of each species. Model projections indicated idiosyncratic responses among food items. Many food items persisted or even increased, although several species were found to be vulnerable based on declines or geographic shifts in suitable habitat. These included *Hedysarum alpinum* (alpine sweet vetch), a critical spring and autumn root-digging resource when little else is available. Potential habitat loss was also identified for three fruiting species of lower importance to bears: *Empetrum nigrum* (crowberry), *Vaccinium scoparium* (grouseberry), and *Fragaria virginiana* (strawberry). A general trend towards uphill migration of bear foods may result in higher vulnerability to bear populations at low elevations, which are also those that are most likely to have human-bear conflict problems. Regardless, a wide diet breadth of grizzly bears, as well as wide environmental niches of most food items, make climate change a much lower threat to grizzly bears than other bear species such as polar bears and panda bears. We cannot exclude, however, future alterations in human behavior and land use resulting from climate change that may reduce survival rates.

Key words: climate change; ecological niche model; food; global warming; grizzly bear; North America; species distribution model; trophic levels; *Ursus arctos*.

INTRODUCTION

Climate change is altering habitats for a wide breadth of organisms, with plants being particularly sensitive given their limited ability to physically follow suitable environmental conditions (Parmesan 2006). While this vulnerability to plants is notable in itself, it also has implications for species that are dependent on plant resources for their habitat. This leaves open the possibility for extinction cascades to be initiated via bottom-up effects, thus increasing vulnerability for species at higher trophic levels that rely on the availability and health of primary producers. Climate change vulnerability assessments for species at higher trophic levels, such as large mammals, may therefore need to include assessments of plant communities and the food web interactions with mammals, under the assumption that food webs related to the target species are consistent in time and environmental space. While

such trophically based vulnerability assessments may be rare in the literature, it is apparent that interspecific interactions among species and trophic levels should be considered when assessing effects of climate change (but see Tuanmu et al. 2013).

For the North American grizzly bear (*Ursus arctos*; see Plate 1), the high energetic requirements of winter hibernation combined with the relatively short foraging season means that habitat tends to be selected based largely on resource availability (Schwartz et al. 2003). While faunal food sources such as ungulate predation are important energy sources, bears also dedicate much effort to foraging on vegetation, particularly in temperate forested habitats (Bojarska and Selva 2012), where isotopic diet assessments demonstrate that grizzly bears in the southern Canadian Rockies are among the most vegetarian of North American populations (Hilderbrand et al. 1999). In spring, and to a lesser extent throughout the active period, root digging for species such as *Hedysarum alpinum* (alpine sweet vetch) dominate the diet and thus the activity of bears (McLellan 1990, Hamer et al. 1991, Munro et al. 2006). As spring progresses with green-up, succulent herbaceous foods

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high in protein, such as young *Equisetum arvense* (horsetail) and *Trifolium* spp. (clovers) become more important. And finally, during the late-summer and early-autumn hyperphagic period, bears in the southern Canadian Rocky Mountains rely predominantly on fruit from perennial shrubs for energy (Munro et al. 2006).

The threat of anthropogenic footprints and activities, such as roads, urban development, and resource extraction, which can all adversely affect grizzly bear survival rates, have been well described (Mattson 1990, McLellan 1990). However, little is known about how climate change may affect the foods and thus the habitats that bears depend on. A variety of empirical models of grizzly bear habitat have been developed, focusing primarily on parameterizing current bear habitat (but see Nielsen et al. 2008), mostly using complex environmental surrogates of food resources and human activity such as land cover type, forest crown closure, slope, aspect, elevation, and metrics of road density or urbanization (e.g., Nielsen et al. 2006, Ciarniello et al. 2007, Graves et al. 2011). Although some studies have focused directly on food resources on which bears depend (e.g., Nielsen et al. 2003, 2004, 2010), few have assessed how climate change would affect those resources and thus grizzly bear habitat. (See, however, the recent review by Butler [2012] on potential linkages between climate and bear foods.) First, woody encroachment of subalpine and alpine meadows threatens sweet vetch habitat and other important alpine sources of bear foods. Second, decreased winter snowpack may limit the number of new avalanche slopes, which also represent quality foraging habitat for bears. Rodriguez et al. (2007) presents the only study to our knowledge of changes in grizzly bear food source consumption in relation to changing climate conditions over a 30-year period in Spain. While the authors found relationships between changes in autumn bear diets and changes in climate regimes over the same period, changes in land use and grazing practices were also noted.

Species distribution models represent a different type of predictive model, often used to project future species ranges under climate change scenarios (Elith and Leathwick 2009). These models relate environmental predictors with the response of observed species presence or absence using any of a number of statistical procedures and then incorporate novel environmental data to project the ranges of suitable species habitat. Because of their empirical nature, species distribution models make a number of assumptions, including equilibrium of a species with its environment and the conservation of species niches over time. They also contain no mechanisms for incorporating biotic interactions such as competition, aside from indirectly through the observed presence and absences of species on the landscape, nor do they consider barriers to or limitations of species migration and colonization (see reviews by Pearson and Dawson 2003, Elith and



PLATE 1. A large adult male grizzly bear (*Ursus arctos*) in the foothills of Alberta, Canada. Forested habitats are common to the region. Photo credit: Gordon Court.

Leathwick 2009). Despite these limitations, species distribution models have been widely used to project future ranges under climate change for a variety of species.

In this study, we assess climate change vulnerability to grizzly bear food plant species using field data on bear food distribution and ecological niche models. Specifically, we project habitat changes for 17 species considered to be key grizzly bear food resources in the southern Canadian Rocky Mountains of Alberta and British Columbia (Fig. 1). To assess risk levels to habitat stability, we also examined seasonal changes in species prevalence across the southern Canadian Rocky Mountains and identified geographic trends of habitat changes. While the extensibility of food resource projections to habitat quality changes, for upper trophic level species like bears, ignores potentially complex adaptive behavioral responses of these habitat generalists, model predictions allow us to make inferences regarding general patterns among species and geographic space of future climate-related vulnerabilities to current key grizzly bear food resources.

METHODS

Ecological niche models

We incorporate eight individual modeling methods into a single, averaged ensemble output, which has been shown to improve accuracy (Araújo and New 2007,

Roberts and Hamann 2012): artificial neural networks, classification tree analysis, generalized additive models, generalized boosting models, generalized linear models, multivariate adaptive regression splines, a boosted regression tree known as Random Forest, and surface range envelopes (not included in the ensemble) (Thuiller 2003). All modeling methods, as an output variable, report a probability of presence (PoP) for each species.

Species niches were parameterized in the models using species presence-absence data from 7088 field vegetation plots located throughout the study area from three independent data sources. A total of 4090 vegetation plots were established in 1977–1979 within Banff National Park, Kootenay National Park, Jasper National Park, and Yoho National Park (Nielsen et al. 2003), 2849 plots were sampled between 2001–2008 in west-central Alberta by Nielsen et al. (2010), and 149 plots were sampled in the Willmore Wilderness Area in 2001–2003 (Gould 2007) and 2009–2010 (J. A. Gould, *unpublished manuscript*). Plots were distributed between 394 m and 2708 m elevation (mean 1603 m) and varied in location (alpine to valley bottoms) and aspect.

Environmental predictors for each plot included nine seasonal and annual climate variables, three topographic/radiative variables, and one remotely sensed variable of forest crown closure. Climate data were generated for the 1961–1990 historic period (prior to the influence of the recent anthropogenic warming signal and a likely period of recruitment for the generally long-lived shrubs that constitute most of the species we considered) using PRISM down-sampling (Daly et al. 1994) via a publically available software package that generates monthly, seasonal, and annual climate variables (Wang et al. 2012). Of the available climate variables, we selected nine that covaried least, including five temperature and precipitation metrics (mean annual temperature, average winter temperature, average summer temperature, winter precipitation, and summer precipitation); two dryness indices (annual heat moisture and summer heat moisture [Hogg 1997]); and two calculated temperature-based metrics (the number of frost-free days and the number of degree days above 5°C). Topographic/radiative predictor variables, which have previously been found important in describing species distributions for bear foods in the region (Nielsen et al. 2003, 2010), included a compound topographic index that incorporates moisture and drainage (Moore et al. 1991), a topographic heat load index that measures annual solar radiation with a lagged heat load effect for southwestern aspects using slope, aspect, latitude (McCune 2007), and finally a general slope/aspect topographic radiation based only on slope and aspect using the topographic radiation aspect (TRASP) index of Roberts and Cooper (1989) within the Geomorphometric and Gradient Metrics ArcGIS Toolbox (Evans 2011). Last, we included a remotely sensed metric of forest crown closure from McLane et al. (2009), as forest structure has been identified as an important local

predictor of occurrence for our species of interest (Nielsen et al. 2010).

Ecological niche models were validated using a random cross-validation of training data, where two-thirds of training points were used to build models, and the remaining one-third used to evaluate model projections. While cross-validations have been shown to be optimistic measures of model accuracy (Araújo et al. 2005), they have also been shown to be effective in selecting among modeling techniques (Roberts and Hamann 2012). Validations were performed using the area under the curve (AUC) of the receiver operating characteristic (Fawcett 2006). The AUC provides a threshold-independent evaluation of true presences vs. false presences for all probability of presence outputs simultaneously, where an AUC value of 1.0 is a perfect match, and where random PoP data would produce an AUC of 0.5.

Species habitat projections

Present day and future species' habitats were projected at 300×300 m resolution, with environmental predictor data generated as described previously. Future-climate grids were estimated for the area by calculating the arithmetic average of 14 general circulation model (GCM) outputs as temperature and precipitation anomalies from the present day, averaged across the 2071–2100 period (hereafter referred to as the “2080s”). The effectiveness of averaged multi-GCM climate projections has been questioned (Fordham et al. 2011), as using multi-model averages of climate has the effect of centralizing more extreme climate projections, which may be equally likely to occur. As a means of bookending the extent of potential future warming, two emissions scenarios, the aggressively warming A2 scenario and the moderately warming B1 scenario (IPCC 2007), were averaged separately, and results from both emissions scenario projections are presented.

Apart from the climate variables, future predictor data were left unchanged from present-day values, with the exception of estimates of crown closure. Projections of future crown closure were estimated using a separate niche modeling procedure, incorporating the same predictor variables as described above for the species models, but using only the Random Forest bootstrapped regression tree method (Breiman 2001). Crown closure models were evaluated by training the model with data from the northern half of the study area, and validating models with data from the southern half, to simulate a projection into warming climates. The correlation between modeled and observed crown closure in the southern half of the study area was $r = 0.49$.

Areas of agricultural use, surface water, and high alpine rock and ice were removed from the species habitat projections, as they were considered unsuitable future habitat. These areas were masked as absences and were not considered in any of the summary analyses.

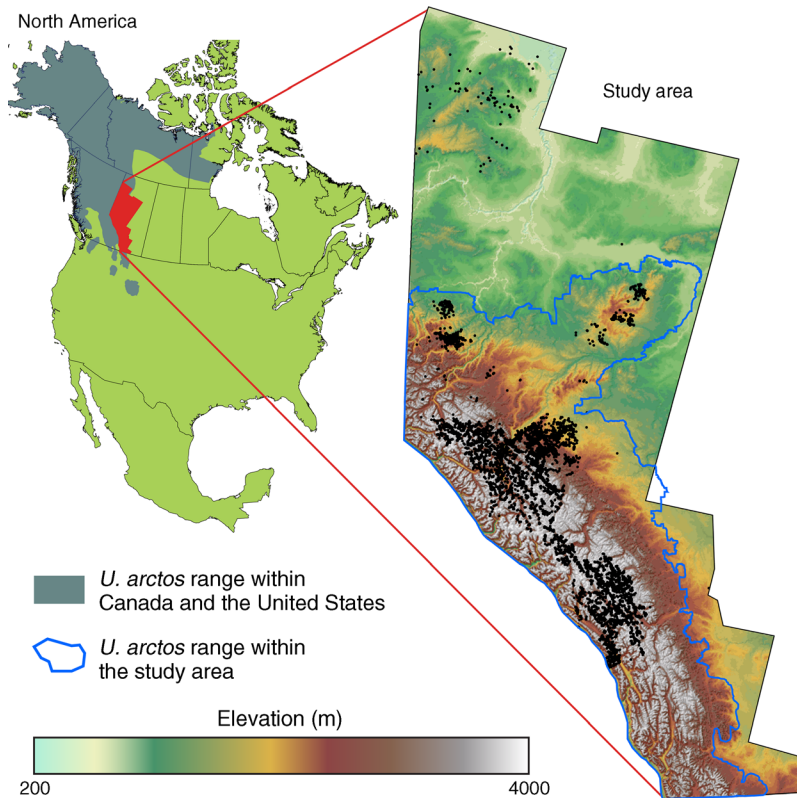


FIG. 1. Location of the study area in the western Canadian Rocky Mountains, showing topographic profile. Present-day grizzly bear range for the southern Canadian Rockies (Nielsen et al. 2009) is outlined in blue.

Masking these areas did not affect model validation statistics, as neither training nor validation data were located in these areas. To convert all other PoPs to binary presence-absence outputs, a threshold PoP was selected for each species. Threshold criteria that balance sensitivity and specificity have been shown to be more accurate than arbitrary thresholds or those based on maximizing Cohen's kappa statistic (Jimenez-Valverde and Lobo 2007), but tend to favor errors of commission in the data (i.e., favoring sensitivity, or potential overestimates of species presence). To select a threshold for presence-absence delineation from the PoP data, the average of two methods was used: (1) the PoP that maximized the sum of sensitivity and specificity, and (2) the PoP that minimized the difference between the absolute values of sensitivity and specificity.

While maps show species projections for the entire study area, summary statistics of elevation profile and change in total distribution (area) were completed only for data within the boundary of present-day grizzly bear habitat (as defined by Nielsen et al. 2009) in order to quantify threats to bear foods for their currently inhabited range (shown in blue in Fig. 1).

Software

All modeling, analysis of results, and generation of output files were done within the R programming

environment (R Development Core Team 2013): all eight individual models were generated with the *BIO-MOD* package (Thuiller et al. 2009), AUC and associated statistics were calculated using the *ROCR* package (Sing et al. 2005), the PCA was performed using the base stats package, and rasters and graphics were generated using the *raster* package (Hijmans and van Etten 2012) and the *ggplot2* package (Wickham 2009).

RESULTS

Model validation

Area under cover (AUC) for all methods within each species is shown in Fig. 2. All AUC values for all species and all methods, including the number of observed presences and absences, are provided in Appendix A. With the exception of the surface range envelopes, which showed very poor model performance (median AUC = 0.61; maximum AUC = 0.68), model validations indicated good to excellent model fit for all methods, with median AUC values ranging from 0.74 for the classification tree method to 0.83 for Random Forest. The ensemble method of averaging outputs from all other methods performed better than any individual method (median AUC = 0.84). While it has previously been shown that including even poor-performing models in the ensemble calculations may increase the accuracy

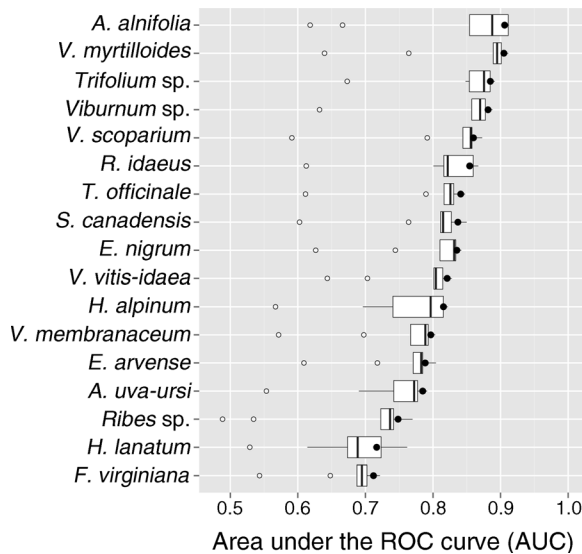


FIG. 2. Boxplot showing model accuracy as measured by the area under the curve (AUC) of the receiver operating characteristic (ROC) for each species and all modeling methods, including the ensemble mean method, the AUCs for which are shown as black circles. The boxes represent the interquartile range, with heavy lines as the median. Whiskers represent the range of the data, omitting Tukey outliers (greater than 1.5 \times the interquartile range), which are shown as open circles. A complete table of AUC values for each species within each method and number of observed presences and absences, including complete scientific names, is provided in Appendix A.

of the ensemble (Roberts and Hamann 2012), including the surface range envelope outputs in the ensemble decreased its accuracy and was thus omitted from the calculation. AUC values for individual species for the ensemble method ranged from 0.72 for *Fragaria virginiana* (wild strawberry) to 0.91 for *Amelanchier alnifolia* (saskatoon). As a simple metric of model agreement, we also examined the standard deviations of PoPs in the ensemble model. Within present-day grizzly habitat, PoP standard deviations tended to be low to moderate, with the greatest model agreement occurring in areas of higher elevation. The highest model disagreements in both B1 and A2 scenarios appear in the low-elevation prairies in the southern extent of the study area, along the bottoms of some southern river valleys, and in some of the warmer and drier low-elevation areas in the north.

Changes in species distributions

Complete summaries of habitat gained and lost for each species are shown in Table 1. Maps of PoP and plots of the distribution for each species along the observed elevation gradients for the modern and future periods are presented in Appendix B. Within present-day grizzly bear range, most species (with some notable exceptions) experienced increased PoPs in the 2080s projections for both the B1 and A2 warming scenarios relative to the 1961–1990 period. PoPs also typically increased from the B1 to the A2 scenario, suggesting a trend of increased habitats with increased warming. When PoPs were converted to presence or absence, most species demonstrated a corresponding increase in

TABLE 1. Summary of species' projected elevation and area changes within occupied grizzly bear habitat (Nielsen et al. 2009) for the 2080s period for two emissions scenarios: B1 (moderate warming) and A2 (aggressive warming).

Species	Common name	Season	Elevation (m)		
			1961–1990		
			p10	p50	p90
<i>Amelanchier alnifolia</i>	saskatoon	aut	880	1378	1822
<i>Arctostaphylos uva-ursi</i>	bearberry	aut	1096	1497	1995
<i>Empetrum nigrum</i>	crowberry	aut	1587	1901	2176
<i>Equisetum arvense</i>	horsetail	spr	766	1036	1360
<i>Fragaria virginiana</i>	strawberry	aut	794	1219	1776
<i>Hedysarum alpinum</i>	sweet vetch	spr–aut	1219	1518	2111
<i>Heracleum lanatum</i>	cow parsnip	sum	809	1237	1846
<i>Ribes</i> spp.	gooseberry	aut	808	1218	1733
<i>Rubus idaeus</i>	raspberry	aut	778	1080	1493
<i>Shepherdia canadensis</i>	buffaloberry	aut	803	1459	1921
<i>Taraxacum officinale</i>	dandelion	spr–sum	791	1127	1582
<i>Trifolium</i> spp.	clover	spr–sum	781	1099	1552
<i>Vaccinium membranaceum</i>	huckleberry	aut	1139	1616	2035
<i>Vaccinium myrtilloides</i>	blueberry	aut	773	1046	1386
<i>Vaccinium scoparium</i>	grouseberry	aut	1634	1940	2239
<i>Vaccinium vitis-idaea</i>	lingonberry	aut	792	1134	1711
<i>Viburnum</i> spp.	cranberry	aut	786	1105	1501

Notes: Median elevations for the 1961–1990 period and the projected changes (Δ elev.) in 10th percentile (p10), median (p50), and 90th percentile (p90) elevation under each future-climate scenario are listed, as are total range area (Area) and percentage change in range area (Δ area) for the 1961–1990 observed climate and the two 2080s climate projections. The percentage of stable area (Stable area) represents the proportion of the species' 1961–1990 range that is maintained in the projections for the 2080s. Trends of species' seasonal use by bears (Season) are based on findings of Munro et al. (2006). Seasons are abbreviated as: aut, autumn; spr, spring; sum, summer.

projected range for the 2080s period for both scenarios (again, typically larger in the A2 than B1 scenario). *Amelanchier alnifolia* gained the most suitable habitat, increasing in projected area by 186% and 199% in the B1 and A2 scenarios, respectively. *Vaccinium membranaceum* (huckleberry) and *Vaccinium myrtilloides* (blueberry) also showed substantial increases in habitat, by 84–112% and 66–78%, respectively. Notable exceptions to increased trends include *Vaccinium scoparium* (grouseberry), which was projected to lose 92–95% of its habitat, *Empetrum nigrum* (crowberry), which was projected to lose 72–89% of its habitat, and wild strawberry, which was projected to lose 30–58% of its habitat. The remaining species gained or lost projected habitat in more moderate amounts, ranging from losses of 18% to gains of 70%.

In addition to the area of total habitat by species, the amount of stable habitat was also summarized within present-day grizzly bear range. The measure of stable area represents the proportion of a species' 1961–1990 habitat that remains suitable habitat in future projections (Table 1). While most species were projected to maintain between 94% and 100% of their 1961–1990 habitat, some species were projected to lose substantial amounts of habitat. *Empetrum nigrum*, *Vaccinium scoparium*, *Fragaria virginiana*, and *Arctostaphylos uva-ursi* (bearberry) in both scenarios, and *Hedysarum alpinum* in the A2 scenario, all lost considerable amounts of stable habitat (retaining between 3% and 67%). *Hedysarum alpinum* in the B1 scenario predicted an

increase in habitat area of 45% but a loss of stable area (only 56% stable), indicating that, while net habitat area may increase, just over half of the present-day range of the species remains suitable habitat in future projections.

In addition to changes in projected area of habitat, all species showed changes in their elevation profile, with a general future trend towards increasing median elevation, increasing 10th percentile elevation (the trailing downslope edge), and increasing 90th percentile elevation (the leading upslope edge) (Table 1; Appendix B). The largest increases in median elevation were projected in the A2 scenario for *Hedysarum alpinum* and *Fragaria virginiana*, with increases of 525 m and 423 m, respectively. With only one exception, the 90th percentile elevation of all species increased in both emissions scenarios. Median and 10th percentile elevation decreases were projected for some species including *Vaccinium membranaceum* (median decrease of 203 m in the A2 scenario), *Arctostaphylos uva-ursi* (median decrease of 101 m in the A2 scenario), and *Amelanchier alnifolia* (median decrease of 68 m in the A2 scenario). All three of these species are wide ranging in their present-day elevation profile. *Empetrum nigrum* was the only species exhibiting contradictory trends in elevation profiles for different emissions scenarios. Projected 10th percentile and median elevations for the species increased moderately in the B1 scenario (by 242 m and 193 m, respectively), but decreased substantially in the A2 scenario (by 993 m and 767 m, respectively).

TABLE 1. Extended.

Δ elevation (m)						Area 1961–1990 (×10 ⁵ km ²)	Δ area 2080s (%)		Stable area 2080s (%)	
2080s (B1)			2080s (A2)				B1	A2	B1	A2
p10	p50	p90	p10	p50	p90					
(−57)	−96	(+91)	(−51)	−68	(+153)	4.47	+186	+199	100	100
(−136)	−57	(+70)	(−109)	−101	(+49)	5.42	−11	−18	67	58
(+242)	+193	(+181)	(−993)	−767	(+201)	2.89	−72	−89	22	3
(+25)	+96	(+315)	(+34)	+152	(+513)	6.94	+30	+45	100	100
(+244)	+212	(+187)	(+440)	+423	(+329)	9.71	−30	−58	61	34
(+133)	+357	(+108)	(+449)	+525	(+207)	1.37	+45	−15	56	31
(+20)	+74	(+131)	(+20)	+74	(+131)	11.42	+17	+17	100	100
(+20)	+92	(+233)	(+21)	+94	(+245)	11.34	+17	+18	100	100
(+23)	+89	(+169)	(+44)	+192	(+404)	8.10	+28	+55	99	100
(+33)	−66	(+87)	(+19)	−124	(+61)	7.40	+42	+70	97	100
(+15)	+69	(+221)	(+31)	+153	(+374)	9.23	+16	+36	99	100
(+11)	+42	(+107)	(+20)	+80	(+244)	8.27	+13	+22	99	99
(−114)	−111	(+24)	(−335)	−203	(−4)	4.96	+84	+112	100	100
(+49)	+224	(+480)	(+56)	+265	(+591)	7.50	+66	+78	100	100
(+382)	+288	(+296)	(−414)	+171	(+319)	2.11	−92	−95	7	3
(+6)	+24	(+57)	(+17)	+85	(+107)	8.75	+13	+30	94	97
(+37)	+176	(+390)	(+43)	+205	(+474)	8.85	+44	+51	100	100

Changes in distribution of seasonal resources

When summarized by foraging season for grizzly bears (as per Munro et al. 2006), the diet richness (number of species present) during spring (hypophagia), summer (early hyperphagia), and autumn (hyperphagia) periods tended to be either stable or increasing (Fig. 3; Appendix C). It should be noted that these summaries reflect only the net balance of diet items (species counts), and do not reflect the loss of one species that is replaced by the arrival of another species (i.e., community turnover in diet composition). Springtime conditions showed no major change in diet richness for most of the present-day grizzly bear range, with the exception of some high mountainous areas that gain habitat for one species and for some regions along the eastern slopes and river valleys of the Rocky Mountains that lose a single species, reflecting the loss of *Hedysarum alpinum* habitat (Fig. 3). Grizzly bear habitat in the summertime is projected to maintain present-day diet richness or increase diet richness in the higher-elevation areas of the Rocky Mountains, with up to four additional species. Decrease in diet richness in summer occurs in the southernmost valley bottoms, losing up to two of the four summer species considered. The same trends as in the spring and summer were also present during the fall: a general stability of diet richness within present-day grizzly bear range. Decreases in habitat of up to three species occurred in the eastern slopes, while increases in high-elevation habitat of up to 11 of the 12 species considered.

DISCUSSION

Climate change vulnerability of grizzly bear food items

The lack of extensive projected range loss due to climate change for most plant-based grizzly bear food items suggests that widespread collapse of habitats due to losses in trophic web linkages on which bears depend is unlikely. In fact, the general trend within present-day grizzly bear range of the southern Canadian Rocky Mountains is towards more widespread availability and increased diet richness of bear foods. Changes in model projections that have high uncertainty could, however, alter responses. For instance, the general projection of increased diet richness ignores key species interactions such as competition, which may, despite environmental suitability for a new site, prevent future establishment (successful colonization).

Our models also assume an “equilibrium and perfect dispersal” scenario where species are expected to reach all suitable habitats by the 2080s. Owing to steep elevation clines in the area, this may be a reasonable assumption for many species, since emerging habitat would be geographically proximate to current habitat. However, some bear food items, particularly the ericaceous shrubs that are an important source of fruit (energy) to bears, are known to have low dispersal–establishment capacity, with their long-term persistence

in an area predominantly due to vegetative reproduction (Vander Kloet and Hill 1994, Regan et al. 2012). These species may therefore only persist in habitats that they currently occupy, and are projected to be within the environmental niche of the species in the 2080s (i.e., zero dispersal scenario). Less topographically diverse locations may be vulnerable to losing a large complement of their species richness, since the rate of migration would need to be higher, especially considering that these areas are more likely to be fragmented by anthropogenic barriers.

In addition to changes in specific locations of habitats, there were notable changes in the elevation profile of food items that have meaningful implications for bears. A general trend of uphill migration of species may increase habitat quality at higher elevations, thus offsetting losses elsewhere, and further providing a source population for rescue effects of sink populations. Given the propensity for human interactions to negatively affect bears and bear survival rates (Mattson 1990), the persistence of grizzly populations under such a scenario relies on the continued preservation of upslope habitats free from anthropogenic disturbance and human activity, as is a feature of the National Parks and other protected areas within current grizzly bear range. However, due to this trend of upslope movement, many downslope locations, such as lower foothills and valley bottoms, are projected to lose species richness by as much as 50% for summer species or 25% of the seasonally important hyperphagic season in late summer and autumn. In locations where increased upslope foraging is not possible or convenient, this may increase human–bear conflict, since food may be more limiting in these areas, as periods of food scarcity are known to increase human–bear conflict rates (Mattson et al. 1992, Pease and Mattson 1999, Gunther et al. 2004). However, given the mobility of the species and the general availability of higher-elevation habitats in the bear range examined here, bears may be able to adapt to these losses by using upslope resources or alternate food items. Indeed, prior studies have demonstrated seasonal adaptations in diet to interannual changes in resources, illustrating their dietary plasticity. For instance, in Yellowstone National Park, whitebark pine nuts are an important seasonal food source for grizzly bears when abundant, but when scarce, are replaced by false-truffles (*Rhizopogon* spp.) (Fortin et al. 2013). Overall, our models predict general increases in seasonal food resources, although changes in habitat for individual food items are predicted to occur, necessitating seasonal adaptation in resources consumed by bears or spatial adjustments in their habitat use relative to changes in food resource distribution.

While not entirely positive, our prognosis for the overall vulnerability of northern Rocky Mountain grizzly bears to climate change is markedly better than those for similar high-trophic-level mammals, including other species of bears. Recent assessments of food

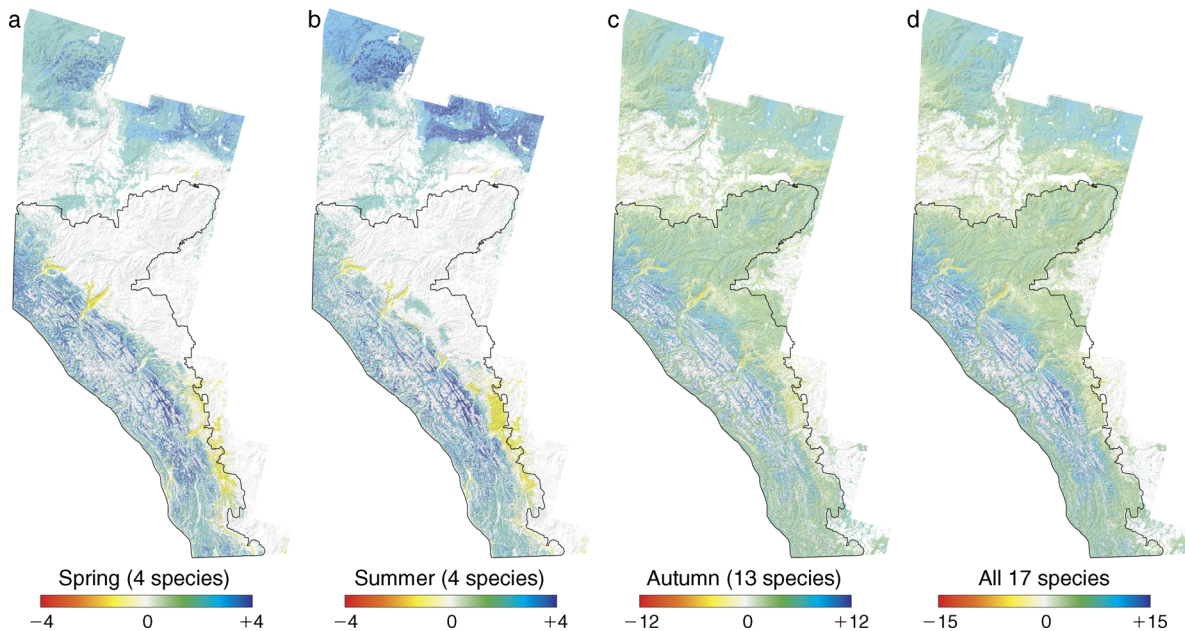


FIG. 3. Maps showing the change from the 1961–1990 period in number of species projected present for the A2 scenario of the 2080s period. Changes are shown by season for (a) spring, (b) summer, and (c) autumn, with the seasonally important bear food source species (see Table 1). (d) Changes in counts of all 17 species considered (all seasons together), are also shown. Areas of unsuitable range (agriculture, rock, ice, water, etc.) are masked in white. The range of present-day grizzly bear habitat in the southern Canadian Rockies is shown as a black outline. Maps of absolute counts of species are shown in Appendix C.

resources for a population of giant pandas (*Ailuropoda melanoleuca*) in China project substantial reductions in availability of many bamboo species (Tuanmu et al. 2013), representing an acute threat to this species. As a second example, the polar bear (*Ursus maritimus*) is a species of conservation concern that has received extensive public exposure in terms of its sensitivity to climate change (Courtland 2008). Primary threats to polar bears from climate warming relate to habitat loss, and in particular, losses of sea ice, which can adversely affect hunting and breeding. Less sea ice coverage and earlier spring sea ice breakup results in less ideal seal-hunting conditions, shorter on-ice feeding periods, and more energy expended in swimming activities, leading to a general decrease in reproduction rates and litter sizes (Derocher et al. 2004). While grizzly bears in the Canadian Rockies do not appear to face such challenges, the implications for all upper-trophic-level species is one of general uncertainty regarding the availability of food resources and habitat quality. A reiteration of the conclusions by Tuanmu et al. (2013) would serve well here: it is important to consider interspecific interactions when assessing effects of climate change.

Most vulnerable species

Species considered in our study that could be labeled “vulnerable” take two forms. First, we identify noncritical bear food species that show major reductions and/or changes in habitat. In this case, the species in question may itself be at high risk, but the effect of its loss on the

overall quality of bear habitat may be minimal due to the availability of other food resources and low use by grizzly bears. Second, we identify critical bear food species, such as those that form a substantial proportion of diets throughout the year, or those that are highly important to bears in a given season, which are projected to have reduced range sizes or to have limited stable habitat between the present and future.

An example in the first case, *Vaccinium scoparium*, shows the largest habitat loss of any species considered in the B1 and A2 scenarios for the 2080s (92% and 95% loss, respectively) and the smallest amount of stable habitat (only 7% and 3% for B1 and A2, respectively). While not a critical food source by itself, bears rely heavily on fruit from all forms of ericaceous shrubs during the autumn hyperphagic period. Other ericaceous species such as *Vaccinium myrtilloides*, *Vaccinium vitis-idaea* (lingonberry), and the more critical *Vaccinium membranaceum* all show increases in habitat and nearly complete maintenance of their present-day ranges, thus suggesting lower vulnerability and risk to climate change. Projections for *Empetrum nigrum* are similar to *Vaccinium scoparium*, with habitat losses of up to 89% and amount of stable habitat as low 3%. Not surprisingly, these two species have the highest-elevation ranges in the present day of all species considered. This, in combination with projected upward elevation shifts in suitable climate conditions, suggests that suitable habitat for these species may be pushed out of alpine areas and “off” mountain tops entirely by future

warming. Other high-elevation species considered, including *Vaccinium membranaceum*, do not exhibit the same increases in elevation and habitat losses under future-climate scenarios. *Vaccinium membranaceum* is less elevation restricted than either *Vaccinium scoparium* or *Empetrum nigrum*, as is evident by their much lower 10th percentile elevations. This wider climate niche may make them less sensitive to changes, particularly in temperature.

Hedysarum alpinum, the other notable high-elevation species considered in our study, is of particular concern, as root digging of this species represents an important spring and autumn food source for bears (Munro et al. 2006). While this species exhibits a less-restrictive elevation profile, much like *Vaccinium membranaceum*, habitat projections shows large increases in elevation in future scenarios, similar to *Vaccinium scoparium* and *Empetrum nigrum*. However, corresponding changes in area of habitat are not consistent between future scenarios, with *Hedysarum alpinum* gaining 45% area of habitat in B1, while losing 15% area in A2. This difference is explained by the increased amount of habitat lost along the east slopes of the Rocky Mountains in the A2 scenario, while new upslope habitat emerges in roughly equal amounts in both scenarios. Density plots of elevation for future-climate scenarios (Appendix B), show equal probabilities of high-elevation habitat in both scenarios but disappearing habitats of mid-elevation in the A2 scenario. The net result for *Hedysarum alpinum* is that, while available habitat may not be drastically restricted in the future, proportions of stable area suggest that half to two-thirds of populations will be required to physically migrate into new locations to be maintained within the landscape. While these migrations may only be short upslope distances, the simple necessity of physical migration for the survival of the majority of this species raises concern, especially given the species' critical importance as a bear food source. Future research exploring the ecological niche of this species is needed given its seasonal importance to bears and the contradictory results observed here for different magnitudes of climate warming.

Two less critical food sources for bears, *Fragaria virginiana* and *Arctostaphylos uva-ursi*, are predicted to decrease in range. In both cases, this result was unexpected, as these species are widespread within the present-day study area as well as throughout western North America, suggesting a tolerance for warmer conditions such as those projected for our future study area. In these cases, the projected habitat losses could be a result of the limits of the model training data, which may not adequately capture the full climate niche of these species, particularly the warmer end of the niche that would be represented to the south of our study area. This is especially visible in *Fragaria virginiana*, which loses extensive habitat through the warmest areas of its present-day range through the center of the study area.

By contrast, future projections for *Arctostaphylos uva-ursi* suggest substantial loss of habitat in the low-elevation river valleys throughout the Rocky Mountains, with no emergence of higher-elevation habitats, as is the case with other widespread species such as *Taraxacum officinale* (dandelion). This would be an expected trend if the range of *Arctostaphylos uva-ursi* is not temperature driven, but rather defined by other environmental predictors, which may be the case.

CONCLUSIONS

This first examination of grizzly bear plant food resources under anthropogenic climate warming provides reasons for optimism, but also reasons for concern. With only a few exceptions, most species considered in this study appear to be at low risk of widespread extirpation, and often do not have large migration requirements to reach locations of suitable future habitat given regional topographic heterogeneity. In fact, many species show the potential to increase in range under future climate warming. This would suggest that the majority of plant-related grizzly bear food items should continue to be available to bears within their current range through the coming century. We have, however, identified a few species of particular interest that show severe projected range losses under future climate warming: high-elevation, restricted species such as *Empetrum nigrum* and *Vaccinium scoparium*, both of which are projected to lose nearly all their range within present-day grizzly bear habitat. However, the effect of the loss of these individual species on bear habitat quality is difficult to assess, given the continued availability of most other autumn fruit resources (including the fact that these species are less commonly used by bears) and the uncertainty around the species' capacity to adapt to these losses through changes in foraging behavior. Of greater concern are the high rates of projected habitat loss or instability of *Hedysarum alpinum*, a spring and autumn food resource for grizzly bears when little else is available.

It should be noted that this study does not consider food quality (i.e., energetics), local abundance, or the potential introduction of new, invasive food resources, which may also be affected in unpredictable ways by anthropogenic alterations in the climate regime. We also did not consider how climate change may affect local sources of animal protein that bears rely on, including ungulates and ants (Munro et al. 2006), although generally warmer climates for cool mountain environments would be expected to benefit these species, particularly ants. Future investigations into how climate change will affect quality and abundance of these food resources, as well as research into potential behavioral responses of bears to changing resource availability, both seasonally and spatially, is needed to fully understand the impacts of climate change on grizzly bear habitats.

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SUPPLEMENTAL MATERIAL

Appendix A

Table of validation statistics for all modeling methods for all species, including the area under the curve of the receiver operating characteristic (AUC), sensitivity, specificity, and sample sizes ([Ecological Archives A024-065-A1](#)).

Appendix B

Maps and summary plots of model projections for each species for the present and future, including (A) maps of model projections of probability of presence (PoP) for the present and future scenarios; (B) maps of projected change in habitat based on changes of modeled species presence/absence; (C) probability density function plots for projected PoPs; and (D) probability density function plots for elevations of projected suitable habitat ([Ecological Archives A024-065-A2](#)).

Appendix C

Seasonal and annual maps showing counts of projected species for the present and future periods ([Ecological Archives A024-065-A3](#)).

RESEARCH

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Serological signature of tick-borne pathogens in Scandinavian brown bears over two decades

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Abstract

Background: Anthropogenic disturbances are changing the geographic distribution of ticks and tick-borne diseases. Over the last few decades, the tick *Ixodes ricinus* has expanded its range and abundance considerably in northern Europe. Concurrently, the incidence of tick-borne diseases, such as Lyme borreliosis and tick-borne encephalitis, has increased in the human populations of the Scandinavian countries.

Methods: Wildlife populations can serve as sentinels for changes in the distribution of tick-borne diseases. We used serum samples from a long-term study on the Scandinavian brown bear, *Ursus arctos*, and standard immunological methods to test whether exposure to *Borrelia burgdorferi* sensu lato, the causative agent of Lyme borreliosis, and tick-borne encephalitis virus (TBEV) had increased over time. Bears had been sampled over a period of 18 years (1995–2012) from a southern area, where *Ixodes ricinus* ticks are present, and a northern area where ticks are uncommon or absent.

Results: Bears had high levels of IgG antibodies against *B. burgdorferi* sensu lato but not TBEV. Bears at the southern area had higher values of anti-*Borrelia* IgG antibodies than bears at the northern area. Over the duration of the study, the value of anti-*Borrelia* IgG antibodies increased in the southern area but not the northern area. Anti-*Borrelia* IgG antibodies increased with the age of the bear but declined in the oldest age classes.

Conclusions: Our study is consistent with the view that ticks and tick-borne pathogens are expanding their abundance and prevalence in Scandinavia. Long-term serological monitoring of large mammals can provide insight into how anthropogenic disturbances are changing the distribution of ticks and tick-borne diseases.

Keywords: *Borrelia burgdorferi*, *Ixodes ricinus*, Lyme disease, Scandinavia, Serology, Tick-borne diseases, Tick-borne encephalitis virus, *Ursus arctos*, Vector-borne diseases, Zoonoses

Background

The incidence of tick-borne diseases, such as Lyme borreliosis (LB) and tick-borne encephalitis (TBE), has increased over the last few decades in a number of European countries [1–3]. One explanation for the increase in tick-borne infections is that the distributional area and abundance of the principal vector, *Ixodes ricinus*, have increased [4–8]. Consistent with this

explanation, studies in Norway and Sweden have shown that the abundance and prevalence of ticks and tick-borne diseases have increased during this time [9, 10]. The distribution of ticks and tick-borne diseases has expanded northward, to higher altitudes, and to new inland regions [9]. In addition, ticks have increased in abundance where they were already present in central and south Sweden [10, 11]. Studies in other parts of the world also have reported changes in the distribution of ticks and tick-borne diseases [12–15].

Climate change could drive changes in the distribution of ticks because these arthropods are very sensitive to temperature and humidity [4, 7]. In southern Sweden,

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the increase in the incidence of LB was positively correlated with a rise in monthly mean temperature [16]. Climate change could also influence the distribution and abundance of ticks and tick-borne diseases via indirect effects on vegetation [15, 17] and important reservoir hosts like rodents [1]. The climate change hypothesis for the emergence of tick-borne diseases in Europe is controversial [2, 7, 18, 19]. Alternative anthropogenic explanations include changes in agriculture and land use that have increased the amount of suitable tick habitat [3, 19]. Additional explanations include improved reporting, diagnosis, and awareness of tick-borne diseases [9, 20], changes in human behaviour that increase contact with ticks [7, 16, 19], and even the socio-political changes in Eastern Europe following the collapse of communism [3, 21].

Immunological methods are widely used to determine whether vertebrate populations have been exposed to tick-borne pathogens [22–24]. The study of changes in the IgG antibody response over time can provide insight into the temporal dynamics of tick-borne diseases [25]. The purpose of our study was to test whether the observed increase in the incidence of tick-borne diseases over the last two decades in Scandinavia could be detected in wild animal sera.

To address this question, we used standard immunological methods to quantify the IgG antibody response against two common tick-borne pathogens in the brown bear (*Ursus arctos*). Long-lived mammals, such as brown bears, can be repeatedly exposed to ticks and are therefore expected to amplify the immunological signature of tick-borne pathogens. Previous studies in Europe and North America have shown that bears can be used as sentinels for tick-borne diseases [26–29]. We investigated the strength of the IgG antibody response against the spirochete bacterium *Borrelia burgdorferi* sensu lato (s. l.), the causative agent of Lyme borreliosis, and the tick-borne encephalitis virus (TBEV). We chose these two tick-borne pathogens because they are present in Scandinavia [2, 17, 18, 30–34] and because reliable ELISA tests are commercially available [35–37].

The brown bears were captured at a southern and a northern area in Sweden over a period of 18 years (1995 to 2012). In the southern area, populations of *I. ricinus* have increased substantially from the early 1990s to 2008 [10]. In the northern area, by contrast, there have been much fewer reports of *I. ricinus* as of 2008 [10]. We therefore predicted that the immune response against tick-borne pathogens would be much stronger in bears from the southern area than bears from the northern area. We also predicted that the immune response against tick-borne pathogens in bear sera would increase over the 18 years of the study in the southern area but not the northern area.

Methods

Collection of bear serum samples

The serum samples were obtained from a long-term study of the brown bear in Sweden. These samples spanned 18 years (1995 to 2012) and came from two distinct regions that are approximately 600 km apart. The southern area was centred in Dalarna and Gävleborg counties in central Sweden (61°30'0"N, 17°0'0"E), with a rolling landscape of coniferous forest dominated by commercial plantations of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The northern area, centred in Norrbotten County (66°36'23"N, 19°49'23"E), is mountainous, with altitudes up to 2000 m and is covered by coniferous forest of Scots pine and Norway spruce at lower altitudes and subalpine forests dominated by birch (*Betula pubescens*) and willows (*Salix* spp.) at higher altitudes (Fig. 1). Details of how the bears were captured have been described elsewhere [38]. Briefly, bears were immobilized by darting from helicopter in the early spring upon emergence from their winter dens. We determined the sex and age of the individuals, collected blood samples, and gave them a unique identification marking. We combined our data into five age groups: yearlings (0–1 years), juveniles (2–3 years), young adults (4–9 years), adults (10–14 years), and old adults (15–29 years). Our data set contained 1,172 serum samples collected from 569 individual bears (mean = 2.06 samples/bear; range = 1 to 9 samples/bear). The bear serum samples were kept at –20 °C until further analysis.

Detection of antibodies against *Borrelia* pathogens

We used an ELISA assay (*Borrelia* microplate IgG) to test whether the bears had developed specific antibodies against *Borrelia* pathogens. The 1172 bear serum samples were randomly assigned to one of 14 96-well commercial ELISA plates (Virion; SERION ELISA). Each ELISA plate contained 84 wild bear serum samples, four positive controls (sera from laboratory mice experimentally infected with *B. afzelii*), four negative controls (sera from uninfected laboratory mice), and four bear serum samples from zoological parks. The serum samples from the zoo bears and the positive and negative controls functioned as a quality control of the ELISA assay. The laboratory mice (positive controls) had been infected with *B. afzelii* by infesting them with *B. afzelii*-infected *I. ricinus* nymphs (unpublished data). To determine the repeatability of the ELISA assay, we also repeated the assay for one randomly selected plate.

Ethical approval

The Ethical Committee on Animal Experiments, Uppsala, Sweden (# C 7/12) and the National Animal Research Authority, Oslo, Norway (# 2013/33387) approved the sampling of blood from captured bears. All experiments involving mice respected the Swiss legislation on animal experimentation and were authorized by the Veterinary

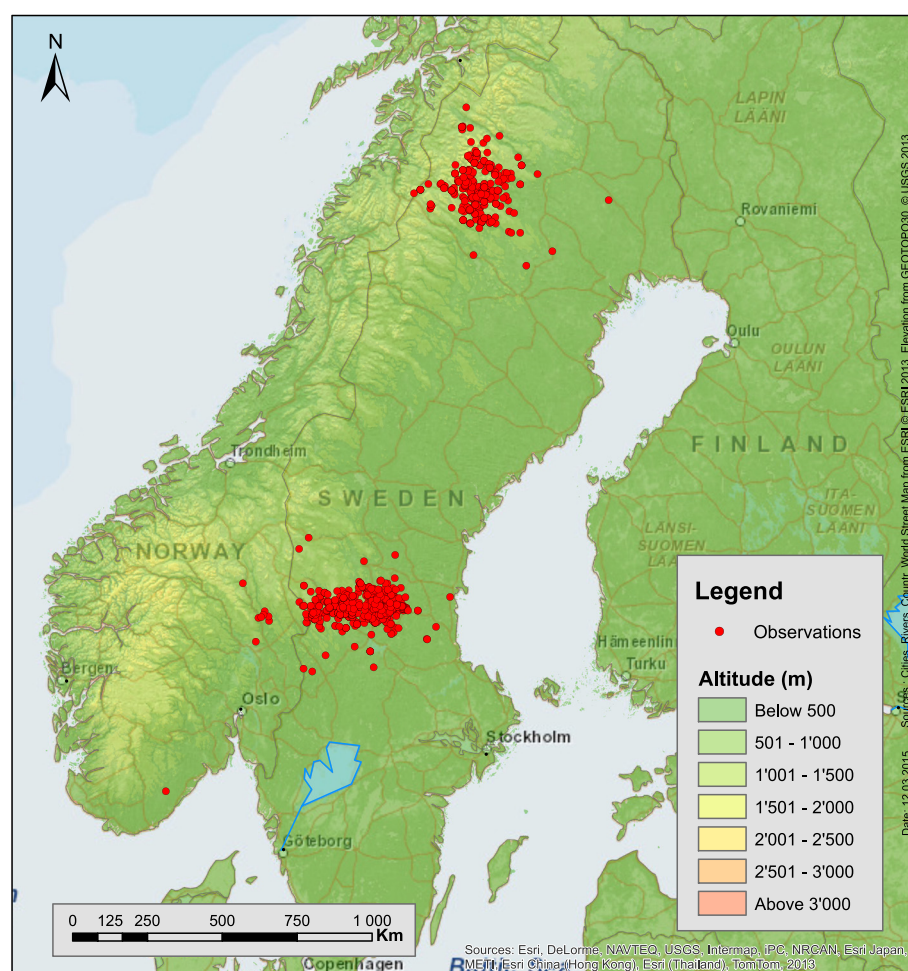


Fig. 1 Map showing the study area in Sweden. Map showing the geographic location of the northern and southern area in Scandinavia where the wild brown bears were captured. Each bear serum sample is represented by one dot

Service of the Canton of Neuchâtel (Authorization number NE2/2012).

Most serological studies on bears and other wild animals use serum dilutions of 1:50 to 1:200 [39–44]. Following the recommendations of the manufacturer, we used a serum dilution of 1:100 by adding 10 µl of serum to 990 µl of 1× PBS. We incubated the plates with 100 µl of the diluted sera for 45 min. We removed the sera and washed the wells three times with 200 µl of washing solution (1× PBS with 0.1 % Tween). We used Protein A conjugated to horseradish peroxidase (INVTROGEN, Thermo scientific) as the secondary antibody because it has been shown to bind the IgG antibodies of a variety of mammals [45]. We confirmed independently that Protein A was capable of binding to IgG antibodies of bears and mice. We added 100 µl of the secondary antibody diluted 1:5000 in 1× PBS and incubated the plates at room temperature for 45 min. We again washed the plates three times with washing solution. We added 100 µl of TMB solution (Thermo scientific) to

each well to produce a colour reaction. The absorbance was read at a wavelength of 652 nm every 2 min for 1 h with a plate reader (BIO-TEK Instruments, program KC4™ v3.2).

Detection of antibodies against TBEV

We used an ELISA assay (FSME (TBE) Microtiter plates IgG) to test whether the bears had developed specific antibodies against TBEV. The ELISA protocol was the same as described for *Borrelia*. For the positive and negative controls, we used goat serum samples from a previous study [46] in addition to the bear serum samples from the zoological park. The seropositive status of these goat serum samples had been determined using a serum neutralization test, which is considered the gold standard in the diagnosis of TBEV. We found that Protein G was much more effective than Protein A at binding goat IgG. For the TBEV ELISA assay, we therefore used two different secondary antibodies: Protein A for the bear samples and Protein G for the goat samples.

Collection of tissue samples from bears

We used quantitative PCR (qPCR) to test bear tissue samples for infection with *Borrelia* pathogens. We collected tissue samples from 16 bears that had been killed legally by private hunters on different days during the last three weeks of the month of August 2014 in the southern area. No bears were killed for the purpose of this study. For each bear, all tissue samples were collected within a few hours following death from the following organs: skin, liver, kidney, bladder, and arteries. One tissue sample was unusable, resulting in a total of 79 tissue samples. Tissue samples were frozen on ice and brought to the laboratory. We used aseptic dissection to obtain ~25 mg of tissue from each sample. To avoid contamination, we disinfected and autoclaved the dissection tools after dissecting the samples from each bear and cleaned the tools with 70 % ethanol and 5 % bleach between dissecting the different tissues from the same bear. The 25-mg tissue samples were placed in individual Eppendorf tubes (1.7 ml) and were kept at -20 °C until further analysis.

DNA extraction of tissue samples

We extracted the DNA from the bear tissue samples using the DNeasy Blood and Tissue extraction kit (QIAGEN) and following the manufacturer's instructions. We eluted the DNA in 200 µl of AE buffer. We also extracted DNA from the ear tissue samples of four laboratory mice that had been infected experimentally with *B. afzelii* (positive controls) and four laboratory mice that had not been infected with *B. afzelii* (negative controls).

Quantitative PCR

We used qPCR to detect *Borrelia* spirochetes in the bear tissue samples. We amplified the *flagellin* gene (132 bp) of the *B. burgdorferi* s. l. genospecies complex. Details of the primers and probe, qPCR reaction mixture, and thermocycling conditions have been described elsewhere [47, 48]. For amplification we used a LightCycler® 96 (Roche Applied Science, Switzerland). The qPCR plates contained 80 bear tissue samples, the 4 mouse positive DNA extraction controls, the 4 mouse negative DNA extraction controls, 3 negative qPCR controls (pure water), and three standards containing 10^3 , 10^4 , and 10^5 copies of the *flagellin* gene (three standards on each plate). All samples were run in duplicate using two different qPCR plates.

Statistical analysis

We used the software program R (version 3.1.2) for the statistical analysis [49]. We calculated the strength of the antibody response against each tick-borne pathogen as the area under the curve of the absorbance versus time plot by using the 'auc' function of the R package 'MESS' [50]. We refer to this antibody response variable as the

optical density. The log-transformed optical densities followed a normal distribution. We therefore analysed this response variable as a linear mixed effects model by using the 'lme' function of the R package 'nlme' [51]. The log-transformed optical density was modelled as a function of four explanatory variables: study area, age group, year of capture, and bear identity. Study area was a fixed factor with two levels: the northern area and the southern area. Age group was a fixed factor with five levels: yearlings, juveniles, young adults, adults, and old adults. Year of capture was a continuous covariate and was rescaled so that the years 1995 and 2012 corresponded to years 1 and 18, respectively. Bear identity was modelled as a random factor.

We ran 19 candidate models that differed in the structure of the fixed effects, but always with the same random effects structure. The full model contained the three main effects, the three 2-way interactions, and the one 3-way interaction. For the other models, we removed one or more factors and interactions. The corrected Akaike information criterion (AICc) was used to compare models by running the 'dredge' function in the R package 'MuMIn' [52]. The AICc weight indicated the support for each model. To calculate the support for each explanatory variable, we summed the supports for all the models containing that particular explanatory variable. We used model averaging to calculate a weighted average of the parameter estimates across the set of candidate models. This approach incorporates the uncertainty due to model selection in the calculation of the confidence intervals and provides robust parameter estimates [53].

We tried adding sex as a fourth fixed factor but the models had trouble converging. To test whether the fixed factor sex was important, we repeated the above analyses by replacing the covariate year of capture with the fixed factor sex. All models with the fixed factor sex had lower AICc values than the corresponding models with the fixed factor year of capture. We therefore did not further consider the fixed factor sex in our model selection results.

Repeatability of the optical density

For the *B. burgdorferi* s. l. ELISA assay, we estimated the repeatability of the optical density for (1) the bear serum samples (two plates) and (2) the controls (14 plates). For the repeatability of the bear serum samples, we used the data from the randomly selected samples of 80 bear sera that were processed twice in two independent ELISA plates. For the repeatability of the controls, we used the data from the positive and negative controls (four *B. afzelii*-infected laboratory mice, four uninfected laboratory mice, and four brown bears from a zoo) that had been used in all 14 ELISA plates.

We used Pearson's correlation test to determine whether there was a correlation between the optical densities of

Table 1 Anti-*Borrelia* IgG values of the Scandinavian brown bears and the negative and positive controls

Serum type	N	Mean	SE	Minimum	Maximum
Wild bears	1172 serum samples (569 individuals)	43.25	0.59	10.17	130.47
Negative controls	56 serum samples (4 individuals)	13.19	0.29	9.10	18.46
Positive controls	56 serum samples (4 individuals)	155.09	2.76	110.60	196.43

The negative controls were uninfected laboratory mice and the positive controls were laboratory mice that had been experimentally infected with *B. afzelii* (Jacquet M, Durand J, Rais O, Voordouw M: Cross-reactive acquired immunity influences transmission success of the Lyme disease pathogen, *Borrelia afzelii*, submitted). The anti-*Borrelia* IgG response was measured in units of optical density (OD units). The sample size (N), mean optical density, standard error (SE), minimum and maximum values are also shown

the *B. burgdorferi* s. l. ELISA assay and the TBEV ELISA assay for the same sample.

(15 to 25 %). The repeatability of the controls among the 15 plates was 0.99 ($F_{11, 168} = 1071.00$, $p < 0.001$).

Results

Repeatability of the optical density of the *Borrelia* ELISA assay

For the *B. burgdorferi* s. l. ELISA, the repeatability of the optical density between the two plates was 0.85 with the controls ($F_{95, 96} = 12.10$, $p < 0.001$) and 0.75 without the controls ($F_{83, 84} = 6.96$, $p < 0.001$). Thus there was substantial repeatable variation among the bear serum samples and the measurement error was not very large

Anti-*Borrelia* IgG antibody values of the bear sera

The mean anti-*Borrelia* IgG antibody value of the bear sera was 3.28 times higher than the negative controls (uninfected mice sera), whereas the mean anti-*Borrelia* IgG antibody value of the positive controls (infected mice sera) was 11.76 times higher than the negative controls (Table 1). Thus the antibody values of the bear sera were intermediate between the seronegative and seropositive mice sera. The eight bears with the highest antibody values (range = 110.73 to 130.47 units of optical density)

Table 2 Model selection results of the anti-*Borrelia* IgG response of the Scandinavian brown bears

Rank	Fixed effects structure	df	LL	AICc	Δ AICc	Weight 1	Weight 2
1	OD ~ S + A + Y + S:A + S:Y	14	-442.26	912.53	0.00	0.54	0.54
2	OD ~ S + A + Y + S:A	13	-444.28	914.55	2.02	0.20	0.74
3	OD ~ S + A + S:A	12	-445.36	914.73	2.20	0.18	0.92
4	OD ~ S + A + Y + S:A + S:Y + A:Y + S:A:Y	22	-437.00	917.99	5.46	0.04	0.96
5	OD ~ S + A + Y + S:Y	10	-449.27	918.53	6.00	0.03	0.99
6	OD ~ S + A + Y + S:A + S:Y + A:Y	18	-442.01	920.02	7.49	0.01	1.00
7	OD ~ S + A + Y + S:A + A:Y	17	-444.04	922.09	9.56	0.00	1.00
8	OD ~ S + A + Y	9	-452.70	923.40	10.87	0.00	1.00
9	OD ~ S + A	8	-453.79	923.58	11.05	0.00	1.00
10	OD ~ S + A + Y + S:Y + A:Y	14	-448.95	925.89	13.36	0.00	1.00
11	OD ~ A + Y	8	-455.03	926.06	13.53	0.00	1.00
12	OD ~ A	7	-456.27	926.55	14.02	0.00	1.00
13	OD ~ S + A + Y + A:Y	13	-452.29	930.58	18.05	0.00	1.00
14	OD ~ A + Y + A:Y	12	-454.52	933.04	20.51	0.00	1.00
15	OD ~ S + Y + S:Y	6	-576.20	1164.4	251.87	0.00	1.00
16	OD ~ S + Y	5	-581.93	1173.86	261.33	0.00	1.00
17	OD ~ Y	4	-583.91	1175.81	263.28	0.00	1.00
18	OD ~ S	4	-586.54	1181.07	268.54	0.00	1.00
19	OD ~ 1	3	-588.91	1183.81	271.28	0.00	1.00

The log-transformed optical density (OD) is a measure of the anti-*Borrelia* IgG response and was modelled as a linear mixed effects model. Fixed factors included study area (S), age group (A), and capture year (Y), and the random factor was bear identity. Shown for each model are: the model rank (Rank), the structure of the fixed effects, the degrees of freedom (df), the log-likelihood (LL), the corrected Akaike information criterion (AICc), the difference in AICc value from the top model (Δ AICc), the model weight (Weight 1), and the cumulative weight (Weight 2)

were higher than the least seropositive mice sera. The antibody values of our ELISA assay suggested that brown bears had been exposed to the *Borrelia* pathogen.

Model selection

In our candidate set of 19 models, the confidence set containing the top four models (1, 2, 3, 4) had a combined support of 96.0 % (Table 2). None of the remaining 15 models had more than 3.0 % of the support (Table 2). The top model had 2.7 times more support than the second-best model (Table 2). There was strong support for the main effects of study area (>99 %), age group (>99 %), and the interaction between study area and age group (>96 %). There was weaker support for the main effect of capture year (>82 %) and the interaction between study area and capture year (>62 %).

Age group and study area

There was substantial variation in the anti-*Borrelia* IgG immune antibody response across age groups (Fig. 2). All other age groups had a higher anti-*Borrelia* IgG antibody response than yearlings (Fig. 2). The immune response in the older age groups was 4.7 to 12.4 % higher than the yearlings, depending on the particular combination of age group and area (Fig. 2). The immune response peaked in the young adult bears (Fig. 2), before declining

by 1.4 to 5.0 % in the older age classes, depending on the particular combination of age group and area. The immune response in the south was 0.9, 2.0, and 5.6 % higher than the north for the juveniles, young adults and adults, respectively. In contrast, the immune response in the south was 2.3 and 0.1 % lower than the north for the yearlings and old adults, respectively. Our analysis found that age group and study area were important predictors of the anti-*Borrelia* IgG response in bear sera.

Capture year and study area

In the southern area, the anti-*Borrelia* IgG response increased slightly over time (Fig. 3). By contrast, in the northern area there was too much variation among years to detect any temporal trend (Fig. 3). For the yearlings in the northern area, the slope of the regression of the anti-*Borrelia* IgG immune response versus time was essentially zero (slope = -0.002 OD units/year, 95 % CL = -0.013 to 0.009 OD units/year; Table 3). For the yearlings in the southern area, the slope was positive and greater than that of the yearlings in the northern area (contrast in slope = 0.011 OD units/year, 95 % CL of the contrast = -0.001 to 0.023 OD units/year) and the lower 95 % confidence limit overlapped zero by a very small amount (Table 3). Our analysis suggested that the anti-*Borrelia* IgG response increased over time, but only in the southern study area.

Other interaction terms

Support for the interaction between capture year and age group was weak. The two models that contained this interaction had a combined support of 5 % (Table 2). Thus there was little evidence that the interaction between capture year and age group influenced variation in the anti-*Borrelia* IgG response of the bears. Support for the three-way interaction between area, age class, and capture year was also weak. The one model that contained this three-way interaction had a support of 4 % (Table 2).

Repeatability of the optical density of the TBEV ELISA assay

Difference in background absorbance between the two plates overwhelmed the variance in absorbance among the samples. The repeatability between the two plates was therefore calculated after standardizing the optical density values to z-scores for each plate. For the TBEV ELISA assay, the repeatability of the standardized optical density between the two plates was 0.80 with the controls ($F_{95, 96} = 9.24$, $p < 0.001$) and 0.58 without the controls ($F_{76, 77} = 3.80$, $p < 0.001$). Thus there was substantial repeatable variation among the bear serum samples and the measurement error was moderate (20 to 42 %). The repeatability of the controls among the 15 plates was 0.97 ($F_{10, 165} = 462.80$, $p < 0.001$).

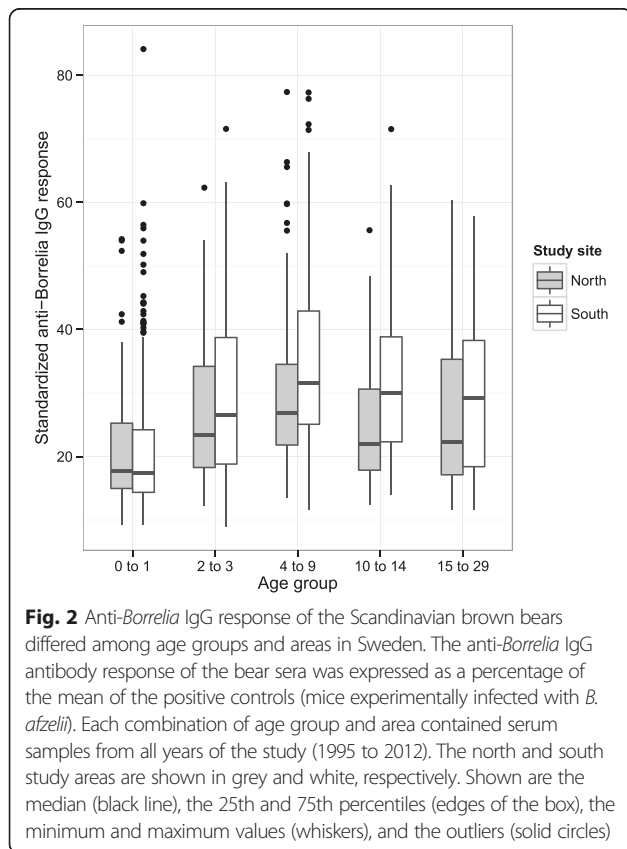


Fig. 2 Anti-*Borrelia* IgG response of the Scandinavian brown bears differed among age groups and areas in Sweden. The anti-*Borrelia* IgG antibody response of the bear sera was expressed as a percentage of the mean of the positive controls (mice experimentally infected with *B. afzelii*). Each combination of age group and area contained serum samples from all years of the study (1995 to 2012). The north and south study areas are shown in grey and white, respectively. Shown are the median (black line), the 25th and 75th percentiles (edges of the box), the minimum and maximum values (whiskers), and the outliers (solid circles)

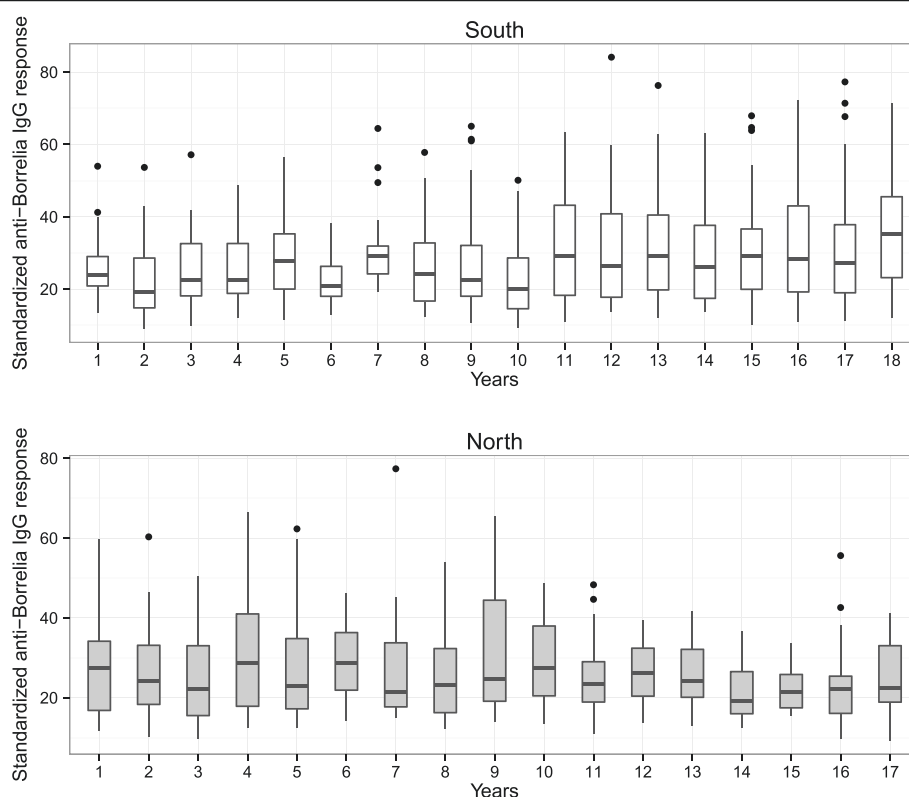


Fig. 3 Anti-*Borrelia* IgG response of the Scandinavian brown bears over time differed between areas. The anti-*Borrelia* IgG response in the bear sera is shown for the entire study (year 1 = 1995 and year 18 = 2012). The anti-*Borrelia* IgG antibody response of the bear sera (optical density) was expressed as a percentage of the mean of the positive controls (mice experimentally infected with *B. afzelii*). Each combination of age group and area contains serum samples from all age classes. The north and south study areas are shown in grey and white, respectively. Shown are the median (black line), the 25th and 75th percentiles (edges of the box), the minimum and maximum values (whiskers), and the outliers (solid circles)

Anti-TBEV IgG antibody values of the bear sera

The mean anti-TBEV IgG antibody value of the bear sera was 2.31 times lower than the negative controls (uninfected goat sera) and 16.37 times lower than the positive controls (infected goat sera) (Table 4). The twelve bears with the highest antibody values (range 23.04 to 39.77 units of optical density) were higher than the mean antibody value of the seronegative goat sera (22.75 units of optical density). The ELISA results suggested very weak exposure of brown bears to TBEV and we therefore did not further analyse these data.

Correlation in optical density between *Borrelia* and TBEV assays

There was a significant, positive correlation between the anti-*Borrelia* IgG immune response and the anti-TBEV IgG immune response across the bear serum samples (Pearson's correlation coefficient = 0.156, $N = 1141$, $p < 0.001$). For the twelve combinations of age group and area, the correlation between the two immune responses was always positive and in some cases statistically significant (Table 5).

Analysis of the bear tissue samples using qPCR

The qPCR worked well, as 90 % of the positive controls tested positive for *Borrelia* spirochetes (9 positive/10 total; 6/6 standards and 3/4 ear tissue samples from experimentally infected mice tested positive for *B. afzelii*) and all negative controls tested negative. None of the bear tissue samples tested positive for *B. burgdorferi* s. l. pathogens.

Discussion

The anti-*Borrelia* immune response was higher in the southern bears than the northern bears for all age groups (except yearlings and old adults). This pattern is consistent with the geographic distribution of *I. ricinus*, which is more common in southern Scandinavia where the climate is warmer [9, 11]. The bears in the southern area were captured primarily in the counties of Dalarna and Gävleborg. In these two counties, populations of *I. ricinus* increased substantially from the early 1990s to 2008 [10]. The bears in the northern area were captured primarily in the northwestern corner of Norrbotten County. In 1990, there were reports of *I. ricinus* in the coastal area of Norrbotten County bordering the Gulf

Table 3 Model-averaged parameter estimates of the anti-*Borrelia* IgG response of the Scandinavian brown bears

Parameter	Model-averaged coefficients	Estimate	% Change	SE	Adj SE	z value	p	Sig
Intercept ^a	Intercept (yearlings in northern area)	3.421		0.0574	0.0575	59.513	<0.0001	***
Contrast	Juveniles	0.216	6.3 %	0.0613	0.0614	3.524	0.0004	***
Contrast	Young adults	0.350	10.2 %	0.0531	0.0532	6.569	<0.0001	***
Contrast	Adults	0.160	4.7 %	0.0871	0.0872	1.832	0.0669	
Contrast	Old adults	0.237	6.9 %	0.1240	0.1242	1.91	0.0561	
Contrast	Southern area	-0.079	-2.3 %	0.0790	0.0791	0.994	0.3202	
Contrast	Juveniles in southern area	0.113	3.3 %	0.0724	0.0725	1.559	0.1189	
Contrast	Young adults in southern area	0.154	4.5 %	0.0643	0.0645	2.389	0.0169	*
Contrast	Adults in southern area	0.292	8.5 %	0.0997	0.0999	2.92	0.0035	**
Contrast	Old adults in southern area	0.074	2.2 %	0.1552	0.1555	0.477	0.6335	
Slope ^b	Capture year (yearlings in northern area)	-0.002		0.0054	0.0054	0.315	0.7525	
Contrast	Capture year in southern area	0.011	0.3 %	0.0059	0.0059	1.942	0.0521	
Contrast	Capture year in juveniles	0.006	0.2 %	0.0108	0.0108	0.571	0.5681	
Contrast	Capture year in young adults	-0.003	-0.1 %	0.0095	0.0095	0.306	0.7595	
Contrast	Capture year in adults	0.014	0.4 %	0.0147	0.0147	0.95	0.3421	
Contrast	Capture year in old adults	0.024	0.6 %	0.0195	0.0195	1.217	0.2238	
Contrast	Capture year in juveniles in southern area	-0.011	-0.3 %	0.0133	0.0133	0.858	0.3907	
Contrast	Capture year in young adults in southern area	0.010	0.3 %	0.0122	0.0122	0.816	0.4145	
Contrast	Capture year in adults in southern area	-0.025	-0.7 %	0.0172	0.0172	1.43	0.1529	
Contrast	Capture year in old adults in southern area	-0.043	-1.3 %	0.0215	0.0215	2.019	0.0434	*

The parameter estimates for the anti-*Borrelia* IgG response of the brown bears were averaged over the candidate models in Table 2. Anti-*Borrelia* IgG values were measured in units of optical density (OD units) and were modelled as a function of study area, age group, capture year and their interactions. The intercept and slope are defined for the reference group (yearling bears in the northern area). The contrasts refer to the difference in the intercepts (or slopes) between each particular combination of age group and area and the reference group. The percentage change (% Change) expresses each contrast as a percentage of the intercept (3.421 OD units). Also shown are the standard error (SE), the adjusted standard error (Adj SE), the z value, the p value (p), and the statistical significance (Sig)

^aIntercept refers to the mean OD for the yearling bears in the northern area

^bSlope refers to the change in OD per year for the yearling bears in the northern area

Significance codes: **** = $p < 0.001$; *** = $0.001 < p < 0.010$; ** = $0.010 < p < 0.050$

of Bothnia [10]. In 2008, *I. ricinus* was reported in central Norbotten County, and this focus overlapped with some of the sampling locations of the bears. In summary, the range maps of *I. ricinus* in the study by Jaenson et al. [10] suggest that the bears in the southern area are more likely to encounter ticks than the bears in the northern area. Furthermore, stable, high-density populations of ticks are more favourable for the introduction and maintenance of tick-borne pathogens [54]. The higher anti-*Borrelia* IgG response in the southern bears was therefore consistent with the expected higher abundance of ticks in southern Scandinavia. We also found that the anti-*Borrelia* IgG immune response in the bear population was much stronger than

the anti-TBEV IgG immune response. This difference was not surprising because *Borrelia* pathogens are much more common than TBEV in populations of *I. ricinus* ticks [20].

The mean anti-*Borrelia* IgG immune response in the bears increased over time, but only in the southern area. This observation is consistent with the literature documenting that the prevalence of ticks and tick-borne diseases (e.g. LB and TBE) has increased in Scandinavia over the last three decades [1–7, 9, 14]. Numerous authors have suggested that climate change is causing this increased burden of tick-borne diseases [11, 55, 56], whereas others have argued against this view [3, 19]. The temporal increase in anti-*Borrelia* IgG levels in the

Table 4 Anti-TBEV IgG values of the Scandinavian brown bears and the negative and positive controls

Serum type	N	Mean	SE	Minimum	Maximum
Wild bears	1172 serum samples (569 individuals)	9.86	0.11	1.93	39.77
Negative controls	60 serum samples (4 individuals)	22.75	0.99	7.59	47.53
Positive controls	60 serum samples (4 individuals)	161.37	2.85	82.84	185.83

The negative controls were uninfected goats and the positive controls were goats that tested positive for TBEV [46]. The anti-TBEV IgG response is measured in units of optical density (OD units). The sample size (N), mean optical density, standard error (SE), minimum and maximum values are also shown

Table 5 Correlation in optical density for *Borrelia* and TBEV ELISA assays in the Scandinavian brown bears

Area	Age group	N	r	p
North	Yearlings (0–1)	124	0.066	0.4642
North	Juveniles (2–3)	58	0.110	0.4101
North	Young (4–5)	56	0.188	0.1661
North	Middle (6–9)	86	0.409	<0.0001
North	Old (10–14)	40	0.126	0.4398
North	Older (15–29)	20	0.188	0.4265
South	Yearlings (0–1)	245	0.130	0.0414
South	Juveniles (2–3)	130	0.198	0.0240
South	Young (4–5)	114	0.175	0.0631
South	Middle (6–9)	129	0.069	0.4340
South	Old (10–14)	86	0.171	0.1164
South	Older (15–29)	53	0.341	0.0124

Pearson's correlation coefficient for the optical density between the *Borrelia* and TBEV assays is positive for all 12 combinations of age group and area for brown bears in Sweden. The area, age group, sample size (N), Pearson's correlation coefficient (r) and p-value (p) are shown

southern bears over the last 18 years is consistent with an increased abundance of *Borrelia*-infected ticks in southern Scandinavia. An alternative explanation for the time-dependent increase in the anti-*Borrelia* immune response is time-dependent, cumulative damage to the bear serum samples. However, if this explanation was true, we should have observed the same time-dependent increase in the anti-*Borrelia* IgG response in the northern area.

The older bears generally had a stronger anti-*Borrelia* IgG immune response than younger bears. Age-related increases in seropositive status are commonly observed, because the probability of encountering a pathogen increases throughout an individual's lifetime [57, 58]. Similar patterns have been observed in wild mice, where adult individuals typically have higher anti-*Borrelia* IgG levels than sexually immature individuals [59, 60]. The observation that the anti-*Borrelia* IgG immune response increased over the first three age classes may be explained by the development of the immune system. Mammals build up their immune system by encountering a wide variety of pathogens during development [61, 62]. The decrease in the immune response of the older bears suggests immuno-senescence. Such age-related declines in the acquired immune response also have been observed in human populations [63, 64].

Ixodes ticks are capable of feeding on bears [26, 29, 65–68]. Numerous studies in North America have collected *I. scapularis* and other tick species from the American black bear (*Ursus americanus*) [26, 28, 29, 65, 66]. Serological studies further suggest that *U. americanus* is frequently

exposed to *Borrelia* pathogens [69, 70]. A molecular screening of brown bears in Slovakia found that 24.3 % (18/74) of the animals tested were positive for the tick-borne pathogen *Anaplasma phagocytophilum* [67]. A serological survey of brown bears in Slovakia found that 65.2 % (15/23) of the animals were seropositive for *A. phagocytophilum* [68]. As *I. ricinus* is the principal vector of *A. phagocytophilum*, these two studies provide indirect evidence that *I. ricinus* ticks are capable of feeding on brown bears [67, 68].

Mammalian hosts differ substantially in their ability to maintain systemic infections with *Borrelia* pathogens [71]. Competent hosts, such as rodents, can maintain long-lived, chronic infections in their tissues [72, 73]. Incompetent hosts, such as deer, do not develop systemic infections [74–76], but such hosts can still develop a strong antibody response to *Borrelia* pathogens [77, 78]. Whether or not bears are competent hosts for *Borrelia* pathogens is currently unknown. A study on Lyme disease in the American black bear isolated spirochetes from blood and kidney samples, but no PCR was conducted to confirm pathogen identity [26]. In our study, none of the tissue samples from the 16 bears tested positive for *B. burgdorferi* s. l. DNA. Consistent with our results, previous studies also have shown that bears develop antibodies against *Borrelia* pathogens [69, 70]. It is possible that bears, like deer, may act as sentinel hosts for *Borrelia* pathogens without developing a systemic infection.

Cross-immunity is a potentially confounding factor in any serological survey. Antibodies developed against other pathogens could be cross-reactive with the antigens used in our assays. For example, antibodies developed against *Treponema* sp. in humans can cross-react with the antigens of *Borrelia burgdorferi* s. l. pathogens [79, 80]. Thus we cannot exclude the possibility that unknown microbial pathogens of the brown bear may have contributed to the background absorbance observed in the serum samples of this study. Future studies should use immunoblotting to further confirm the specificity of the anti-*Borrelia* IgG antibody response in brown bears and other wild animal populations.

Conclusions

Our long-term serological study of the Scandinavian brown bear provides evidence consistent with the observation that ticks and tick-borne pathogens are expanding their abundance and prevalence, respectively, in northern Europe. Bears in the southern area, where *I. ricinus* ticks have been reported, had higher values of anti-*Borrelia* IgG antibodies than bears at the northern area, where *I. ricinus* ticks are believed to be less common. Over the 18 years of the study, the value

of anti-*Borrelia* IgG antibodies increased in the southern area, but not the northern area. Our study suggests that long-term serological monitoring of large mammals can provide insight into changes in the distribution of ticks and tick-borne diseases, and perhaps the reasons for these changes.

Abbreviations

AICc: Akaike information criterion; LB: Lyme borreliosis; TBE: tick-borne encephalitis; TBEV: tick-borne encephalitis virus.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

ALE, KLJ, and JMA initiated this study. JES and JMA are chief scientists of the Scandinavian Brown Bear Research Project. JES, JMA, ALE, and KLJ all participated in the collection of serum samples. JMA and ALE planned the blood sampling and biobanking of the bears. KLJ organized the biobank, sorted the serum samples and transported them to Switzerland. JB collected the bear tissue samples for PCR analysis. LP, RL, and MJV planned the immunological component of the study. LP conducted the ELISA and PCR assays. MJ experimentally infected the mice with *B. afzelii* via tick bite and provided the positive control sera. LP and MJV conducted the statistical analyses and wrote the manuscript. MB created the map of the bear sampling locations. All authors helped edit the manuscript. All authors read and approved the final manuscript.

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A Comprehensive Review of the Ecological and Human Social Effects of Artificial Feeding and Baiting of Wildlife



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February 2003

A Comprehensive Review of the Ecological and Human Social Effects of Artificial Feeding and Baiting of Wildlife

including an

Annotated Bibliography of the Scientific Literature



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Executive Summary

The Ecological and Human Social Effects of Artificial Feeding and Baiting of Wildlife

In recent years, events within Canada and the United States have drawn attention to potential negative consequences of feeding and baiting wild animals, especially enhanced transmission of infectious diseases such as bovine tuberculosis and chronic wasting disease. This report was prepared to gather available science-based information on the ecological and human social effects of artificial feeding and baiting of wildlife into one readily accessible document. The contracting agencies, Parks Canada and Saskatchewan Environment, recognize that an objective review of existing literature may help to answer questions and concerns within and outside the agencies, and help to guide subsequent decision-making concerning management and research pertaining to feeding and baiting.

Although the objectives for artificial feeding and baiting with feed often differ, the effects of these practices are considered together. In essence, both provide natural or artificial food for wildlife at specific locations in the environment.

Significant ecological effects of providing feed to wildlife have been documented through observation and experimentation at the individual, population, and community levels. In Saskatchewan and Manitoba, the increased potential for disease transmission and outbreak is perhaps of greatest and immediate concern. Nevertheless, even if spread of disease is prevented, other significant ecological concerns exist. Disruption of animal movement patterns and spatial distribution, alteration of community structure with reduced diversity and abundance, the introduction and invasion of exotic plant species, and general degradation of habitat are all major negative effects that have been documented at different locations throughout North America. Although information gaps exist, current information appears sufficient to conclude that the potential for negative ecological effects as a result of providing food to wildlife through artificial feeding or baiting is high. Nevertheless, our current understanding of the specific mechanisms operating between cause (feeding or baiting) and effect is often too crude to allow accurate prediction of the nature or magnitude of effect.

The human social effects of providing food to wildlife concern numerous issues (economics, human safety, wildlife ownership, etc.), and perceptions regarding specific issues can be quite disparate. The science-based information is limited in part because philosophical differences lie at the root of many of the issues and science is not the appropriate tool for resolution, e.g., science cannot determine whether hunting over bait is ethical or not.

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Introduction

Brief Statement of Report Objective

This report provides a comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. The peer-reviewed scientific literature has been the primary source of information for this report. Nevertheless, “non-scientific” information from varied sources (e.g., government websites, expert personal opinion, and the popular press) is included too. This latter information has helped to identify information gaps in the scientific literature, and uncover common misconceptions regarding artificial feeding and baiting of wildlife.

Brief History and Background of the Request

Food is provided to wildlife in Saskatchewan and Manitoba both as a method to stabilize the effects of winter mortality and control wildlife damage to agricultural produce, and as a method to attract wildlife for the purpose of hunting. In recent years, events within both provinces (e.g., chronic wasting disease in wild deer within Saskatchewan, bovine tuberculosis in elk in Manitoba) and broader have drawn attention to potential negative consequences of feeding and baiting wild animals, and have raised concern about the potential impact of these practices. Although perspectives may differ between the two contracting agencies, Parks Canada Agency and Saskatchewan Environment, both have recognized a need to gather available science-based information on the positive and negative impacts of feeding and baiting into one readily accessible document. Such an objective review may help to answer questions and concerns within and outside the agencies, and help to guide subsequent decision-making concerning management and research pertaining to feeding and baiting in respective jurisdictions.

Artificial Feeding of Wildlife

Artificial feeding is defined broadly as placing natural or artificial food into the environment that supplements the food source contained naturally in the home range of a given wild species. Artificial feeding is practiced with intent at various scales and for many reasons: from the maintenance of an active bird feeder in the backyard of a private citizen, to the mass feeding of approximately 14,000 elk and 600 bison during winter at the National Elk Refuge and Grand Teton National Park, Wyoming. Numerous terms are synonymous with intentional artificial feeding, each giving some clue as to the purpose for feeding. These are:

- **Supplemental feeding** – the provision of food to enhance individual and population features, e.g., antler size, number and survival of young, etc.;
- **Emergency feeding** – the provision of food when natural food sources become inaccessible or severely restricted;

- **Winter feeding** – the provision of food to offset reduced food availability caused by winter conditions (Fig. 1), i.e., snow cover, snow depth, etc.; and
- **Intercept feeding** – the provision of food to reduce damage to agricultural crops, livestock, or timber stands (Fig. 2).

It is important to realize that artificial feeding may also occur unintentionally. Garbage dumps, compost heaps, standing agricultural crops, and artificial environments such as golf courses are all potential sources of food used by wild species.



Figure 1. White-tailed deer at winter feeding site in Wisconsin.



Figure 2. Intercept feeding white-tailed deer as part of the Wildlife Landowner Assistance Program in Saskatchewan.

Baiting of Wildlife

Like artificial feeding, baiting can involve placing natural or artificial food, or alternatively non-food materials such as scent lures and decoys, to attract or entice wild animals to a specific area. However, baiting differs in purpose from artificial feeding. It is used as a technique to:

- Aid hunters and trappers (Fig. 3);
- Vaccinate wild populations against disease;
- Poison problem wildlife; and
- Capture of wildlife for management or research purposes (Fig. 4).



Figure 3. Black bear at bait site used for hunting.



Figure 4. Black bear captured for research by bait and a leg-hold snare.

Occurrence of Artificial Feeding and Baiting of Wildlife in Canada

The occurrence of artificial feeding and baiting of wildlife in Canada varies among the provinces and territories (Table 1). In recent years, as these practices have come under increased scrutiny, regulations have been changed within some jurisdictions. For example, the Ontario spring black bear hunt was banned in early 1999 by the provincial government following increased pressure from environmental activists including World Wildlife Fund Canada and the Animal Alliance of Canada. Most recently, Manitoba Conservation has banned the baiting of cervids (deer, elk, moose, and caribou) for hunting to support efforts to prevent the spread of bovine tuberculosis and to keep chronic wasting disease (CWD) out of the province (see Appendix A).

Table 1. Occurrence of artificial feeding and baiting of wildlife in Canada by province or territory as of September 2002.

Jurisdiction	Artificial Feeding Practiced	Hunting by Bait Permitted
Yukon Territory	No	Yes, for wolf and coyote
Northwest Territories	No	Yes, for bear ^A
Nunavut	No	No
British Columbia	No	No
Alberta	Yes	Yes, for bear and wolf
Saskatchewan	Yes	Yes, for bear and cervids
Manitoba	Yes	Yes, for bear
Ontario	Yes	Yes, for bear
Quebec	Yes	Yes, for bear and deer
New Brunswick	No	Yes, no species restrictions
Nova Scotia	No	Yes, for bear and deer
Prince Edward Island	No	Yes, for coyote and red fox
Newfoundland & Labrador	No	Yes, for bear and cervids

^A Legislation in the Northwest Territories allows baiting for bears by permit. However, issuance of a permit is contingent upon approval by the local community. To date, no permits have been issued because most communities are opposed to hunting bear by bait (Lynda Yonge¹, personal communication).

¹ Lynda Yonge – Wildlife Management Specialist, Government of the Northwest Territories, Yellowknife, NT

The Ecological Effects of Artificial Feeding and Baiting

For the sake of this report a distinction is made between ecological and human social effects. In general, many of the potential ecological effects discussed are based on scientific study and substantiated by empirical data. In contrast, many of the human social effects reflect the perceptions or beliefs of different groups, views that conflict in some cases. Although quantitative or semi-quantitative data are presented sometimes as evidence to support or refute specific effects, it is unlikely that resolution of these conflicts will ever be inferred from the factual findings of science. Instead, hope for resolution will likely depend upon broad education and meaningful discourse.

Although the objectives for artificial feeding and baiting with feed often differ, the effects of these practices are considered together. In essence, both provide natural or artificial food for wildlife at specific locations in the environment. Although baiting has not been studied as widely as artificial feeding, we believe many research results from the study of artificial feeding also are applicable to baiting. This is because differences in ecological effects from one feed or bait site to another are less likely to be explained by the objective for providing food (i.e., supplement or bait?) and more likely to be explained by the cumulative influence of many factors including: type, quantity, and distribution of food; duration of feeding; social behavior of target species; and population and community composition. Nevertheless, despite our lack of distinction between artificial feeding and baiting when considering ecological effects, every effort has been made when providing specific examples from scientific studies to indicate which of the two practices was employed.

The ecological effects of artificial feeding and baiting concern:

- Physical condition and reproductive success;
- Population processes;
- Disease;
- Community processes; and
- Wildlife mortality by hunting.

Detailed discussion of each of these follows:

Physical Condition and Reproductive Success

Physical condition and reproductive success are closely linked; animals in good condition generally have better reproductive success than animals in poor condition. Artificial feeding has been used in attempt to improve the physical condition and reproductive success of a variety of wild species (Fig. 5). However, the success of these efforts have not always been consistent and suggest that many other factors, in addition to food availability and quality, also influence physical condition and reproductive success. Specific examples illustrating the varied effects include:

- Black bears (*Ursus americanus*) that frequented garbage dumps to supplement their diet were found to be heavier, and their reproductive rates were higher, than bears eating only a natural diet (Rogers et al., 1974).
- Artificial feeding programs in Canada and the United States have improved the nutritional status and reproductive success of ungulate populations (Robinette et al., 1973; Ozoga and Verme, 1982; Carpenter et al., 1984; Boutin, 1990).
- Artificial feeding during winter does not improve fecundity in elk (*Cervus elaphus*) (Smith, 2001).
- The effect of artificial feeding on the physical condition of deer is variable depending on density of deer, the feeding practices related to the sex and age ratios, and the severity of the winter (Tarr and Perkins, 2002).
- Artificial feeding during winter increases the fecundity and fawn survival of white-tailed deer (*Odocoileus virginianus*) (Verme, 1965; Murphy and Coates, 1966; Ozoga and Verme, 1982).
- Artificial feeding does not increase the birth weights of elk calves (Smith et al., 1997). Birth weights appear to be largely density dependent, so increased birth weight as a result of artificial feeding is likely only to be detected when population densities of elk approach the carrying capacity of winter yards (Smith, 2001).
- Artificial feeding improved nesting success of bald eagles (*Haliaeetus leucocephalus*) in Alaska (Hansen, 1987) and white-tailed eagles (*Haliaeetus albicilla*) in Sweden (Helander, 1978).
- Winter feeding did not improve reproductive success of bald eagles in Maine (McCollough et al., 1994)

Lewis (1990) suggests that although improved physical condition and reproductive success are generally perceived as beneficial effects of artificial feeding, they may prove detrimental in the long term. This is because, as physical condition and reproductive success improve, population growth will eventually exceed the carrying capacity of the range.



Figure 5. Artificial feeding is used to improve physical condition and reproductive success in a variety of wild species.

Population Processes

The provision of food for wildlife at focal locations in the environment has been demonstrated to affect numerous processes at the population level. The spatial distribution of animals can be altered so that population density is significantly increased in the vicinity of the food source (Boutin, 1990; Schmidt and Gossow, 1991; Easton, 1993; Tarr and Perkins, 2002). As animals converge toward focal food sources, their normal daily or seasonal movements can be disrupted (Baker and Hobbs, 1985; Lewis, 1990; Paquet, 1991; Fersterer et al., 2001). As density of animals increases around a focal food source, competition among individuals can also increase (Jarman, 1974; Schmitz, 1990; Grenier et al., 1999). Ultimately, survival may be enhanced or reduced depending on the purpose for providing food, the manner in which food is distributed, and the level of competition or interaction among population members.

Specific examples of effects on population processes include:

- Relative to central areas within Riding Mountain National Park, the density of bears is greater at the periphery of the park close to bait sites located on adjacent agricultural lands (Paquet, 1991). In addition, the home ranges of female bears in Riding Mountain National Park are larger than home ranges in other parks where baiting does not occur. These observations suggest a source-sink model of population regulation (Pulliam, 1988; Pulliam and Danielson, 1991) in which the park represents a territory suitable for the production of dispersing offspring, and the sinks are baited areas around the park periphery where the expected rate of reproduction is insufficient to replace the parents.
- In the short term, intercept feeding was successful in altering the movements of bears in spring to include feeding sites in their travels and, consequently, reduce damage to saplings (Fersterer et al., 2001). However, as the number of bears attracted to feeding sites increased, the effectiveness of intercept feeding decreased.
- Artificial feeding was not observed to prevent or delay any white-tailed deer from migration, although the longer a feeder was in operation, the proportion of non-migratory deer increased (Lewis, 1990).
- Winter mortality of elk on feeding grounds in Wyoming was lower than occurred in unfed populations of elk (Smith, 2001).
- Artificial feeding may help to maintain and support some endangered species including trumpeter swans (*Cygnus buccinator*) (Gale, 1989; Gomez and Scheuring, 1996), and local “at-risk” populations including bald eagles (Hario, 1981; Helander, 1981; Helander, 1985; McCollough et al., 1994).
- Artificial feeding increased the carrying capacity of habitat for bald eagles during times of decreasing prey population and was effective at drawing eagles away from contaminated food sources (McCollough et al., 1994).

Disease

The provision of food to wildlife has been implicated widely as a causative factor that increases the occurrence of infectious and non-infectious disease. Animals are attracted to artificial sources of feed in higher density than normally occurs under natural conditions (Thorne and Herriges, 1992; Williams et al., 1993; Fischer et al., 1997). As animal density increases, competition for food also increases resulting in more frequent contact among individuals (Baker and Hobbs, 1985; Schmitt et al., 1997). Contact can be direct through physical contact, or indirect as occurs when two animals share the same portion of food. If one or more animals are harboring an infectious organism or prion, its transmission to uninfected individuals is facilitated by the increased frequency of contact among animals congregating at the feeding site (Miller et al., 1998; Michigan Bovine TB Eradication Project, 2002). It is also suggested stress from crowding reduces

immunocompetence in some animals, increasing the likelihood of disease (Smith and Roffe, 1992; Smith, 2001). Disease can affect individual animals, populations, or communities. Depending on the nature of the disease and the feeding location, disease can be transmitted within or between species (Schmitt et al., 1997; Smith, 2001), between wildlife and domestic animals (Thorne and Herriges, 1992), or even between wildlife and humans (Rupprecht et al., 1995). Non-infectious disease also can occur when wild species are fed foods incompatible with their digestive function (Wobeser and Runge, 1975), foods of poor nutritional quality (Ohio Wildlife Center, 2000; see www.ohiowildlifecenter.org/WildlifeInfo/nuisancewaterfowl.htm), or spoiled foods that have become toxic (Perkins, 1991; Davis, 1996; Breed, 2002).

Specific examples of disease occurrence attributed to artificial feeding or baiting include:

1. *Bovine tuberculosis in wild cervids* – In 1994, bovine tuberculosis (TB) was detected in a population of white-tailed deer in an area of Michigan where there were no infected livestock or bison to serve as a reservoir (Schmitt et al., 1997). Focal sources of concentrated feed and high densities of deer were determined to be the factors maintaining this disease and increasing its prevalence. High concentrations of deer around feeding and baiting sites facilitate disease transmission through increased animal-to-animal contact and possibly through contamination of feed (Palmer et al., 2001; Schmitt et al., 2002). Bovine TB also has been detected in wild mule deer (*Odocoileus hemionus*) in Montana (Rhyen et al., 1995). However, in contrast to deer in Michigan, infection of deer in Montana appears to have occurred as a result of contact between wild deer and infected livestock. In 1998, a bovine TB surveillance program was established in west-central Manitoba following detection of the disease in wild elk within and around Riding Mountain National Park. High densities of elk around bait sites and hay bales or standing crops on agricultural lands adjacent to the park coupled with increased interaction between elk and livestock are believed to play a role in maintaining the disease in cattle and elk from this area (Parks Canada Agency, 2001b). In Michigan, a variety of environmental and farm management factors have been identified to be associated with increased risk of bovine TB on cattle farms including higher TB prevalence among wild deer and cattle farms in the area, herd size, and ponds or creeks in cattle housing areas (Kaneene et al., 2002).
2. *Chronic wasting disease in deer* – In Fort Collins, Colorado, artificial feeding by private citizens is believed to have contributed to the infection of 49 free-ranging cervids with chronic wasting disease (CWD) (Spraker et al., 1997). Experimental and circumstantial evidence suggests infected animals probably transmit the disease through animal-to-animal contact, and through contamination of food or water sources with body fluids (saliva, urine) and feces (Williams and Young, 1980; Miller et al., 1998). Further, conditions of high animal density or confinement can create conditions where transmission of CWD occurs at a faster rate than under natural conditions (Fig. 6) (Miller et al., 2000). Several government agencies in Canada (Appendix A – see www.gov.mb.ca/chc/press/top/2002/08/2002-08-16-01.html) and the United States (Michigan Department of Natural Resources, 2002 – see www.michigan.gov/dnr/0,1607,7-153-10370_12150-29070--,00.html; Wisconsin

Department of Natural Resources, 2002 – see www.dnr.state.wi.us/org/land/wildlife/regs/02CWDregs.pdf; New York Department of Environmental Conservation, 2003 – see www.dec.state.ny.us/website/regs/part189.htm) have recently changed their regulations regarding artificial feeding and baiting in an effort to prevent or reduce infection of wild cervids with CWD.



Figure 6. Captive elk infected with chronic wasting disease.

3. *Bovine brucellosis in elk and bison* – In the western United States, brucellosis in wildlife of the Greater Yellowstone Ecosystem is an issue of national importance to the National Park Service as well as other federal and state agencies. At issue is the risk of transmission of brucellosis from wildlife to domestic animals (Cheville et al. 1998; Smith, 2001), the health and welfare of wildlife under National Park Service stewardship, and management of federal lands. Brucellosis in elk in the ecosystem is enhanced as a direct result of management actions that cause dense winter aggregations of elk on feeding-grounds (Thorne and Herriges 1992; Williams et al., 1993; Smith, 2001). The disease, however, is not found among free-ranging elk herds subsisting on natural forage because the route of transmission requires contact with reproductive products. The feeding-grounds of the Greater Yellowstone Ecosystem include the National Elk Refuge and 22 sites in Wyoming. Together, these sites are home to an estimated 22-25,000 elk. Once introduced to bison (*Bison bison*) the disease is maintained via their naturally gregarious behavior.

4. *Carbohydrate overload in wild ruminants* – Wild ruminants can die from feeding on highly digestible, low-fiber feed (Wobeser and Runge, 1975). Ruminants need to change their diet of roughage to grain slowly to give the bacteria in their gut a chance to adjust to changes in feed type. Otherwise, rapid exposure to a concentrated grain diet will often cause a fatal disruption of the body's acid-base balance. Animals that survive the immediate effects of "carbohydrate overload" often die in the days or weeks that follow due to secondary complications of the disease. A variety of feeds can cause carbohydrate overload (also called grain overload, lactic acidosis, or enterotoxemia), including grains, lentils, bread, and corn. In Saskatchewan from 1995 to 2001, two to four wild deer submitted each year to the diagnostic pathology service of the Canadian Cooperative Wildlife Health Centre were diagnosed as dying of carbohydrate overload. Given the small likelihood of finding a wild animal that is either dying of or has recently died of carbohydrate overload, it is likely a considerably larger number of wild deer that succumb to this disease go undetected.
5. *Psoroptic mange in elk* – Elk at the National Elk Refuge in Wyoming have survived on artificial feeding during the winter months for approximately 90 years. Each year, 20-30 adult male elk die from psoroptic mange (Samuel et al., 1991; Smith, 2001). Infected elk have also served as a reservoir for infection of a sympatric population of bighorn sheep (*Ovis canadensis*).
6. *Demodectic mange in white-tailed deer* – White-tailed deer receiving artificial feed in Maine have suffered from outbreaks of demodectic mange caused by the spread of mites while at feeding stations (Maine Department of Inland Fisheries and Wildlife, 2002; see www.state.me.us/ifw/hunt/deerfeed.htm).
7. *Starvation of white-tailed deer* – Winter feeding of white-tailed deer can lead to starvation of some individuals if the feeding delays the migration of deer to their winter yards, or if artificial feeding is terminated abruptly (Ozoga and Verme, 1982).
8. *Mycoplasmal conjunctivitis in house finches* – Since 1994, mycoplasmal conjunctivitis has been found in a variety of bird-feeder type birds, especially house finches (*Carpodacus mexicanus*). In the past 8 years, the disease has spread westward from the eastern United States (Fischer et al., 1997; Hartup, 1998). Although it is not fully understood how the disease is transmitted among house finches, artificial feeding is suspected to facilitate transmission (Fischer et al., 1997; Hartup et al., 1998). The use of tube feeders that offer few perches increases contact among birds. Further, seed contaminated by the infectious organism *Mycoplasma gallisepticum* is protected from moisture within the tube feeders.
9. *Salmonellosis in passerine birds* – Outbreaks of salmonellosis in Michigan occur mostly in passerine birds concentrated around feeders during winter. (Michigan Department of Natural Resources, 2001; see www.michigan.gov/dnr/1,1607,7-153-10370_12150_12220-27268--CI,00.html). The disease is transmitted directly through ingestion of feed contaminated with feces containing the bacterium *Salmonella typhimurium*.

10. *Nutritional deficiencies in fed birds* – Many people feed wild birds, including waterfowl, to supplement their diet. However, birds maintained on artificial feed are frequently submitted to wildlife rehabilitation centers as a result of severe nutritional deficiencies and metabolic bone disease (Ohio Wildlife Center, 2000; see www.ohiowildlifecenter.org/WildlifeInfo/nuisancewaterfowl.htm).

Although provision of food to wildlife is more commonly associated with increasing the occurrence of disease, it has also been used effectively in some circumstances to prevent disease. For example, the widespread dispersal of bait containing vaccine has been an effective and feasible method of preventing the spread of rabies in areas of Ontario and Texas (Farry et al., 1998a; Farry et al., 1998b; Rosatte et al., 2001).

Community Processes

The potential effects of providing food to wildlife typically extend well beyond the population of the targeted species, especially if food is provided over a prolonged period. Disease has already been described to affect multiple species in a community. Competition among species for limited resources often increases as the density of animals increase in a feeding area (Williamson, 2000). Over many years, the composition of a community can change markedly – plant and animal diversity is reduced, and plant abundance declines (Casey and Hein, 1983; DeCalesta, 1994). The ability of a habitat to support animal life, its carrying capacity, is diminished (Doenier et al., 1997; Williamson, 2000). Further, if plant materials are provided for artificial feed, there is increased likelihood of invasion by exotic plant species (Fig. 7) (Kosowan and Yungwirth, 1999; Alien Plant Working Group, 2000; Spurrier and Drees, 2000). Processing of plant materials into pellets through crushing and steaming greatly reduces, but does not entirely eliminate, the presence of viable weed seeds (Cash et al., 1998). The effects of invasion can be devastating (IUCN, 1999; Alien Plant Working Group, 2000) and include:

1. Reduction of biodiversity;
2. Loss of and encroachment upon endangered and threatened species and their habitat;
3. Loss of habitat for native insects, birds, and other wildlife;
4. Loss of food sources for wildlife;
5. Changes to natural ecological processes such as plant community succession;
6. Alterations to the frequency and intensity of natural fires;
7. Disruption of native plant-animal associations such as pollination, seed dispersal and host-plant relationships; and
8. Alterations in soil characteristics resulting in soil erosion.

The prevention of introducing biological invaders into the environment has been identified to be of the highest priority by the International Union for the Conservation of Nature (1999).



Figure 7. Exotic plant seeds left remaining and germinating at ungulate bait site in Saskatchewan.

Specific examples of effects on community processes include:

- In Wyoming, moose (*Alces alces*) suffered a reduction in the carrying capacity of their habitat because elk maintained on artificial feed had reduced the amount of willow in the area (Williamson, 2000).
- Casey and Hein (1983) studied the effects of 27 years of artificial feeding of ungulates on the community structure of an eastern deciduous forest. Populations of white-tailed deer, elk and mouflon sheep (*Ovis musimon*) were maintained at higher densities in feeding areas than in neighboring areas where artificial feeding did not occur. Further, the amount of under-story was decreased, little ground cover remained, trees were larger, and there were an increased number of dead trees in feeding areas. As a result, ground-nesting birds such as wild turkeys (*Meleagris gallopavo*) were less abundant in the feeding areas. There also was an increase in bark-foraging species and cavity-nesting species because of the change in the composition of the trees.
- The provision of supplemental food for deer on rangelands in Texas may negatively impact populations of neighboring wild turkeys and other ground-nesting birds by concentrating potential nest predators, such as raccoons and skunks, near feeders (Cooper and Ginnett, 1998; Cooper and Ginnett, 2000).
- Doenier et al. (1997) studied the browse pressure exerted by deer around artificial feeding sites. The effects of over-browsing, such as loss of plant species and increases in less desirable plant species, were seen within a one mile radius of feeding sites.
- Weeds contained in the feed at artificial feeding sites and seeds deposited in the area by birds, animals, or wind, threaten the integrity of a community. If the invading

plant species have a high rate of reproduction, means of dispersal, and disturbed areas caused by over-browsing, biological invasion is a distinct possibility (Spurrier and Drees, 2000). This possibility has been recognized in numerous areas of Saskatchewan and Manitoba where exotic plant species appear to have been introduced into communities through baits used for ungulates (see, for example: “Wildlife Feed May Be Weedy, Diseased” by Karen Briere in Western Producer, March 23rd, 2000). The spread of exotic plant species is facilitated by the species feeding on the bait, as well as by transport of seeds on vehicles and other equipment (Adam Kosowan², personal communication). Invasion of native grassland by exotic plant species is considered a major problem in Saskatchewan (Thorpe and Godwin, 1999 – see http://www.serm.gov.sk.ca/ecosystem/biodiversity/threats_bio.pdf). Exotic invasion is not yet a serious threat in the forest regions, but there is some invasion of species such as Kentucky blue grass, quack grass, Canada thistle, and caragana in the southern edge of the forest, which is affected by proximity to settlement and livestock grazing.

Wildlife Mortality by Hunting

Baiting, and to a lesser extent artificial feeding, are believed by some to influence the numbers of wild animals killed by hunting. In fact, a basic question of concern to resource managers is does baiting lead to an increase in wildlife mortality by hunting, either for the population as a whole or for specific segments of the population, and if so what impact could this have on the population over the short and long term. Unfortunately, answers to these questions are not easily determined. Considerable debate and differing opinion remain on exactly how or if wildlife mortality by hunting is affected by providing food, as illustrated in the following examples:

- The numbers of black bears killed by hunters over bait around Riding Mountain National Park (RMNP), Manitoba, is high. Given the low reproductive rate of black bears, the mortality resulting primarily from hunting is likely to be unsustainable (Paquet, 1991). The immediacy of this concern, however, might be obscured in the short term by source-sink population dynamics (Pulliam, 1988) where the protected area within the park provides a source of bears that disperse toward the baiting areas. However, over many years, it is possible that the genetic pool for black bears of RMNP will be reduced through high hunting success coupled with the selective killing of larger bears. Alternatively, the severe hunting pressure on local black bears could be offset by immigration from other outlying populations (Lamport, 1996).
- Hunting black bears over bait can potentially enable hunters to better discriminate target animals and avoid killing of sensitive sex and age classes, e.g., lactating females (Obbard, 2002). However, based on hunter survey data from Ontario, Lamport (1996) concluded that the ability of the average hunter to correctly determine the sex of a bear over bait is poor (Fig. 8). The results from this survey, as well as results from other studies (Litvaitis and Kane, 1994), suggest selectivity is

² Adam Kosowan – Boreal Ecologist, Saskatchewan Environment, Prince Albert, SK

less important to hunters than successfully killing a bear, regardless of its sex or age class.



Figure 8. Shooting stand and bait site constructed for hunting black bears in Ontario.

- Winterstein (1992) reported that hunters in Michigan were 20 percent more effective in harvesting deer when using bait than those not using bait (3.8 versus 3.1 deer harvested per 100 days of hunting). A 1999 phone survey found that 44 percent of hunters were successful using bait, while 52 percent were successful without bait (Michigan Department of Natural Resources, 1999 – see www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99baiting.pdf). A more recent survey in Michigan indicated that archers using bait required fewer days to harvest a deer than non-baiters (4.9 ± 4.3 versus 1.8 ± 2.1 deer/100 days) (Frawley, 2002). In contrast, firearm hunters using bait required approximately the same time to harvest a deer than non-baiters (8.3 ± 3.3 versus 7.4 ± 2.5 deer/100 days). Overall, baiting appeared to contribute more towards greater harvest rates among archers than firearm hunters (Frawley, 2002).
- A survey by the Wisconsin Department of Natural Resources in 1993 found that 50% of hunters were successful with bait, while 54% were successful without bait (Wisconsin Bureau of Wildlife Management, 1993).

- Deer that were provided artificial feed during summer were more likely than unfed deer to seek out bait sites providing similar feed during hunting season (Lewis, 1990).

Conclusions Regarding The Ecological Effects of Artificial Feeding and Baiting

Significant ecological effects of providing food to wildlife have been documented through observation and experimentation at the individual, population, and community levels. The increased potential for disease transmission and outbreak is perhaps of greatest and immediate concern; recent outbreaks of bovine tuberculosis and chronic wasting disease in Canada and the United States giving credence to this point.

Nevertheless, even if disease is prevented, other significant ecological concerns exist.

Disruption of animal movement patterns and spatial distribution, alteration of community structure with reduced diversity and abundance, the introduction and invasion of exotic plant species, and general degradation of habitat are all major negative effects that have been documented at different locations in North America.

Further, it would appear the costs of such effects are unlikely to be outweighed by any long-term benefits. For example, the record of success for artificial feeding programs has been generally low (Carhart, 1943; Doman and Rasmussen, 1944; Dahlberg and Guettinger, 1956; Keiss and Smith, 1966; Lewis and Rongstad, 1998). In many instances, large-scale feeding efforts have created feed-dependent populations existing in numbers that exceed the carrying capacity of their environment (Ozoga and Verme, 1982; Ontario Ministry of Natural Resources, 1997 – see www.mnr.gov.on.ca/mnr/pubs/deer2.pdf; Williamson, 2000).

The Human Social Effects of Artificial Feeding and Baiting

The human social effects of providing food to wildlife through artificial feeding or baiting are not as amenable to scientific research as the ecological effects. In many cases, social effects reflect the sometime conflicting perceptions or beliefs of different groups. Acceptance of perceived effects or resolution of conflicting views is more likely to occur through broad education and meaningful discourse than through scientific study. The major human social effects concern:

- Economics;
- Human safety;
- Regulations – compliance and enforcement;
- Wildlife ownership;
- Hunter success;
- Discord among hunters; and
- Discord between jurisdictions.

Detailed discussion of each of these follows:

Economics

Providing food to wildlife can involve transactions of large sums of money and perhaps this as much as anything has encouraged continuation of artificial feeding and baiting despite compelling evidence for significant negative ecological effects. Although reported statistics are scattered and few, the following examples illustrate the scale of business (Fig. 9).

- In 1991, hunters in Michigan used over 13 million bushels of bait for deer, with a net value in excess of 50 million dollars (\$U.S.) (Winterstein, 1992).
- In 1995, artificial feeding and baiting in Michigan generated a minimum value to farmers of about 15 million dollars (\$U.S.) and two to three times that amount to retailers (Michigan Department of Natural Resources, 1999 – see www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99feeding.pdf; Williamson, 2000).
- In 1993, approximately 13 million dollars (\$CAN) was spent in Ontario for supplies and services associated with the spring and fall black bear hunting season, much of which is done over bait (Lamport, 1996).
- Outfitting (includes hunting, angling, and touring) is the largest single source of export dollars in the Saskatchewan tourism industry. The direct income from the industry is about 80 million dollars (\$CAN) annually (Sask Net Work, 2003 – see http://www.sasknetwork.gov.sk.ca/pages/lmi/sectorstudies/inetsectors/Tourism/outfit_sp.htm)

- Recent statistics on bird feeding in the United States indicate people spend nearly \$4.7 billion (\$U.S.) annually on bird feeding and watching wildlife. Of that, they spend: \$3.2 billion on birdseed and wildlife food; \$832 million on birdfeeders, birdbaths and nesting boxes; and \$636 million on binoculars and spotting scopes (see – www.franchisegator.com/cgi-bin/profile.php?key=58).



Figure 9. Bagged corn sold for the baiting of white-tailed deer in Wisconsin.

The cost of supplies and services are largely transparent – the manufacturer, distributor, or service sets a price and the consumer knowingly pays it. In contrast, the costs of maintaining artificial feeding programs or dealing with the negative ecological effects of providing food to wildlife (e.g., disease containment, habitat degradation) are often obscure, but generally considerable, long term, and borne by society as a whole. This is illustrated in the following examples:

- The financial cost of feeding mule deer is estimated at \$183.37 (\$U.S.) per deer saved, and may prove cost-prohibitive to some wildlife managers (Baker and Hobbs, 1985)
- In 1997, the cost of feeding bears to protect trees in western Washington was \$300,000 (\$U.S.) (Partridge, 2001).
- By the end of 2001, the Canadian Food Inspection Agency had paid close to \$30 million (\$CAN) in compensation to elk farmers for losses in association with chronic wasting disease (CWD) (Inch, 2002 – see

www.inspection.gc.ca/english/anima/heasan//cahcc/cahcc2001/plen-aj-e.shtml).

Although this cost was in association with captive elk only, the disease is transmitted between and among both captive and free-ranging cervids (Miller et al., 1998; Miller et al., 2000) and considerable amounts of money also have been spent in association with CWD surveillance and depopulation of wild deer. In Saskatchewan, total costs for CWD testing of hunter- and control-killed deer since 1999 are close to \$500,000 (\$CAN) (Trent Bollinger³, personal communication).

- Albeit unintentional, standing agricultural crops, stored hay and grain, and livestock all represent potential sources of food for wildlife (Fig. 10). Failure of agricultural producers to prevent access by wildlife to these food sources can be costly. In 2000 and 2001, over \$2.2 million (\$CAN) was paid in compensation to producers in Saskatchewan for crop damage caused by large game (Saskatchewan Crop Insurance Corporation, 2002 – see www.saskeropinsurance.com/pdf/SCICannualreport0102.pdf). A further 2.8 million (\$CAN) was paid for damage caused by waterfowl. During the same period, 3.4 million (\$CAN) was paid to producers in Manitoba for damage caused by wildlife (large game and waterfowl combined) (Manitoba Crop Insurance Corporation, 2002 – see www.mcic-online.com/Downloads/Financials.pdf). Further, wildlife agencies in both provinces have been forced at times to use intercept feeding in attempt to reduce damage to agricultural products.
- Although the recovery of the trumpeter swan (*Cygnus buccinator*) is a great success story for wildlife conservation, the increased number of birds wintering in southern British Columbia is putting pressure on the agricultural lands they have come to depend on. Since each swan can eat up to 1.2 kilos of grass per day, their foraging habits might translate into substantial forage losses to the farmer (Environment Canada, 2002; see www.ecoinfo.ec.gc.ca/env_ind/region/swan/swan_e.cfm).
- Impacts of invasive plant and animal species on native habitats in the United States range from insidious to catastrophic, and cost Americans about \$138 billion (\$U.S.) annually (Fig. 11) (Pimental et al., 2000; Spurrier and Drees, 2000; also see – <http://biology.usgs.gov/cro/invasives.pdf>).

³ Trent Bollinger – Wildlife Disease Specialist, Canadian Cooperative Wildlife Health Centre, Saskatoon, SK



Figure 10. Albeit unintentional, standing agricultural crops, stored hay and grain, and livestock all represent potential sources of food for wildlife.



Figure 11. From native forest to introduced plants – exotic plant species thriving along an ungulate shooting lane in Saskatchewan.

Human Safety

Various issues of human safety have been identified in association with providing food to wildlife, including artificial feeding and baiting. However, conclusive information is lacking in many instances. Issues include:

- Deer feeding sites located near well-traveled highways may increase deer/vehicle collisions (Wisconsin Conservation Congress, 2000 – see www.dnr.state.wi.us/org/land/wildlife/hunt/deer/deer2000/b&freport.pdf; Stewart, 2001 – see <http://msucare.com/pubs/infosheets/is1624.pdf>; also see – www.state.me.us/ifw/hunt/deerfeed.htm; Manitoba Conservation, 2002 – see www.gov.mb.ca/natres/wildlife/huntingg/general_information/notice.html).
- Wild animals conditioned to human food sources may lose their natural wariness of people and become aggressive toward people either in protection of, or in seeking other, human food sources, e.g., camp food, garbage (Fig. 12) (The Humane Society of the United States, 2002 – see <http://www.hsus.org/ace/12810>; Pennsylvania Game Commission, 2003 – see http://sites.state.pa.us/PA_Exec/PGC/newsroom/2003/nr002-03.htm). Black bears conditioned to human food sources have been associated with injury to humans, particularly inside national parks where carrying of firearms is restricted (Herrero, 1970; Herrero, 1985). Although there are few published data available demonstrating a causal relationship between feeding and the creation of nuisance bears, the circumstantial evidence has been broad enough to convince many government agencies to develop policies on the feeding of bears. For example, in the United States, the U.S. Forest Service (USFS), the Bureau of Land Management (BLM), the U.S. Fish and Wildlife Service, and the National Park Service all publish materials telling the public not to feed bears, materials that warn: “Do Not Fed Bears!,” “Bears Are Dangerous!,” and “A Fed Bear Is A Dead Bear” (Examples from each of these agencies are found at <http://www.fs.fed.us/r4/sc/yankeefork/Bear.html>, <http://www.or.blm.gov/Rogueriver/WildRogueOnly/Bears.htm>, <http://www.r6.fws.gov/endspp/grizzly/factsheets/grizz%20foods.pdf>, and <http://www2.nature.nps.gov/nps77/health.new.html>). A troublesome finding is that two of these agencies (the USFS and BLM) also permit baiting for bears on federal lands in nine of the 27 states that allow bear hunting, the nine states being Alaska, Idaho, Maine, Michigan, Minnesota, New Hampshire, Utah, Wisconsin, and Wyoming (Scheick, 2002). Clearly, the allowance of baiting in these states contradicts federal policies on the feeding of bears. Contradicting policies on feeding and baiting bears are also found in Canada where a number of provincial government agencies that permit baiting of black bears for hunting also warn against providing food to these animals as it can lead to dangerous human-bear interactions or damage to human property (Nova Scotia Department of Natural Resources, 1996 – see <http://www.gov.ns.ca/natr/wildlife/conserva/20-01-1.htm>; Ontario Ministry of Natural Resources, 2000 – see <http://www.mnr.gov.on.ca/mnr/bears/index.html>; Saskatchewan Environment, 2000 – see <http://www.serm.gov.sk.ca/media/saskatchewan%20environmentnewsline/bears.htm>

and

http://www.serm.gov.sk.ca/media/saskatchewan%20environmentnewsline/reduce_bear_encounter.htm; Alberta Sustainable Resource Development, 2002 – see <http://www3.gov.ab.ca/srd/fw/bears/manage.html>; and Manitoba Conservation, 2002 – see www.gov.mb.ca/natres/wildlife/huntingg/general_information/notice.html).



Figure 12. Black bears conditioned to human food sources may lose their natural wariness of people and become aggressive either in protection of, or in seeking other, human food sources.

- In Ontario, 82 municipalities have recently joined together with the Canadian Outdoor Heritage Alliance (COHA) to pressure the provincial government to reinstate the spring black bear hunt as many believe cancellation of the spring hunt in 1999 has resulted in an increase of nuisance bears (COHA, 2002; see http://www.coha.net/press/press_release16.html and http://www.coha.net/published_articles/published_articles8.html). The Ontario Ministry of Natural Resources attributes the abnormally high incidence of problem bears over the past 5 years to a reduction in natural foods due to unusual weather conditions and point out that similar events have been recorded in years prior to cancellation of the spring hunt (Ontario Ministry of Natural Resources, 1998 – see <http://www.mnr.gov.on.ca/MNR/csb/news/sept28nr98.html>; Martyn Obbard⁴,

⁴ Martyn Obbard – Research scientist in predators/conservation biology, Ontario Ministry of Natural Resources, Peterborough, ON

personal communication). Nevertheless, the COHA advocates that hunting (over bait) is the only well regulated management tool for keeping an “out of control black bear population at a safe and sustainable size.” Apparently, wildlife officials from various agencies in North America also share the view that baiting is needed to help control bear populations (see [http://www.biggamehunt.net/sections/Politics/Congressman Announces Plan to End Bear Baiting 01060312.html](http://www.biggamehunt.net/sections/Politics/Congressman%20Announces%20Plan%20to%20End%20Bear%20Baiting%2001060312.html)). Most recently, Karen Noyce, a bear researcher with the Minnesota Department of Natural Resources, was quoted widely in the media as saying that “bear baiting has helped keep the population in check.” In response to public pressure in Ontario, the Ontario Ministry of Natural Resources has recently established a Nuisance Bear Review Committee to undertake an independent review of scientific information related to the nuisance bear issue in the province (Further information available at <http://nuisancebear.mnr.gov.on.ca/index.html>).

- After a prohibition of hunting black bears with bait or hounds came into effect in 1993 in Colorado, neither the geographic distribution of bear kill nor the size or growth rate of the statewide bear population changed (Beck, 1997).
- In general, jurisdictions that permit the feeding of wildlife through artificial feeding or baiting have restrictions concerning type and amount of feed, location and identification of feed/bait site, and duration of feeding/baiting. These restrictions are placed in part to minimize human injury. Still, it is unlikely any persons injured as a result of wildlife conditioned to human food sources would have legal recourse (Brendan Delehanty⁵, personal communication).
- Hunting over bait is presumed to be safer than other hunting techniques because it allows hunters to remain stationary near their bait pile instead of moving about and encountering other hunters. Hunters frequently have a clear line of sight to their bait pile allowing them a better view of their target and reducing the chance of an accident (Michigan Department of Natural Resources, 1999; see www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99baiting.pdf).

Regulations – Compliance and Enforcement

Where artificial feeding or baiting is permitted, regulations are often maintained concerning type and amount of feed, location and identification of feed/bait site, and duration of feeding/baiting. However, although wildlife agencies are aware that not all persons will comply fully with regulations, it is nearly impossible to assess the level of compliance within a jurisdiction. Further, enforcement of regulations is sometimes problematical. Examples that illustrate these points include:

- In a letter to Michigan deer hunters, Peter Bull writes, “Unfortunately, many hunters were not as comfortable with the baiting compliance survey which accompanied the

⁵ Brendan Delehanty – Lawyer, MacPherson Leslie & Tyerman, Saskatoon, SK

baiting survey. In fact, we have concluded that our attempt to determine the percentage of Michigan's deer hunters who violate the baiting regulations (either intentionally or unintentionally) was unsuccessful. Too many hunters obviously were uncomfortable with our methodology.” (Bull, 2002; see http://www.fw.msu.edu/faculty/peyton/october_update.pdf)

- Use of bait may also facilitate illegal activities such as shooting deer at night. Shooting deer at night over bait is perceived by Michigan Department of Natural Resources law enforcement to be a widespread problem and is probably more common than spotlighting deer from vehicles (cited as a personal communication by R. Asher in Michigan Department of Natural Resources, 1999; see – www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99baiting.pdf). Lighted bait piles occur primarily on private land, making it difficult to catch violators.
- A ban on baiting may be easier for Michigan Department of Natural Resources law enforcement personnel to enforce than a quantity restriction on the amount of bait used (Fig. 13). However, field personnel in DMU 452 reported good compliance with the five-gallon quantity restriction in place during the 1998 hunting season (Michigan Department of Natural Resources, 1999; see – www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99baiting.pdf).
- Because baiting is a dispersed activity and hounding is still legal for other species, Measure 18 (a regulation introduced in Oregon in 1994 banning the use of hounds and bait for hunting bears) has proven difficult to enforce. Compliance with special bear hunting regulations in the Indigo Wildlife Management Unit was poor and may represent poor compliance with all bear regulations, including the ban on the use of hounds and bait (Boulay et al., 1997).



Figure 13. A Wisconsin conservation officer surveys a bait pile that exceeds the legal quantity restriction.

Wildlife Ownership

In all jurisdictions of Canada and the United States, wildlife is held in public trust and is supposed to be managed for the benefit of all citizens. It is a resource too important to be owned by any one individual. However, artificial feeding and baiting are forms of wildlife privatization as animals are attracted to and held on private lands (Michigan Department of Natural Resources, 1999 – see www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99feeding.pdf; Williamson, 2000; Maine Department of Inland Fisheries and Wildlife, 2002 – see www.state.me.us/ifw/hunt/deerfeed.htm). As wild animals become dependent on food provided by private individuals or government agencies, the principles of animal husbandry replace those of wildlife management (D. Langford, quoted in Brown, 2001).

Hunter Success

In general, the effect of baiting on hunter success (i.e., the proportion of hunters who harvest an animal) has been considered in two ways. One way has been to compare hunter success between those who use bait and those who don't while hunting for the same species at roughly the same point in time. The other way has been to look at the change in hunter success rate in an area where baiting was once legal but has since been banned. Unfortunately, it has been difficult to draw any general conclusions about hunter success because "hunter success rates" are affected by many other factors in addition to whether or not bait was used, e.g., method of kill, different seasons and localities, residency status of hunter, number of hunters, etc. The following points illustrate some of the different analyses regarding the effect of baiting on hunter success:

- Winterstein (1992) reported that hunters in Michigan were 20 percent more effective in harvesting deer when using bait than those not using bait (3.8 versus 3.1 deer harvested per 100 days of hunting). A more recent survey in Michigan indicated that archers using bait required fewer days to harvest a deer than non-baiters (4.9 ± 4.3 versus 1.8 ± 2.1 deer/100 days) (Frawley, 2002). In contrast, firearm hunters using bait required approximately the same time to harvest a deer than non-baiters (8.3 ± 3.3 versus 7.4 ± 2.5 deer/100 days). Overall, baiting appeared to contribute more towards greater harvest rates among archers than firearm hunters (Frawley, 2002).
- A survey by the Wisconsin Department of Natural Resources in 1993 found that 50% of hunters were successful with bait, while 54% were successful without bait (Wisconsin Bureau of Wildlife Management, 1993).
- A Texas study reported higher success rates, reduced kill distances, more deer observed, and less time required to harvest a deer when hunting over bait (Synatzske, 1981). Further, baiting was determined to be an effective tool for increasing deer harvest in areas where higher harvest rates are required.
- Information from the 1998 white-tailed deer rifle-hunting season in Saskatchewan shows that resident hunters (the majority of who do not use bait) had an average success rate of 92% in the Forest and Forest Fringe Wildlife Management Zones, compared to 76% for non-resident hunters (the majority who hunt over bait) (Schmidt, 2001). However, resident hunters spent an average of 8.6 days hunting per deer harvested compared to 5.1 days per deer harvested by non-resident hunters. Although resident and non-resident hunters killed similar proportions of bucks (81% versus 86%), non-resident hunters killed a greater proportion of older bucks than resident hunters (92% versus 72% of the buck harvest older than yearlings).
- After a prohibition of hunting black bears with bait or dogs came into effect in Colorado in 1993, the annual harvest rate changed little, hunter success rate decreased, and hunter participation increased (Beck, 1997). Since 1993, the annual harvest rate has averaged 563 bears compared to 551 annually from 1985 to 1992 (Colorado Division of Wildlife, 2001; see

http://wildlife.state.co.us/huntrecap/HistoricalHarvest/bear_1957to2000.htm). Hunter success decreased from 15% before to 6% after the prohibition, whereas the number of hunters per year increased 86% over the same period.

- After a prohibition of hunting black bears with bait or dogs came into effect in Oregon in 1995, the annual harvest rate decreased, hunter success rate decreased, harvest efficiency (i.e., time required to kill a bear) increased, and hunter participation increased (Boulay, 1997). Since 1995, the annual harvest rate has averaged 804 bears compared to 993 annually from 1989 to 1994 (Oregon Division of Fish and Wildlife, 2001; see http://www.dfw.state.or.us/ODFWhtml/Wildlife/StatBooks/2001Stats/01bear_summary.pdf). Hunter success decreased from 8% before to 4% after the prohibition, whereas the number of hunters per year increased 71% over the same period. Prior to 1995, hunters expended about 194 days per bear killed compared to 395 days since the prohibition.
- Washington also banned the hunting of black bears with bait or dogs in 1997 (Washington Department of Fish and Wildlife, 2002; see http://www.wa.gov/wdfw/wlm/game/management/final_gmp_27nov02.pdf). Hunter success rates during 1999 and 2000 were around 3% compared to success rates of 10% or higher for most years preceding the prohibition. Hunter days per bear killed ranged from 60 to 100 days before the prohibition to 100 to 400 or more afterwards. Hunter participation prior to the ban ranged from 11000 to 14000 hunters per year. In 2000, more than 37,000 hunters participated in the black bear hunt.
- In Saskatchewan, hunter success rates for black bear averaged more than 50% from 1994 to 1998 (Arsenault, 2001). License sales ranged from about 3000 to 4200 annually for the same period. In 1998 about 4200 hunters killed an estimated 2300 bears, expending about 7 days of hunting effort per bear killed.

Discord Among Hunters

In recent years, there has been much heated debate in the popular literature among hunters about ethical considerations regarding hunters who bait (Petersen, 1996; McCaffery, 2000; Stewart, 2001 – see <http://msucare.com/pubs/infosheets/is1624.pdf>). Reasons for opposition to baiting include:

- Some hunters and many non-hunters think that hunting over bait is too easy and “unfair” to animals (Lamport, 1996; Michigan Department of Natural Resources, 1999; see www.michigandnr.com/publications/pdfs/huntingwildlifehabitat/Issue_Reviews/99baiting.pdf). This practice goes against the principles of “fair chase”, a set of hunting conditions that advocate fair hunting requires the taking of prey as acceptably uncertain and difficult for the hunter (Posewitz, 1994; Peyton, 1998a). In many places, fair chase issues have served to draw non-hunters’ attention to the

controversies of baiting, penned hunts, shooting preserves, hunting with dogs, etc. Non-hunter perceptions of “unfair” hunting behaviors can also create a poor image of those who participate in or allow the practice and, as a consequence, erode credibility of the agency and its hunting constituents (Peyton, 1998b). In some jurisdictions, animal rights activists have effectively used the public forum and government policy processes to affect changes in hunting regulations, e.g., cancellation of the Ontario spring black bear hunt in 1999.

- There is a perception that baiting increases interference and competition among hunters. For example, in past years, the erection of permanent tree stands over bait sites in the provincial forests of Saskatchewan restricted access to some hunters and sparked a growing conflict between resident hunters and outfitters catering to non-resident hunters (Fig. 14) (Saskatchewan Environment, 1999; see www.serm.gov.sk.ca/fishwild/Outfitting/outfitting.htm).



Figure 14. A permanent tree stand in the provincial forest of Saskatchewan.

- Hunter opinion for baiting as an acceptable hunting technique varies widely among jurisdictions. A 1999 survey of Michigan deer hunters indicated 61% of respondents supported deer baiting for hunting, while 28% disapproved (Frawley, 2000). About 48% of the hunters surveyed used bait for deer hunting. In Mississippi, a survey of deer/turkey license buyers indicated 63% of respondents were opposed to, and 36% supported, a change in hunting regulations that would allow hunting deer over bait in the state (Mississippi Department of Wildlife, Fisheries and Parks, 2001; see <http://www.mdwfp.com/wildlifeissues/articles.asp?vol=6&article=54>). Of these respondents, 67% agreed that hunting over bait negatively influences non-hunter attitudes towards hunting, and 65% agreed that hunting over bait is not considered fair chase. In Saskatchewan, a recent survey of hunters indicated 59% of those surveyed supported the use of bait for hunting bear, while 26% did not (Saskatchewan

Environment, 2002; see <http://www.serm.gov.sk.ca/fishwild/MarketResearchStrat.pdf>). The same survey indicated 34% support for baiting of deer, and 57% opposed. 12% of the hunters surveyed indicated they have used bait for deer hunting in the past three years.

Discord Between Jurisdictions

In general, free-ranging wildlife can move back and forth across jurisdictional boundaries without restriction. However, this can pose problems if neighboring jurisdictions have markedly different regulations regarding artificial feeding and baiting. For example, in 1979, Parks Canada introduced “ecological integrity” as a guiding principle for the management of national parks, a principle that was formally recognized as an amendment to the National Parks Act in 1988. Ecological integrity implies “ecosystems have integrity when they have their native components (plants, animals, and other organisms) and processes (such as growth and reproduction) intact” (Parks Canada Agency, 2001a – see http://parkscanada.pch.gc.ca/EI-IE/index_e.htm). Although artificial feeding and baiting are not permitted in national parks, many of the provinces and territories permit artificial feeding, baiting, or both activities in the areas immediately surrounding national parks (Fig. 15). Aside potential for conflict over wildlife management issues between provincial and federal authorities, there is the threat that the ecological effects of artificial feeding and baiting (disease, invasion by exotic plant species, altered community structure, etc.) will impact directly upon the ecological integrity of national parks.

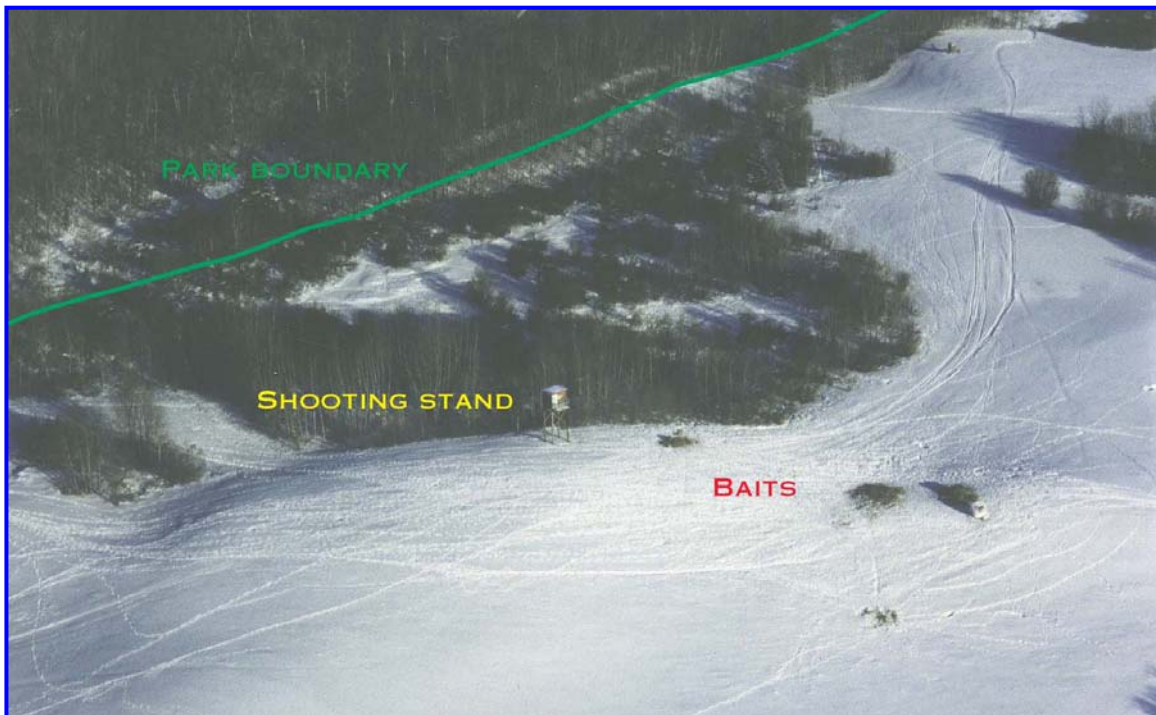


Figure 15. Shooting stand and bait sites in close proximity to boundary of Riding Mountain National Park, Manitoba.

Conclusions Regarding The Human Social Effects of Artificial Feeding and Baiting

The human social effects of providing food to wildlife concern numerous issues including economics, human safety, compliance with and enforcement of feeding or baiting regulations, wildlife ownership, hunter success, discord among hunters, and discord between jurisdictions. Because philosophical differences lie at the root of some of these issues, resolution of conflicting views is more likely to occur through broad education and meaningful discourse than through scientific study. For example, research cannot determine whether the short-term economic gains of feeding wildlife are outweighed by the potential long-term costs of ecological change (e.g., disease, introduction of exotic plant species, etc.), or whether hunting over bait is ethical or not.

Although scientific data on human injury as a result of feeding wildlife is limited, a disturbing finding is the apparent contradiction in policies on feeding and baiting maintained by numerous government agencies in Canada and the United States. Some of the same agencies that warn the public of the dangers of wildlife (especially bears) conditioned to human food sources and regulate against (intentional and unintentional) feeding of wildlife also permit the use of bait for the purpose of hunting. And yet, from a biological perspective, there is likely little difference between a garbage dump, a garden plot, an intercept feeder, round bales, or a bait site.

Information Gaps

Information gaps were considered only in regard to ecological effects (and not human social effects) where scientific research has potential to provide missing information. Although many gaps exist, current information is sufficient to conclude that the potential for negative ecological effects as a result of providing food to wildlife through artificial feeding or baiting is high. Nevertheless, our current understanding of the specific mechanisms operating between cause (feeding or baiting) and effect is often too crude to allow accurate prediction of the nature or magnitude of effect. Thus, for example, although we know providing artificial sources of feed to wild deer in Saskatchewan has potential to increase transmission of chronic wasting disease, we do not know what influence the type, quantity, and distribution of food, or the timing and duration of feeding will have on disease transmission. If this information were available, it could be used along with other biological and physical information to develop prediction models where measurements of a number of key determinants are plugged into an equation to predict the probability of an ecological effect. This approach is similar in principle to resource selection functions (RSF) where empirical data is used to estimate models of the responses of animals to resources (Manly et al., 1993). RSF models have been particularly useful for conservation and land management planning, and can be applied to examine impacts of human activity.

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Annotated Bibliography

Note: Not all of the citations described in the following section are referenced in the main body of the report. Nevertheless, these citations collectively provide an overview representative of many of the ecological and human social aspects of artificial feeding and baiting.

1. **Adams, CE, N Wilkins, and JL Cooke. 2000. A place to hunt: organizational changes in recreational hunting, using Texas as a case study. Wildlife Society Bulletin 28: 788-796.**

This article concerns attitudes toward hunting in Texas, attitudes that are representative of a general trend seen in recent years throughout the United States and Canada. Social pressures from urban dwellers and dwindling recruitment of young hunters are creating pressure for change in the methods of wildlife management. As a result, the policies of wildlife management are becoming influenced more by the general public and non-governmental organizations, and less by hunters, than in past.

2. **Asher, J. 2000. War on weeds: winning it for wildlife. Transactions of the 65th North American Wildlife and Natural Resource Conference, Washington DC, USA. 65: 42-54.**

The author draws attention to ongoing and widespread degradation of our environment through invasion by non-native plant species, and the urgent need to employ qualified people to remedy this situation. He uses examples, such as leafy spurge (*Euphorbia esula* L.), to illustrate the economic impact these non-native plants have on people and wildlife. He emphasizes that success in the “war on weeds” will require education of the general public and prevention of invasion of non-native species. I feel that general adherence with his proposal could significantly improve wildlife habitat across the country reducing need for wildlife support programs, such as supplemental feeding.

3. **Baker, DL, and NT Hobbs. 1985. Emergency feeding of mule deer during winter: tests of a supplemental ration. Journal of Wildlife Management 49: 934-941.**

The authors examine the effectiveness of emergency feeding of mule deer (*Odocoileus hemionus*) during winter to prevent mortality. Although emergency feeding helped to reduce mortality, the mortality rate remained significant (20%) even when deer were fed *ad libitum*. The authors conclude that emergency feeding cannot prevent all winter deaths, but can be used to prevent high mortality in extreme weather conditions. This is a very thorough examination of diet requirements of mule deer and wildlife managers could use this information when designing an emergency feeding program.

4. **Bellhouse, TJ. 1991. The influence of weather and feeder design on the behavior and consumption of supplementary feed by white-tailed deer (*Odocoileus virginianus*) in north-central Ontario. MSc Thesis, Laurentian University, Sudbury, Ontario.**

Among numerous methods available for feeding deer, the barrel feeder was found to be the most economical and the least likely to invoke aggressive interactions among white-

tailed deer (*Odocoileus virginianus*). In addition, provision of adequate numbers of feeders helped significantly to reduce competition among deer seeking food. Although the frequency of aggressive interactions among deer increased as the winter progressed, independent of feeder type and number, the intensity of aggression decreased. I recommend reading this study before attempting to initiate a supplemental feeding program.

5. Brittingham, MC, and SA Temple. 1992. Use of winter bird feeders by black-capped chickadees. Journal of Wildlife Management 56: 103-110.

The authors investigate the use of feeders by black-capped chickadees (*Parus atricapillus*). They describe the use of feeders in relation to the sex, social dominance, and home range of birds, as well as in relation to ambient temperature. The authors advocate supplemental feeding of wild birds as a method of increasing positive human/wildlife interactions without causing negative effects on the bird population.

6. Brittingham, MC, and SA Temple. 1992. Does winter bird feeding promote dependency? Journal of Field Ornithology 63: 190-194.

The authors investigate if the use of feeders by black-capped chickadees (*Parus atricapillus*) results in birds becoming dependent on artificial food sources. Dependency was not seen, however. The authors attribute this finding to the fact that chickadees are opportunistic feeders and routinely visit a variety of different food sources, never relying on only a single source. However, the study was conducted in a rural environment, and the findings may not be applicable to birds occupying an urban habitat.

7. Brown, TL, DJ Decker, SJ Riley, JW Enck, TB Lauber, PD Curtis, and GF Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. Wildlife Society Bulletin 28: 797-807.

The authors investigate the effectiveness of hunting to control the size of white-tailed deer (*Odocoileus virginianus*) populations. They believe the potential for hunting as a mechanism for population control has not been achieved to date. Because public perceptions directly affect how wildlife managers deal with the growing problem of urban and suburban deer, the authors recommend greater effort must be given to educating hunters and non-hunters alike on deer biology and the value of hunting. .

8. Bruning-Fann, C, SM Schmitt, SD Fitzgerald, JS Fierke, PD Friedrich, JB Kaneene, KA Clarke, KL Butler, JB Payeur, DL Whipple, TM Cooley, JM Miller, and DP Muzo. 2001. Bovine tuberculosis in free-ranging carnivores from Michigan. Journal of Wildlife Diseases 37: 58-64.

In recent years, an intensive surveillance program for bovine tuberculosis (TB) in Michigan wildlife has identified infection among animals representing a variety of carnivore species. The authors provide evidence to suggest that bovine TB is not endemic in carnivore populations. Instead, it appears that carnivores have become exposed to the causative organism, *Mycobacterium bovis*, as a result of feeding upon infected white-tailed deer (*Odocoileus virginianus*). Further research is required to confirm the validity of this hypothesis.

9. Casey, D, and D Hein. 1983. Effects of heavy browsing on a bird community in deciduous forest. Journal of Wildlife Management 47: 829-836.

The authors investigate the effect of long-term supplemental feeding of white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and mouflon sheep (*Ovis musimon*) upon co-existing bird populations in a deciduous forest community. This study provides strong evidence that supplemental feeding affects biodiversity. High concentrations of ungulates around feeding sites alter the local habitat which, in turn, leads to changes in the species composition of co-existing bird populations.

10. Cooper, SM, and TF Ginnett. 2000. Potential effects of supplemental feeding of deer on nest predation. Wildlife Society Bulletin 28: 660-666.

The authors investigate the effect that supplemental feeding of deer has had upon the nests of ground-nesting turkeys located in close proximity to feeding sites. The results of this study illustrate clearly that supplemental feeding can have far-reaching effects on non-target species.

11. DeCalesta, DS. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management 58: 711-717.

The author investigates how increases in white-tailed deer (*Odocoileus virginianus*) density, as a result of supplemental feeding, have affected songbird abundance and diversity. His results indicate that intermediate canopy-nesting songbirds begin to decrease in abundance at a threshold deer density of between 7.9 and 14.9 deer/km². In addition to the decline in bird numbers, there was a progressive loss of tree species that resulted in habitat fragmentation and reduced biodiversity.

12. Doenier, PB, GD DelGuidice, and MR Riggs. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildlife Society Bulletin 25: 235-243.

The authors investigate the effects of winter supplemental feeding on browse consumption by white-tailed deer (*Odocoileus virginianus*). They find that there are year-to-year differences in browse consumption that are influenced by winter conditions, independent of the availability of supplemental feed. The ability for browse plants to recover from grazing differs from one species to the next. Consequently, long-term annual variation in browse pressure alters the diversity and availability of browse and, more generally, the carrying capacity of the environment. This study provides another example of the potentially far-reaching effects of supplemental feeding programs.

13. Doman, ER, and DI Rasmussen. 1944. Supplemental winter feeding of mule deer in northern Utah. Journal of Wildlife Management 8: 317-338.

Despite the age of this report, many of the issues identified in this study remain relevant today. The authors recommend that priority be given to habitat restoration and maintaining deer within the carrying capacity of the environment over supplemental feeding. Supplemental feeding is identified as costly from both a financial and ecological perspective. This study is a key piece of research cited by many researchers today.

14. Enck, JW, DJ Decker, and TL Brown. 2000. Status of hunter recruitment and retention in the United States. Wildlife Society Bulletin 28: 817-824.

In recent years, the number of hunters is declining progressively in the United States. As the number of hunters has decreased, so to has financial support for wildlife programs. These changes are placing pressure on wildlife managers to expand public understanding of the population controls (i.e., hunting) necessary to maintain viable populations of game animals.

15. Farry, SC, SE Henke, AM Anderson, and MG Fearneyhough. 1998. Responses of captive and free-ranging coyotes to simulated oral rabies vaccine baits. Journal of Wildlife Diseases 34: 13-22.

This study is an extension of Farry et al. (1998 – see 16.) and provides more evidence to show that vaccine baits provide an efficient method of disease control among wild animals. However, the focus of the authors is solely from a public safety perspective. They do not consider that, from an ecological standpoint, disease may serve as a population control mechanism (Randy Dibblee⁶, personal communication). They also give little consideration to the implications of vaccine bait consumption by non-target species.

16. Farry, SC, SE Henke, SL Beasom, and MG Fearneyhough. 1998. Efficacy of bait distributional strategies to deliver canine rabies vaccines to coyotes in southern Texas. Journal of Wildlife Diseases 34: 23-32.

The authors investigate the efficacy of vaccinating free-ranging coyotes (*Canis latrans*) against rabies using bait (dog food) containing canine rabies vaccine. The study illustrates the one of the applications of baiting in wildlife management, and draws attention to the consumption of bait by non-target species.

17. Fersterer, P, DL Nolte, GJ Ziegler, and H Gossow. 2001. Effect of feeding stations on the home ranges of American black bears in western Washington. Ursus 12: 51-53.

The authors investigate the effects of intercept feeding on a population of American black bears (*Ursus americanus*). Intercept feeding was found to result in increased population size, greater concentrations of bears in the vicinity of feeding sites, and changes in bear movement patterns over time. The authors discuss the broad implications of their findings for the baiting of bears in general.

18. Grenier, D, C Barrette, and M Crête. 1999. Food access by white-tailed deer (*Odocoileus virginianus*) at winter feeding sites in eastern Quebec. Applied Animal Behavior Science 63: 323-337.

The authors investigate how the number and distribution of feeding sites in supplemental feeding programs can affect access of individual white-tailed deer (*Odocoileus virginianus*) to food. In general, competition at feeding sites prevents less aggressive individuals access to feed. In contrast, the high social dominance of bucks gives them

⁶ Randy Dibblee – Wildlife Biologist, Prince Edward Island Fisheries, Aquaculture and Environment, Charlottetown, PEI

priority at feeding sites. However, through the provision many, well-distributed feeding sites, subordinate deer were able to gain free access to food.

19. Gross, JE, and MW Miller. 2001. Chronic wasting disease in mule deer: disease dynamics and control. Journal of Wildlife Management 65: 205-215.

There is little known about how chronic wasting disease (CWD) is transmitted making prevention of this disease difficult. At present, intense management of wild and captive populations, selective culling of wild herds, and restrictions on the supplemental feeding of wild herds offer the best approaches to preventing the spread of CWD. In addition, the authors advocate the development and application of prediction models to prevent an epidemic since detection of infected populations is difficult.

20. Hartup, BK, HO Mohammed, GV Kollias, and AA Dhondt. 1998. Risk factors associated with mycoplasmal conjunctivitis in house finches. Journal of Wildlife Diseases 34: 281-288.

The authors investigate the spread of mycoplasmal conjunctivitis in house finches (*Carpodacus mexicanus*) and identify risk factors associated with the disease. Bird feeders are implicated as significantly facilitating transmission of this disease for two reasons. First, house finches and other species congregate in large numbers at feeders increasing the likelihood of transmission from infected to non-infected individuals. Second, the design of tube feeders protects the causative organism, *Mycoplasma gallisepticum*, from the stresses of the environment and increases the likelihood of non-infected birds consuming contaminated feed.

21. Holsman, RH. 2000. Goodwill hunting? Exploring the role of hunters as ecosystem stewards. Wildlife Society Bulletin 28: 808-816.

The author advocates the need for more research into the relationship between hunting and stewardship values. He asserts that the education of hunters should include a stewardship ethic and promotion of stewardship through social norms. The author's views are quite relevant to the topic of this review because ultimately the public perception of hunters will influence the practice of baiting and supplemental feeding programs.

22. Inglis, JE. 1993. An analysis of human-black bear conflicts in Algonquin Provincial Park, Ontario (1973-1990). Proceedings of the 11th Eastern Black Bear Workshop, New Hampshire, USA.

Based on a decade of study of black bears (*Ursus americanus*) in Algonquin Provincial Park, Ontario, the author concludes that education about safe methods of storing food, bear-proof garbage containers, and relocation programs have contributed significantly to reducing bear/human conflicts in the park. Nevertheless, more research is warranted to find effective methods for problem bear control as relocation of problem bears has met with limited success.

23. Koerth, BH, and JC Kroll. 2000. Baiting type and timing for deer counts using cameras triggered by infrared monitors. Wildlife Society Bulletin 28: 630-635.

This study illustrates another of the applications of baiting in wildlife management, and draws attention to the sex and seasonal biases associated with this method of estimating population size and demography.

24. Krausman, PR. 2000. Wildlife management in the twenty-first century: educated predictions. Wildlife Society Bulletin 28: 490-495.

The author identifies the need for further research into the management of wildlife populations in a manner that is consistent with the principals of ecology, not economics. Current methods of wildlife management are becoming increasingly ineffective as more and more wildlife habitat is destroyed through human activities. A deeper understanding of the interrelationships between humans, habitat, and wildlife is required as a basis for the successful management of wildlife.

25. Lamport, C. 1996. Black bear in Ontario status and management. Federation of Ontario Naturalists, Don Mills, Ontario.

This review of black bear (*Ursus americanus*) hunting in Ontario resulted in response to a growing negative view in the province concerning the spring bear hunt, the baiting of bears, and use of dogs to hunt bear. The author has provided a very thorough report that encompasses recommendations from biologists, law makers, economists, and educators.

26. Leighton, FA. 2002. Foreign animal diseases and Canadian wildlife: Reasons for concern and the elements of preparedness. Canadian Veterinary Journal Volume 43: 265-267.

The author makes the case that the threat of foreign animal diseases to the wildlife of Canada will not only affect wildlife but also the economy of the country. The likelihood of wildlife contracting disease, or infecting humans or livestock, has increased as human activities (e.g., agriculture, eco-tourism, and hunting) encroach more and more on wildlife habitat. The author provides measures that officials should take to prevent the occurrence of epidemics. Some of these measures have direct bearing on the decision to provide supplemental feed to wildlife.

27. Lewis, TL. 1990. The effects of supplemental feeding on white-tailed deer in northwestern Wisconsin. PhD Thesis, University of Wisconsin, Madison, Wisconsin.

The author investigates the effect of supplemental feeding upon the migration, survival, and recruitment of white-tailed deer (*Odocoileus virginianus*) in relation to deer feeding programs was the focus of this paper. He concludes: (1) the effect of supplemental feeding on migration is minimal as deer did not travel more than 2.5 km to feed regularly at feeders; (2) the survival of deer is improved through winter feeding; and (3) summer-feeding increases fawn recruitment more than winter feeding. The author also notes that a greatly overlooked benefit of supplemental feeding is the educational value to the public, increasing their awareness and appreciation of wildlife and their management.

- 28. Lewis, TL, and OJ Rongstad. 1998. Effects of supplemental feeding on white-tailed deer, *Odocoileus virginianus*, migration and survival in northern Wisconsin. The Canadian Field-Naturalist 112: 75-81.**

As an extension of the work presented in Lewis (1990 – see 27.), the authors argue that the increased survival rate resulting from winter feeding is not significant enough to warrant governmental support of supplemental feeding programs. They recommend instead that wildlife managers make adjustments to harvest rates to ensure that deer populations are maintained within the carrying capacity of their habitat.

- 29. Litvaitis, JA, and DM Kane. 1994. Relationship of hunting technique and hunter selectivity to composition of black bear harvest. Wildlife Society Bulletin 22: 604-606.**

The hunting of black bears (*Ursus americanus*) over bait is believed to bias the sex ratio of hunters harvest with more male being killed than females. The authors advocate close monitoring of this trend by wildlife managers and the creation of different hunting opportunities to adjust the harvest composition when required. Although the authors identify problems with current hunting practices, they do not offer any solutions.

- 30. McBryde, GL. 1995. Economics of supplemental feeding and food plots for white-tailed deer. Wildlife Society Bulletin 23: 497-501.**

Using examples, the authors illustrate the great financial expense associated with different supplemental feeding programs. Supplemental feeding is regarded as the most expensive of available methods for increasing the carrying capacity of a habitat.

- 31. McCollough, MA, CS Todd, and RB Owen, Jr. 1994. Supplemental feeding program for wintering bald eagles in Maine. Wildlife Society Bulletin 22: 147-154.**

The authors investigate the effectiveness of a supplemental feeding program to increase survival of bald eagles (*Haliaeetus leucocephalus*). They conclude that supplemental feeding programs may be required under special circumstances only, but should not be used routinely. The authors note that non-target species also routinely visited feeding sites.

- 32. McLaughlin, CR, and HL Smith. 1991. Baiting black bears: hunting techniques and management issues. Proceedings of the 10th Eastern Workshop on Black Bear Research and Management, University of Arkansas, Arkansas. 10: 110-119.**

The authors present the results of a survey indicating which states and provinces permit the hunting of black bears (*Ursus americanus*) over bait. They also provide details about jurisdictional restrictions on how baiting is conducted including types of baiting, the quantity of bait, and how baits are set. Although this report is over 10 years old, it illustrates the great variation among locales in legislation concerning baiting.

- 33. Miller, MW, ES Williams, CW McCarty, TR Spraker, TJ Kreeger, CT Larsen, and ET Thorne. 2000. Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. Journal of Wildlife Diseases 36: 676-690.**

Based on information gathered from surveillance of wild cervid populations in Wyoming and Colorado and mathematical modeling of epidemics, the authors conclude that chronic wasting disease (CWD) has been infecting wild populations for over 30 years. They further discuss the strengths and weaknesses of surveillance approaches to determine disease prevalence. This paper underscores the great difficulty encountered when attempting to determine the history and prevalence of CWD in wild cervids.

- 34. Muth, RM, and WV Jamison. 2000. On the destiny of deer camps and duck blinds: the rise of the animal rights movement and the future of wildlife conservation. Wildlife Society Bulletin 28: 841-851.**

The authors discuss the changing social acceptance of hunting and examine the forces influencing this change in public perception. They state clearly that wildlife managers must address the concerns of the entire public, not just hunters. In this regard, it is important to recognize that the animal rights movement has proven to be a strong force influencing public perception. Further, public perception is also being shaped by large numbers of urban dwellers that live in cities and are quite remote from wildlife and wild places. Because hunting is no longer a family tradition, the onus is on wildlife managers to educate the public and maintain support for their programs. Otherwise, the focus of wildlife management will be reduced to not much more than pest management for urban areas.

- 35. Obbard, ME. 2002. Do suspended baits enable hunters to better discriminate between male and female black bears? Proceedings of the 16th Eastern Workshop on Black Bear Research And Management, South Carolina. 16: 109.**

The ability of hunters to correctly identify the reproductive class of black bears (*Ursus americanus*) when hunting over bait influences the population dynamics of the black bear population. The author proposes that suspended bait should increase the accuracy of hunters and sets out to determine if this is the case. Although the author's assertion holds some promise, the sample number of bears that he investigates is too small to draw any firm conclusions regarding this alternative method of baiting.

- 36. Organ, JF, and EK Fritzell. 2000. Trends in consumptive recreation and the wildlife profession. Wildlife Society Bulletin 28: 780-787.**

Public perception and the role of wildlife management are changing. The focus of wildlife management curricula has shifted from a consumptive perspective to a non-consumptive perspective, in part, as a result of the declining number of hunters in society. Although the authors present statistics based on the United States population, the trends are undoubtedly similar in Canada.

- 37. Ozoga, JJ. 1972. Aggressive behavior of white-tailed deer at winter cuttings. Journal of Wildlife Management 36: 861-867.**

The author investigates the effect of supplemental feeding on the social behaviour and survival rates of white-tailed deer (*Odocoileus virginianus*). He finds that aggressive

behavior around feeding sites does not prevent subordinate animals from obtaining feed. Further, the frequency of aggressive interactions diminishes as social stability develops among the deer. The author recommends supplemental feeding programs use cuttings from trees close to deer yards rather than grain. The use of natural browse in close proximity to deer yards should reduce the energy that is typically expended in traveling to feeding sites that provide grains.

38. Ozoga, JJ, and LJ Verme. 1982. Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. Journal of Wildlife Management 46: 281-300.

The authors investigate the effects of supplemental feeding on competition, growth, reproduction, mortality, and fawn sex ratios of white-tailed deer (*Odocoileus virginianus*). This detailed study also provides information regarding the effects of supplemental feeding on the sociobiology and habitat of deer. The authors place priority on the health of does as the primary objective of a supplemental feeding program.

39. Partridge, ST, DL Nolte, GJ Ziegltrum, and CT Robbins. 2001. Impacts of supplemental feeding on the nutritional ecology of black bears. Journal of Wildlife Management 65: 191-199.

Although this study lacks the depth presented by Fersterer et al. (2001 – see 17.), the authors add support to the effectiveness of intercept feeding to prevent damage to agricultural crops by black bears (*Ursus americanus*). Further, they present data to show that supplemental feeding does not appear to increase physiological condition of bears beyond the condition that would be attained on a diet acquired naturally.

40. Perkins, JR. 1991. Supplemental feeding. Texas Parks and Wildlife Department Fisheries and Wildlife Division. 9 pp. (see http://www.tpwd.state.tx.us/wildlife_pubs/supplemental_feeding.pdf).

The author examines the practice of supplemental feeding in Texas, and makes recommendations for different types of feed to be considered in feeding operations. Most importantly, he concludes that, whenever possible, habitat management is a better choice than supplemental feeding.

41. Peyton, RB. 2000. Wildlife management: cropping to manage or managing to crop? Wildlife Society Bulletin 28: 774-779.

The author presents the case that public support for sport hunting is changing and this will ultimately affect wildlife management. In recent years, animal rights groups have had increasing input into wildlife management issues. Further, there is growing demand by hunters that issues concerning fair chase are addressed by wildlife managers to ensure that non-consumptive wildlife users distinguish between those who hunt by “fair chase” and those who hunt by other means (e.g., bait hunting) when providing input into wildlife management issues.

- 42. Rhyan, J, K Aune, B Hood, R Clarke, J Payeur, J Jarnagin, and L Stackhouse. 1995. Bovine tuberculosis in a free-ranging mule deer (*Odocoileus hemionus*) from Montana. *Journal of Wildlife Diseases* 31: 432-435.**

The authors document the transmission of bovine tuberculosis (TB) from the infected livestock of a game ranch to free-ranging mule deer (*Odocoileus hemionus*). This case study highlights the serious concern of disease transmission between sympatric animal populations, and more specifically illustrates transmission of disease from livestock to wild animals. Many believe that the practices of supplemental feeding and baiting increase the probability of disease transmission in this manner. The authors advocate continuous surveillance and the implementation of disease management plans to eliminate bovine TB from wild and captive populations.

- 43. Rogers, LL, DW Kuehn, AW Erickson, EM Harger, LJ Verme, and JJ Ozoga. 1974. Characteristics and management of black bears that feed in garbage dumps, campgrounds, or residential areas. *Conference Proceedings of the 3rd IBA - Bears--Their Biology and Management Conference, Binghamton/Moscow.***

The authors captured 126 black bears (*Ursus americanus*) that included problem bears known to frequent dumps, campsites and residential areas. All bears were weighed and categorized according to sex and breeding condition to determine if the supplemental food obtained by problem bears affected their growth rate and fecundity. Problem bears were biased toward male bears. Relative to bears that were not receiving supplemental food, problem bears were heavier and had better success with reproduction. The authors conclude that supplemental feeding had an obvious effect on bear growth and reproduction.

- 44. Rosatte, R, D Donovan, M Allan, LA Howes, A Silver, K Bennett, C MacInnes, C Davies, A Wandeler, and B Radford. 2001. Emergency response to raccoon rabies introduction into Ontario. *Journal of Wildlife Diseases* 37: 265-279.**

The authors describe the approach used by the Ontario Ministry of Natural Resources to prevent an epidemic of rabies from occurring in the province. Through a combined approach that included capture, vaccinate, and release, coupled with widespread dispersal of bait laced with vaccine, provincial officials were able to successfully vaccinate a large number of wild animals. This report provides an example of the use of baiting to benefit both wildlife and people.

- 45. Rupprecht, C, JS Smith, M Fekadu, and JE Childs. 1995. The ascension of wildlife rabies: a cause for public health concern or intervention? *Emerging Infectious Diseases* 1: 107 – 114.**

The authors present an historical global perspective of the effects of rabies infection on the human population. They clearly illustrate the enormous financial expense incurred to prevent wild animal populations from infecting humans and domestic animals. The authors also examine the positive and negative effects of using vaccine baits to prevent rabies.

- 46. Schmitt, SM, SD Fitzgerald, TM Cooley, CS Bruning-Fann, L Sullivan, D Berry, T Carlson, RB Minnis, JB Payeur, and J Sikarskie. 1997. Bovine tuberculosis in free-ranging white-tailed deer from Michigan. *Journal of Wildlife Diseases* 33: 749-758.**

The authors document an outbreak of bovine tuberculosis in free-ranging white-tailed deer (*Odocoileus virginianus*) in Michigan that could not be directly linked to infected livestock. Supplemental feeding is identified as a key factor contributing to the spread of disease by concentrating deer by into unnaturally high densities that readily facilitate animal-to-animal transmission. This case history should serve as a clear warning to wildlife managers of the potential disease risks associated with supplemental feeding programs.

- 47. Schmitz, OJ. 1990. Management implications of foraging theory: evaluating deer supplemental feeding. *Journal of Wildlife Management* 54: 522-532.**

The author conducts an experiment in a northern deer yard to compare the foraging behavior of naturally wintering and supplementally fed white-tailed deer (*Odocoileus virginianus*) and to assess when supplemental feeding might be warranted. He examines the effects of browse depletion and accumulating snow on diet selection across three winter sampling periods. In all time periods, both naturally wintering and supplementally fed white-tailed deer maximized their energy intake through browse consumption. The author concludes that the supplemental feeding program employed may have been inefficient, perhaps because feed was delivered in a few large feeders creating a limited resource.

- 48. Schwantzkopf, KS. 1990. Behaviour, social organization and feeding patterns of white-tailed deer (*Odocoileus virginianus* Rafinesque, 1832) in Saskatchewan as related to climate and supplemental feeding. MSc Thesis, University of Regina, Regina, Saskatchewan.**

The author presents a case to support the use of supplemental feeding programs in wildlife management. She acknowledges that although there are inherent problems with many feeding programs, careful consideration and planning can help to avoid problems and increase the overall effectiveness of feeding programs.

- 49. Smith, BL. 1998. Antler size and winter mortality of elk: effects of environment, birth year, and parasites. *Journal of Mammalogy* 79: 1028-1044.**

The author investigates the effects of numerous factors, including supplemental feeding, on the antler size and winter mortality of elk (*Cervus elaphus*). Supplemental feeding does not appear to influence antler size, nor does it affect birth weight and winter survival of elk. The author concludes that increased winter survival cannot be used to justify the implementation of supplemental feeding programs for elk.

- 50. Smith, BL. 2001. Winter feeding of elk in western North America. *Journal of Wildlife Management* 65: 173-190.**

Elk (*Cervus elaphus*) at the National Elk Refuge, Wyoming, have been provided supplemental feed for 90 years providing excellent opportunity to investigate the effects of feeding on elk populations, behaviour, and the surrounding environment. The author

uses long-term information collected from this elk population to clearly illustrate many of the positive and negative effects associated with supplemental feeding.

51. Smith, BL, RL Robbins, and SH Anderson. 1997. Early development of supplementally fed, free-ranging elk. Journal of Wildlife Management 61: 26-38.

The authors investigate the contributions of animal density, weather conditions, and supplemental feeding on the reproduction of the elk (*Cervus elaphus*) in the Grand Teton National Park, USA. Annual rates and duration of supplemental feeding had no measurable effect on birth weight of elk calves. However, winter feeding may have improved the milk yield of cows resulting in calf weight gains that exceeded values previously reported for elk calves raised without winter feeding.

52. Smith, BL, and T Roffe. 1994. Diseases among elk of the Yellowstone Ecosystem, USA. In: van Hoven, W, H Ebedes, and A Conroy (eds). Wildlife ranching: a celebration of diversity - Proceedings of the 3rd International Wildlife Ranching Symposium. Pretoria: Centre for Wildlife Management, University of Pretoria.

Elk (*Cervus elaphus*) at the National Elk Refuge, Wyoming, have been provided supplemental feed for 90 years providing excellent opportunity to investigate the effects of feeding on elk populations, behaviour, and the surrounding environment. In this paper, the authors document the diseases that have been transmitted among elk and attributed to the unnaturally high density of elk in the area. They point out the potentially serious consequences to the livestock industry that could occur if some of these diseases were transmitted from elk to neighbouring populations of livestock.

53. Spraker, TR, MW Miller, ES Williams, DM Getzy, WJ Adrian, GG Schoonveld, RA Spowart, KI O'Rourke, JM Miller, and PA Merz. 1997. Spongiform encephalopathy in free-ranging mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*) in north-central Colorado. Journal of Wildlife Diseases 33: 1-6.

The authors discuss the occurrence of chronic wasting disease (CWD) in wild cervids in Colorado illustrating the paucity of knowledge concerning the origin, transmission, and control of this disease. They suggest that supplemental feeding by the public may enhance horizontal transmission of CWD and emphasize the need for further research on the epidemiology of CWD.

54. Spurrier, C, and L Drees. 2000. Hostile takeovers in America: invasive species in wildlands and waterways. Transactions of the 65th North American Wildlife And Natural Resources Conference 65: 315-325.

The authors provide an historical and broad ecological perspective on the invasion of non-native plant species into North America. They underscore the great financial cost incurred when attempting to combat an existing invasion, and emphasize the need to prevent introduction of non-native species rather than attempting to eliminate them following invasion. They stress that current international trade agreements are founded

on short-sighted economic policies that do not consider the long-term ecological effects of invasive plant species.

55. Steffen, DJ, DW Oates, MC Sterner, and VL Cooper. 1999. Absence of tuberculosis in free-ranging deer in Nebraska. Journal of Wildlife Diseases 35:105-107.

The authors report on their surveillance of white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) in Nebraska for the presence of bovine tuberculosis (TB). No evidence of bovine TB was found. This surveillance was carried out in response to the report of bovine TB in white-tailed deer in four counties of Michigan, possibly as a result of supplemental feeding programs initiated by private citizens.

56. Tarr, ME, and PJ Perkins. 2002. Influences of winter supplemental feeding on the energy balance of white-tailed deer fawns in New Hampshire, USA. Canadian Journal of Zoology 80: 6-15.

The authors demonstrate that provision of highly nutritious feed to white-tailed deer (*Odocoileus virginianus*) during winter raises their metabolic rate to a point where energy demands cannot be met by natural browse alone. In effect, the deer become dependent on supplemental feeding. The authors find that the effectiveness of supplemental feeding programs is influenced by a number of factors including herd density, food availability and winter conditions.

57. Thomas, JW, and DH Pletscher. 2000. The convergence of ecology, conservation biology, and wildlife biology: necessary or redundant? Wildlife Society Bulletin 28: 546-549.

The authors examine the history of wildlife management and emphasize the need for a change in perspective. They recommend an ecosystem management approach that encompasses biological disciplines combined with social, legal and economic knowledge. They make strong points supporting the need for a multidisciplinary approach to wildlife management.

58. Wobeser, G, and W Runge. 1975. Rumen overload and rumenitis in white-tailed deer. Journal of Wildlife Management 39: 596-600.

The authors present the results of a survey of 108 dead white-tailed deer (*Odocoileus virginianus*) where 30 animals were found to have died as a result of carbohydrate engorgement (grain overload). This potential for this disease is greatly increased when people provide supplemental feed or bait that is high in carbohydrates to deer.

59. Woolf, A, and JL Roseberry. 1998. Deer management: our profession's symbol of success or failure? Wildlife Society Bulletin 26:515-521.

The authors discuss some of the social issues of wildlife management. Their view is that governmental policies on wildlife management are influenced too much by public opinion, and too little by science. They argue that wildlife management today should emphasize the conservation of ecosystems in relation to all human activities, not just hunting. These views have obvious implications for the implementation of supplemental feeding programs to support an individual species.

60. Wundram, IJ. 1981. Urban ethology: an anthropological approach to wildlife in the city. Human Organization 40: 168-171.

The author explains that urban ethology is a growing field examining the interrelationship between humans and animals living in the city. She emphasizes that many city dwellers are far removed from understanding wildlife in the context of a natural environment. To rectify this lack of understanding, the author identifies the need to develop programs to educate urban dwellers about the interdependency between humans, wildlife, and the environments they co-habit.

APPENDIX A

Manitoba Government **NEWS RELEASE**



Information Services, Room 29, Legislative Building, Winnipeg, Manitoba R3C 0V8
Telephone: (204) 945-3746
Fax: (204) 945-3988

August 16, 2002

HUNTING REGULATIONS CHANGED TO ADDRESS BOVINE TUBERCULOSIS AND CHRONIC WASTING DISEASE

Manitoba Conservation has amended hunting regulations for cervids (deer, elk, moose and caribou) to support efforts to prevent the spread of bovine tuberculosis and to keep chronic wasting disease (CWD) out of the province.

The actions will help prevent the possible spread of disease by reducing contact between deer, elk and cattle and by addressing situations that might risk bringing CWD into Manitoba. The regulations apply to baiting, feeding, using attractants and bringing whole, killed animals into the province.

The baiting of cervids for hunting is illegal in all areas of the province, as is hunting near crops left in the field for the purpose of luring cervids. A hunter education and enforcement awareness program is being developed concerning the new baiting regulations.

Beginning this fall, a hunter will be charged for placing cervid bait for the purpose of hunting or for hunting within 800 metres of a cervid bait.

If a natural resource officer believes that farm produce is being used to attract cervids for the purpose of hunting, the officer may:

- issue an order to remove or fence the farm produce; or
- post the area to prohibit hunting, the discharge of a firearm or the possession of a loaded firearm within 800 metres of the farm produce.

Under the new regulations, it is illegal to possess a substance that contains the urine, feces, saliva or scent glands of a cervid. These attractants may transmit diseases, including CWD, to wild cervids. Most of the commercially available attractants used by hunters are produced in areas where wild or farmed cervids have tested positive for CWD. This measure is one of several initiatives to prevent the spread of this disease to Manitoba.

It is also now illegal to bring a cervid that has been killed in another province, territory or country into Manitoba without first removing the head, hide, hooves, mammary glands, entrails, internal organs and spinal column.

The antlers and the connecting bone plate that has been detached from the remainder of the skull can be imported only if all hide and other tissue has been removed and the skull plate disinfected. Capes may be brought into Manitoba but must be immediately chemically processed into a tanned product.

Further restrictions specific to game hunting areas (GHA) 23 and 23A around Riding Mountain make it illegal to use cervid feed or attractants for any purpose. Bovine TB and other diseases are more easily spread where cervids gather, such as at feed sites.

These changes support a recently announced doubling of the elk harvest in GHA 23 and 23A as part of the TB Management Strategy, developed over the last two years.

Other steps to help reduce the occurrence of bovine TB in the area include:

- the placement of barrier fencing at hay storage sites;
- research on elk movement and cattle/elk interactions; and
- increased public education.

Hunters can call 945-6784 in Winnipeg or toll free 1-800-214-6497 for more information.

WILEY



Excavation of Red Squirrel Middens by Grizzly Bears in the Whitebark Pine Zone

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Journal of Applied Ecology

Excavation of red squirrel middens by grizzly bears in the whitebark pine zone

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Summary

1. Whitebark pine seeds *Pinus albicaulis* are an important food of grizzly *Ursus arctos horribilis* bears wherever whitebark pine is abundant in the contiguous United States of America; availability of seeds affects the distribution of bears, and the level of conflict between bears and humans. Almost all of the seeds consumed by bears are excavated from middens where red squirrels *Tamiasciurus hudsonicus* have cached whitebark pine cones.
2. Relationships among the occupancy of middens by squirrels, the excavation of middens by bears, and site features were investigated in this study. Data were collected from radio-marked bears and from middens located from line transects on two study sites in the Yellowstone ecosystem.
3. Densities of active middens were positively related to lodgepole pine *Pinus contorta* basal area and negatively related to steepness of slope.
4. The probability that a midden was occupied by a squirrel (i.e. active) was positively related to lodgepole pine basal area in the surrounding stand, size of the midden and size of the whitebark pine cone crop, and negatively related to elevation and to bear excavation during the previous 2–12 months.
5. The probability that a midden had been excavated by a bear during the previous 12 months was positively related to size of the midden, and to whitebark pine basal area and cone crop, and negatively related to nearness of roads and town sites.
6. The influence of midden size on bear use was attributable to a positive relationship with the number of excavated cones. The positive association between bear excavations and whitebark pine basal area or cone crops was attributable to availability of pine seeds.
7. Grizzly bears would benefit from the minimization of roads and other human facilities in the whitebark pine zone and from increases in the availability of whitebark pine seeds, potentially achieved by increasing the numbers of cone-producing whitebark pine trees, especially in lower elevations of the whitebark pine zone where red squirrels are more abundant.

Key-words: avoidance of humans, diet selection, foraging strategies, habitat relationships, Yellowstone National Park.

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Introduction

Whitebark pine *Pinus albicaulis* Engelm. seeds are an important food of grizzly bears *Ursus arctos horribilis* Ord. in parts of the contiguous United States that experience a continental climate (Mattson & Reinhart 1994). When whitebark pine seeds are abundant, grizzly bears eat virtually nothing else (Craighead, Sumner & Scaggs 1982; Mattson, Blanchard & Knight 1991). Approximately one-half of the kernel of white-

bark pine seeds consists of fats (Lanner & Gilbert 1994) that are potentially important to the reproduction of female grizzly bears (Mattson & Reinhart 1994; Mattson 1997a).

Availability of whitebark pine seeds has a major indirect effect on grizzly bear survival in the Yellowstone ecosystem. When pine seeds are available, most grizzly bears forage in high-elevation whitebark pine stands that are typically remote from human facilities (Mattson, Blanchard & Knight 1992). When pine

seeds are scarce, grizzly bears are active closer to roads and town sites, and roughly two to three times as many bears are killed by humans compared to years when pine seeds are abundant (Mattson *et al.* 1992). Because humans kill between 80 and 90% of all adult and subadult grizzly bears that die in the contiguous United States (Mattson *et al.* 1996), use of whitebark pine seeds by grizzly bears has become a prominent management consideration, especially in the Yellowstone ecosystem.

Yellowstone grizzly bears obtain virtually all (> 90%) of the pine seeds they eat by excavating cone caches made by red squirrels *Tamiasciurus hudsonicus* (Mattson & Reinhart 1994). Whitebark pine cones require two years to mature and remain on the tree with seeds retained within unless harvested by seed or cone predators such as squirrels (McCaughey & Schmidt 1990). Red squirrels harvest the cones of whitebark pine after they mature, typically in early August, and cache them in larder hoards (Kendall 1983; Hutchins 1994). These hoards are identified by a prominent accumulation of cone debris from previous caches and typically mark the centre of a territory that is vigorously defended by a single resident squirrel (Smith 1968; Kemp & Keith 1970). The accumulated debris is called a 'midden' and constitutes the defining feature of squirrel territories which may persist through the tenures of several individuals (Rusch & Reeder 1978; Price *et al.* 1986). Red squirrels and their middens have thus become a focus of management attention in grizzly bear habitat.

Managers are also concerned with the under-use of available bear foods where grizzly bears seem to avoid humans and human facilities. Previous research in the contiguous United States has shown that grizzly bears routinely avoid areas within 500 m of roads, and within up to 5 km of town sites and major recreational developments (Mattson *et al.* 1996). Questions remain, however, whether this research based on day-time telemetry locations of radio-marked animals adequately documents night-time use. There is also concern that habitat selection primarily related to the distribution of native foods may be mistaken for 'avoidance' of humans, especially if poor quality habitat is spatially correlated with human facilities (Mattson *et al.* 1996).

This study was designed to provide managers with critical information on grizzly bear use of pine seeds and the potential under-use of habitat near humans by bears. To facilitate habitat assessments, information on the density of squirrel middens excavated by grizzly bears was stratified by commonly used classifications of site potential and forest stand structure. Data were collected to allow midden use by bears and midden occupancy by squirrels to be modelled. The models were designed to help managers anticipate the consequences of management actions and the reaction of grizzly bears to other phenomena, such as natural forest succession and global climate change.

Finally, this study provided an opportunity to test whether grizzly bears in the Yellowstone ecosystem were avoiding roads and town sites.

Whitebark pine seeds are the most abundant of only two high-quality foods commonly available to grizzly bears in forests at high elevations (> 2360 m). The other food source is meat obtained from ungulate carrion & kills (Mattson & Knight 1989; Mattson 1997a). Whitebark pine seeds are consumed by bears almost exclusively from middens. Middens therefore correlate well with the availability of high quality bear foods in whitebark pine forests. Because bear excavations are durable and visually prominent, they can be detected at any time, irrespective of the time of day that either bears or researchers are active.

Study area

The study area consisted of two sites located one each in the states of Wyoming and Montana, United States of America, in or near Yellowstone National Park. One site, 9.5 km² in size, was located on the Mt Washburn mountain massif in north-central Yellowstone Park (44°47'N 110°24'W). A second site, 12 km² in size, was located immediately north-east of the Park, within 2 km of the town of Cooke City (45°00'N 109°58'W). The Mt Washburn site was transected by a paved highway. During the study, Cooke City had a population of 100 year-round residents, although this number increased during the summer due to visitors and seasonal residents. The town was reached by a paved highway that defined the lower elevational boundary of the nearby study site. Neither site had been harvested for timber by humans.

Both sites encompassed the range of elevations where mature whitebark pine is common, between 2360 m and the upper extent of forest growth at 2870 m. Forest cover was broken by a few meadows and rock-strewn slopes and consisted primarily of lodgepole pine *Pinus contorta* Dougl., subalpine fir *Abies bifolia* A. Murray, Engelmann spruce *Picea engelmannii* Parry, and whitebark pine. Douglas-fir *Pseudotsuga menziesii* (Merbel) Franco was common in places on the Mt Washburn site. Whitebark pine and Douglas-fir usually occurred intermixed with other tree species, but they could dominate wind-exposed sites at high and low elevations, respectively (Mattson & Reinhart 1990). Undergrowth was short-statured (< 50 cm) and typically dominated by forbs such as western meadow-rue *Thalictrum occidentale* Gray, and ericaceous shrubs such as globe huckleberry *Vaccinium globulare* Rydb. and grouse-whortleberry *V. scoparium* Leiberger.

Both sites were steep and predominantly west- to north-facing. As a consequence, much of the study area was exposed to the prevailing west- to south-west winds (Dirks & Martner 1982). This accentuated the harsh climate of the whitebark pine zone, typified by average annual temperatures near 0°C, annual pre-

precipitation of 600–800 mm and only 4 months without continuous snow cover (Weaver 1990). These conditions coincided with the extreme upper-elevational limits of red squirrel distribution (Streubel 1989).

Some data used in this analysis were collected in conjunction with a radio-telemetry study that included all of the known range of Yellowstone's grizzly bears. This range was *c.* 23000 km² in size, and consisted of high-elevation (>1650 m) mountains and plateaus surrounded by valleys and plains more intensively settled or used by humans. Features of this larger study area are described by Knight & Eberhardt (1985), Blanchard & Knight (1991) and Mattson *et al.* (1991).

Materials and Methods

FIELD METHODS

Data were collected from 1984 to 1987 along transects that were systematically placed throughout the elevational range of whitebark pine (Mattson & Reinhart 1996). Transects were 500–1000 m long, depending on topography and the occurrence of non-forest vegetation. Sampling occurred between 10 August and 28 September, during peak harvest and use of whitebark pine seeds by squirrels and bears (Kendall 1983; Mattson & Reinhart 1994), and before winter snow accumulation each year. Transects and sites were sampled in the same order each year. During 1984, 35 transects totalling 18.9 km and 15 transects totalling 16.4 km were sampled on the Mt Washburn and Cooke City sites, respectively. During the remaining years, 57 and 21 transects, totalling 29.8 and 21.1 km, were sampled at each respective site. More transects were established in 1985 to increase sample sizes in certain stand types (see below) especially in lower elevations of the whitebark pine zone.

These transects intersected 50 and 84 forest stands on Mt Washburn, and 57 and 69 stands on the Cooke City site (for 1984 and remaining years, respectively). Stands were delineated by interpretation of 1:20 000 aerial photographs and field checked for accuracy. Stands were classified according to habitat type (Steele *et al.* 1983) and cover type (Despain 1990). Habitat type reflected the biophysical site, and cover type described the current forest structure, including dominant species and successional status.

The stratification by habitat and cover type, and the related importance of sampling by stands, affected the layout of transects. Initial placement was systematic, parallel at about 150-m intervals. However, layout was subsequently adjusted to minimize the edge effects between different types of habitat and cover on parameter estimates by type (cf. Eberhardt 1978). This was done by maximizing the number of right-angle intersections with stand boundaries and the proportion of transects contained within stand interiors (Mattson & Reinhart 1996).

Two individuals sampled the transects; one observer (the co-author) sampled all years. All observed middens were noted, along with the perpendicular distance of each from the transect line. All but one of these middens were <50 m from a transect; the exception was 64 m away. Middens were distinguished according to whether they were currently used by a squirrel [based on the criteria of Finley (1969; fresh cones and clippings) and on sightings and vocalizations], and by whether they had been excavated by a bear within the previous 2 or 12 months. Excavations which were less than 2 months old were associated with use of the current year's crop of cones, while excavations 2–12 months old were associated with use of cones from the previous year's crop. Dimensions of the midden (length and width in decimetres) were also measured. The percentage of the midden surface disturbed by bear digging was assessed by eye.

Forest canopies were sampled by variable-radius plots placed at regular intervals along transect lines. Common US Forest Service techniques (cf. Finch 1957) were used to simplify subsequent management recommendations. The age of the oldest tree in a stand, based on counts of annual rings from an extracted core, was used to indicate the time since the last stand-replacement fire, excluding trees that had obviously survived this fire. Mature cones were also counted each year on 10 permanently marked whitebark pine trees at each of the Mt Washburn and Cooke City study sites. Blanchard (1990) describes the methods that were used for marking trees and counting cones.

Grizzly bears were radio-collared and tracked throughout the Yellowstone ecosystem from 1986 to 1992. These bears were located by aerial-telemetry and locations were subsequently visited by ground crews as part of a larger-scale study to document feeding behaviour and diet (Mattson 1997a,b). Wherever a radio-tagged bear had excavated a squirrel midden, the number of visible cones used by the bear was counted. These cones were identifiable by the ragged fracturing of bracts and by their close association with bear excavations. In small middens, all cones were counted. In larger middens, counts were based on subsamples from regularly placed (5-m spacing) 25-m² plots. Midden dimensions were also measured in the same way as for middens observed on transects. Knight & Eberhardt (1985), Blanchard & Knight (1991) and Mattson (1997b) provide further details on methods for radio-tagging bears and sampling telemetry locations.

ANALYSIS

Thirty-five habitat type/cover type combinations were present in the study area. These were consolidated into six classes (Table 1) based on similar forest structures. Consolidation was based on cluster analysis of data

Table 1. Description of forest types used to stratify the analysis of red squirrel habitat relationships and excavation of red squirrel middens by bears on the Mt Washburn and Cooke City sites, Yellowstone area, 1984–87

Type	Description*	Syntaxonomic composition†
WBP	High-elevation wind-exposed sites dominated by whitebark pine, immediately below upper timberline, but extending down exposed ridges.	Habitat types (hts) of the whitebark pine climax series.
WBP/LPP	High-elevation sites on northerly exposures with ground-layer vegetation dominated by ericaceous shrubs; whitebark pine abundant in diverse canopies.	Whitebark pine cover types (cts) of the subalpine fir/grouse-whortleberry ht, whitebark pine phase, and subalpine fir/globe-huckleberry ht.
LPP/WBP	Mid- to high-elevation sites on northerly or easterly exposures with diverse ground-layer vegetation; lodgepole and whitebark pines common or abundant in diverse canopies.	Lodgepole pine cts of the subalpine fir/grouse-whortleberry ht, whitebark pine phase and subalpine fir/globe huckleberry ht; subalpine fir/bluejoint reedgrass <i>Calamagrostis canadensis</i> and subalpine fir/twisted stalk <i>Streptopus amplexifolius</i> hts.
ABLA/VAGL	Mid-elevation sites on northerly or westerly exposures with ground-layer vegetation dominated by globe-huckleberry; lodge-pole pine abundant.	Lodgepole pine cts of the subalpine fir/globe-huckleberry ht.
LPP	Mid- to low-elevation sites on moderate to gentle slopes dominated by lodge-pole pine.	Subalpine fir/grouse-whortleberry ht, grouse-whortleberry phase, and lodgepole pine cts of the subalpine fir/western meadowrue ht.
ABLA/SPBE	Low- to mid-elevation wind-exposed sites with diverse ground-layer vegetation and Douglas-fir typically present.	Subalpine fir/birch-leaf spirea <i>Spirea betulifolia</i> ht.

* Descriptions are based on Mattson & Reinhart (1990).

† Habitat types are described by Steele *et al.* (1983) and cover types by Despain (1990).

from each site [average linkage (SAS Institute, Inc. 1989)] using total forest basal area, whitebark pine basal area, and canopy species diversity [by the Margalef diversity index (D_{Mg}); Magurran 1988; Table 2]. Basal area was calculated as the cross-sectional area of

all stems > 1.4 m tall. Information on lodgepole pine basal area and stand age (Table 2) is relevant to explaining the results of the following statistical analyses.

Densities of middens were estimated using the computer program TRANSECT (Burnham, Anderson &

Table 2. Characteristics of canopies on forest types used to stratify the analysis of red squirrel habitat relationships and excavation of red squirrel middens by bears on the Mt Washburn and Cooke City sites, Yellowstone area, 1984–87. Sample size is for the number of plots. Canopies changed after the wild-fires of 1988. Means followed by the same letter in columns are not different among habitat types within sites at $\alpha = 0.1$

		Total Basal area (m ² ha ⁻¹)		Whitebark pine Basal area (m ² ha ⁻¹)		Lodgepole pine Basal area (m ² ha ⁻¹)		Margalef's Diversity Index (<i>D</i> _{Mg})		Age of oldest tree (years)	
Forest type*	<i>n</i>	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mt Washburn											
WBP	34	23.7b†	14.2	16.0a‡	11.3	3.9c‡	8.6	0.385b‡	0.427	151b†	38
WBP/LPP	230	41.9a	19.0	23.4a	18.0	5.1c	9.7	0.550a	0.388	192a	36
LPP/WBP	314	43.2a	17.9	8.1b	11.8	16.8b	16.0	0.518a	0.333	182a	37
LPP	206	40.4a	17.4	2.2c	7.1	28.2a	17.5	0.313b	0.323	179a	35
ABLA/SPBE	96	28.7b	15.3	6.2bc	8.7	15.8b	12.8	0.416b	0.413	202a	76
Cooke City											
WBP/LPP	154	37.0ab	17.9	17.6a	15.9	6.8b	11.3	0.538a	0.358	158a	30
LPP/WBP	52	40.7a	21.3	7.1a	9.0	11.6b	16.1	0.528a	0.346	150a	40
ABLA/VAGL	267	34.9ab	16.5	3.4b	7.7	16.9a	15.4	0.458a	0.355	165a	34
LPP	72	32.4b	14.7	1.0b	5.0	16.6a	15.4	0.254b	0.326	148a	47

* Forest types are described in Table 1.

† Results of parametric tests that used natural log transformations of the data. Untransformed values are displayed.

‡ Results of non-parametric ANOVA (Kruskal–Wallis) and multiple comparisons (Zar 1984).

Laake 1980). Estimates were made for each of the six forest type classes on each site for each of the four study years. Stands rather than transects were used as replicates because the study was stratified by habitat types. Serial correlation did not pose a problem because adjacent stands were mapped as different types. In most cases, the Fourier series was used to estimate probability detection functions (Mattson & Reinhart 1996).

Analysis-of-variance (ANOVA) was used to test for differences in mean densities of middens and to test for differences in the means of forest canopy variables, among habitat types, sites and years. A type I error rate (α) of 0.1 was chosen for not rejecting differences, recognizing that P will always be an approximation of reality, and that α is chosen based on individual considerations and scientific norms (Gilbert 1989). Non-parametric ANOVA (the Kruskal–Wallis test) and a non-parametric equivalent of the Tukey multiple-comparisons test (Zar 1984) were used where data were *a priori* non-normal. An analogue of the Tukey test was also used for multiple-comparisons among proportions (Zar 1984). In all other cases, parametric ANOVA was used, followed by the Ryan Q or Tukey–Kramer multiple-comparisons test, depending upon whether cell sample sizes were equal or not (Day & Quinn 1989). Analyses for values averaged by habitat type were weighted by the length of transects (km) or number of plots to correct for the potential effects of unequal variances induced by unequal sampling of different habitat types.

Multiple linear regression was used to analyse the relationship of midden density to site and stand features. Observations were based on averages over all years by type for each site, excluding 1984 when fewer transects were sampled compared to 1985–87. Site effects were tested by analysis-of-covariance. Weighted regression (by km of transects) was used to account for unequal sampling effort among habitat types (Weisberg 1985). Linear regression was also used to analyse the relationship between the number of cones excavated per midden at aerial-telemetry locations of radio-tagged bears and midden size (length \times width).

Models were developed that related the probability of squirrel activity or bear excavations in each midden to site features, size of the whitebark pine cone crop, and midden dimensions. These probabilities were modelled as logits $\{\ln [p/(1-p)]\}$, able to be back-transformed by: $\hat{p} = e^{\beta}/(1 + e^{\beta})$ (Demaris 1992). Model fit was judged by the likelihood ratio statistic (Demaris 1992) and parameter significance was judged by the Wald χ^2 test (Wald 1943). Maximum likelihood estimates were used for all parameters. Logistic regression and contingency-table analyses, as appropriate, were used to describe single-factor relationships prior to building models with multiple independent variables. Independence was judged by the G^2 -test. Where independence was rejected, classes that

exhibited significant differences between dependent states were identified using simultaneous Bonferroni confidence intervals that varied with the sample sizes of each dependent class (Miller 1981).

Log-linear models with multiple independent variables allowed for a more reliable description of partial relationships because the effects of other factors could be controlled. Site and year effects attributable to differences in size of the whitebark pine seed crop and frequency of bear excavations were simultaneously considered. However, there were potential problems with this approach because observations were not wholly independent. Non-independence could have arisen from bears foraging in adjacent squirrel middens, from the occupancy of one midden by a squirrel affecting the occupancy of other middens around it and by repeat sampling of some middens during different years. Control of this potential effect was difficult because middens were not marked. As a result, the probability of type I error was underestimated (Garson & Moser 1995). A more conservative α (0.01) was adopted for these models.

Results

DISTRIBUTION OF ACTIVE MIDDENS

Densities of active middens were highest in forest types dominated by lodgepole pine (the LPP type) and lowest in forest types dominated by a mix of whitebark and lodgepole pines (the WBP/LPP type) on both the Mt Washburn and Cooke City sites (Tables 2 and 3). Densities were also low in forest types characterized by high coverages of Douglas-fir and birch-leaf spirea (the ABLA/SPBE type) and in the LPP/WBP type on the Cooke City site. Individual middens were consistently smallest (length \times width) in the ABLA/SPBE type and in forest types dominated by whitebark pine (the WBP type) (Table 3). Middens were largest on both sites in the WBP/LPP and LPP/WBP types.

The density of active middens, by forest type ($n = 9$), was positively related to lodgepole pine basal area ($LPPBA$) and negatively related to steepness of slope ($SLOPE$):

$$\hat{y} = 1.32 + 0.116\sqrt{LPPBA} - 0.350 \ln(SLOPE)$$

($F_{2,6} = 33.5$, $R^2 = 0.918$, $P = 0.001$). There was no effect ($P = 0.796$) attributable to the study area site (Mt Washburn vs. Cooke City). $LPPBA$ and $SLOPE$ potentially conveyed information about other stand and site features, calculated as Pearson's correlations using square root transformations of basal areas and natural log transformation of $SLOPE$. $LPPBA$ was negatively correlated with whitebark pine basal area ($r = -0.836$, $P = 0.005$) and elevation ($r = -0.658$, $P = 0.058$). $SLOPE$ was positively correlated with Douglas-fir basal area ($r = 0.685$, $P = 0.042$), and negatively correlated with subalpine fir ($r = -0.869$,

Table 3. Sizes and densities of active middens and densities of middens excavated by grizzly bears, for forest types of the Mt Washburn and Cooke City sites, Yellowstone area, 1984–87. Coefficients of variation (CV) are expressed as SD mean⁻¹ and are for among-years' variation ($n = 4$). Means followed by the same letters in columns are not different among habitat types within sites, controlling for year effects where evident, at $\alpha = 0.1$

		Active midden density ($n \text{ ha}^{-1}$)		Active midden size (m^2)		Excavated midden density ($n \text{ ha}^{-1}$)	
Forest type*	n	Mean	CV	Mean	CV	Mean	CV
Mt Washburn							
WBP	8	0.50bc†	0.37	10.0c‡	0.001	0.057b†	1.12
WBP/LPP	34	0.23c	0.25	84.4a	0.02	0.138a	0.38
LPP/WBP	126	0.72ab	0.16	82.3a	0.06	0.291a	0.30
LPP	103	1.09a	0.19	56.7b	0.05	0.207a	0.42
ABLA/SPBE	4	0.37c	0.30	12.1c	0.08	0.000b	–
Cooke City							
WBP/LPP	50	0.44bc	0.22	81.3a	0.03	0.160a	0.76
LPP/WBP	12	0.44c	0.42	120.1a	0.03	0.048ab	2.10
ABLA/VAGL	83	0.66ab	0.24	42.5b	0.02	0.029b	1.16
LPP	24	0.86a	0.01	52.8b	0.02	0.000b	–

* Descriptions of forest types are given in Tables 1 and 2.

† Tests used square root transformations of the data. Untransformed values are displayed.

‡ Tests used natural log transformations of the data. Untransformed values are displayed.

$P = 0.002$) and Engelmann spruce ($r = -0.703$, $P = 0.035$) basal areas.

PROBABILITY OF SQUIRREL ACTIVITY

The probability that a midden was being used by squirrels to feed or cache cones was related to elevation, midden size, basal area of lodgepole pine in the surrounding stand, and whether the midden had been excavated within the last 2–12 months by bears (Table 4). The probability of activity was positively related

to lodgepole pine basal area and negatively related to elevation (Fig. 1). Of the more immediate features, the probability of activity was positively related to midden size and negatively related to excavation by bears (Fig. 2). The nature of these relationships was the same on the Mt Washburn and Cooke City sites. However, all of the relationships, except for midden size, were stronger on Mt Washburn (Table 4).

These relationships were evident in a log-linear model with multiple independent variables (Table 5). In addition, the probability of squirrel activity was

Table 4. Statistics for tests of goodness-of-fit and for whether parameters (β_1) = 0 (Wald χ^2 tests), for single-variable logistic regression models. The probability of a squirrel being active in a midden or that a midden was excavated by bears was related to site, stand or midden features. Models were developed for each of the Cooke City and Mt Washburn study sites from observations along transects, 1984–87

	Goodness-of-fit			β_1 (d.f. = 1)	
	d.f.	G^2	P	χ^2	P
<i>Probability of squirrel activity</i>					
Lodgepole pine basal area ($\text{m}^2 \text{ ha}^{-1}$)					
Cooke City	40	36.3	0.638	1.9	0.172
Mt Washburn	61	68.0	0.250	43.0	<0.001
Elevation (m)					
Cooke City	51	53.4	0.380	3.7	0.056
Mt Washburn	52	59.2	0.231	47.8	<0.001
Midden length \times width (size) (m^2)					
Cooke City	92	101.8	0.228	28.4	<0.001
Mt Washburn	117	156.7	0.008	10.9	0.001
<i>Probability of bear excavation</i>					
Whitebark pine basal area ($\text{m}^2 \text{ ha}^{-1}$)					
Cooke City	31	53.9	0.007	21.4	<0.001
Mt Washburn	42	100.1	<0.001	12.8	0.001
Midden length \times width (size) (m^2)					
Cooke City	78	71.2	0.693	18.3	<0.001
Mt Washburn	99	110.5	0.202	40.3	<0.001

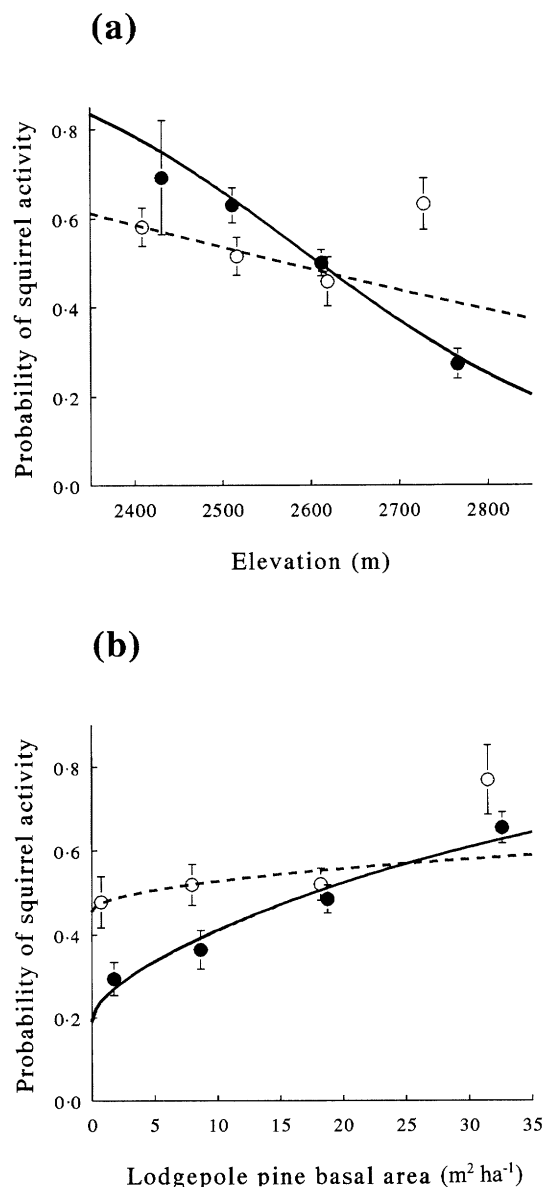


Fig. 1. Relationships between the probability of a red squirrel using a midden for caching or feeding and (a) elevation and (b) basal area of lodgepole pine in the surrounding forest stand, for two study sites in the Yellowstone ecosystem between 1984 and 1987. The curved lines depict relationships estimated by logistic regression. Point probability estimates (± 1 SE) are also shown for four percentiles, to illustrate the fit of regression lines to observed midden activity. The dashed line and open points depict the relationship for the Cooke City site and the solid line and points depict the relationship for Mt Washburn.

positively related to the size of the current-year's cone crop. At $\alpha > 0.01$, squirrel activity was also positively related to the previous year's whitebark pine cone crop and negatively related to being located on the Cooke City vs. Mt Washburn site (Table 4). Model fit was acceptable (d.f. = 666, $G^2 = 662.6$, $P = 0.530$).

DISTRIBUTION OF BEAR EXCAVATIONS

Bears consumed whitebark pine seeds exclusively from cones excavated in middens. In no instance were they

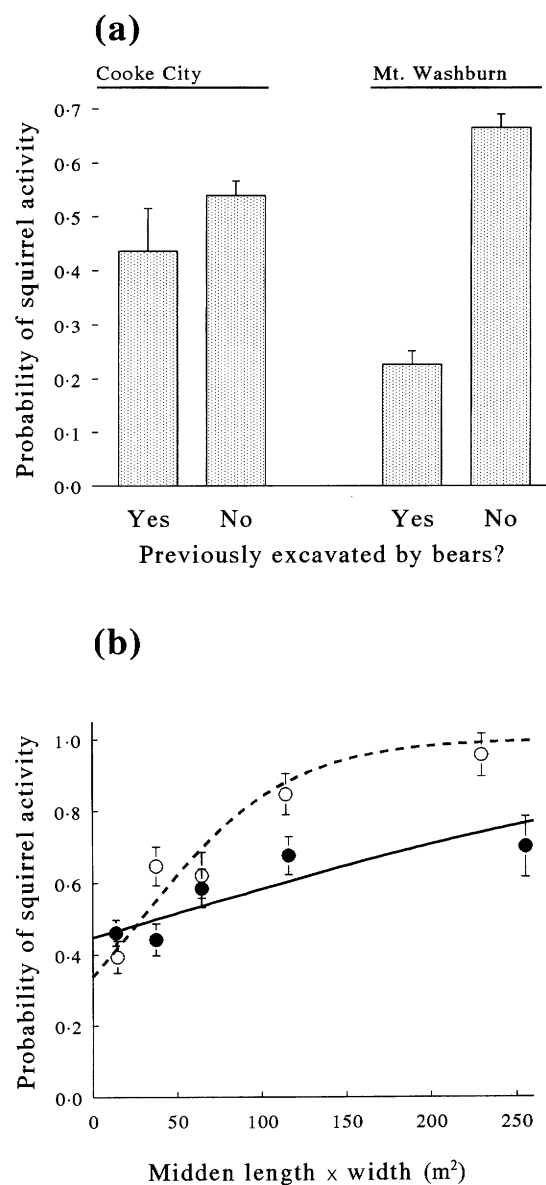


Fig. 2. Relationships between the probability of a red squirrel using a midden for caching or feeding and (a) excavation by bears within the previous 2–12 months and (b) midden size, for two study sites in the Yellowstone ecosystem between 1984 and 1987. The curved lines depict relationships estimated by logistic regression. Point probability estimates (± 1 SE) are also shown for five percentiles, to illustrate the fit of regression lines to observed midden activity. The dashed line and open points depict the relationship for the Cooke City site, and the solid line and points depict the relationship for Mt Washburn.

observed to consume seeds from fallen cones or cones obtained directly from tree canopies. Excavations therefore represented total consumption of pine seeds by bears in the transect study area. The density of middens excavated by bears was highest in forest types dominated by a mix of whitebark and lodgepole pines (the WBP/LPP and LPP/WBP types) on both study sites (Table 3). Densities were lowest in stands dominated by whitebark pine (the WBP type) or where Douglas-fir was abundant (the ABLA/SPBE) on the Mt Washburn site, and in stands dominated by lodge-

Table 5. Estimates of β parameters and the results of tests (P -values from Wald χ^2 tests with d.f. = 1) for whether parameters = 0 for two multi-variable log-linear models. These models describe relationships between the probability of a squirrel being active in a midden or the probability that a midden was excavated by bears and site features, stand features, size of the whitebark pine cone crop and midden characteristics. Data were collected from middens observed along transects on the Mt Washburn and Cooke City study sites from 1984–87

Parameter	Probability of squirrel activity (coefficients)			Probability of bear excavation (coefficients)		
	Estimate	SE	P	Estimate	SE	P
Intercept	98.8	24.5	<0.001	−7.98	0.73	<0.001
Midden length \times width (size) (m^2)	0.016	0.0023	<0.001	1.12*	0.14	<0.001
Current-year's whitebark pine cone crop ($n \text{ tree}^{-1}$)	0.191	0.030	<0.001	0.072	0.020	<0.001
Previous-year's whitebark pine cone crop ($n \text{ tree}^{-1}$)	0.034	0.014	0.014	0.053	0.017	0.002
Lodgepole pine basal area ($\text{m}^2 \text{ ha}^{-1}$)	0.211†	0.074	0.005	—		
Elevation (m)	−12.9*	3.11	<0.001	—		
Bear excavation within the previous 2–12 months						
Yes	−0.846	0.125	<0.001			
No	0.846‡					
Site effect						
Cooke City	−0.320	0.130	0.014	—		
Mt Washburn	0.320‡					
Whitebark pine basal area ($\text{m}^2 \text{ ha}^{-1}$)	—			0.374†	0.080	<0.001
Squirrel active in the midden						
Yes	—			0.664	0.142	<0.001
No	—			−0.664‡		
Within 500 m of a road						
Yes	—			−0.877	0.288	0.002
No	—			0.877‡		
Within 5 km of a town site						
Yes	—			−1.67	0.310	<0.001
No	—			1.67‡		

* Coefficient estimated for natural-log transformed values.

† Coefficient estimated for square-root transformed values.

‡ Coefficient calculated by difference.

pole pine (the LPP type) on the Cooke City site. The lowest densities of bear excavations coincided with the smallest mean sizes of middens on both sites.

Based on observations of radio-tagged grizzly bears, the number of cones excavated per midden was highest in the WBP and LPP/WBP types, and lowest in the ABLA/SPBE and LPP types (Table 6). Thus,

Table 6. Number of cones, by forest type, that were excavated by grizzly bears from red squirrel middens. The sample was obtained while visiting telemetry locations of radio-tagged bears in the Yellowstone area from 1986 to 1992. Means followed by the same letter are not different, controlling for year effects where evident, at $\alpha = 0.1$. Natural log transformations of the data were used, although untransformed values are displayed

Forest type*	Cones excavation ^{−1}		
	Mean	SD	n
WBP	137a	132	27
WBP/LPP	74ab	65	46
LPP/WBP	83a	74	28
LPP	57b	17	37
ABLA/SPBE	56b	74	3

* Forest types are described in Tables 1 and 2.

even though bear excavations could be relatively common in lodgepole pine-dominated stands (as on Mt Washburn), food rewards tended to be small. Conversely, even though middens were small and excavations relatively infrequent in whitebark pine-dominated stands, food rewards tended to be large. Overall, however, the LPP/WBP and WBP/LPP types were distinguished by the highest unit-area densities of cones excavated by bears.

PROBABILITY OF BEAR EXCAVATION

The probability that a bear had excavated a midden within the previous 12 months was positively related to the size of the midden and the basal area of whitebark pine in the surrounding stand (Fig. 3), and negatively related to its location within 500 m of road or 5 km of Cooke City (Fig. 4). Single-variable relationships based on logistic regression analyses were strong on both sites, although the fit of these single-variable models was sometimes not adequate (Table 4). The probability of bear excavation increased with midden size and whitebark pine basal area on both the Mt Washburn and Cooke City sites.

Pooling observations from both study sites and

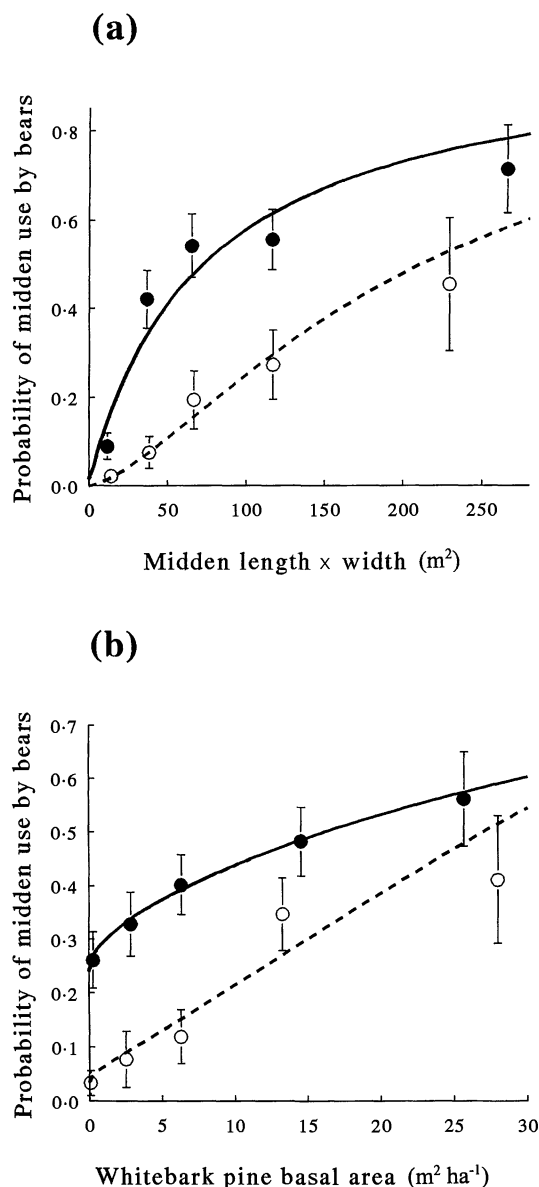


Fig. 3. Relationships between the probability of a red squirrel midden being excavated by bears during the previous 12 months, and (a) midden size and (b) basal area of whitebark pine in the surrounding forest stand, for two study sites in the Yellowstone ecosystem, 1984–87. The curved lines depict relationships estimated by logistic regression. Point probability estimates (± 1 SE) are also shown for five percentiles, to illustrate the fit of regression lines to observed bear excavations. The dashed line and open points depict the relationship for the Cooke City site, and the solid line and points depict the relationship for Mt Washburn.

jointly considering hypothesized zones of influence (ZOIs) associated with roads and town sites, no midden excavations were observed within overlapping road and town site ZOIs, and excavation was 1.3 and 2.6 times as likely away from road and town site ZOIs, respectively. Coefficients associated with town site, but not road, effects were significant (d.f. = 1, $\chi^2 = 19.6$, $P < 0.001$, and $\chi^2 = 5.5$, $P = 0.019$, respectively). At $\alpha > 0.01$, road effects were also significant. Model fit was not acceptable (d.f. = 1, $G^2 = 5.3$, $P = 0.021$).

These relationships were strong in a log-linear model that included multiple independent variables and provided a very good fit to the observed patterns (d.f. = 657, $G^2 = 507.0$, $P = 1.000$) (Table 5). The probability of excavation by bears within the previous 12 months was also positively related to the size of the whitebark pine cone crop during the previous and current year, and to the probability that a midden was being used by a squirrel at the time of observation. No effects attributable to study site were evident ($P > 0.25$). Holding all other effects constant at mean values for the study area, this model predicted that nearness to roads and town sites reduced the probability of bear use by 66 and 92%, respectively. Overlapping ZOIs from roads and town sites reduced bear use by 98%.

CORRELATES OF MIDDEN AND CONE CROP SIZE

The number of cones excavated from a midden by radio-tagged grizzly bears was positively related to midden size ($r^2 = 0.151$, $F_{1,126} = 68.0$, $P < 0.001$) (Fig. 5). The relationship was calculated for natural log transformed values of midden area and number of cones, excluding seven potentially anomalous very large (> 600 m²) middens.

The percentage of midden area disturbed by bear digging was recorded during 1986 and 1987, following large and small whitebark pine cone crops during the previous year, respectively (Table 7). Most bear excavations recorded during these years were attributable to bears foraging on the previous year's crop during the preceding 12 months. The relative frequency of different digging intensities differed between the two years (d.f. = 4, $G^2 = 15.1$, $P = 0.005$) (Fig. 6). Excavations were more extensive during 1986 compared to 1987, and differed in that relatively more excavations disturbed 61–80% of the midden and relatively few disturbed 21–40% of the midden during 1986. Excavations were also relatively more common during the year that preceded sampling in 1986 compared to all other years, including 1987 (Table 7). Midden densities were lower, especially on the Mt Washburn site, during 1986 compared to 1985.

Discussion

RED SQUIRREL ACTIVITY AND ABUNDANCE

The number of resident territorial red squirrels is closely associated with the number of active middens in an area (Kilham 1954; Smith 1968; Wolff & Zasada 1975; Vahle & Patton 1983). Active middens are thereby good indicators of red squirrel abundance (Mattson & Reinhart 1996) and inferences about populations of territorial red squirrels based on observations of middens are justified.

The establishment and use of middens by red squir-

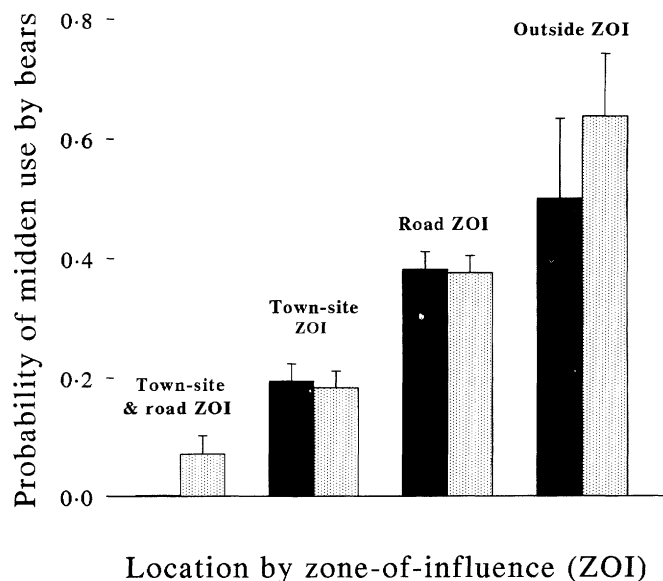


Fig. 4. The relationship between the probability (± 1 SE) of a red squirrel midden being excavated by bears during the previous 12 months and its location within zones-of-influence (ZOIs) for roads and town sites that had been identified by previous research with grizzly bears. Data were pooled from the Mt Washburn and Cooke City study sites in the Yellowstone ecosystem from 1984–87. The road ZOI included areas within 500 m and the town site ZOI included areas within 5 km. The black bars depict observed proportional use by bears and the stippled bars depict use predicted by a maximum-likelihood log-linear model.

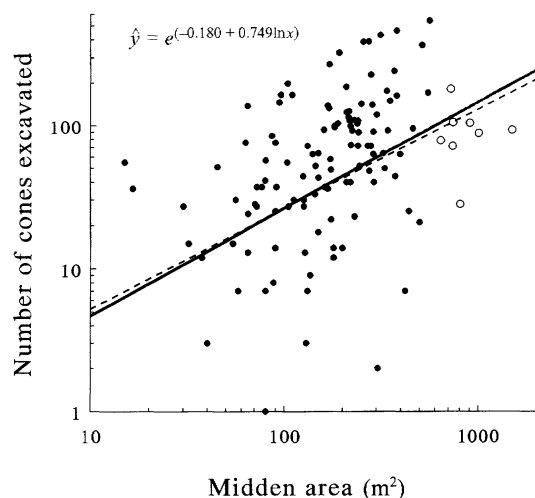


Fig. 5. The relationship between the number of cones excavated by radio-marked grizzly bears from red squirrel middens and the surface area of the midden for the Yellowstone ecosystem between 1986 and 1992. The solid line depicts the estimated relationship, excluding potentially anomalous very large (> 600 m²) middens (shown as ○). The dashed line depicts the relationship including these middens.

rels in the whitebark pine zone was positively associated with lodgepole pine basal area. Previous work with squirrels in conifer forests found that similar relationships existed between squirrel abundance or midden-site selection and the basal area of either the entire stand or of certain species within the stand (Wolff & Zasada 1975; Vahle & Patton 1983; Sullivan & Moses 1986; Smith & Mannan 1994). The mechanism behind these relationships was assumed to be unit-area food abundance or micro-site amelioration. However, the energetic benefits of using lodgepole

pine seeds are less than those of using the seeds of any other tree species in the study area (Smith 1968; Finley 1969; Lanner & Gilbert 1994). Other studies have also found that red squirrels living in stands dominated by lodgepole pine or the closely related jack pine *Pinus banksiana* Lamb. existed at much lower densities compared to squirrels living in Douglas-fir or spruce-dominated stands (Smith 1968, 1970; Finley 1969; Rusch & Reeder 1978). Thus, interpreting the positive relationship observed in this study between squirrels and lodgepole pine is complicated because it both contradicts and agrees with expectations based on previous research.

The relationship between red squirrel activity or abundance and lodgepole pine basal area was probably caused, in part, by non-biotic features that were correlated under natural conditions with abundance of lodgepole pine in the whitebark zone. Within this zone, lodgepole pine was more abundant at lower elevations or, more generally, where climate was less extreme (Mattson & Reinhart 1990). Comparatively mild conditions probably also favoured red squirrels in an otherwise harsh environment (Gurnell 1987). If so, then these results should not be construed to imply that red squirrel populations can be increased simply by increasing the abundance of lodgepole pine on a site. On the other hand, red squirrels may have directly benefitted from lodgepole pine because seed crops of this species are comparatively stable from one year to the next (Finley 1969; Smith 1970). As evidence of this potential effect, densities of active middens were least variable among years on sites where lodgepole pine was most abundant.

Annual variation in the frequency of red squirrel

Table 7. Annual estimates of the whitebark pine cone crop, percentage of active middens that were excavated by grizzly bears during the previous 2 months, and density of active middens, Mt Washburn and Cooke City sites, Yellowstone area, 1984–87. Sample size is for the number of active middens. Percentages followed by the same letter in columns are not different among years within sites at $\alpha = 0.1$, controlling for habitat type effects

Year	<i>n</i>	Cone crop (<i>n</i> tree ⁻¹)		Excavated middens (%)	Active midden density (<i>n</i> ha ⁻¹)
		Mean	SD		
Mt Washburn					
84	50	7.5b	2.6	26.0bc	0.447
85	90	28.3a	6.8	48.9a	0.557
86	65	0.9c	1.6	16.9c	0.219
87	138	3.4c	3.6	27.5b	0.453
Cooke City					
84	30	—	—	6.7b	0.428
85	54	46.6a	9.3	24.1a	0.682
86	40	3.8c	2.4	0.0c	0.548
87	39	11.8b	2.6	13.3ab	0.544

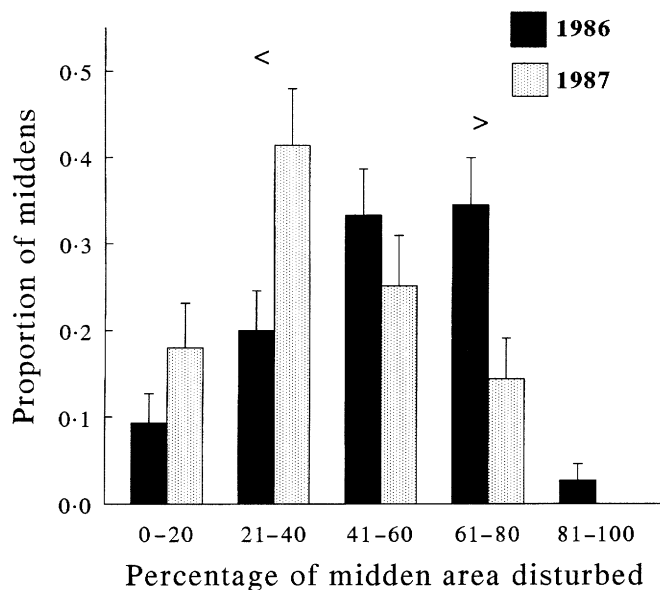


Fig. 6. The proportion of red squirrel middens excavated by bears during 1986 and 1987 relative to different levels of disturbance. Data were pooled from the Mt Washburn and Cooke City study sites in the Yellowstone ecosystem. Disturbance was measured as the percentage of a midden's surface that had been excavated or covered with back-cast debris by the bear. The '<' denotes a category where the relative frequency during 1987 exceeded that during 1986 while the '>' denotes the opposite.

activity in established middens was positively related to the size of whitebark pine cone crops and negatively related to the frequency of bear excavations. Both of these relationships were plausible. Whitebark pine seeds are large, fatty and favoured by squirrels over the seeds of other tree species (Kendall 1983; Hutchins 1994). Greater amounts of a high energy-content food, such as whitebark pine seeds, probably allowed a greater number of vulnerable and otherwise dispersing juveniles to survive and establish middens (Klenner & Krebs 1991).

Bears, on the other hand, deprived squirrels of food that represented a substantial amount of invested energy. Bear excavations in middens were often exten-

sive and affected more than one-half of the middens in some forest types during some years. Kendall (1983) observed that some middens were repeatedly excavated during a given year. Mattson & Jonkel (1990) also noted that some squirrels were killed and eaten by bears in the process. It is therefore possible that red squirrel populations declined after heavy exploitation of middens by bears. If so, then bears induced changes in squirrel populations that were detrimental to their own future foraging success.

Evidence of squirrel demography and behaviour from this study was largely circumstantial. Because we did not collect information on the total number of whitebark pine cones cached in middens, the import-

ance of whitebark pine seeds to red squirrel reproduction and survival is not clear; although the results of Kendall (1983) and Hutchins (1994) suggest they represent a major influence. The summary of information on hoarding by North American and Eurasian red squirrels *Sciurus vulgaris* Linnaeus by Wauters & Casale (1996) similarly suggests that larger hoards, in general, may be critical to red squirrel survival (cf. Smith 1968; Kemp & Keith 1970; Rusch & Reeder 1978). Although the percentage of middens disturbed by bear excavations was indicative, we did not directly estimate the percentage of cached cones that were consumed by bears, and so do not have a direct estimate of depredation. Also, as we did not observe marked squirrels, it is unclear what induced midden abandonment by the squirrels, and the extent to which this was due to mortality rather than movement to a new territory. The currently unknown relationship between midden size and age has additional bearing on this issue.

BEAR EXCAVATIONS

Both black bears *Ursus americanus* Pallas and grizzly bears excavate whitebark pine cones from red squirrel middens (Kendall 1983). Some of the excavations observed during this study were therefore attributable to black bears. However, this fraction is probably small. Black bears are inherently less prone to dig compared to grizzly bears (Herrero 1978). Grizzly bears also comprised 65% of the 168 bear sightings made in or near the Mt Washburn study site from 1984 to 1989 (K. Gunther, Bear Management Office, Yellowstone National Park, personal communication). In addition, where signs of bears were identified to species level in and near the Cooke City site during 1991, grizzly bears accounted for twice as many observations as black bears [D. P. Reinhart & D. J. Mattson, 1992, unpublished Interagency Grizzly Bear Study Team Report, Bozeman, Montana).

Midden size was important in determining whether bears excavated a midden; larger middens were used relatively more often than smaller middens. It may be that bears were more likely to excavate larger middens simply because they encountered them proportionately more often. On the other hand, large middens were more likely to be the site of squirrel activity and also tended to yield more excavated cones compared to small middens. It is possible therefore that bears selected for large middens, and that this behaviour was rewarded and reinforced. However, it is unclear whether red squirrels cached more cones in larger middens compared to smaller middens, given that we did not count the total number of exploited and unexploited cones in sampled middens.

The frequency of bear excavation was apparently affected by spatial and temporal variation in the availability of whitebark pine seeds. Availability of seeds would be obvious from the size of the cone crop.

Although seed production was less obviously related to whitebark pine basal area, Forcella & Weaver (1980), Weaver & Forcella (1986) and Shimanyuk (1963; for the closely related Siberian stone pine *Pinus sibirica* Rupr.) found good correlation between unit-area cone production and abundance of mature trees.

Assuming that whitebark pine basal area indicated the availability of seeds, bears excavated middens more often during years when, and on sites where, seed crops were larger. These results also suggest that bears excavated a given midden more intensively during years when more pine cones were available and presumably more were cached by squirrels. Given the plausible assumption that duration use and spatial extent of excavations in a given midden were correlated, bears resided longer in a 'patch' when resources were concentrated and more abundant. All of these patterns are consistent with the general predictions of optimal foraging theory (Stephens & Krebs 1986).

The results of this study are consistent with previous observations of grizzly bears avoiding roads and town sites. In common with bears foraging on ungulate carcasses during the spring (Green, Mattson & Peek, in press) and bears foraging on spawning cut-throat trout *Oncorhynchus clarki* Richardson during the early summer (Reinhart & Mattson 1990), bears during this study made virtually no use of resources in areas affected by close proximity to both a road and a town site. Proximity to town sites had a greater apparent impact on bears than did proximity to roads. These results also corroborate a previous assessment of human impacts in Yellowstone Park based on the analysis of telemetry locations from radio-tagged bears (Mattson, Knight & Blanchard 1987). This study is thus part of a growing body of research indicating that grizzly bears avoid areas near human facilities (Mattson *et al.* 1996).

In conclusion, grizzly bears will be affected both by human activity and management of forest stands in the whitebark pine zone. For example, a recent proposal which would have placed a gold mine near Cooke City, largely in or near areas used by bears to forage on whitebark pine seeds (Mattson 1995), would have had a negative impact on access by bears to this important food. Timber harvest also occurs in the whitebark pine zone, especially on lower-elevation sites (Eggers 1990). Depending on the harvest system, squirrel abundance as well as the numbers of whitebark pine cones cached in squirrel middens may be reduced, as may the opportunities for bears to obtain seeds. Two other factors, global climate change and white pine blister rust *Cronartium ribicola* J.C. Fisch. ex Rabenh. could also have a negative impact on grizzly bear abundance. Both pose major threats to whitebark pine in areas where grizzly bears currently consume substantial amounts of whitebark pine seeds. Under predicted scenarios of global climate warming, the whitebark pine zone would diminish to approximately one-tenth of its current extent (Romme &

Turner 1991). Blister rust has also virtually eliminated whitebark pine from much of its former range and is present in the Yellowstone ecosystem (Kendall 1995). Even a small increase in mortality of mature whitebark pine could negatively affect both the occupancy of pre-established middens by squirrels and the excavation of cones by bears.

MANAGEMENT IMPLICATIONS

This study is one of several confirming that grizzly bears avoid human facilities even when using high quality foods. By controlling for a number of intervening habitat-related factors, these results, along with those of Reinhart & Mattson (1990) and Green *et al.* (in press), indicate that the location of human facilities in the whitebark pine zone will almost certainly have a detrimental effect on grizzly bear access to an important food. Given that grizzly bears obtain more pine seeds per unit area under diverse canopies containing substantial amounts of both whitebark and lodgepole pines, these types of stands should receive protection.

In addition, these results suggest that grizzly bears would probably benefit from the propagation of blister rust-resistant whitebark pine in lower elevations of the whitebark pine zone (cf. Hoff, Hagle & Krebill 1994), in areas where red squirrel middens are more abundant. Similarly, grizzly bears would be vulnerable to incremental losses of cone-producing whitebark pine, whether due to forest succession, blister rust or climate warming. Managers should consider the potential effects of future losses of whitebark pine in their strategic conservation planning (Mattson & Reid 1991); the prospect of such losses introduces added uncertainty into population and habitat projections (Mattson & Reinhart 1994).

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Intraspecific Predation in Scandinavian Brown Bears Older than Cubs-of-the-Year

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INTRASPECIFIC PREDATION IN SCANDINAVIAN BROWN BEARS OLDER THAN CUBS-OF-THE-YEAR

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Abstract: Intraspecific predation of bears >1 year old is observed occasionally, but the mechanisms behind it are poorly understood and often debated. We documented 13 cases of intraspecific predation in brown bears (*Ursus arctos*) in 2 Scandinavian study areas during 668 bear-years of radiotracking 238 brown bears. We found area differences in the rates of intraspecific predation only for yearling females. Annual yearling female mortality due to intraspecific predation was higher (0.162, 6 of 38) in the south than in the north (no mortality recorded, 28 yearlings followed). No older subadult females were killed by other bears. Annual mortality rates due to intraspecific predation for males, areas combined, were: 0.032 for yearlings, 0.040 for 2-year-olds, and 0.061 for 3-year-olds, for a combined rate from age 1 through 3 years of 0.127. One adult female was killed. Staying with their mother did not significantly reduce intraspecific predation among yearlings. Neither population density, at the levels we observed, nor reduced food abundance influenced rates of intraspecific predation on yearlings in our areas. In our study areas, intraspecific predation on yearling females was correlated positively with the number of adult males that had died 3 years previously and whether any adult male had died 2 years previously. In an earlier study, we found that cub mortality was elevated during the breeding season 2 years after the death of adult males. As we found a similar pattern for intraspecific predation on yearling females, we speculate that infanticidal males may be prone to kill subadult bears. Although based on a relatively small sample of mortalities, our results strengthen our earlier conclusion that the killing of adult males may have a population consequence that managers should consider.

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Key words: brown bear, intraspecific predation, management, population dynamics, Sweden, *Ursus arctos*

Bears kill other bears, both cubs-of-the-year (called “cubs” in this paper) and older bears, but most authors consider the killing of bears older than cubs by conspecifics to be rare (Rogers 1983, Mattson et al. 1992, Garshelis 1994, McLellan 1994). However, McLellan et al. (1999) found that 5 of 12 natural mortalities among subadult and adult female brown bears in the Rocky Mountains were apparently due to conspecifics. Garshelis (1994) reported that about 2 North American black bears (*U. americanus*) per year were reported killed by conspecifics during the last 20 years, which is a low number considering the multitude of telemetry studies that have been conducted on this species. Intraspecific predation has also been reported occasionally in polar bears (*U. maritimus*; Lunn and Stenhouse 1985, Derocher and Wiig 1999). Two attempts have been made to quantify intraspecific predation in brown bears using scat analysis. Mattson et al. (1992) found that 0.17% of 6,976 brown bear scats in Yellowstone National Park, USA, contained remains of conspecifics (meat or >50% indigestible remains). Zhiryakov (1993) found that a similar proportion, 0.1%, of brown bear feces contained bear hair in and near the Alma-Ata State Reserve, Tian-Shan Mountains, Kazakhstan. McLellan et al. (1999) found that 5 of 34 total known mortalities of radiomarked subadult and adult female brown bears were due to conspecifics, but did not report whether the 2 natural mortalities of 25 total mortalities of males were due to intraspecific predation. In some areas of Russia, intraspecific predation is much more common among brown bears in years when the major food crops, usually berries and the very important seeds of stone pines (*Pinus sibirica*

and *P. pumila*), fail simultaneously. Smirnov and Shurygin (1991) wrote that intraspecific predation and cannibalism is a typical feature of brown bears in lean years in Tuva, central Siberia. Intraspecific predation during starvation years was reported to reduce adult survival and population size in central Siberia (Zavatskii 1993) and the Baikal region (Ustinov 1993), although these conclusions were not based on studies of radiomarked bears. In addition, Bunnell and Tait (1981) hypothesized that the killing or evicting of subadult males by adult males could be important in the regulation of bear populations.

Mattson et al. (1992) encouraged bear researchers not only to report instances of intraspecific predation, but also to report sample sizes and effort, such that mortality rates could be analyzed with respect to demographic and environmental parameters. Here we report mortality rates due to intraspecific predation in 2 brown bear populations in Scandinavia based on 13 instances of intraspecific predation during 668 bear-years (1 bear-year is the equivalent of 1 bear followed for 12 months, $n = 238$ bears) of radiotelemetry tracking during 1984–99. We use the term “intraspecific predation” to mean intraspecific killing. Because we usually recovered the carcass quickly, we are unsure how much of it would finally have been consumed by the perpetrator. We only considered bears >1 year old here; we considered mortality of cubs earlier (Swenson et al. 1997, 2001). Beyond reporting rates, we addressed the following questions:

Are bears in certain age or sex categories particularly vulnerable to intraspecific predation?—Mordosov (1993) stated that adults killed yearlings in spring, and Mattson

et al. (1992) suggested that young males might be especially vulnerable, but this was based only on 1 dead young male.

Do yearlings that stay with their mothers survive better than those that separate as yearlings, as predicted by Stringham (1983)?

Who are the perpetrators?—The general pattern from literature reviews in North America seems to be that adult males kill other bears of all age and sex classes, but adult females kill few adult males (Garshelis 1994, McLellan 1994), although there is not sufficient evidence to make a definite conclusion.

When does the mortality occur?—Mattson et al. (1992) found a tendency for brown bear feces to contain more bear remains (both brown and black bear) in March–May than later in the year in Yellowstone National Park. Zyryanov (1991) and Mordosov (1993) reported that intraspecific predation among brown bears in Siberia takes place in spring and autumn. There are several reports of bears being killed by conspecifics while in or at the den for American black bears (Rogers 1983, Tietje et al. 1986, Davis and Harestad 1996) and brown bears (Zetterberg 1951, Pearson 1975, Smirnov and Shurygin 1991, Zyryanov 1991, Mordosov 1993).

What is the reason for intraspecific predation?—No universal reason has yet been found, but several explanations have been proposed. (1) The Russian authors cited above have proposed that bears kill conspecifics for food when other food is scarce. This has also been suggested by some North American authors (Tietje et al. 1986, Olsen 1993), although data from Yellowstone National Park did not support this explanation (Mattson et al. 1992). Tietje et al. (1986) hypothesized that a male could improve his breeding success by killing and eating other bears to improve his condition during the breeding season in years of poor food availability. (2) Both adult males and females could benefit from killing unrelated conspecifics of the same sex, usually older bears killing younger ones. This would reduce the number of offspring of competitors, and thus remove future competitors to themselves and their own offspring for space, food, and mates (Rogers 1983, Tietje et al. 1986, LeCount 1987, Garshelis 1994, Hessing and Aumiller 1994). (3) Several authors have suggested that higher density or concentration of bears in of itself leads to increased intraspecific predation (Stringham 1983, Tietje et al. 1986, Davis and Harestad 1996). The pattern of intraspecific predation in Yellowstone did not contradict this hypothesis (Mattson et al. 1992).

These explanations were usually based on a few observed cases of intraspecific predation. There are certainly other valid explanations and it is reasonable to believe that there are actually several reasons for intraspe-

cific predation and that there may be different reasons in different circumstances.

STUDY AREAS

The study areas were located in northern Sweden and central Sweden–southeastern Norway, as described in Bjärvall and Sandegren (1987). These study areas are about 600 km apart and are near the northern and southern edges of the species' range in Sweden. The northern study area was about 8,000 km² in central Norrbotten County in northern Sweden, around Kvikkjokk (66°–68° N, 16°–20° E). It included alpine vegetation in the mountains, which were up to 2000 m high, in the western part of the area. Birch (*Betula pubescens*) formed the timberline at about 800 m. Boreal forest dominated and consisted primarily of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) in the U-shaped valleys and the lower (down to 300 m) and more rolling terrain in the eastern part of the study area. The southern study area was about 13,000 km² in northern Dalarna County and western Gävleborg County in Sweden and eastern Hedmark County in Norway (60°–61° N, 11°–16° E). The area was dominated by gently rolling terrain between 200 and 1000 m in elevation. Only a small part of the study area was above timberline. Intensively managed boreal forest dominated the study area, and the important tree species were Scots pine, Norway spruce, and the exotic lodgepole pine (*Pinus contorta*). The study populations belong to separate mitochondrial DNA lineages (Taberlet et al. 1995). However, nuclear DNA analyses have revealed that, although there are differences between the populations, there has been extensive gene flow throughout Scandinavia (Waits et al. 2000). An analysis of reproductive and mortality data indicated rapid growth in both populations during 1984–95: $\lambda = 1.14$ in the north and $\lambda = 1.16$ in the south (Sæther et al. 1998).

Bear hunting was generally allowed during the autumn in both areas, but the northern area included 3 national parks, where bear hunting was forbidden throughout the study period. Hunting pressure has increased in the southern study area in recent years, from an average of 2.8 bears killed legally per year in the 2 provinces encompassing the study area (Dalarna and Gävleborg) during 1985–95, to 23 in 1998. There was evidence of considerable illegal killing of bears, especially in the northern area (Swenson and Sandegren 1999). Illegal killing appeared to be less on the study areas than in the surroundings, and it appeared to have a major limiting effect on the population in the north. We have documented this in the north through the loss of radiomarked bears, especially males leaving the study area, and changes in the distribution of females, as determined from the distribution of legally killed fe-

male bears (Sandegren and Swenson 1997, Swenson and Sandegren 1999). Swenson *et al.* (2001) concluded that a higher immigration rate of newly recruited males occurred in the southern study area than in the northern area after adult males died. This was based on an apparent stable population trend for adult males in the south, in spite of the loss of adult males, and the decline in number of adult males in the north after adult males died.

METHODS

During 1984–99, 101 bears were marked in the northern study area and during 1985–99, 137 were marked in the south. All were immobilized early in the spring from a helicopter and marked with radiotransmitters (Telonics, Mesa, Arizona, USA). Most of the subadult bears captured after 1994 were equipped with a transmitter with a mortality sensor, which changed the pulse rate of the transmitter after it had not been moved for 4.7 hours. Growing bears were recaptured each spring to provide them with larger collars, although in the latter years of the study, yearlings received a transmitter that was implanted into the body cavity. Except for yearlings of radiomarked females, we collected a premolar tooth, which we sent to Matson, Inc., Milltown, Montana, USA, for age estimation based on the cementum annuli (Craighead *et al.* 1970). Bears were weighed every time they were captured. During 1988–91, 86% of the females observed in the company of radiomarked males during the breeding season in the north had functioning radiotransmitters. The corresponding value in the south, based on this type of observations made in 1988, 1989, and 1993, was 47% (Swenson *et al.* 1994, 1995). Judging from observations of males with radiomarked females in the breeding season, Swenson *et al.* (2001) concluded that virtually all adult males in the north and about 56% of them in the south were marked.

As marking occurred only during one short period each year, we calculated annual survival rates using the Kaplan–Meier procedure (Kaplan and Meier 1958). In this method, survival is calculated each month based on the number of radiomarked bears alive each month, and the monthly survival rates are multiplied to obtain an annual survival rate. Because we were only interested in intraspecific predation, we censored other causes of mortality, as recommended by Pollock *et al.* (1989). The rates of intraspecific predation reported here are 1 minus the censored annual survival rates. All bears were located at least once a week from the ground or from an aircraft, weather permitting. When a mortality pulse was received or death was suspected, the site was visited as soon as possible, usually within a day in the south and a few days in the north. All carcasses were examined by veterinarians at the National Veterinary Institute of Sweden. Determining intraspecific

predation was based on bite marks, particularly in the skull. Most carcasses were found so quickly that there was no question as to the cause of death. However, some dead bears in the north were found later, due to the wilderness character of the study area and poor weather that often hindered telemetry work from aircraft and access to the carcass with a helicopter. In cases where decomposed carcasses were found, judgment regarding cause of death was based on bite marks on the bones, particularly the skull. Thus, our estimate of mortality due to intraspecific predation may have been somewhat low in the north, although we do not believe it caused a major bias. During this study we documented 12 cases of intraspecific mortality of radiomarked subadult bears, 1 of a yearling that had been ear-tagged but had no radiotransmitter, and 1 of an adult (>3 years old).

Almost half of the bears in the north (43%, $n = 35$ to 1998) and almost all in the south (89%, $n = 57$) separated from their mothers as yearlings (Swenson *et al.* 1994). It can be difficult to decide whether a yearling killed by another bear in the spring had separated from its mother before being killed. We attempted to locate bears at least once a week, and we considered a yearling to have been with its mother when killed if it had been with her during the last time it was located alive.

Following Garshelis (1994) and Swenson *et al.* (2001), we used yearling body mass as a surrogate measure of food abundance the previous year. Yearlings were weighed to the nearest 0.5 kg shortly after den emergence ($n = 62$ in the north and 80 in the south). A body mass index for a given year was calculated as the mean of the deviations in body masses for yearlings from the appropriate area, expressed in standard deviation units, from the overall mean for all yearlings for all years for that sex and area. Thus, body masses from both sexes in an area were standardized and could be combined. The yearling body mass index was termed “fall condition index”, because most of the body mass was gained during the previous fall season. The body mass index was also considered to provide a “spring condition index” for the year in which yearlings were weighed. Thus for example, a body mass index obtained in early spring 1997 was used as a “spring condition index” for 1997 and as a “fall condition index” for 1996.

Loss of cubs has been correlated with the death of adult males in our study areas (Swenson *et al.* 1997, 2001). We therefore examined for this effect among subadult bears. The locations where adult males (>5 years old) were known to have died were compared with the locations of radiomarked females with cubs for a given year, called a “cub area”. A high proportion of the adult males were radiomarked: almost all (>90%) in the north and about 56% in the south (Swenson *et al.* 2001). In addition, all

bears killed by hunters must be shown to the authorities, the exact location of the kill must be reported (and can be verified), and samples must be turned in, including a tooth. We tallied the number of adult males known to have died within each cub area and within 1 male home-range diameter from it at time lags of 1, 2, and 3 years. This method is described in more detail and data are presented elsewhere (Swenson et al. 2001).

Indices of the trend in density of all adult females were derived by estimating the densities of breeding adult females and correcting these estimates for the proportion of radiomarked adult females that were breeding that year. Density of breeding adult females was estimated from the ratio of marked and unmarked females seen in the company of marked adult males during the breeding season using a simple Petersen estimate (Swenson et al. 1994). This was expanded to all adult females using the observed proportion of adult females that were breeding that year. We calculated a mean density from the years we have estimates (6 years in the north, 3 years in the south) and assigned this density to the year that was the mid-point of the years for which we had obtained estimates. With this starting point, we calculated annual density estimates before and after that year using the rates of population growth found from a demographic analysis of our data, $\lambda = 1.14$ in the north (1984–95) and $\lambda = 1.16$ in the south (1985–95; Sæther et al. 1998).

We also estimated the relative bear density in the home ranges of the subadults in a spatial manner, not temporally as above. In Sweden, female bears are concentrated in four geographically isolated areas termed female core areas (Swenson et al. 1994). These core reproductive areas are defined as the 90% harmonic mean areas (Dixon and Chapman 1980) of hunter-killed female bears during 1981–93 (Swenson et al. 1998a). In general, the relative density of bears is halved about every 24 km from the center of a core reproductive area toward the edge (Swenson et al. 1998a). This density gradient is a result of a sustained increase in population size, both in density and in distribution (Swenson et al. 1995, 1998a). In the south, our field station is located approximately in the center of the southernmost core reproductive area in Sweden. For practical reasons, to reduce the effect of a mismatch between the location of the center of the core reproductive area and the location of our field station, bear density was considered to be constant within 15 km from our field station. Outside this area, the relative density of bears was estimated as $0.5^{((x-10)/24)}$, where x = the distance (in km) of a home range center from our field station (Swenson 1998a). We were not able to obtain this relative spatial density for the northern study area.

Estimated survival functions from radiomarked bears were compared using the z test recommended by Pollock

et al. (1989). Pollock et al. (1989) recommended a sample size of 40–50 animals to obtain a mortality estimate with good precision. This exceeds our sample sizes for every age–sex–area category, so we accepted an α level of 0.10 for statistical significance.

We used stepwise multiple logistic regression to investigate correlates of annual rates of intraspecific predation mortality among radiomarked yearlings. Yearling fate (killed by another bear or not) was treated as the dependent variable. The independent variables were: area, sex, spring body mass of the yearling, annual spring condition index, annual fall condition index, adult female bear density, number of adult males known to have died in or near the cub areas (with time lags of 1, 2, and 3 years), and whether or not adult males were known to have died in or near the cub areas (with time lags of 1, 2, and 3 years). Independent variables were entered into the model, and removed by backward elimination using the Wald χ^2 statistic for removal (Norušis 1997). Statistical tests were carried out in SPSS.

RESULTS

Are Bears in Certain Age or Sex Categories More Vulnerable to Intraspecific Predation?

Yearlings—The mortality rate due to intraspecific predation was not significantly different for yearling males in the north and south ($z = 0.17$, 1 df, $P = 0.91$, Table 1). The combined mortality rate for yearling males in all areas was 0.032 (SE = 0.022, $n = 64$). In yearling females,

Table 1. Mortality rates of radiomarked brown bears in Scandinavia due to intraspecific predation by age, sex, and study area (north and south), 1984–98.

Age (years)	Sex	Area	Mortality (SE)	N ^a
1	M	N	0.037 (0.036)	30 (1)
		S	0.029 (0.029)	34 (1)
	F	N	0	28 (0)
		S	0.162 (0.061)	38 (6)
2	M	N	0.082 (0.056)	31 (2)
		S	0	28 (0)
	F	N	0	23 (0)
		S	0	26 (0)
3	M	N	0	18 (0)
		S	0.096 (0.064)	25 (2)
	F	N	0	21 (0)
		S	0	22 (0)
>3	M	N+S	0	179 ^b (0)
	F	N+S	0.0037 (0.004)	268 ^c (1)

^a Number of radiomarked bears for subadults and number of years and partial years the bears were followed for adults. The number in parentheses is the number documented as killed by another bear.

^b The actual time was 136.9 bear-years.

^c The actual time was 251.0 bear-years.

however, the bear-caused mortality was higher in the south than in the north ($z = 2.66$, 1 df, $P = 0.008$, Table 1). When comparing sexes of yearlings within an area, we found no statistical difference in mortality rate between males and females in the north ($z = 1.00$, 1 df, $P = 0.32$). In the south, however, females had a mortality rate due to intraspecific predation that was over 5 times higher than males ($z = 1.97$, 1 df, $P = 0.049$, Table 1). Female yearlings were 25% smaller than males in the north and 18% smaller in the south (Swenson et al. 2001).

Subadult bears.—Intraspecific predation was also observed in 2- and 3-year-old bears, but only in males (Table 1). In both areas combined, the annual rate of intraspecific predation was 0.040 (SE = 0.028, $N = 59$) among 2-year-old males and 0.061 (SE = 0.042, $N = 43$) among 3-year-old males. Thus, the cumulative rate of intraspecific predation for male bears from age 1 through 3 years (i.e., the second through fourth years of life) in both areas combined was 0.127. No radiomarked female 2-year-olds ($N = 49$) or 3-year-olds ($N = 43$) were killed by other bears. When combining areas and ages (2- and 3-year-olds), we found a significantly higher intraspecific predation rate among males (0.048, SE = 0.024, $N = 102$) than females (0 mortalities, 92 females followed, $z = 2.03$, 1 df, $P = 0.042$).

Adult bears.—We followed bears older than 3 years for a total telemetry time of 388 bear-years and recorded only a single death due to another bear. This was a 12-year-old female with 3 cubs. The annual mortality rate for females older than 3 years due to intraspecific predation was 0.0037 (SE = 0.0037, based on 251 bear-years of radiotelemetry (Table 1).

Who Are the Perpetrators?

As with most studies of bear mortality, identifying the perpetrator was difficult. We identified 3 potential perpetrators, but do not have conclusive evidence for any of them: (1) an adult male likely killed a male yearling; (2) a 5-year-old female with 3 cubs may have killed a female yearling, who was her half-sister; and (3) an 11-year-old resident male probably killed a 12-year-old female, who had 3 cubs. Details of these incidents are given below.

Case 1.—An adult male was the most likely killer of yearling male (W9405). The yearling was located with its mother on 27 May 1994, but was located alone and inactive on 28 and 29 May at the site where the partially eaten bear carcass later was found. A large Scots pine tree at the kill site had many fresh claw marks from what appeared to be a large bear and a smaller bear, suggesting that a large bear had dragged a smaller bear out of the tree. We assume that the smaller bear was W9405, but his littermate (W9404, female) was also in the vicinity at the time. Tracks from a large male bear and a female with

cubs were observed in mud on a road about 400 m from the kill site. These indications suggest that an adult male may have killed W9405, although the female with cubs or other bears can not be ruled out. We concluded that this bear had been with its mother when killed, but it is possible that it had separated from her less than a day before it was killed.

Case 2.—Some evidence suggests that a female with cubs may have killed yearling female W9805. This yearling was observed alone on 11 June 1998. The next day, a radiotelemetry position was obtained at 21:30 and was, according to the activity sensor on the transmitter, inactive at the site where it was later found dead; it may have already been dead at this time. Another bear, W9404, a 5-year-old female with 3 cubs, was recorded, using radiotelemetry, to have passed this site about 20:30 on the same day. No other radiomarked bears were located in the area, but an unmarked bear can not be excluded as the killer. The kill site was visited on 13 June. It was evident that W9805 had been chased for about 50 m, based on torn up moss and tufts of hair. The bite marks suggested that she had been killed by an adult bear and the carcass was partially consumed. W9404 and W9805 were half-sisters born in separate litters to the same mother.

Case 3.—An adult male most likely killed adult female W8905. The 12-year-old female was observed with 3 cubs 300 m from their den on 21 May 1999. At 05:25 on 25 May, she was located at the same site with a passive signal (her transmitter did not have a mortality function), together with an 11-year-old male (W9807), who had an active signal. The site was checked by airplane the same day. The activity signals were the same; one adult bear was seen (probably W9807) and 2 cubs were observed in a tree. A visit to the site in the evening revealed that the adult female was dead, covered with moss, and the posterior portions had been eaten. The site showed evidence of a fight. Two of the young were found alive in a tree. They were kept alive by providing dog food at the den site, but were killed by an unknown bear on 11 June. They were in good condition when killed.

Do Yearlings that Stay with their Mothers Survive Better?

In the south, where 89% of the yearlings separated from their mothers during the spring, we were unable to reject the hypothesis of no difference in the rate of intraspecific predation among yearlings with their mothers (0.200, SE = 0.179, $N = 5$) and those separated from their mothers, sexes combined, (0.090, SE = 0.035, $N = 68$, $z = 0.60$, 1 df, $P = 0.55$). Likewise, in the north, where 43% of the yearlings separated from their mother, there was no statistical difference in intraspecific predation between those with their mother (no mortalities, $N = 26$) and those sepa-

rated from their mother (0.037, SE = 0.036, $N = 31$, $z = 0.96$, 1 df, $P = 0.30$). Similarly, for both areas combined, yearlings with their mother had an intraspecific predation rate (0.032, SE = 0.032, $N = 31$) that was not significantly different from those not with their mother (0.074, SE = 0.027, $N = 99$, $z = 1.00$, 1 df, $P = 0.32$).

When Does the Mortality Occur?

Of the 14 bears identified as killed by conspecifics, 13 of which were radiomarked and 1 earmarked, 86% were killed during May–July (Table 2). This pattern seemed to hold for all age and sex classes of victims. One bear, a 3-year-old male, was killed at his den site. He was located there alive in October; we thought that the subsequent mortality signal was due to hibernation, but he was found dead outside the den the following spring. He had obviously been killed there before the snow arrived, i.e. be-

Table 2. Months in which brown bears were killed by conspecifics in Scandinavia, according to age and sex, 1984–99. Data from both study areas are combined.

Month	Females		Males			Total
	Yearling	Adult	Yearling	2-yr old	3-yr old	
May	1	1	1	1		4
Jun	4 ^a					4
Jul	2		1		1	4
Aug					1	1
Sept						0
Oct				1		1

^a One of these bears was ear-tagged but not radiomarked and was found without the help of radiotelemetry.

fore he had entered the den.

Factors Correlated with Intraspecific Predation

In the stepwise multiple logistic regression, using yearlings of both sexes and areas and including sex and area as independent variables, 3 independent variable were statistically significant: the number of adult males known dying in the area 3 years earlier, sex, and fall condition index. A positive relationship was found between intraspecific predation and the 2 continuous variables (Table 3). Because sex was a significant variable, similar regressions were performed on the sexes separately. No significant independent variables were found for yearling males. However for yearling females, a positive relationship was found between intraspecific predation and both the number of adult males known dying 3 years previously and the fall condition index (Table 4). In the south, the relative density of bears within the yearlings' home ranges did not influence the probability of being killed by another bear for males (Wald $\chi^2 = 0.004$, 1 df, $P = 0.95$) or females (Wald $\chi^2 = 0.165$, 1 df, $P = 0.68$). The data, including the independent variable and the selected dependent variables, are presented in Table 5.

Because we earlier found a relationship between cub mortality and whether any adult males had died (Swenson et al. 2001), we also compared intraspecific predation rates for yearlings where any adult male had died (using time lags of 1, 2, and 3 years) to those where no adult male was known to have died. No significant results were found

Table 3. Results of a stepwise multiple logistic regression with whether a radiomarked yearling brown bear was killed by another bear in two study areas in Sweden as the dependent variable. Independent variables were study area, sex of the yearling, spring body mass of the yearling, annual spring condition index, annual fall condition index, bear density (based on adult females), number of adult males known to have died in or near the cub areas, with time lags of 1, 2, and 3 years, and whether or not adult males were known to have died in or near the cub areas, with time lags of 1, 2, and 3 years.

Variable	Slope	SE	Wald χ^2	df	P
Constant	-8.149	2.668	9.33	1	0.002
Number of adult males dying 3 years earlier	0.671	0.322	4.35	1	0.037
Sex	2.584	1.352	3.66	1	0.056
Fall condition index	1.320	0.699	3.56	1	0.059
Entire model			10.29	3	0.016

Table 4. Results of a stepwise multiple logistic regression with whether a radiomarked yearling female brown bear was killed by another bear in two study areas in Sweden as the dependent variable. Independent variables were study area, spring body mass of the yearling, annual spring condition index, annual fall condition index, bear density (based on adult females), number of adult males known to have died in or near the cub areas, with time lags of 1, 2, and 3 years, and whether or not adult males were known to have died in or near the cub areas, with time lags of 1, 2, and 3 years.

Variable	Slope	SE	Wald χ^2	df	P
Constant	-3.476	0.955	13.24	1	0.000
Number of adult males dying 3 years earlier	0.891	0.378	5.57	1	0.018
Fall condition index	2.209	1.053	4.40	1	0.036
Entire model			9.83	2	0.007

for males (Table 6). For yearling females, however, the rate of intraspecific predation was higher when adult males had died than if none were known to have died 2 years previously and a tendency in that direction was found with a 3-year time lag (Table 7).

In a similar test, we examined whether a 2- or 3-year-old male being killed by another bear was related to any of the same dependent variables used for the test for yearlings, except that age was included and sex excluded. Body mass was also excluded, as it was not available for several individuals. None of these variables entered into the final model. In the south, the relative density of bears within the subadult males' home ranges did not influence the probability of being killed by another bear (Wald $\chi^2 = 0.062$, 1 df, $P = 0.80$). There may have been too few instances of intraspecific predation in these subadult males in our data set to adequately test the effects of the independent variables.

DISCUSSION

In our 2 study areas, intraspecific predation was almost entirely confined to yearlings and subadults, as also reported by Mordosov (1993) and suggested by Mattson *et al.* (1992). The probability of being killed by another bear from our sample was 0.127 for males during ages 1 through 3 years (both areas), 0.162 for yearling females in the south, and 0 for yearling females in the north. Thus, intraspecific predation can be an important demographic factor in some populations. Yearling females were the most vulnerable to intraspecific predation. As they were

the smallest subadult bears, it is possible that they were the easiest to kill.

In spite of our relatively large sample sizes, we were unable to demonstrate a survival advantage to yearlings of staying with their mothers, contrary to that predicted by Stringham (1983). Furthermore, we found that 3 orphaned cubs from 2 litters experienced normal growth in the north (Swenson *et al.* 1998b). We do not know why some females keep yearlings for an additional year, when it means also postponing reproduction for an additional year. Factors that may influence this situation are that our populations are growing rapidly (Sæther *et al.* 1998) and they are expanding in distribution, with no evidence that carrying capacity has been reached in any areas (Swenson *et al.* 1998a).

The one adult female that was killed by a conspecific most probably was killed by an adult male and likely was killed while defending her young, as has been recorded elsewhere for American black bears and brown bears (Garshelis 1994, McLellan 1994). The annual rate of intraspecific predation for females >3 years old in our relatively large sample (251 bear-years) was only 0.0037. No adult males were killed by conspecifics, as also found by McLellan *et al.* (1999).

Intraspecific predation was greatest during the spring breeding season, as also reported by Mattson *et al.* (1992). Although intraspecific predation may be associated with breeding behavior, it may also be associated with a greater probability for bears to encounter each other during the breeding season. At this time, adult males and adult females without cubs travel the greatest distances (Zakrisson 2001).

Table 5. Loss of radiomarked yearling female brown bears to intraspecific predation in the northern and southern study areas in Sweden, 1987–98, including the yearling masses (i.e., spring condition index) and number of adult (>5 years) males dying within the cub areas 1, 2, and 3 years previously. (One female yearling was followed in the north in 1984. She survived the year.)

Year	North					South				
	Yearling female loss ^b	Spring index ^c	No. males dying ^a			Yearling female loss ^b	Spring Index	No. males dying		
			-1 yr	-2 yr	-3 yr			-1 yr	-2 yr	-3 yr
1987	0/0	—				0/2	—	0	0	0
1988	0/0	—	0	0	0	0/0	—	0	1	0
1989	0/2	-0.17	2	0	0	0/1	-0.39	0	0	3
1990	0/0	+0.17	0	1	0	0/1	+0.60	0	0	0
1991	0/0	+2.07	0	0	1	0/2	-1.68	1	2	0
1992	0/1	+0.69	0	0	0	1/4	-0.46	4	1	2
1993	0/3	+0.19	0	0	0	0/3	-0.48	2	4	1
1994	0/4	-0.28	0	0	0	2/5	-0.34	0	2	4
1995	0/8	+0.27	0	0	0	0/4	-0.21	1	0	2
1996	0/2	-0.98	0	0	0	1/1	-0.19	0	1	0
1997	0/1	-0.47	1	0	0	0/1	+2.01	3	1	1
1998	0/2	+0.35	0	1	0	1/6	+0.41	0	3	0
1999	0/4	-0.38	0	0	1	1/8	+0.52	4	3	3

^a Adult males. Numbers can change when tracked diagonally because the cub areas were different each year.

^b Number killed by intraspecific predation/total number followed with radiotelemetry.

^c Spring condition index in 1989 corresponds to fall condition index in 1988.

Table 6. Annual rate of intraspecific predation in yearling male brown bears in Scandinavia, in relation to whether adult (>5 years) males were known to have died within the cub areas at various time lags, 1984–99. Data are combined from both study areas.

Time before the mortality of yearlings	Following known adult male death			No known adult male death			<i>z</i>	<i>P</i>
	Mortality	SE	<i>N</i>	Mortality	SE	<i>N</i>		
1 year	0.029	0.029	36	0.037	0.036	27	0.17	0.86
2 years	0.027	0.027	37	0.044	0.042	26	0.34	0.73
3 years	0.039	0.038	26	0.029	0.029	37	0.21	0.83

^a Two-tailed *z* test as described in Pollock et al. (1989).

Table 7. Annual rate of intraspecific predation in yearling female brown bears in Scandinavia, in relation to whether adult (>5 years) males were known to have died within the cub areas at various time lags. Data are combined from both study areas.

Time before the mortality of yearlings	Following known adult male death			No known adult male death			<i>z</i>	<i>P</i>
	Mortality	SE	<i>N</i>	Mortality	SE	<i>N</i>		
1 year	0.114	0.054	36	0.069	0.047	30	0.63	0.53
2 years	0.182	0.067	33	0	0	33	6.14	0.007
3 years	0.132	0.055	38	0.037	0.036	28	1.45	0.15

^a Two-tailed *z* test as described in Pollock et al. (1989).

We did not find an unequivocal reason for intraspecific predation. However, it is probably not possible to find one explanation for all intraspecific predation in bears. In our study areas, we only found significant relationships, among the factors we tested, for intraspecific predation on yearling females. In a multivariate analysis, positive relationships were found between this and the number of adult males known to have died in the area 3 years previously and the fall condition index. In a univariate analysis, a positive relationship was found between intraspecific predation and whether any adult male was known to have died 2 years earlier, with a tendency in that direction after 3 years. As both variables had been included in the multivariate analysis, the number of males dying 3 years previously was the factor that best explained the observed variation. However, both results suggest that disruption of the adult male social organization, perhaps resulting in the immigration of new males (Swenson et al. 1997, 2001), may have been involved in elevating the rates of intraspecific predation.

The pattern of intraspecific predation of yearling females in relation to mortality of adult males was similar to the pattern we observed for loss of cubs in our 2 study areas (Swenson et al. 2001). Mortality of cubs was also considerably higher in the south, where mortality of adult males was higher, than in the north, and cub mortality in the south was correlated with number of adult males dying 2 years earlier in a multivariate analysis. Cub mortality was also higher when any adult males had died 2 years earlier in a univariate analysis. Swenson et al. (2001) concluded that there was a higher immigration rate of new males in the south than in the north. This was based on a high emigration rate of radiomarked subadult males and no significant change in the number of adult males, de-

spite an annual mortality rate of about 10%. The conclusion was that infanticide caused by these immigrating males was probably the most important cause of cub loss. Intraspecific predation on yearling females was correlated with the number of adult males dying 3 years earlier in the multivariate analysis, in contrast to the 2-year time lag found for cubs. However, the same result, higher mortality after 2 years, was found in the univariate analyses. Based on these results, we speculate that infanticidal males might be more prone to kill young bears, including subadults. Also, the 2-year time lag for cub mortality and 3-year time lag for yearling mortality means that the cohort that experiences an elevated mortality rate as cubs following the loss of adult males on the area, also experiences a higher mortality the following year, at least the females in the cohort. Subadult bears were also killed by conspecifics most often in the breeding season, which is the same pattern we observed regarding cub loss (Swenson et al. 2001).

A higher loss of subadults with a time lag following high adult mortality also appears to have occurred in grizzly bears in the Yellowstone Ecosystem. Stringham (1983) analyzed data from the Yellowstone brown bear study during 1959–79 and found that the mean number of adult males censused before and after a cohort was born was negatively correlated with the cohort sizes at ages 0.5 years ($r^2 = 0.31$), 1.5 years ($r^2 = 0.50$), and 2.5 years ($r^2 = 0.82$). The highest numbers of censused adult males were in 1968–70 (Stringham 1983). The known mortality of adult males in the Yellowstone Ecosystem was also highest during these 3 years, mean of 9/year, compared to 1959–67, with a mean of 2.7/year (Craighead et al. 1995:278). Thus, low cohort size may also have been correlated with high losses of adult males with the reported time lags. The

elevated losses of cubs and subadults apparently continued for 2 or 3 years after many adult males were killed. Again, the high losses may have been related to a disruption of the adult male social organization, and perhaps occurred after new males entered the studied subpopulation of bears using the garbage dumps.

A second factor that was correlated with intraspecific predation in yearling females was fall condition. However, it was difficult to interpret this result, because the relationship was positive. It is not intuitively obvious why better condition in the fall should lead to higher intraspecific mortality, especially when most of the mortality occurs in the spring. A similar relationship was found for cubs (Swenson et al. 2001). Thus, there may be a factor involved here that we have not identified. Loss of cubs and intraspecific predation on yearling females may be correlated with a factor or factors other than intraspecific predation that is also correlated with the death of adult males 2 or 3 years earlier. We have not identified such a factor, but our results suggest that it is not poor food availability.

Relative population density was not found to influence the probability of intraspecific predation in either yearlings of both sexes or subadult males. We tested for density effects both temporally and spatially. We conclude that population density, within the range of densities observed in our study, was not an important factor influencing intraspecific predation. We earlier failed to find evidence that brown bears had reached carrying capacity in any areas in Sweden (Swenson et al. 1998a).

MANAGEMENT IMPLICATIONS

There has been considerable debate in the scientific literature about potential negative or positive effects on population growth of killing adult males. After reviewing the evidence and presenting his own data, Miller (1990) recommended that managers should not assume that the killing of adult males would have a positive effect on cub survivorship. Wielgus and Bunnell (1994, 2000) went even further, suggesting that killing adult males might even decrease cub survival. Our studies of cub survival (Swenson et al. 1997, 2001) have led us to agree with Wielgus and Bunnell (1994, 2000). However, this debate has only been concerned with cub survival.

The similarity of the results for cubs and yearling females leads us to speculate that the killing of adult males and disruption of the resident adult male social organization, with presumed immigration of new males, has even a greater demographic effect on a bear population than we proposed previously (Swenson et al. 1997, 2001). Loss of cubs was 0.35 in the south and 0.04 in the north (Swenson et al. 2001). Loss of female yearlings due to

intraspecific predation was 0.162 in the south and 0 in the north. Assuming that many of the cubs were killed by other bears, we conclude that intraspecific mortality can be an important demographic factor in some bear populations. As the level of intraspecific predation can be related to the killing of adult males, we repeat the caution we have given earlier (Swenson et al. 2001): "Until this question is adequately resolved, managers should act conservatively and assume a population consequence of harvesting adult male bears."

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Sport Hunting, Predator Control and Conservation of Large Carnivores

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Abstract

Sport hunting has provided important economic incentives for conserving large predators since the early 1970's, but wildlife managers also face substantial pressure to reduce depredation. Sport hunting is an inherently risky strategy for controlling predators as carnivore populations are difficult to monitor and some species show a propensity for infanticide that is exacerbated by removing adult males. Simulation models predict population declines from even moderate levels of hunting in infanticidal species, and harvest data suggest that African countries and U.S. states with the highest intensity of sport hunting have shown the steepest population declines in African lions and cougars over the past 25 yrs. Similar effects in African leopards may have been masked by mesopredator release owing to declines in sympatric lion populations, whereas there is no evidence of overhunting in non-infanticidal populations of American black bears. Effective conservation of these animals will require new harvest strategies and improved monitoring to counter demands for predator control by livestock producers and local communities.

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Introduction

Management agencies typically skew harvests toward males in order to protect adult females. However, in species with extensive paternal investment such as African lions (*Panthera leo*), trophy hunting can increase the rate of male replacement (and associated infanticide) to the point of reducing population size unless off-takes are restricted to males old enough to have reared their first cohort of dependent offspring (≥ 5 –6 yrs of age) [1–3]. Solitary felids have none of the “safety nets” provided by the cooperative cub rearing strategies of African lions [4–5], and Fig. 1ab illustrates the greater vulnerability of solitary species by examining the effects of trophy hunting on a hypothetical population of “solitary lions” while leaving other demographic parameters from ref. [1] unchanged (Supporting Information Table S1, also see ref. [6]). Leopards (*Panthera pardus*) may be more sensitive to sport hunting than solitary lions (with a safe minimum age of 6–7 yrs of age, Fig. 1c), whereas cougar (*Felis concolor*) males can be safely harvested as young as 4 yrs of age (Fig. 1d).

We tested whether infanticidal species are vulnerable to over-hunting by focusing on four large carnivore species with sizable markets for sport-hunted trophies, comparing three infanticidal felids (lions, cougars and leopards) to American black bears (*Ursus americanus*). We used black bears as a control case because males do not kill cubs in order to increase mating opportunities (sexually-selected infanticide – SSI), so rates of infanticide are not increased

by male-biased trophy hunting; in fact, among ursids, SSI has been documented in only one population of European brown bears (*U. arctos*) [7–9].

We extracted data from the UNEP World Conservation Monitoring Centre (WCMC) CITES trade database (See Materials and Methods). Data on total trophy harvests of lions and leopards are not available, so we used CITES-reported exports, which in cougars and black bears were highly correlated with domestic sport-hunting totals (Supporting Information Fig. S1); likewise CITES-reported trade in Tanzania's lion trophies showed a close match between imports and exports. Given sustained market demand, harvest trends should provide a reasonable proxy of population trends since sport hunters use intensive methods such as baits and hounds to locate these animals, and quotas on annual off-takes are either too high to limit harvests or (for black bears) reflect the management agency's perception of population trend [10].

Results

Fig. 2 shows the annual CITES exports for lions and leopards and US off-takes of cougars and black bears (See Materials and Methods). The reported number of trophies increased rapidly across all four species as markets grew during the 1980's and 1990's [11–12]. Off-takes have continued to increase for black bears, reflecting the sustained growth of bear populations

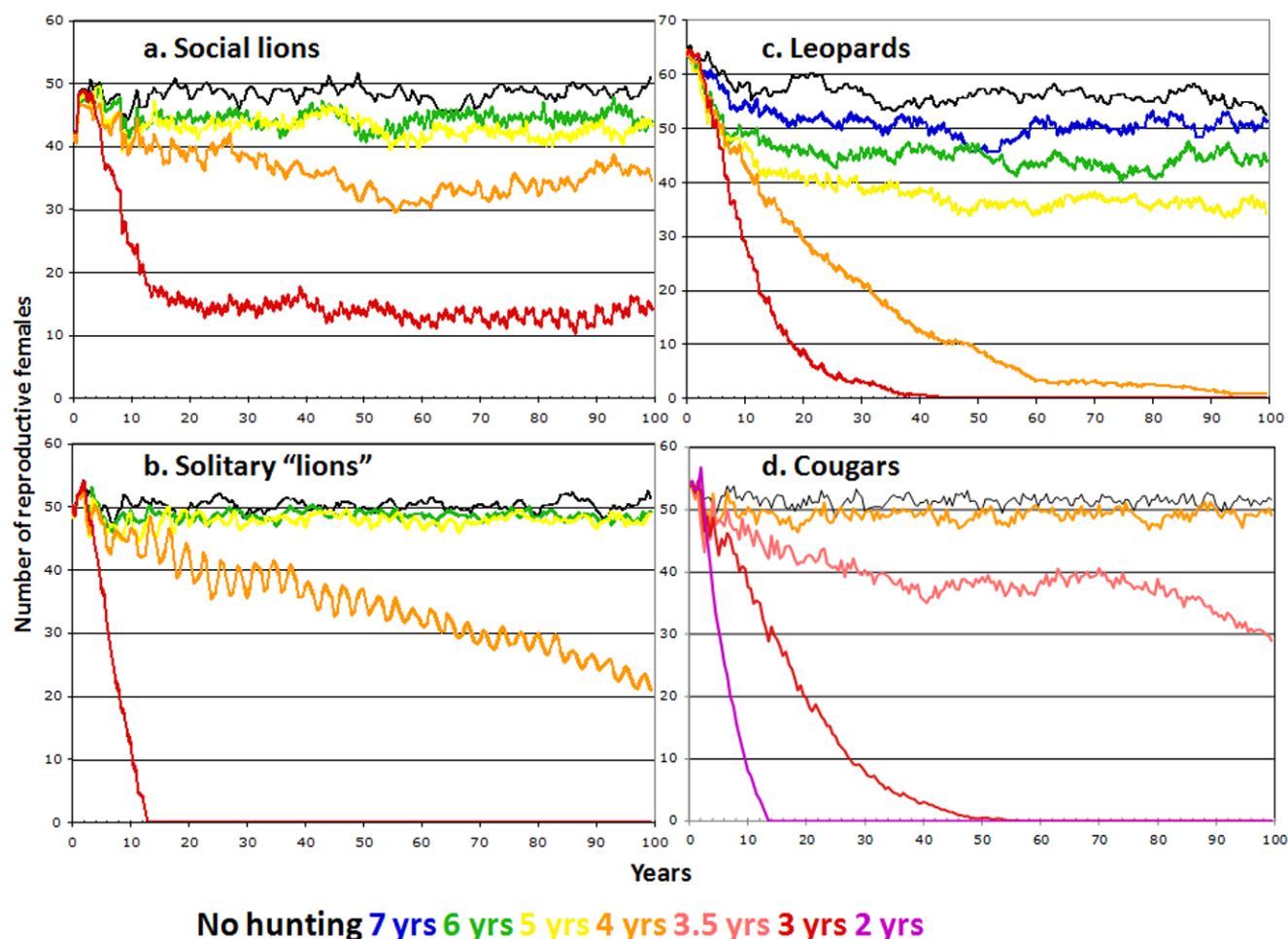


Figure 1. Average number of adult females in population simulations where all eligible males are removed during a 6-mo hunting season each year for 100 yrs. Colors indicate outcomes for different age minima for trophy males; each line indicates average from 20 runs. **A.** Population changes for “social lions” follow the assumptions and demographic variables in ref. [1] except to restrict hunting to 6-mo seasons and to incorporate additional details of dispersal, survival and reproduction [44–46]. **B.** Population changes for a hypothetical lion population where males and females are solitary and each territorial male controls one female. **C.** Population changes for leopards based on long-term data from Phinda Private Game Reserve [33,47] and other sources [37,48]. **D.** Population changes for cougars based on demographic data from refs. [27,49–53]. doi:10.1371/journal.pone.0005941.g001

throughout North America [13]. Leopard offtakes reached an asymptote in most countries, except for declines in Zambia in the 1980’s and Zimbabwe in the 1990’s and a recent CITES-granted increase to Namibia. In contrast, lion offtakes peaked then fell sharply in the 1980’s and 1990’s in Botswana, Central African Republic, Namibia, Tanzania, Zambia and Zimbabwe. Cougar offtakes showed similar peaks and declines in the 1990’s in Arizona, Colorado, Idaho, Montana and Utah (Fig. 2).

The downward harvest trends for lions and cougars (highlighted in Supporting Information Fig. S2) most likely reflected declining population sizes: success rates (as measured by harvest/quota) have fallen for both cougars and lions (Supporting Information Fig. S3). Demand for lion trophies (as measured by total imports from across Africa) has grown in the US and held stable in the EU since the mid-1990s, sustained in recent years by imports of trophies of captive lions from South Africa [12,14] (Supporting Information Fig. S3). Several countries instituted temporary bans on lion trophy hunting (Botswana in 2001–2004, Zambia in 2000–2001 and western Zimbabwe in 2005–2008) or banned female lions from quota (Zimbabwe, starting in 2005), but these measures were implemented well after the major decline in lion offtake in

each country. The harvest trends are also consistent with recent surveys suggesting a 30% continent-wide population decline in African lions [15] and declining cougar populations in several US states [16–17]. Conversely, black bear populations appear to be increasing across their range [13], even in states where cougar populations have declined (Fig. 2). Although not apparent from most hunting offtakes, leopards have undergone an estimated range decline of 35% in Africa [18] and were recently listed as Near Threatened by IUCN due to habitat loss, prey depletion, illegal skin trade and problem animal conflicts [19].

Trophy hunting is likely to have contributed to the declines in lion and cougar populations in many areas. Over the past 25 yrs, the steepest declines in cougar and lion harvests occurred in jurisdictions with the highest harvest intensities (Fig. 3a). Similarly, hunting blocks with the highest lion offtakes per 1000 km² in Tanzania’s Selous Game Reserve showed the steepest declines between 1996 and 2008 ($r^2 = 0.26$, $n = 45$ blocks, $P = 0.0004$). The Selous is the largest uninhabited hunting area in Africa (55,000 km²) and has long been the premier destination for lion trophies. Across jurisdictions, declining harvests were unrelated to habitat loss for either lions or cougars (Fig. 3b) or to snow

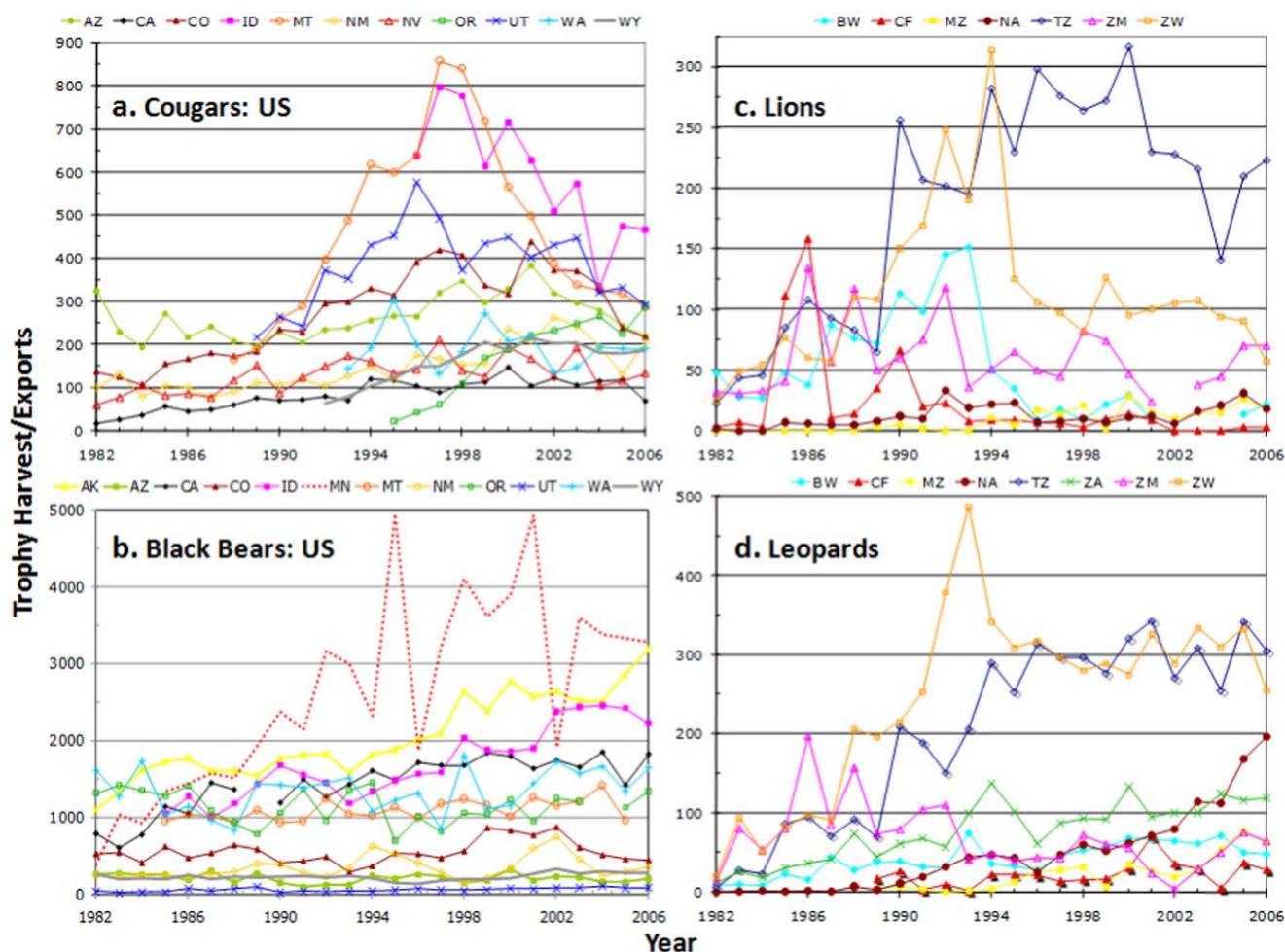


Figure 2. Domestic offtakes of a) cougars and b) black bears and CITES-reported trophy exports of c) lions and d) leopards. For US states: AK=Alaska, AZ=Arizona, CA=California, CO=Colorado, ID=Idaho, MN=Minnesota, MT=Montana, NM=New Mexico, NV=Nevada, OR=Oregon, UT=Utah, WA=Washington, WY=Wyoming. For CITES data: BW=Botswana, CF=Central African Republic, MZ=Mozambique, NA=Namibia, TZ=Tanzania, ZM=Zambia, ZW=Zimbabwe. doi:10.1371/journal.pone.0005941.g002

conditions for cougars. We modified our population simulation models to estimate impacts of sport hunting in a changing environment and found that habitat loss only imposes an additive effect on the impact of trophy hunting (Supporting Information Fig. S4). Note that habitat loss in many African nations has been so extensive (Fig. 3b) that lion offtakes have failed to recover for 10–20 yrs following the peak harvest years except in Namibia.

Although trophy hunting of lions and cougars is often portrayed as an economic strategy for increasing support for carnivore conservation, local communities often seek extirpation of problem animals [15,20–22]. Thus, sport hunting quotas may sometimes reflect pressures to control carnivores rather than to conserve them. Across Africa, countries with the highest intensity of lion offtake also had the highest number of livestock units per million hectares of arable land ($P = 0.047$, $n = 7$). In the US, Oregon announced plans in 2006 to reduce its cougar population by 40% to decrease depredation on livestock, pets and game mammals [23], Washington altered its cougar quotas in response to human-wildlife conflicts in the 1990s–2000s, and recent offtakes have exceeded government-sanctioned eradication programs in several states. For example, Utah's sport-hunting cougar harvests averaged 500/yr in 1995–7

compared to peak culls of 150/yr in 1946–1949 [24], and Montana sport hunters harvested 800/yr in 1997–1999 vs. 140/yr in the peak “bounty” years of 1908–11 [25]. Likewise, South Africa exported 120 leopard trophies per year in 2004–2006, similar to the cull of 133 leopards per year in Cape Province (which covered most of the country) during 1920–1922 [26].

Fig. 4 shows the potential consequences of coupling a 40% cull of cougars with intensive sport hunting if the control program only targets males (reflecting traditional trophy hunting), removes males and females in proportion to their abundance, or only removes adult females. Fig. 4adg show population trends for the maximum fixed offtakes that never resulted in population extinctions during 20 simulations, whereas Fig. 4beh show the minimum fixed harvests that caused extinction in all 20 runs (often within 10 yrs of an initial decline). Fig. 4cfi show the consequences of applying the maximum “safe” offtakes if the population were inadvertently culled by 50% because of inaccurate population estimates. Consistent with population viability analyses [27–28], a female-only harvest comes closest to maintaining a persistent population reduction; a mixed male-female strategy allows the largest number of trophies to be harvested; a male-only harvest never maintains a

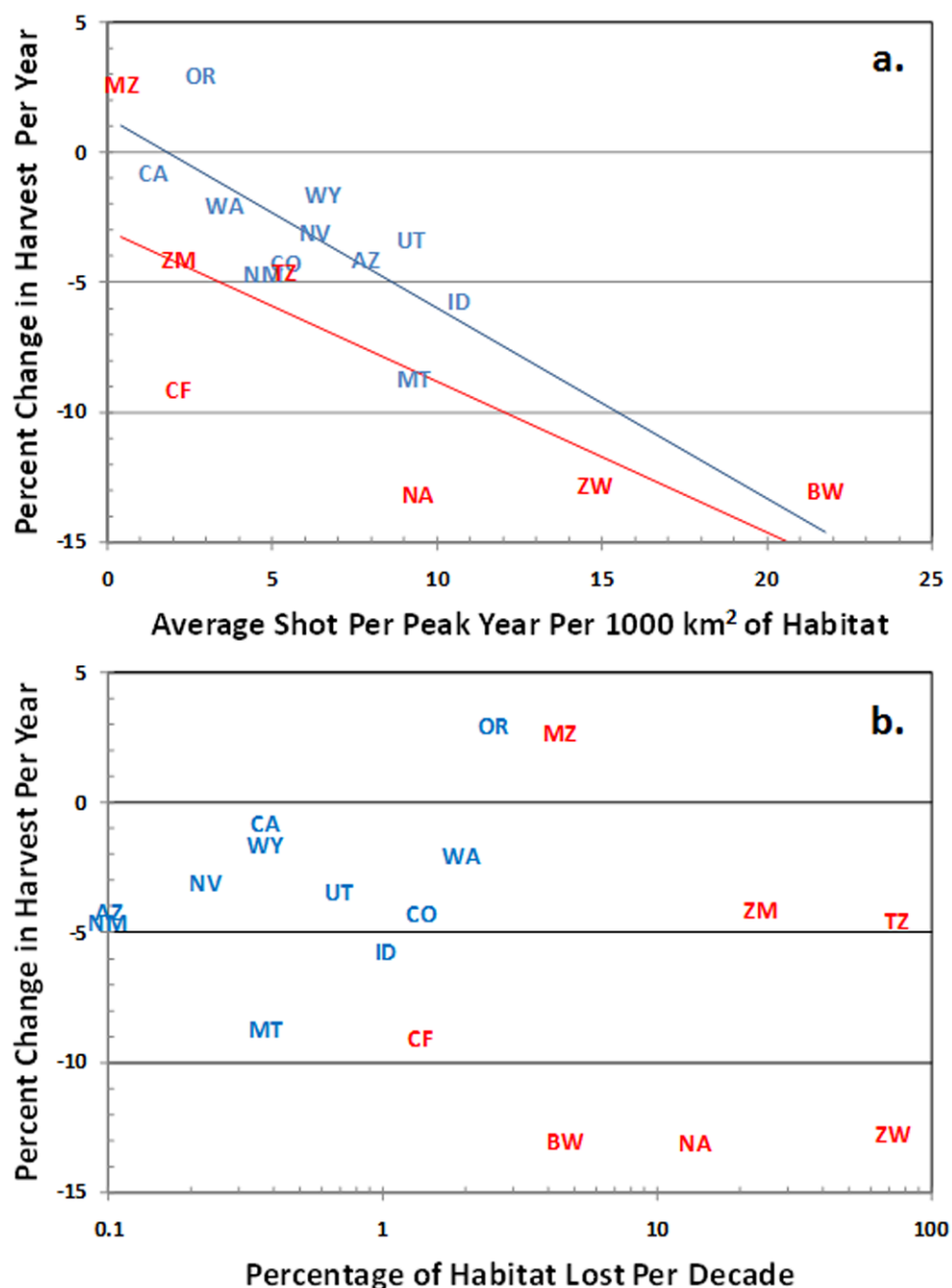


Figure 3. Recent trends in cougar off-takes (blue) and lion off-takes (red) as functions of a) harvest intensity and b) habitat loss. Jurisdictions with the highest harvest intensity showed the greatest decline in cougar off-takes ($r^2 = 0.5151$, $P = 0.0129$) and lion off-takes ($r^2 = 0.5796$, $P = 0.0468$). Habitat loss is plotted on a log scale to allow comparison between the African countries and the US states. doi:10.1371/journal.pone.0005941.g003

40% reduction in population size and has the smallest margin of error (male-only harvests can have catastrophic effects even in non-infanticidal species [29]).

These simulations assume a fixed harvest whereas many wildlife agencies reduce their quotas in response to lowered off-takes (Supporting Information Fig. S3 also see ref. [30]). However, off-takes may often be maintained at constant levels through compensatory increases in hunting effort, running the risk of an “anthropogenic Allee effect” [31–32]. Hunters in Zambia, Zimbabwe and Tanzania maintain their lion harvests by shooting males as young as 2 yrs of age (Fig. 5). In Zimbabwe, high lion off-takes were sustained from 1995 until 2005 by allowing females

on quota [3], and the duration of lion safaris increased by nearly 18% from 1997 to 2001 (Supporting Information Fig. S3). Similarly, hounds have been used to hunt leopards in Zimbabwe since 2001, potentially masking a continued population decline.

Discussion

Mortality from state-sanctioned and illegal predator control likely contributed to the overall population declines of cougars and lions; while leopards are also killed as pests, the leopard’s CITES Appendix I status requires international approval for national export quotas, potentially providing safeguards against overhar-

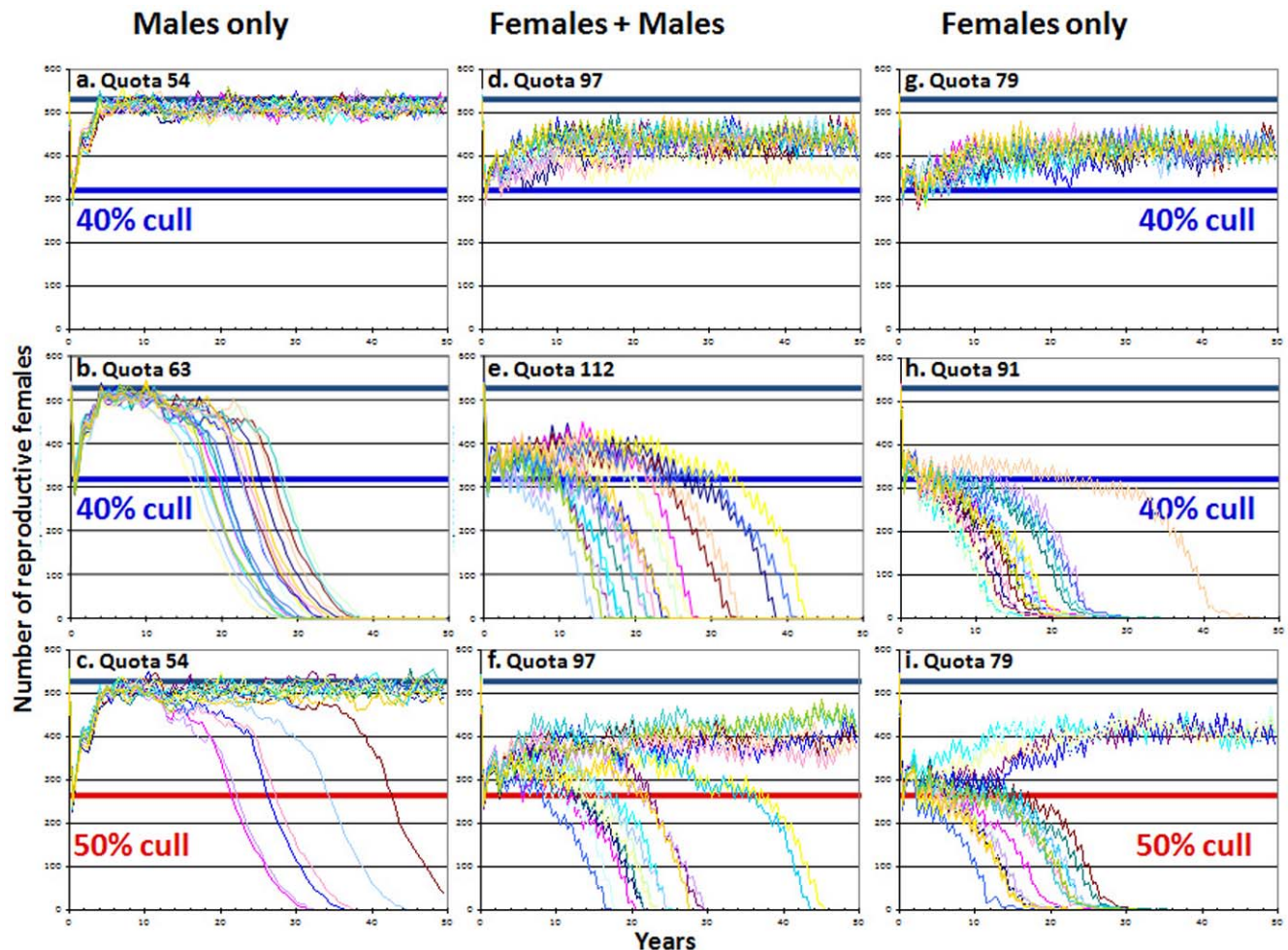


Figure 4. Simulated cougar populations subjected to an initial cull followed by fixed offtakes for 50 yrs. The initial cull is either 40% (top and middle rows) or 50% (bottom row), and the subsequent harvests are either the maximum offtake that incurred no extinctions in 20 runs following a 40% cull (top and bottom rows) or the minimum that produced 20 extinctions in 20 runs following a 40% cull (middle row). In the absence of sport hunting, the stable population size in these simulations is 527 reproductive females (indicated by the heavy black line in each graph); a 40% reduction in population size is indicated by blue lines, a 50% reduction by red lines. Each column represents a different harvest strategy: male only (left column), males and females (middle) and female only (right). Demographic parameters are set as in Fig. 1; quotas allow offtake of animals as young as 2 yrs; each graph shows outputs from 20 runs.
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vest. However, leopard exports have declined in some countries, quotas have risen in others, and concerns have been raised over the level of problem animal offtakes and the management of leopard hunting practices [33–35]. Further, leopard populations in many areas may have been “released” [36] by large scale declines in lion numbers: lions inflict considerable mortality on leopards [37]; consequently, hunting blocks in Tanzania’s Selous Game Reserve with the highest lion harvest intensities showed the largest increases in leopard harvests ($P=0.0059$ after controlling for declines in lion offtakes, $n=45$ blocks). Thus the full impact of current trophy hunting practices on leopards may not be fully apparent for several more years.

Harvest policies for infanticidal species such as lions, cougars and leopards that relied on “constant proportion” or “fixed escapement” could help protect populations but require accurate information on population size and recruitment rates, which are virtually impossible to collect; a harvest strategy of “constant effort” can more easily be achieved by measuring catch rates and regulating client days [38–40]. Hunting efficiency could be reduced by banning or limiting the use of baits and hounds, but

the absence of direct oversight in remote hunting areas would make enforcement difficult. Alternatively, the age-minimum harvest strategies illustrated in Fig. 1 could be implemented without risk of over-hunting, assuming that ages can be reliably estimated before the animals are shot [41] rather than afterwards [42]. Unsustainable levels of trophy hunting of lions and cougars appear to be driven by conflicts with humans and livestock: the intensity of lion hunting was highest in countries with the most intensive cattle production, and wildlife managers are under similar pressure from US ranchers to raise cougar offtakes. Thus an even more fundamental challenge for carnivore conservation will be to build community tolerance for predators by reducing the need for retaliatory predator control and by improving benefit sharing from well managed trophy hunting [15].

Materials and Methods

We analyzed trophy exports (<http://www.unep-wcmc.org/citestrade/>) by using the term “trophy” and restricting the analysis to countries that exported at least 25 trophies of a particular



Figure 5. Sample of under-aged male African lions shot by sport hunters in various countries from 2004–2008.
doi:10.1371/journal.pone.0005941.g005

species for at least 2 yrs from 1982 to 2006 (excluding captive-bred lion trophies from South Africa). Other types of exports (skins) were also analyzed for lions, since non-standard terms are sometimes used by reporting countries [43], but these did not alter overall export trends. Data on Tanzanian hunting quotas were provided by the CITES office at the Division of Wildlife headquarters in Dar es Salaam; data on duration of hunting safaris in Zimbabwe were from the head office of Parks and Wildlife Management Authority in Harare.

Offtake data for black bears and cougars were provided by the Alaska Dept. of Fish & Game, Arizona Game & Fish Dept., California Dept. of Fish & Game, Colorado Division of Wildlife, Idaho Fish & Game, Minnesota Dept. of Natural Resources, Montana Fish, Wildlife & Parks, New Mexico Game & Fish, Nevada Dept. of Wildlife, Oregon Dept. of Fish & Wildlife, Utah Division of Wildlife Resources, Washington Dept. of Fish & Wildlife, and Wyoming Game & Fish. Note that all cougar offtakes in California are due to predator control.

“Harvest intensity” is the average harvest of the three peak offtake years divided by the extent of habitat in that state/country. Regression coefficients were calculated across the time period beginning with the earliest of the three peak harvests and ending in 2006 for cougars or the last of the three lowest subsequent harvest years for lions (Supporting Information Fig. S3); percent change is the regression coefficient divided by the peak harvest. Limited lion and leopard offtake data were available from 1996–2008 in Tanzania’s hunting blocks; trends were only calculated for blocks reporting ≥ 5 yrs of activity.

Cougar habitat is forest cover taken from the National Land Cover Database (NLCD) www.mrlc.gov/changeproduct.php; lion habitat is the extent of GLOBCOVER land classification categories 42, 50, 60, 70, 90, 100, 110, 120, 130, 134, 135, 136, 160, 161, 162, 170, 180, 182, 183, 185, 186 and 187 in each country, see <http://postel.mediasfrance.org/en/DOWNLOAD/Biogeophysical-Products/>. Habitat loss is based on change in forest cover in the US 1990–2000 and in woodland/forest habitat in Africa 1990–2005 from FAO Global Forest Resources Assessment 2005, <http://www.fao.org/forestry/32185/en/>. Snow conditions for cougars are taken from <http://www.wrcc.dri.edu/Climsum.html> and African livestock production is taken from http://www.fao.org/es/ess/yearbook/vol_1_1/pdf/b02.pdf, using production levels from years of peak lion offtake in each country.

Supporting Information

Figure S1 The number of CITES-reported exports of a) cougar trophies and b) black bear trophies from the US were highest in years when the most animals were harvested domestically in the western states ($P < 0.001$ for each species).

Found at: doi:10.1371/journal.pone.0005941.s001 (0.69 MB EPS)

Figure S2 Trendlines for the population declines of a) cougars and b) lions. Individual states with statistically significant declines in cougar offtakes: MT, ID, AZ, UT and CO; individual countries with significant declines in lion offtakes: BW, TZ and ZW.

Found at: doi:10.1371/journal.pone.0005941.s002 (1.08 MB EPS)

Figure S3 Quotas, offtakes and catch rates each year since the peak harvests for cougars in Colorado, Montana and Utah and lions in Tanzania and Botswana; duration of lion hunts in

Zimbabwe. Catch rates are (offtakes/quotas). Catch rates have generally declined because offtakes have fallen more quickly than quotas. Catch rates briefly improved in Utah and Botswana when quotas were adjusted downwards, but subsequently resumed an overall decline; Montana’s adjustments in quotas are too recent to evaluate. For Zimbabwe, vertical lines indicate standard errors; numbers are sample sizes; duration of lion hunts became significantly longer between 1997 and 2001 ($P < 0.01$). No other data are available on quotas or hunt durations from these or other countries/states. The bottom graphs show that declines in lion trophy exports are unlikely to reflect declining market demand; imports of lion trophies have increased, especially in recent years for captive-bred or “canned” lion trophies for South Africa. The declines in trophy exports are also unlikely to be caused by irregular reporting; adding additional exports of skins from Botswana, Tanzania and Zimbabwe would not significantly change the pattern of decline.

Found at: doi:10.1371/journal.pone.0005941.s003 (1.38 MB EPS)

Figure S4 Simulated impacts of trophy hunting in cougars for varying degrees of habitat loss. Solid lines are the same as in Fig. 1: all available males above the age minimum are harvested each year and available habitat remains unchanged over 100 yrs. Dashed lines show population sizes with the same harvest strategies but with 20% habitat loss in 100 yrs; dotted lines represent outputs with 40% habitat loss.

Found at: doi:10.1371/journal.pone.0005941.s004 (1.49 MB EPS)

Table S1

Found at: doi:10.1371/journal.pone.0005941.s005 (0.03 MB DOC)

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Author Contributions

Conceived and designed the experiments: CP MK KN. Performed the experiments: MK. Analyzed the data: CP MK HB LP KN. Contributed reagents/materials/analysis tools: MK HC HB LP DLG GP MS AS GB LH KN. Wrote the paper: CP DLG KN.

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Status and Ecological Effects of the World's Largest Carnivores

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Background: The largest terrestrial species in the order Carnivora are wide-ranging and rare because of their positions at the top of food webs. They are some of the world's most admired mammals and, ironically, some of the most imperiled. Most have experienced substantial population declines and range contractions throughout the world during the past two centuries. Because of the high metabolic demands that come with endothermy and large body size, these carnivores often require large prey and expansive habitats. These food requirements and wide-ranging behavior often bring them into conflict with humans and livestock. This, in addition to human intolerance, renders them vulnerable to extinction. Large carnivores face enormous threats that have caused massive declines in their populations and geographic ranges, including habitat loss and degradation, persecution, utilization, and depletion of prey. We highlight how these threats can affect the conservation status and ecological roles of this planet's 31 largest carnivores.

Advances: Based on empirical studies, trophic cascades have been documented for 7 of the 31 largest mammalian carnivores (not including pinnipeds). For each of these species (see figure), human actions have both caused declines and contributed to recovery, providing "natural experiments" for quantifying their effects on food-web and community structure. Large carnivores deliver economic and ecosystem services via direct and indirect pathways that help maintain mammal, avian, invertebrate, and herpetofauna abundance or richness. Further, they affect other ecosystem processes and conditions, such as scavenger subsidies, disease dynamics, carbon storage, stream morphology, and crop production. The maintenance or recovery of ecologically effective densities of large carnivores is an important tool for maintaining the structure and function of diverse ecosystems.

Outlook: Current ecological knowledge indicates that large carnivores are necessary for the maintenance of biodiversity and ecosystem function. Human actions cannot fully replace the role of large carnivores. Additionally, the future of increasing human resource demands and changing climate will affect biodiversity and ecosystem resiliency. These facts, combined with the importance of resilient ecosystems, indicate that large carnivores and their habitats should be maintained and restored wherever possible. Preventing the extinction of these species and the loss of their irreplaceable ecological function and importance will require novel, bold, and deliberate actions. We propose a Global Large Carnivore Initiative to coordinate local, national, and international research, conservation, and policy.

ARTICLE OUTLINE

Ecological Effects of Large Carnivores

Ecosystem and Economic Services

Anthropogenic Impacts

Climate Change

Outlook

A Final Word

SUPPLEMENTARY MATERIALS

Figs. S1 to S4

Tables S1 to S3

ADDITIONAL RESOURCES

"Lords of nature: Living in a land of great predators"; www.youtube.com/watch?v=PagO3gmwmA0

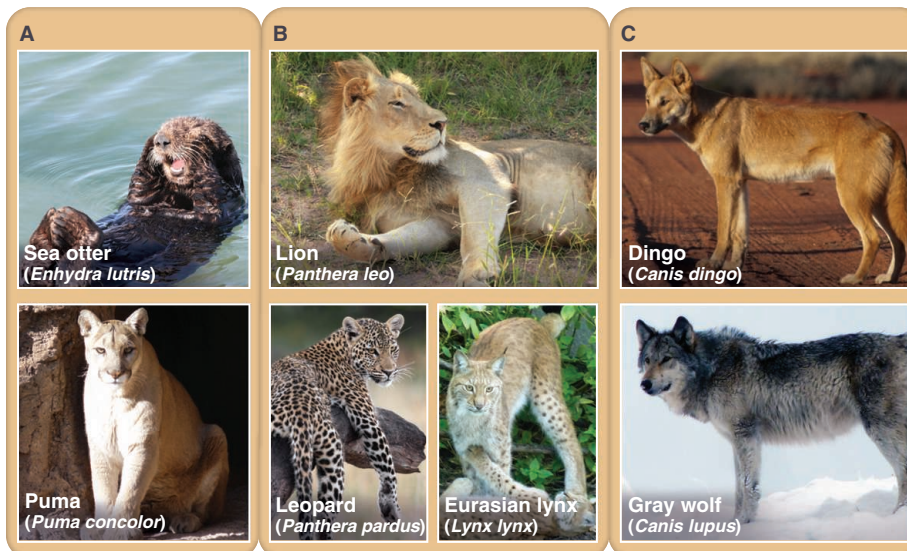
George Monbiot, TED "For more wonder, rewrite the world"; www.youtube.com/watch?v=8rZzHkpyPkc

Trophic Cascades Program, www.cof.orst.edu/cascades/

Large Carnivore Initiative for Europe, www.lcie.org/Home.aspx

RELATED ITEMS IN SCIENCE

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Ecologically important carnivores. Seven species of large carnivores with documented ecological effects involving (A) "tri-trophic cascades" from large carnivores to prey to plants, (B) "mesopredator cascades" from large carnivores to mesopredators to prey of mesopredators, and (C) both tri-trophic and mesopredator cascades. [Photo credits: sea otter (N. Smith), puma (W. Ripple), lion (K. Abley), leopard (A. Dey), Eurasian lynx (B. Elmhagen), dingo (A. McNab), gray wolf (D. McLaughlin)]

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Status and Ecological Effects of the World's Largest Carnivores

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Large carnivores face serious threats and are experiencing massive declines in their populations and geographic ranges around the world. We highlight how these threats have affected the conservation status and ecological functioning of the 31 largest mammalian carnivores on Earth. Consistent with theory, empirical studies increasingly show that large carnivores have substantial effects on the structure and function of diverse ecosystems. Significant cascading trophic interactions, mediated by their prey or sympatric mesopredators, arise when some of these carnivores are extirpated from or repatriated to ecosystems. Unexpected effects of trophic cascades on various taxa and processes include changes to bird, mammal, invertebrate, and herpetofauna abundance or richness; subsidies to scavengers; altered disease dynamics; carbon sequestration; modified stream morphology; and crop damage. Promoting tolerance and coexistence with large carnivores is a crucial societal challenge that will ultimately determine the fate of Earth's largest carnivores and all that depends upon them, including humans.

The order Carnivora consists of 245 terrestrial species inhabiting nearly every major habitat on Earth (1). These mammalian species, which we call carnivores, are generally unified by a shared heritage of subsisting largely on other animals and are naturally rare because of their position at the top of the food web. These are also some of the world's most revered and iconic species. Ironically, they are also some of the most threatened. During the previous two centuries, many carnivores have experienced substantial population declines, geographic range contractions, and fragmentation of their habitat (2, 3).

Carnivores of various sizes play an important role in regulating ecosystems (4–7). These roles, moreover, may not be redundant among carnivore species, because the strength and nature of their impacts are influenced by factors such as the carnivore's size, metabolic demands, density, sociality, and hunting tactics. The larger carnivores especially tend to have large energetic constraints, slow life histories, and low population densities and roam widely in search of larger prey (8–10). This conflation of low population densities and reproductive rates with high food requirements and wide-ranging behavior, bringing them into conflict with humans and livestock, is what makes them vulnerable and poorly able to respond to persecution.

Large carnivores can exert ecological effects despite existing at low densities (11), but persecution can affect their social structure and influence their ecological role (12). Classically, the effects of large carnivores are thought to extend down the food web to herbivores and to plants, but we are learning that their cascading influences propagate broadly to other species as mediated by their controlling effects on mesocarnivores (4, 13, 14). Large carnivores have the dual role of potentially limiting both large herbivores through predation and mesocarnivores through intraguild competition, thus structuring ecosystems along multiple food-web pathways. Together, these controls influence the nature and strength of ecosystem functioning. What makes the conservation of large carnivores exceptionally important, therefore, is both their vulnerability to extinction and their ability to structure ecosystems. With this in mind, our focus here is on the largest carnivores.

We review the conservation status and ecological effects of the 31 largest (average adult

body masses ≥ 15 kg) species of Carnivora (not including pinnipeds). Although most of these species are obligate meat eaters, some are omnivorous and one is herbivorous (Table 1). The remaining 214 carnivore species with body masses <15 kg are not considered here, but we acknowledge they also can play important and varied roles in communities (4, 13). The 31 largest carnivores belong to five families: Canidae, Felidae, Mustelidae, Ursidae, and Hyaenidae. They generally have small population sizes (Fig. 1 and table S1), often due to high levels of range loss (Table 1). Many of these species (61%) are listed by the International Union for the Conservation of Nature (IUCN) as threatened (vulnerable, endangered, or critically endangered) and are at risk of local or total extinction. Most (77%) are undergoing continuing population declines (Table 1). Estimates of range contractions for 17 of the 31 species revealed that they currently occupy on average only 47% (minimum $<1\%$, maximum 73%) of their historical ranges (Table 1). These range losses can result in local population extinctions, which have implications for the maintenance of ecosystem and socioeconomic services. Thus, many of these species are gradually disappearing just as we are beginning to understand and appreciate their roles in ecosystems and the many societal benefits that accrue from their preservation (5, 15).

We report our current understanding of the substantial ecological roles large-carnivore species play in ecosystems and how their population declines, extirpations, and recoveries stand to influence ecological communities and ecosystems across the globe. We further consider how those roles may change as environmental conditions become altered when humans cause habitat loss and climate change. We end by addressing the outlook for the future and the looming uncertainties motivating an urgent need for more research on carnivore interactions in food webs and the conservation of these species.

Ecological Effects of Large Carnivores

Seven of the 31 species of large carnivores are associated with documented trophic cascades. Therefore, we focus on these seven species with analysis and discussion. Each of the seven species is well studied in comparison to other large carnivores (fig. S2). In all cases, these seven species of large carnivores clearly have cascading influences on ecological communities and ecosystems. We assessed the general strength of these effects using available data to calculate the $\log_{10}(X_a/X_p)$ effect magnitudes, where X_a and X_p are the values for the response variables with the large-carnivore species absent and present, respectively [for methods, see (6)]. The effect magnitude of large-carnivore removal on the abundance of prey, plants, and mesopredators ranged from -2.3 to 2.3 (Fig. 2). These are considered large effects. For example, an effect size of 2 or -2 represents a difference of two orders of magnitude (100 times) in the effect

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between when carnivores are absent as compared to present. These values also rank relatively high when compared to a meta-analysis of 114 case studies of predators from both aquatic and terrestrial systems, where effects, expressed in log₁₀ ratios, ranged from −0.3 to 1.0 (16). With the exception of the sea otter, all of the aquatic and terrestrial predators included in that study were ≤2 kg in body mass, suggesting a potential link between carnivore size and ecological influence. Below we provide a brief synthesis for each of the seven large-carnivore species. Following these species accounts is a general discussion of other large-carnivore species, for which less is known about their ecological effects.

Lions and Leopards

The African lion (*Panthera leo*) occupies 17% of its historical range and is listed as vulnerable by

the IUCN. Its abundance has declined dramatically in recent decades because of habitat loss and indiscriminate killing in defense of humans and livestock (17). The leopard (*Panthera pardus*) is near threatened and occupies 65% of its historical range. When sympatric, lions and leopards exert control on mesopredators. In West Africa, olive baboons (*Papio anubis*) increased in abundance at rates most closely correlated with declines in these apex predators relative to seven other environmental variables that might explain baboon abundance and range occupancy (18). Increases in baboons correlated with accelerated declines in small ungulates and primates. Among large mammals, baboons pose the greatest threat to livestock and crops and they use many of the same sources of animal protein and plant foods as humans in sub-Saharan Africa. In some areas, baboon raids in agricultural fields require fami-

lies to keep children out of school so they can help guard planted crops (18).

Dingoes

The dingo (*Canis dingo*), thought to have arrived in Australia around 5000 years ago (19), became the sole remaining mammalian apex predator on the continent after the extinction of the Tasmanian tiger (*Thylacinus cynocephalus*). With European settlement, dingo populations have been affected across the continent, notably by the erection of a 5500-km dingo-proof fence designed to keep dingoes out of Australia's major sheep-grazing region. The presence and absence of dingoes on either side of the fence, along with variation in dingo management practices among properties, has produced a continental-scale experiment. The most significant and well-understood effects of dingoes are in the control of populations of native

Table 1. Large-carnivore species list, body mass (in kilograms), diet, endangerment status, population trend, and percent of historical range occupied. Body masses are from Gittleman (15), Mammalian Species Accounts, and the Animal Diversity Web. Diet categories are from

Hunter (1) as follows: M, meat eater; V, vegetation and/or fruit eater; O, omnivore. Species status and trend are from the IUCN Red List (16): LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered.

Family/species*	Common name	Mass, diet	IUCN status (trend)	% of historical range	Reference for % of historical range
Canidae					
<i>Canis lupus</i>	Gray wolf	33, M	LC (stable)	67	(1)
<i>Canis rufus</i>	Red wolf	25, M	CR (increasing)	<1	(91)
<i>Chrysocyon brachyurus</i>	Maned wolf	23, O	NT (unknown)	68	(2)
<i>Lycan pictus</i>	African wild dog	22, M	EN (decreasing)	10	(17)
<i>Cuon alpinus</i>	Dhole	16, M	EN (decreasing)	—	—
<i>Canis dingo</i> †	Dingo	15, M	VU (decreasing)	84	(20)
<i>Canis simensis</i>	Ethiopian wolf	15, M	EN (decreasing)	2	(17)
Felidae					
<i>Panthera tigris</i>	Tiger	161, M	EN (decreasing)	18	(3)
<i>Panthera leo</i>	Lion	156, M	VU (decreasing)	17	(17)
<i>Panthera onca</i>	Jaguar	87, M	NT (decreasing)	57	(3)
<i>Acinonyx jubatus</i>	Cheetah	59, M	VU (decreasing)	17	(17)
<i>Panthera pardus</i>	Leopard	53, M	NT (decreasing)	65	(3)
<i>Puma concolor</i>	Puma	52, M	LC (decreasing)	73	(3)
<i>Panthera uncia</i>	Snow leopard	33, M	EN (decreasing)	—	—
<i>Neofelis nebulosa</i>	Clouded leopard	20, M	VU (decreasing)	—	—
<i>Neofelis diardi</i>	Sunda clouded leopard	20, M	VU (decreasing)	—	—
<i>Lynx lynx</i>	Eurasian lynx	18, M	LC (stable)	—	—
Mustelidae					
<i>Enhydra lutris</i>	Sea otter	28, M	EN (decreasing)	—	—
<i>Pteronura brasiliensis</i>	Giant otter	24, M	EN (decreasing)	—	—
<i>Aonyx capensis</i>	Cape clawless otter	19, M	LC (stable)	—	—
Ursidae					
<i>Ursus maritimus</i>	Polar bear	365, M	VU (decreasing)	—	—
<i>Ursus arctus</i>	Brown bear	299, O	LC (stable)	68	(3)
<i>Ailuropoda melanoleuca</i>	Giant panda	134, V	EN (decreasing)	—	—
<i>Ursus americanus</i>	American black bear	111, O	LC (increasing)	59	(35)
<i>Tremarctos ornatus</i>	Andean black bear	105, O	VU (decreasing)	—	—
<i>Ursus thibetanus</i>	Asiatic black bear	104, O	VU (decreasing)	—	—
<i>Melursus ursinus</i>	Sloth bear	102, O	VU (decreasing)	—	—
<i>Helarctos malayanus</i>	Sun bear	46, O	VU (decreasing)	—	—
Hyaenidae					
<i>Crocota crocuta</i>	Spotted hyena	52, M	LC (decreasing)	73	(17)
<i>Hyaena brunnea</i>	Brown hyena	43, O	NT (decreasing)	62	(17)
<i>Hyaena hyaena</i>	Striped hyena	27, O	NT (decreasing)	62	(17)

*Changes to taxonomic status have influenced the number of species included in this group, and some less-known and taxonomically ambiguous carnivores may be missing from this analysis because they have yet to be listed by the IUCN. †Currently incorporates the New Guinea singing dog, *C. hallstromi*, whose taxonomic and conservation status is yet to be elucidated.

herbivores, introduced herbivores, and the exotic mesopredator the red fox (*Vulpes vulpes*). The suppression of these species by dingoes reduces total herbivory and predation pressure, in turn benefiting plant communities and smaller native prey (12, 14, 20, 21). The dingo's social stability and associated behavior are thought to be key to its ecological effectiveness (12). Overall, the suppression of dingoes has probably contributed to the endangerment and extinction of small marsupials and rodents over much of the continent (21, 22).

Eurasian Lynx

The Eurasian lynx (*Lynx lynx*) maintains an extensive distribution in eastern and northern Eurasia, but it has been extirpated from large parts of Western Europe (23). At the continental scale, the effects of lynx predation increase with harsh winter conditions (23, 24). Lynx may limit both prey (roe deer *Capreolus capreolus*) and mesocarnivore (red fox) abundance, so changes in lynx status may trigger cascading effects along two pathways, of which the mesocarnivore-mediated cascade is the more explored (25). The recent recovery and enhanced conservation protection of Eurasian lynx in Finland were accompanied by a decline in red fox abundance and a commensurate recovery in the abundance of forest grouse (*Tetrao tetrix* and *T. urogallus*) and mountain hare (*Lepus timidus*) (7, 25). Moreover, where lynx density had recovered to "ecologically effective" levels, the controlling effects of lynx on red foxes and prey increased with ecosystem pro-

ductivity, indicating that the strength of predator control may vary as a function of the net primary productivity of the ecosystem (26, 27).

Sea Otters

Sea otters (*Enhydra lutris*) were hunted to near-extinction during the Pacific maritime fur trade in the 18th and 19th centuries (28). Sea otter populations are presently stable or increasing from about Kodiak Island eastward, deeply depleted [presumably because of killer whale predation (29)] from about Kodiak Island westward through the Aleutian archipelago, and largely recovered in Russia. The earlier recovery of these populations and the more recent decline of recovered populations in southwest Alaska (29) offer natural experiments to study the sea otter's influences on coastal ecosystems. The best-documented cascade of effects involves sea otters limiting herbivorous sea urchins and, in turn, enhancing the abundance and distribution of kelp and other fleshy macroalgae in coastal inshore ecosystems (Fig. 3A) (30). As sea otter populations recover and decline, shifts between the kelp-dominated and urchin-dominated conditions can be abrupt (31). Once reached, these different ecological states tend to persist (32) unless the system is pushed strongly to the other state by substantial increases or reductions in otter abundance. The follow-on effects of these shifts influence numerous other species and ecological processes in coastal ecosystems through three basic mechanisms: the creation of biogenic habitat (i.e., created by living

organisms), the enhancement of primary production, and the influence of kelp forests in dampening coastal waves and currents [reviewed in (31)].

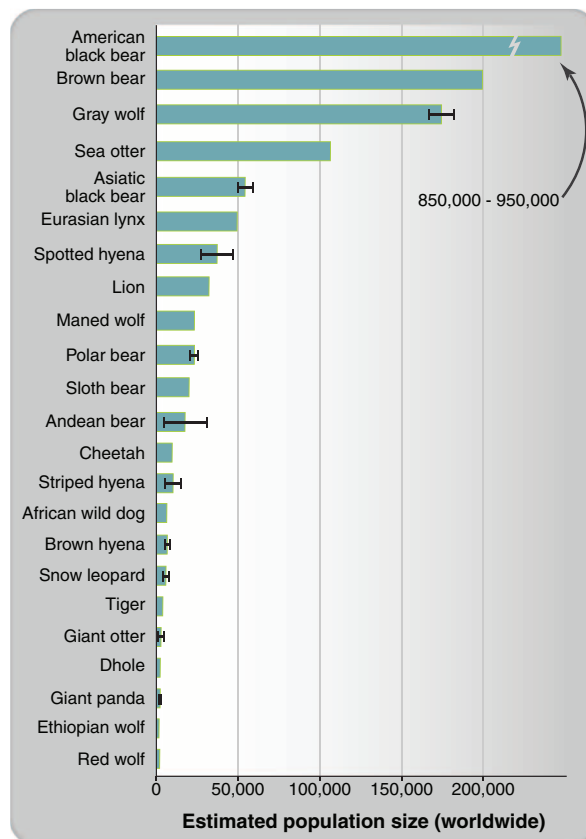
Gray Wolves

The gray wolf (*Canis lupus*) is one of the world's most widely distributed mammals and the most studied large carnivore (fig. S2). It has been extirpated from much of Western Europe, the United States, and Mexico, and its overall range has been reduced by approximately one-third because of persecution by humans and habitat fragmentation (1). In recent decades, wolf population declines have been arrested because of enhanced legal protection, reintroduction programs, and natural recolonization, resulting in population recoveries in portions of the Rocky Mountains, Great Lakes, and southwestern regions of North America, as well as in various parts of Europe. Other than humans, gray wolves, by virtue of their widespread geographic distribution, group hunting, and year-round activity, are the most important predator of cervids in the Northern Hemisphere (33). Predation by wolves with sympatric bears (*Ursus* spp.) generally limits cervid densities (33). In North America and Eurasia, cervid densities were, on average, nearly six times higher in areas without wolves than in areas with wolves (34). As early as the 1940s, cervid irruptions, after wolf and other predator declines, were first documented in various ecosystems of western North America (35). The shifts in plant communities consequent to the cascading effects of wolf extirpations and of recoveries have been found across a variety of areas of North America, representing a wide range of productivity (6). In Yellowstone National Park, wolves were reintroduced in 1995–1996, making this park one of the most predator-rich areas in North America. This reintroduction triggered various direct and indirect effects, as mediated by both mesopredators and cervid prey (Figs. 3B and 4).

Pumas

The range of the puma (*Puma concolor*) in the Western Hemisphere remains larger than that of any other terrestrial mammal, even though they have been extirpated from most of the eastern United States (36). In the absence of pumas and sometimes other large carnivores, hyperabundant cervids [such as the white-tailed deer (*Odocoileus virginianus*)] in the eastern United States and Canada now affect many aspects of ecosystem function, including plant recruitment and survival, endangered species status, forest stand structure, nutrient dynamics, and socioeconomics through vehicle collisions (37). Where pumas are present, they can be important drivers of cervid populations and associated trophic relations, as in canyon settings in western North America, where they locally limit mule deer (*O. hemionus*) densities, releasing woody plants from browsing suppression (38, 39). Pumas also appear to influence processes affecting terrestrial and aquatic species, including hydrophytic plants, wildflowers, amphibians,

Fig. 1. Worldwide population estimates of large-carnivore species. Error bars represent the low and high range of the estimates when available. Population estimates were not available for all species. Species ranges vary widely, and range sizes can have a strong influence on species population levels (table S1). Sources: Gray wolf (90), all other species IUCN (91).



lizards, and butterflies. Their presence may also help to stabilize stream banks and channels (38). Pumas may induce their prey to engage in “human shielding” as an antipredator strategy. Deer at risk from pumas, for example, associated themselves with human development at high densities, in turn causing plant damage (38, 39).

Other Large Carnivores

Little is known about the ecological effects of the other large-carnivore species listed in Table 1, and questions remain about their potential roles in controlling food webs and ecosystem functioning, especially in the tropics and subtropics (Fig. 5). However, some valuable lessons come from the flooding of a forest region in Venezuela to generate hydroelectric power. This once-intact, productive tropical system was composed of a species-rich food web with multiple linkages among species. Flooding fragmented the region to produce mountaintop islands—the Lago Guri

islands—resulting in the loss of an entire predator guild of jaguars (*Panthera onca*), pumas, lesser mammalian predators, large raptors, and snakes (40). This loss of predators had cascading effects on species of pollinators, seed dispersers, seed predators, folivores, and mesopredators, as well as on woody plant recruitment, bird abundance, and soil carbon/nitrogen ratios (41).

Predator species often co-occur, requiring consideration of their joint effects. Multiple predator effects on prey species and on ecosystems can be synergistic (15). Thus, in some cases, the strength of a trophic cascade may be due to synergisms owing to complementarity among species in the top carnivore guild of communities. This implies that the combined effects of predator species may need to be conserved to fully ensure control over communities and ecosystem functioning. For example, bears of northern latitudes (*Ursus* spp.) may control the recruitment of juveniles into populations of their prey species (42). Because

bears are opportunistic omnivores and eat a variety of foods, their effects may complement those of gray wolves (34). In North America, both black (*U. americanus*) and brown (*U. arctos*) bears commonly prey on neonatal cervids, taking a large percentage of the annual offspring that are less than 1 month old, and these effects could be additive. In Yellowstone National Park, bears killed more elk (*Cervus elaphus*) calves than did gray wolves, coyotes (*Canis latrans*), and pumas combined (43). In Europe, roe deer densities were significantly lower in areas with sympatric wolves and lynx than in areas with wolves alone or areas where both predators were absent (24, 34). The effect of multiple predators on prey, however, need not always be synergistic. Adult female elk mortality was similar in areas of western North America with pumas alone as compared to areas with sympatric pumas and wolves (44).

Questions persist about how large-carnivore effects interact with habitat productivity. Theory

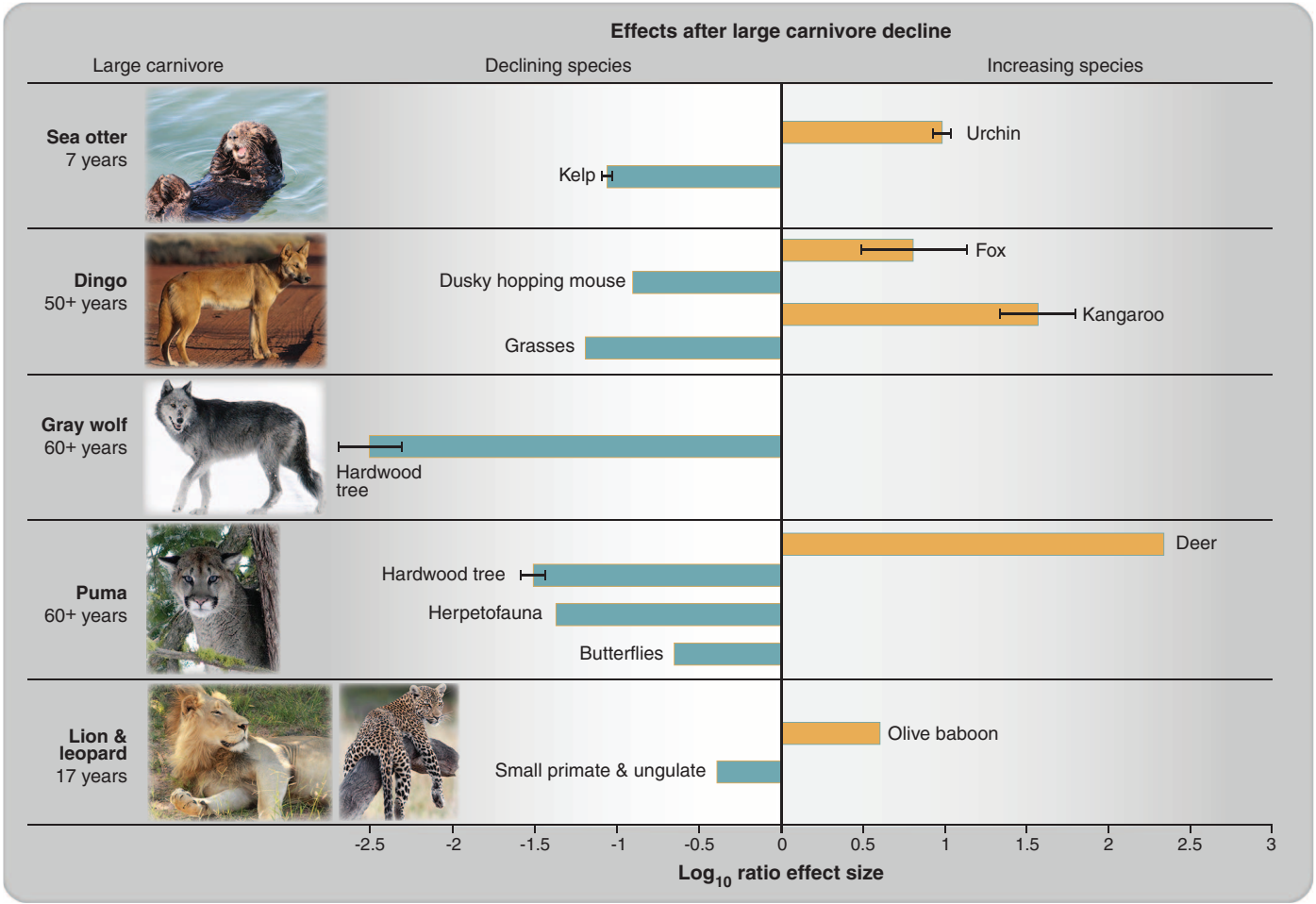


Fig. 2. Examples of effect sizes, shown as \log_{10} ratios, after the removal of large-carnivore species. Sea otters (29, 92), dingoes-foxes and dingoes-kangaroo (21, 93), dingoes-mice (*Notonmys fuscus*) (93), dingoes-grasses (20), gray wolves–hardwood trees (94, 95), pumas–hardwood trees (38, 39), pumas-deer-herpetofauna-butterflies (38), and lions and leopards (38). The number of years refers to the time since large-carnivore extirpation. The \log_{10} ratios were calculated by dividing the values of each response variable without predator by those with predator and then taking the \log_{10} of

that ratio. Positive log ratios₁₀ indicate a positive effect, and negative log₁₀ ratios indicate a negative effect of removing large carnivores. For studies using time-series data, we used the final sampling date in our analysis. The orange bars indicate direct effects and the blue bars indicate indirect effects. Error bars represent standard errors and were only available in some cases. [Photo credits: sea otter (N. Smith), dingo (A. McNab), gray wolf (Yellowstone National Park), puma (Washington Department of Fish and Wildlife), lion (K. Abley), leopard (A. Dey)]

predicts that the strength of cascading effects may vary with the productivity of ecosystems and should show a “humped relationship” with ecosystem productivity (26, 27). That is, we might not expect to see strong trophic cascades in ecosystems such as extreme deserts, high elevations, or high latitudes, where low primary productivity limits herbivore populations and where there is insufficient energy available to support populations of large carnivores (27). The trophic effects of single carnivore species might also be diminished in extremely productive environments, because prey species diversity may also be high in such systems and, consequently, the strength of interspecific interactions is diffused across a greater number of interaction pathways (20, 41, 45). For example, in a productive tropical forest, Sunda clouded leopards (*Neofelis diardi*) had no measurable effect on the abundance of the main large ungulate prey species (46). Conversely, there is also empirical evidence indicating that some canids consistently limit prey densities regardless of ecosystem productivity (34, 47). Accordingly, more analyses of how productivity interacts with trophic interactions are needed. To this end, regions harboring large-carnivore populations with different conservation statuses, including places without them, can be used as broad bioclimatic contexts for natural experiments.

Ecosystem and Economic Services

Large carnivores deliver economic and ecosystem services in a variety of direct and indirect ways. Because of their iconic and charismatic nature, large carnivores provide direct economic

benefits associated with tourism. In both Minnesota and Yellowstone (48, 49) and the African photo-safari industry (50), the opportunity to simply observe large carnivores can drive tourism revenue. In Yellowstone alone, wolf-related tourism expenditures range from \$22 million to \$48 million (in U.S. dollars) per year (49).

Large carnivores also have strong potential to indirectly deliver ecosystem services, such as carbon storage to buffer climate change, biodiversity enhancement, reestablishment of native plant diversity, riparian restoration, and even regulation of diseases. In some ecosystems, large carnivores may enhance carbon storage by limiting the numbers of their herbivore prey, thus allowing plants (all of which absorb and store CO₂) to flourish. Carnivore conservation and restoration might reverse declines in forests stands and production, thereby aiding carbon storage, especially in the highly productive tropics, where declines in plant biomass occur after predator extirpation (40, 41). Maintaining gray wolf populations and their interactions with moose is estimated to help store significant amounts of carbon in boreal ecosystems (51). The restoration of sea otter populations can reduce sea urchin herbivores, thereby allowing kelp ecosystems to flourish at levels that can, in the North American range, lead to a 4.4- to 8.7-teragram increase in stored carbon valued at \$205 million to \$408 million (in U.S. dollars) on the European Carbon Exchange (52). Predators may enhance scavenger diversity (53) and thereby contribute to nutrient cycling, in addition to myriad other documented cascading and ramifying pathways (15). In riparian systems, large carnivores

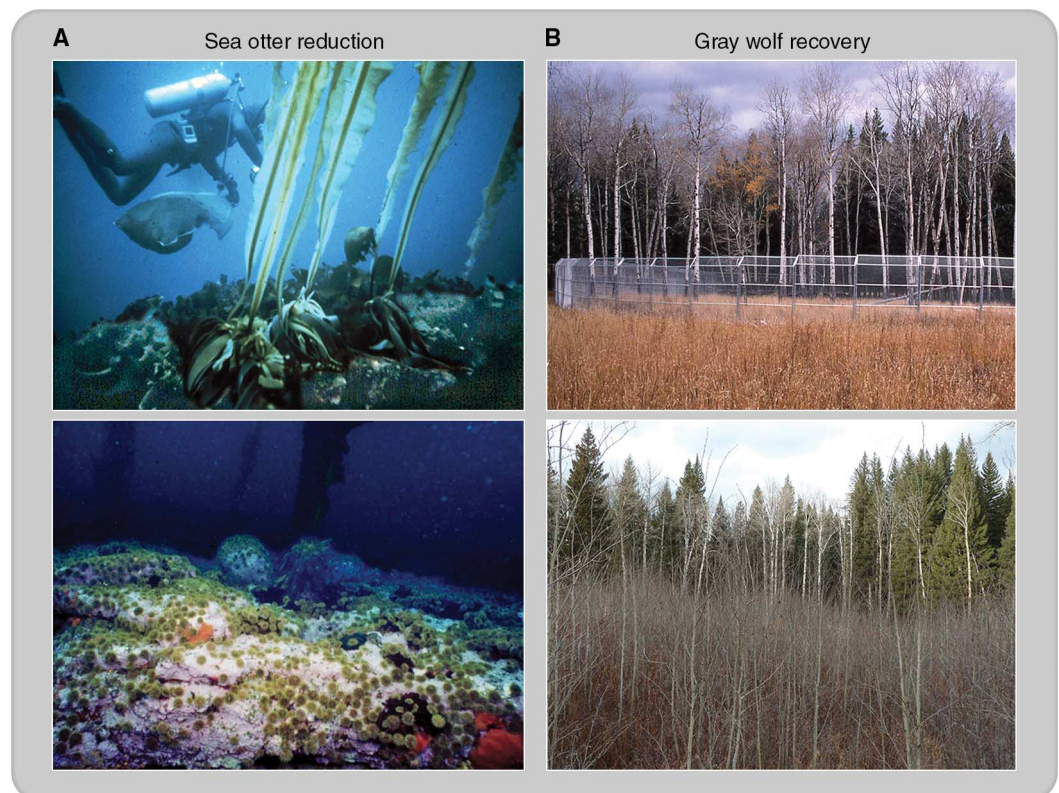
may reduce stream bank erosion through the growth of woody plants and enhance water quality and flood control through the restoration of beaver that benefit from the restored plants (54–57). Large carnivores help reduce disease prevalence in ungulate prey populations, thereby mitigating agricultural costs because of spillover effects on domestic livestock (58). Perhaps counterintuitively, large carnivores may also provide crucial services for the very industry they are perceived to be at most in conflict with: pastoralism. By limiting the density of wild herbivores and promoting productivity, large carnivores may enable pastoral activities that are sustainable (12, 59). This is not to deny that large carnivores also have direct costs, often associated with livestock losses (60), and balancing these costs against potential benefits for human-dominated ecosystems as a whole is a pressing challenge (61). Regardless, the potentially widespread beneficial ecosystem and economic services associated with large carnivores are underappreciated by society.

Anthropogenic Impacts

Large-carnivore population declines are typically precipitated by multiple, and sometimes concurrent, human threats, including habitat loss and degradation, persecution, utilization (such as for traditional medicine, trophy hunting, or furs), and depletion of prey. Globally, the strength of these threats varies substantially by region (Fig. 6 and table S2). These threats are sometimes localized to only parts of a carnivore’s range and, in some cases, may extend beyond its range, thus acting to limit reoccupation of former habitats.

Fig. 3. Examples of plant response after sea otter reduction and after gray wolf recovery. (A)

An area of seafloor near Kirilof Point, Amchitka Island, Alaska, in 1971 (upper left, photo by P. Dayton), at which time sea otters were abundant, and in 2001 (lower left, photo by M. Kenner) at which time sea otter numbers had been reduced by more than 90% by killer whale predation. **(B)** Photos of the Yellowstone Northern Range taken in October 1994 (top right, photo by National Park Service) and November 2012 (bottom right, photo by D. McLaughlin), showing increased recruitment of aspen since wolf re-introduction in 1995–1996 at the site of the Crystal Creek gray wolf holding pen, which was removed in 1998. Young aspen in the 1994 photo were mostly less than 1 m tall and those in the 2012 photo were typically 3 to 4 m tall.



Human actions may dampen or even eliminate cascading effects. For example, Mexican gray wolves in southwestern North America have not yet been restored to an ecologically effective density in relation to that of their main prey, elk, because of ongoing conflicts with livestock grazing and repeated management translocations (62). Likewise, recent wide-scale hunting of recovering gray wolf populations in parts of the Great Lakes region and the western United States may reduce wolf populations below sizes at which they are able to exert their effects on communities and ecosystems (63–65). Furthermore, wolves and other carnivores may have little influence on other species in areas where human hunters have disproportionate effects on prey densities (66). Few large carnivores can persist in parts of Latin America, Asia, and Africa because of the loss of wild ungulate prey species caused by activities such as hunting for bushmeat. The extraction of bushmeat, in turn, has created “empty forests” (1). Conversely, hyperabundant exotic ungulates (domestic livestock) are present in much of the world. These livestock are a potential prey base and thus a continuing source of conflict between humans and large carnivores (17).

Hunting by humans, whether legal as in North America and Europe or illegal as in the pantropical bushmeat trade, may itself cause trophic cascades, because humans are also predators with the potential for ecological impacts. Indeed, human hunting pressure on moose (*Alces alces*) has led to the release of control on willow (*Salix* spp.) shrub production and hence encouraged increases in neotropical migrant bird abundances (42). Although it is often claimed that human hunting substitutes for predators, it remains doubtful whether such substitution actually leads to the same functional consequences for communities and ecosystems. Effects may be different because of differences in the intensity and timing of predation by humans versus predators, as well as hunting effects on the behavior, age, and sex of prey (67). Many carnivores hunt year-round, day or night, and away from human access points. The behavioral responses of prey to predation risk caused by carnivores may create an “ecology of fear” with myriad cascading effects on ecosystems (68). In the end, it is not surprising that various human activities in Australia (12), North America (13, 34), and Eurasia (24) have been unsuccessful in substituting for large carnivores to control populations of native and nonnative herbivores and mesopredators. The huge importance of carnivores is exemplified by the fact that humans typically cannot replicate the effects of carnivores on ecosystems.

Habitat fragmentation, and more generally the intensity of human uses of landscapes, continue to be persistent threats to larger-bodied carnivores, with the potential for cascading impacts on species diversity (5, 38). There exists, therefore, an increasing need to understand the interacting effects of anthropogenic land-use changes and altered large-carnivore guilds on community structure and function. Because of differences in their

ecology and human tolerance, pumas are able to persist in areas with much higher levels of human land use than are gray wolves, even though these two carnivores are of similar size. Such differential predator species loss in the face of landscape changes may be especially critical if synergism among multiple large carnivores within predator guilds is required to maintain control over prey populations (34, 43). These and other carnivore species make kills in different habitats, or scavenge to supplement their diets, which can determine the nature and rates of prey kills and

consumption (53, 69). In addition to altering predator communities, increased human land use can alter nutrient and water availability, thereby mitigating natural controls over ecological communities and ecosystem functioning (70).

Perhaps one of the most insidious threats to carnivores is global human population size and its associated resource consumption, which are expected to continue rising significantly through at least 2050 (Fig. 7). Increased human population size can lead to increased demand for meat. Interestingly, human carnivory competes with

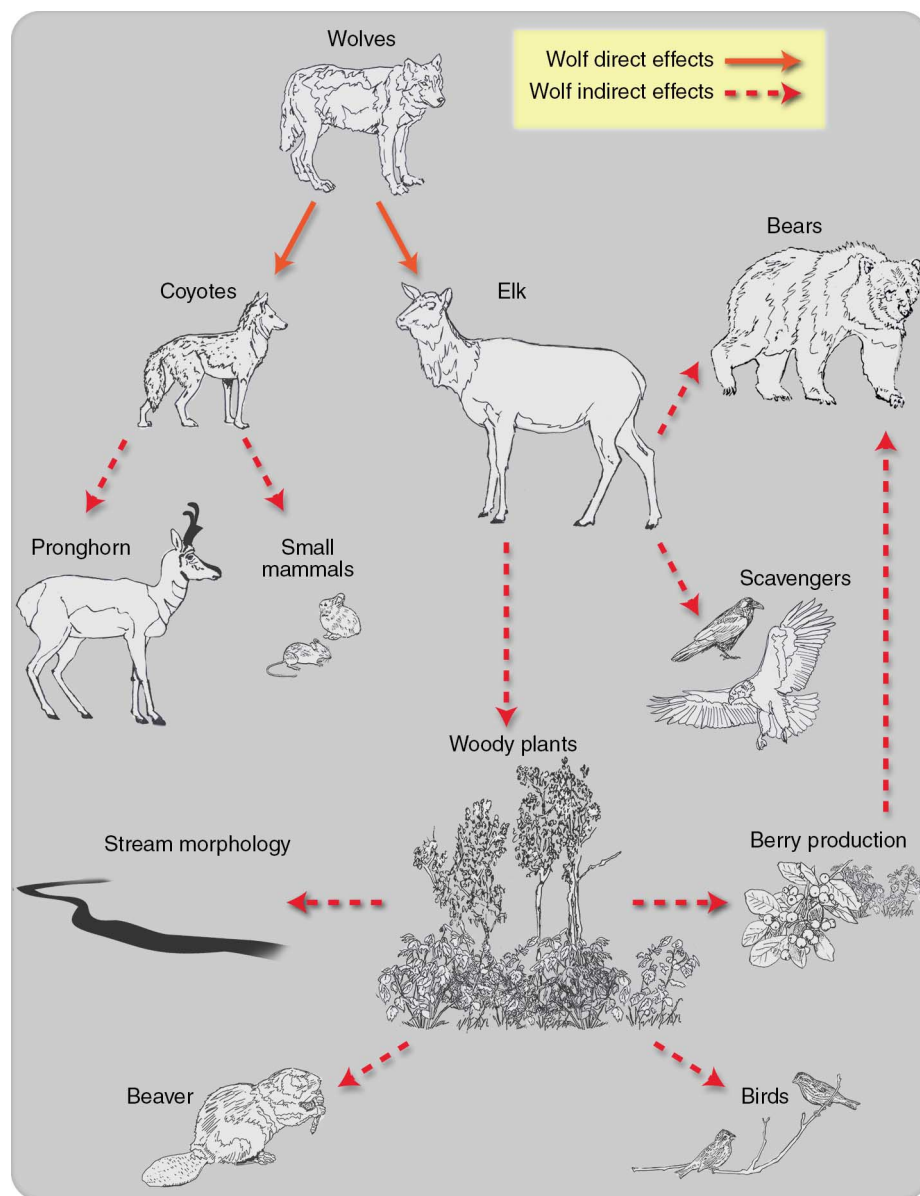


Fig. 4. Conceptual diagram showing direct (solid lines) and indirect (dashed lines) effects of gray wolf reintroduction into the Greater Yellowstone ecosystem. Wolf direct effects have been documented for elk (96) and coyotes (97), whereas indirect effects have been shown for pronghorn (98), small mammals (99), woody plants (100), stream morphology (54), beaver (55), birds (101), berry production (63), scavengers (53), and bears (56, 63). This is a simplified diagram, and not all species and trophic interactions are shown. For example, the diagram does not address any potential top-down effects of pumas, bears, and golden eagles (*Aquila chrysaetos*), which are all part of the Yellowstone predator guild where juvenile or adult elk are prey.

large carnivores. For example, the need for humans to either produce meat through livestock production or to exploit wild sources necessarily puts extra pressure on large carnivores on multiple fronts, including ongoing habitat loss from land conversion, depletion of prey, and direct persecution due to conflicts with livestock. In light of their slow life histories and requirement for large continuous habitat, such trends exacerbate the vulnerability of large carnivores to extinction (9). Increases in both human population and meat consumption can also affect biodiversity, greenhouse gas emissions, food security, deforestation, desertification, and water quality and quantity (71, 72). Therefore, policy for carnivore conservation needs to be joined up with policy addressing these other converging issues having implications at the global scale (71, 72). Ideally, discussions regarding potential decreases in both human fertility rates and per-capita meat consumption would be part of a long-term strategy for overcoming these concurrent challenges.

Climate Change

Looking forward, the status of large carnivores will influence the extent to which individual species, biotic communities, and ecosystems respond to climate change. For example, mesopredators

that have been released from control by the loss of their carnivore predators may increase further in abundance wherever climate change relaxes limitations on their own prey (23). Large carnivores may instrumentally determine resilience against invading species, because both native and introduced species are less likely to become invasive in ecosystems in which food-web interdependencies remain intact (7). These potential buffering capacities remain both poorly appreciated and poorly understood. Widespread modeling approaches forecasting climate change effects on species still simplistically assume that such interactions and interdependencies do not require consideration, let alone quantification (73). Furthermore, climate change is already causing species geographic range shifts that stand to disrupt existing species interactions (74, 75). As species move at different rates and in different directions, novel communities are likely to be created as new combinations of predator and prey species assemble on landscapes. The recently documented change in hunting locations and food habits among polar bears (*Ursus maritimus*) is a case in point. With receding sea ice, polar bears have more difficulty hunting seals, their traditional prey, and are now feeding onshore on the eggs of migratory waterfowl (76).

As climate change progresses, large carnivores might serve as important buffers or amplifiers of effects on ecosystems (77). In Yellowstone National Park, reintroduced gray wolves control the timing and abundance of ungulate carrion resources, on which a suite of scavenger species, ranging in size from grizzly bears to magpies (*Pica hudsonia*), depend for winter survival and reproduction. The return of wolves has buffered the influence of climate change on late-winter carrion availability (77) by shifting the dynamics of carrion availability from a boom-and-bust cycle, linked to climate variability, to a more dependable resource based on shifting patterns of wolf pack size (53). Large carnivores might also help augment ecosystem carbon storage by suppressing herbivores, thereby allowing plants to flourish (34). For instance, the decline of large carnivores in western North America was followed by a decline in hardwood tree recruitment in riparian areas of over two orders of magnitude (6). In northern North America, gray wolves limiting moose populations may be responsible for increased net ecosystem uptake of carbon due to decreased browsing and increased net primary productivity (51). Likewise, the presence of sea otters in near-shore environments suppresses sea urchins, allowing macroalgal kelp to thrive and thereby

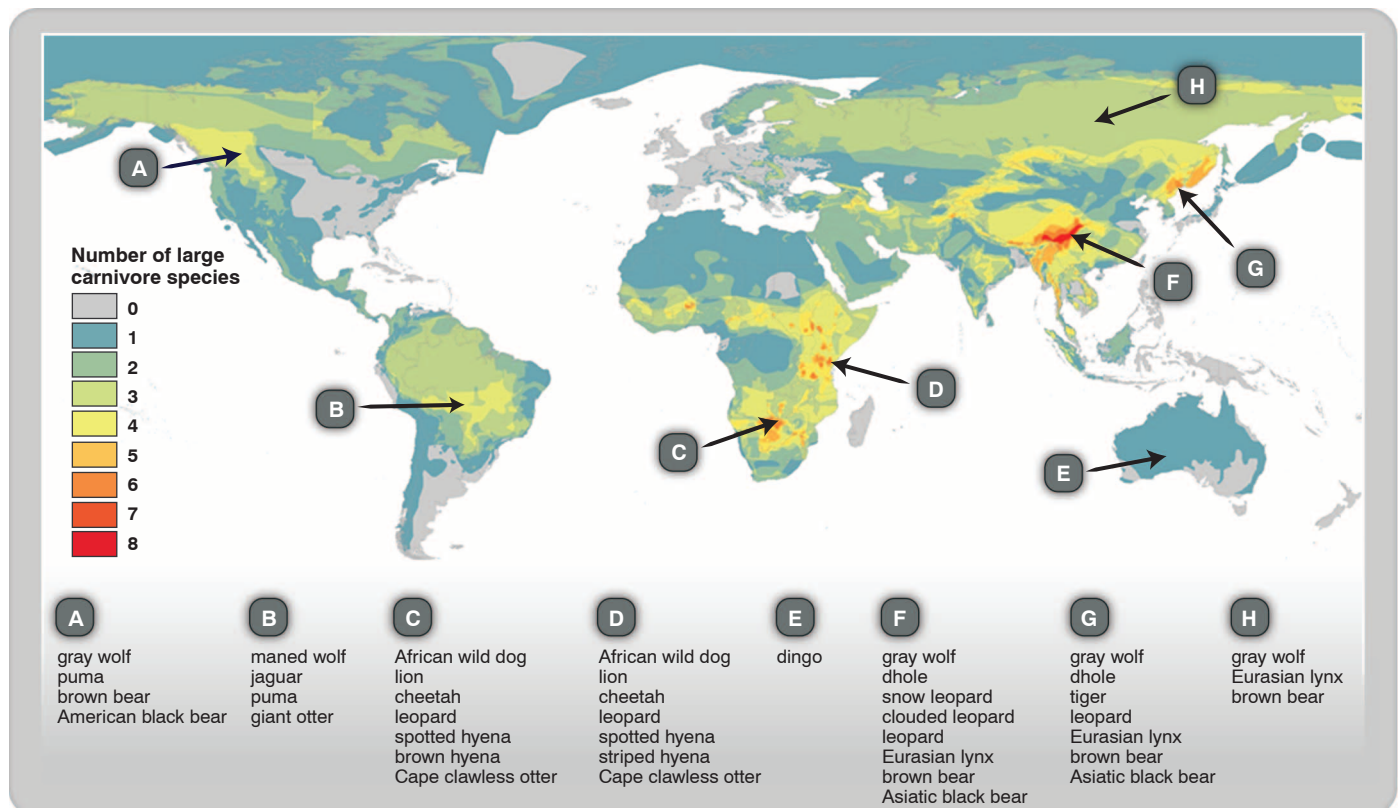


Fig. 5. Contemporary overlap of large carnivore ranges throughout the world. Compared to historical times, large-carnivore range contractions have been most extensive in Europe, southeastern North America, and western and central Africa. The areas with the highest number of species and with intact large-carnivore guilds are some of the best regions for research and conservation (e.g., southeastern Asia, eastern and southern Africa, and northwestern North America).

Northern Eurasia is the region with the most expansive range for a three-species guild (gray wolves, Eurasian lynx, and brown bear). The percent of the total terrestrial land area in each of the eight classes in the map includes 0, 13.3%; 1, 29.1%; 2, 23.5%; 3, 20.5%; 4, 9.1%; 5, 2.8%; 6, 1.1%; 7, 0.4%; 8, 0.1%. Only ~5% of Earth's land surface currently contains more than four overlapping large-carnivore species. See fig. S4 for individual range maps. Source: IUCN (91).

increasing ecosystem carbon production and storage by one to two orders of magnitude (52). Globally, several billion head of ruminating livestock affect global climate change by contributing significant amounts of methane, nitrous oxide, and carbon dioxide (~5.7 gigatons of CO₂ equivalent per year) to the atmosphere, making domestic ruminants a significant contributor to climate change (11.6% of all anthropogenic emissions of greenhouse gases) (72). Decreasing global livestock numbers to reduce greenhouse gas emissions would both mitigate climate change and benefit large-carnivore conservation by reducing ongoing worldwide conflict between large carnivores and livestock.

Outlook

The loss of large carnivores across global ecosystems is predicted to lead to two general outcomes. First, as apex predators are lost, we should expect continued change in cascading controls over communities and ecosystem function. Although these effects will differ with the variation in precipitation, temperature, productivity, diversity, and overall landscape features, the continued loss of carnivores nonetheless will be accom-

panied by changes in plant species diversity, biomass, and productivity. In forest and arid ecosystems, the loss of palatable perennial plant species may interact with global warming to increase the rate of desertification. Because plants are the trophic foundation of all ecosystems, these vegetation changes can be expected to have wide-ranging influences on virtually all other species. The growing list of case studies, some of which we presented above, may well represent the tip of the proverbial iceberg. Changes in species abundance resulting from the loss of large carnivores can be expected to influence numerous other ecological processes, including disease dynamics (78, 79), wildfire (80), and carbon sequestration (51). Furthermore, the effects of large carnivores are now known to have wide ramifications through highly interconnected food-web networks within their associated ecosystems (81). Second, we should expect surprises, because we have only just begun to understand the influences of these animals in the fabric of nature (82).

The classic conception of large-carnivore influences on ecosystems held that predators were responsible for depleting resources such as fish, wildlife, and domestic livestock. This assumption

is still used to justify wildlife management practices aiming to limit or eradicate predators in some regions (83, 84). This conception of carnivore ecology is now outdated and in need of fundamental change. Indeed, evidence shows that their roles are far more complex and varied, and their myriad social and economic effects on humans include many benefits. Conservation decisions must begin to account for these integral roles and the attendant economic costs of carnivore species losses.

Currently, the IUCN Species Survival Commission (SSC) action plan series represents perhaps the most comprehensive attempt to establish priorities for individual species or taxa (84, 85). These action plans not only provide assessments of threats but recommend conservation monitoring and actions for each large-carnivore species (table S3). Action plans are compiled by the taxonomically organized SSC's Specialist Groups (for example, the Canid Specialist Group compiles action plans for all canid species). Large carnivores, however, also share common conservation challenges that cross taxonomic boundaries: slow life histories, requirement for extensive and continuous habitat, low densities, complex

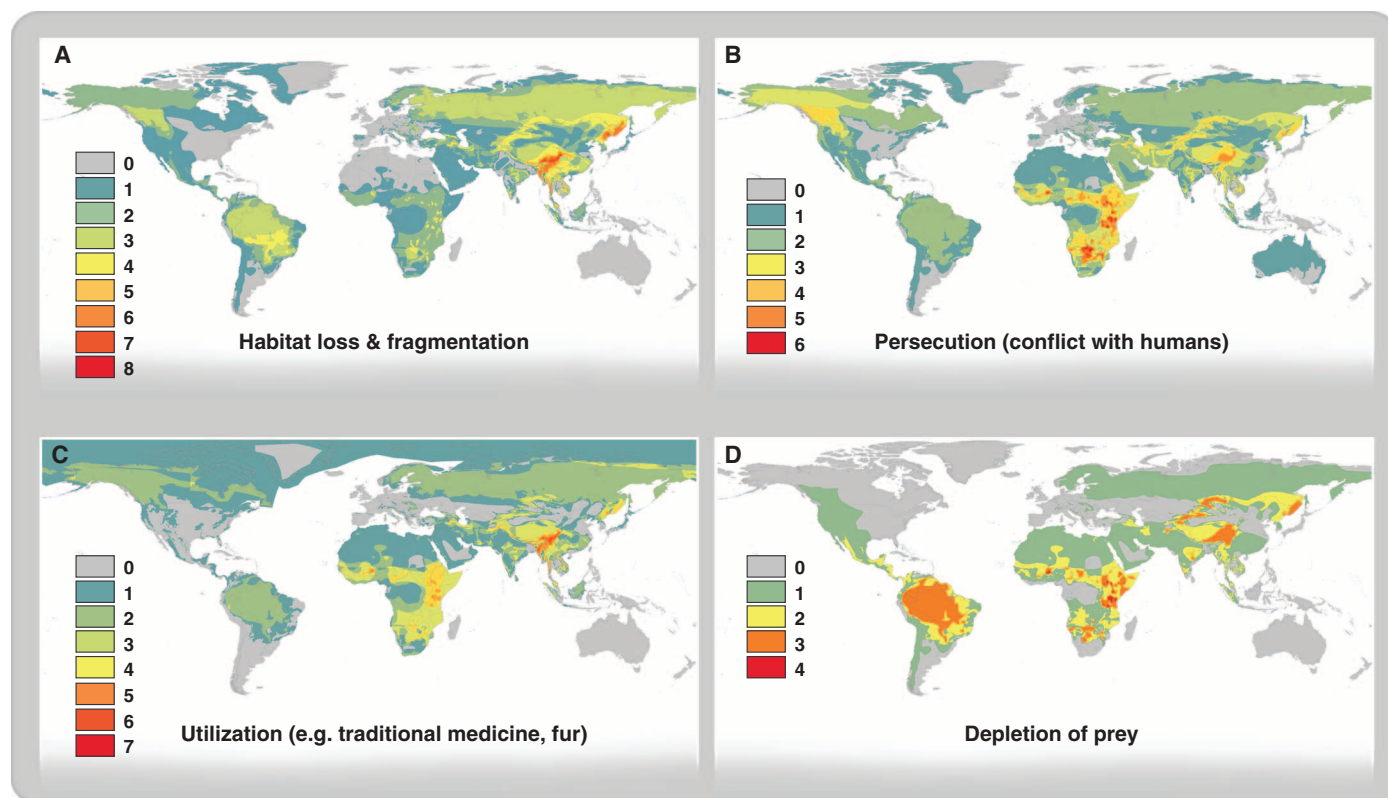


Fig. 6. Maps showing the the spatial overlap for the ranges of large-carnivore species by threat category for habitat loss and fragmentation, persecution, utilization, and depletion of prey. The number of large-carnivore species affected by specific threats is shown in the map legend. Threat categories include: (A) Habitat loss and fragmentation. Forest logging and/or the development of urban, agricultural, and road infrastructure reduces land available to large carnivores and creates barriers between and within populations. (B) Persecution. Culling (poison baiting, trapping, and shooting)

for the purpose of removal or reduction, in some cases reinforced with a government-subsidized bounty system, in response to real or perceived threat to pastoral and agricultural activities and human lives. (C) Utilization. Large carnivores are killed for sport, body parts for traditional medicine, fur, and meat for human consumption, and live animals are captured and sold. (D) Depletion of prey. The decline of prey populations due to human hunting, competition with livestock, habitat loss, and other factors reduces the prey base for large carnivores. See table S2 for raw data. Source: IUCN (91).

social structures, importance to ecological function, and conflict with humans. These common traits and challenges have given rise to the creation of the Large Carnivore Initiative for Europe, a Specialist Group whose vision is “to maintain and restore, in coexistence with people, viable populations of large carnivores as an integral part of ecosystems and landscapes across Europe” (86). We propose the expansion of this initiative, to establish a Global Large Carnivore Initiative (GLCI).

There is now a substantial body of research demonstrating that, alongside climate change, eliminating large carnivores is one of the most significant anthropogenic impacts on nature (5). Unlike climate change, however, large-carnivore conservation has yet to become a focus of widespread public recognition, possibly because they are rare, remote, and in some cases perceived to be dangerous and a threat to economic prosperity. The formation of a GLCI would be an important step for the advancement of international public recognition of the ecological role and inherent value of large carnivores, and for developing and coordinating strategies for conservation actions that promote human/large-carnivore coexistence. Such an organization could be modeled, in part, after the Global Tiger Initiative, which is coordinating local, national, and international tiger conservation policy across their distribution and was endorsed in 2010 by the leaders of all 13 tiger-range countries, with funding from the World Bank (87). These 13 countries and partners have moved well beyond words to accomplishments on the ground, including securing funding, establishing new tiger reserves, passing laws on tiger conservation, creating high-level commissions to improve wildlife law enforcement, addressing habitat loss and fragmentation, promoting connectivity, and more (87). The success of any future GLCI would probably include these types of authoritative actions, orchestrated by politi-

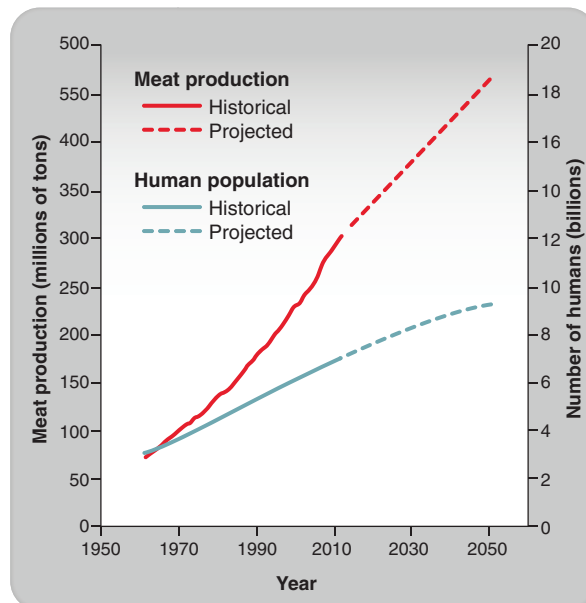
cally bold commitments from nations around the world.

A Final Word

One of the main ecological arguments for the conservation of large carnivores is that they are often capable of exerting strong regulatory effects on ecosystems (5, 15). Although we present evidence that seven of the top carnivore species we reviewed here have such trophic effects, we know much less about the trophic impacts of the 24 other species of large carnivores. More research directed at these species is needed. Also, we need a better understanding of minimum required densities for large carnivores to maintain trophic cascades in different ecosystems, and when and where the strength of those effects is likely to be large versus small. It is also important to understand which human activities are most in conflict with the conservation of specific large carnivores.

A crucial societal challenge is finding creative solutions to maintain viable populations of large carnivores in the face of alternative land uses (7, 59). This is most urgent because global livestock production continues to encroach on land needed by large carnivores, particularly in the developing world, where livestock production tripled between 1980 and 2002 (88). If the world continues to transition into one that replaces top carnivores with livestock and mesopredators, it is incumbent on us to understand more about the ecological effects of such a downward ratcheting on ecosystems. More large and livestock-free protected areas are needed, especially in regions such as southeastern Asia, where large-carnivore richness (Fig. 5) remains the highest in the world. Yet even in these regions, carnivore populations are decreasing (Table 1) and few large reserves exist (fig. S3). More protected areas alone will not be sufficient, so strategies are also needed to facilitate human coexistence with these animals across working landscapes (59).

Fig. 7. Historical and projected global human population and global meat production from 1961 to 2050. Source: FAOSTAT (102) and (103) for projected meat production.



Large-carnivore conservation might best be served by a two-pronged approach. First, there is a need for increased recognition of and focus on conserving the full range of the potential effects provided by large carnivores, because this may lead to broader biodiversity, as well as social and economic benefits (5, 15, 89). In areas where large carnivores have been displaced or locally extirpated, their reintroduction may represent a particularly effective approach for passively restoring those ecosystems. However, harnessing the positive effects of large carnivores while (i) minimizing their impacts on humans and (ii) getting humans to adapt to large-carnivore presence, represents a major sociopolitical challenge. Biodiversity conservation programs intended to retain or reintroduce large carnivores must ultimately address both of these challenges if they are to succeed. Second, large-carnivore conservation might also be seen as a moral obligation—the recognition of the intrinsic value of all species. A 40-year history of the field of environmental ethics has both rigorous and systematic rationales for valuing species and nature itself. Large-carnivore conservation, therefore, might benefit greatly from a more formal relationship with practitioners of environmental ethics. It will probably take a change in both human attitudes and actions to avoid imminent large-carnivore extinctions. A future for these carnivore species and their continued effects on planet Earth’s ecosystems may depend upon it.

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Supplementary Materials

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Figs. S1 to S4

Tables S1 to S3

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Trophic Downgrading of Planet Earth

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Until recently, large apex consumers were ubiquitous across the globe and had been for millions of years. The loss of these animals may be humankind's most pervasive influence on nature. Although such losses are widely viewed as an ethical and aesthetic problem, recent research reveals extensive cascading effects of their disappearance in marine, terrestrial, and freshwater ecosystems worldwide. This empirical work supports long-standing theory about the role of top-down forcing in ecosystems but also highlights the unanticipated impacts of trophic cascades on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles. These findings emphasize the urgent need for interdisciplinary research to forecast the effects of trophic downgrading on process, function, and resilience in global ecosystems.

The history of life on Earth is punctuated by several mass extinction events (2), during which global biological diversity was sharply reduced. These events were followed by novel changes in the evolution of surviving species and the structure and function of their ecosystems. Our planet is presently in the early to middle stages of a sixth mass extinction (3), which, like those before it, will separate evolutionary winners from losers. However, this event differs from those that preceded it in two fundamental ways: (i) Modern extinctions are largely being caused by a single species, *Homo sapiens*, and (ii) from its onset in the late Pleistocene, the sixth mass extinction has been characterized by the loss of larger-bodied animals in general and of apex consumers in particular (4, 5).

The loss of apex consumers is arguably humankind's most pervasive influence on the natural world. This is true in part because it has occurred globally and in part because extinctions are by their very nature perpetual, whereas most other environmental impacts are potentially reversible on decadal to millennial time scales. Recent research suggests that the disappearance of these animals reverberates further than previously anticipated (6–8), with far-reaching effects on processes as diverse as the dynamics of disease; fire; carbon sequestration; invasive species; and biogeochemical exchanges among Earth's soil, water, and atmosphere.

Here, we review contemporary findings on the consequences of removing large apex consumers from nature—a process we refer to as trophic downgrading. Specifically, we highlight the ecological theory that predicts trophic downgrading, consider why these effects have been difficult to observe, and summarize the key empirical evidence for trophic downgrading, much of which has appeared in the literature since the beginning of the 21st century. In

"What escapes the eye ... is a much more insidious kind of extinction: the extinction of ecological interactions"

Daniel H. Janzen (1)

so doing, we demonstrate the influence of predation and herbivory across global ecosystems and bring to light the far-reaching impacts of trophic downgrading on the structure and dynamics of these systems. These findings suggest that trophic downgrading acts additively and synergistically with other anthropogenic impacts on nature, such as climate and land use change, habitat loss, and pollution.

Foundations in Theory

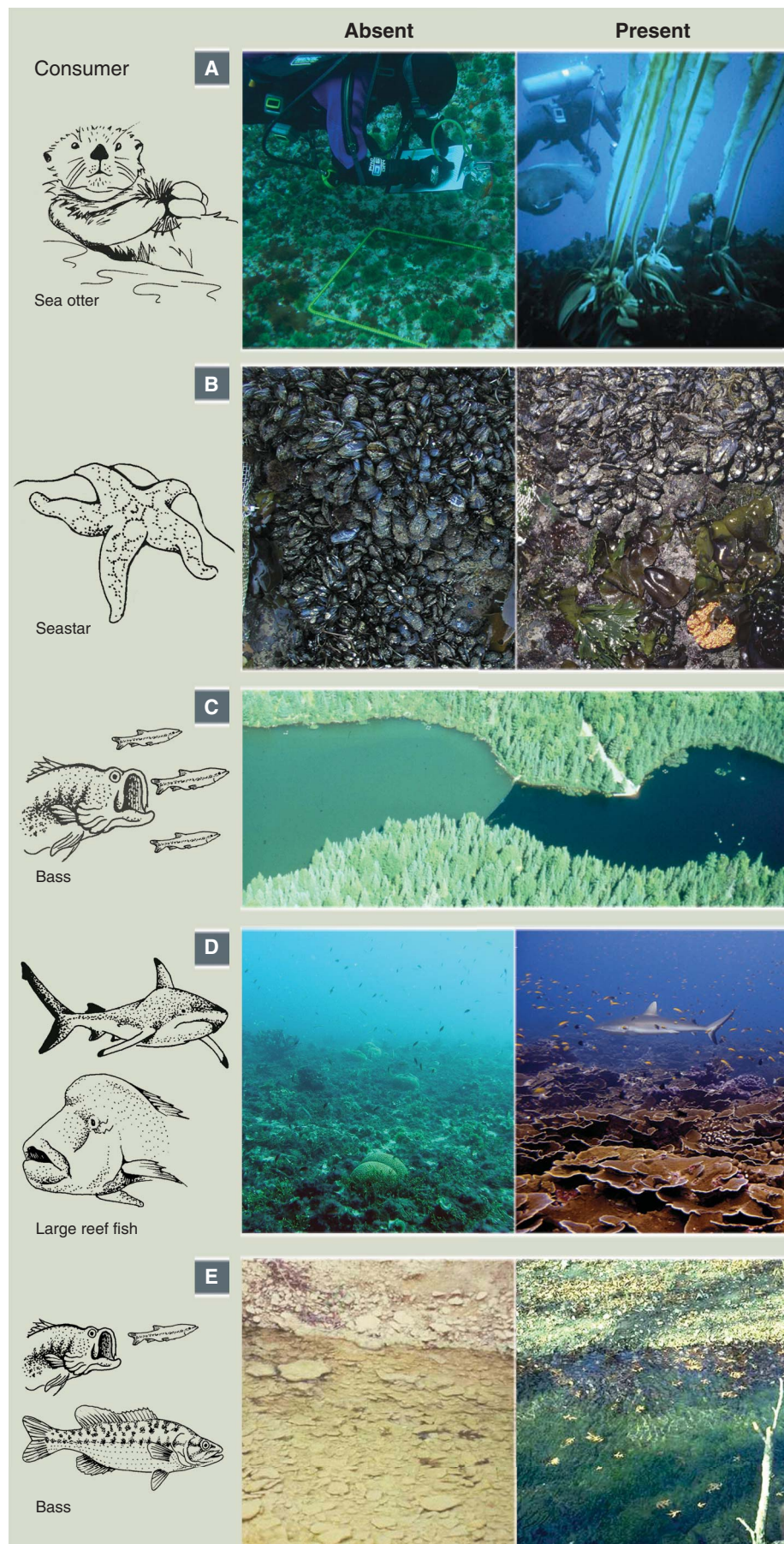
Ecological theory has long predicted that major shifts in ecosystems can follow changes in the abundance and distribution of apex consumers (9, 10). Three key elements of that theory provide the foundation for interpreting recurrent patterns suggestive of trophic downgrading in more recent empirical work across ecosystems. First is the idea that an ecosystem may be shaped by apex consumers, which dates back more than a century but was popularized in the 1960s (9). This concept was later formalized as the dynamic notion of "trophic cascades," broadly defined as the propagation of impacts by consumers on their prey downward through food webs (11). Theoretical work on factors that control ecosystem state resulted in a second key advance, the recognition of "alternative stable states." The topology of ecosystem dynamics is now understood to be nonlinear and convoluted, resulting in distinct basins of attraction.

Alternative stable states occur when perturbations of sufficient magnitude and direction push ecosystems from one basin of attraction to another (12). Tipping points (also known as thresholds or break-points), around which abrupt changes in ecosystem structure and function (a.k.a. phase shifts) occur, often characterize transitions between alternative stable states. Ecosystem phase shifts can also display hysteresis, a phenomenon in which the locations of tipping points between states differ with the directionality of change (13). A third key concept, connectivity, holds that ecosystems are built around interaction webs within which every species potentially can influence many other species. Such interactions, which include both biological processes (e.g., predation, competition, and mutualism) and physicochemical processes (e.g., the nourishing or limiting influences of water, temperature, and nutrients), link species together at an array of spatial scales (from millimeters to thousands of kilometers) in a highly complex network.

Taken together, these relatively simple concepts set the stage for the idea of trophic downgrading.

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The loss of apex consumers reduces food chain length, thus altering the intensity of herbivory and the abundance and composition of plants in largely predictable ways (10). The transitions in ecosystems that characterize such changes are often abrupt, are sometimes difficult to reverse, and commonly lead to radically different patterns and pathways of energy and material flux and sequestration.

The Cryptic Nature of Trophic Downgrading

The omnipresence of top-down control in ecosystems is not widely appreciated because several of its key components are difficult to observe. The main reason for this is that species interactions, which are invisible under static or equilibrium conditions, must be perturbed if one is to witness and describe them. Even with such perturbations, responses to the loss or addition of a species may require years or decades to become evident because of the long generation times of some species. Adding to these difficulties is the fact that populations of large apex consumers have long been reduced or extirpated from much of the world. The irony of this latter situation is that we often cannot unequivocally see the effects of large apex consumers until after they have been lost from an ecosystem, at which point the capacity to restore top-down control has also been lost. Another difficulty is that many of the processes associated with trophic downgrading occur on scales of tens to thousands of square kilometers, whereas most empirical studies of species interactions have been done on small or weakly motile species

Fig. 1. Landscape-level effects of trophic cascades from five selected freshwater and marine ecosystems. **(A)** Shallow seafloor community at Amchitka Island (Aleutian archipelago) before (1971; photo credit: P. K. Dayton) and after (2009) the collapse of sea otter populations. Sea otters enhance kelp abundance (right) by limiting herbivorous sea urchins (left) (20). **(B)** A plot in the rocky intertidal zone of central California before (September 2001, right) and after (August 2003, left) seastar (*Pisaster ochraceus*) exclusion. *Pisaster* increases species diversity by preventing competitive dominance of mussels. [Photo credits: D. Hart] **(C)** Long Lake (Michigan) with largemouth bass present (right) and experimentally removed (left). Bass indirectly reduce phytoplankton (thereby increasing water clarity) by limiting smaller zooplanktivorous fishes, thus causing zooplankton to increase and phytoplankton to decline (26). **(D)** Coral reef ecosystems of uninhabited Jarvis Island (right, unfished) and neighboring Kiritimati Island (left, with an active reef fishery). Fishing alters the patterns of predation and herbivory, leading to shifted benthic dynamics, with the competitive advantage of reef-building corals and coralline algae diminished in concert with removal of large fish (66). **(E)** Pools in Brier Creek, a prairie margin stream in south-central Oklahoma with (right) and lacking (left) largemouth and spotted bass. The predatory bass extirpate herbivorous minnows, promoting the growth of benthic algae (67).

with short generation times that could be manipulated at small spatial scales. Although some influences of apex consumers (e.g., trophic cascades) seen in experiments scale up to systems with larger or more mobile species (14), others are harder to discern at small spatial and temporal scales (e.g., many of the indirect effects of trophic cascades on ecosystem processes described below). As a result, we have an incomplete and distorted picture of the influences of apex consumers across much of the natural world.

The Widespread Occurrence of Trophic Cascades

Despite these challenges, trophic cascades have now been documented in all of the world's major biomes—from the poles to the tropics and in terrestrial, freshwater, and marine systems (table S1). Top-down forcing and trophic cascades often have striking effects on the abundance and species composition of autotrophs, leading to regime shifts and alternative states of ecosystems (15). When the impacts of apex consumers are reduced or removed or when systems are examined over sufficiently large scales of space and time, their influences are often obvious (Figs. 1 and 2). Although purposeful manipulations have produced the most statistically robust evidence, “natural experiments” (i.e., perturbations caused by population declines, extinctions, reintroductions, invasions, and various forms of natural resource management) corroborate the essential role of top-down interactions in structuring ecosystems involving species such as killer whales (*Orcinus orca*) (16), lions (*Panthera leo*) (17), wolves (*Canis lupus*) and cougars (*Puma concolor*) (18), the great sharks (19), sea otters (*Enhydra lutris*) (20), diverse mesopredators (21), and megaherbivores (22). Although the extent and quality of evidence differs among species and systems, top-down effects over spatial scales that are amenable to experimentation have proven robust to alternative explanations (23).

The impacts of trophic cascades on communities are far-reaching, yet the strength of these impacts will likely differ among species and ecosystems. For example, empirical research in Serengeti, Tanzania, showed that the presence or absence of apex predators had little short-term effect on resident megaherbivores [elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), and rhinoceros (*Diceros bicornis*)] because these herbivores were virtually invulnerable to predation (24). Conversely, predation accounted for nearly all mortality in smaller herbivores [oribi (*Ourebia ourebi*), Thompson's gazelle (*Eudorcas thomsonii*), and impala (*Aepyceros melampus*)], and these species showed dramatic increases in abundance and distribution after the local extinction of predators. Thus, top-down forcing in this system is more apparent in some species than others, at least when it is studied on relatively short time scales, although the aggregate ecological impact of apex consumers here, as elsewhere, remains great (24).

Other than the inclusion of top-down forcing, there is no rule of thumb on the interplay between apex consumers and autotrophs in intact ecosys-

tems. This is largely a consequence of natural variation in food chain length (10). In some cases, the influence of apex consumers is to suppress herbivory and to increase the abundance and production of autotrophs. The sea otter/kelp forest system in the North Pacific Ocean (20) (Fig. 1A) and the wolf/ungulate/forest system in temperate and boreal North America (25) (Fig. 2C) function in this manner. Apex consumers in other

systems reduce the abundance and production of autotrophs. The largemouth bass/planktivore/zooplankton/phytoplankton system in U.S. Midwestern lakes (26) (Fig. 1C) functions in such a manner.

Effects on Ecosystem Processes

Apart from small oceanic islands, all regions of our planet supported a megafauna before the

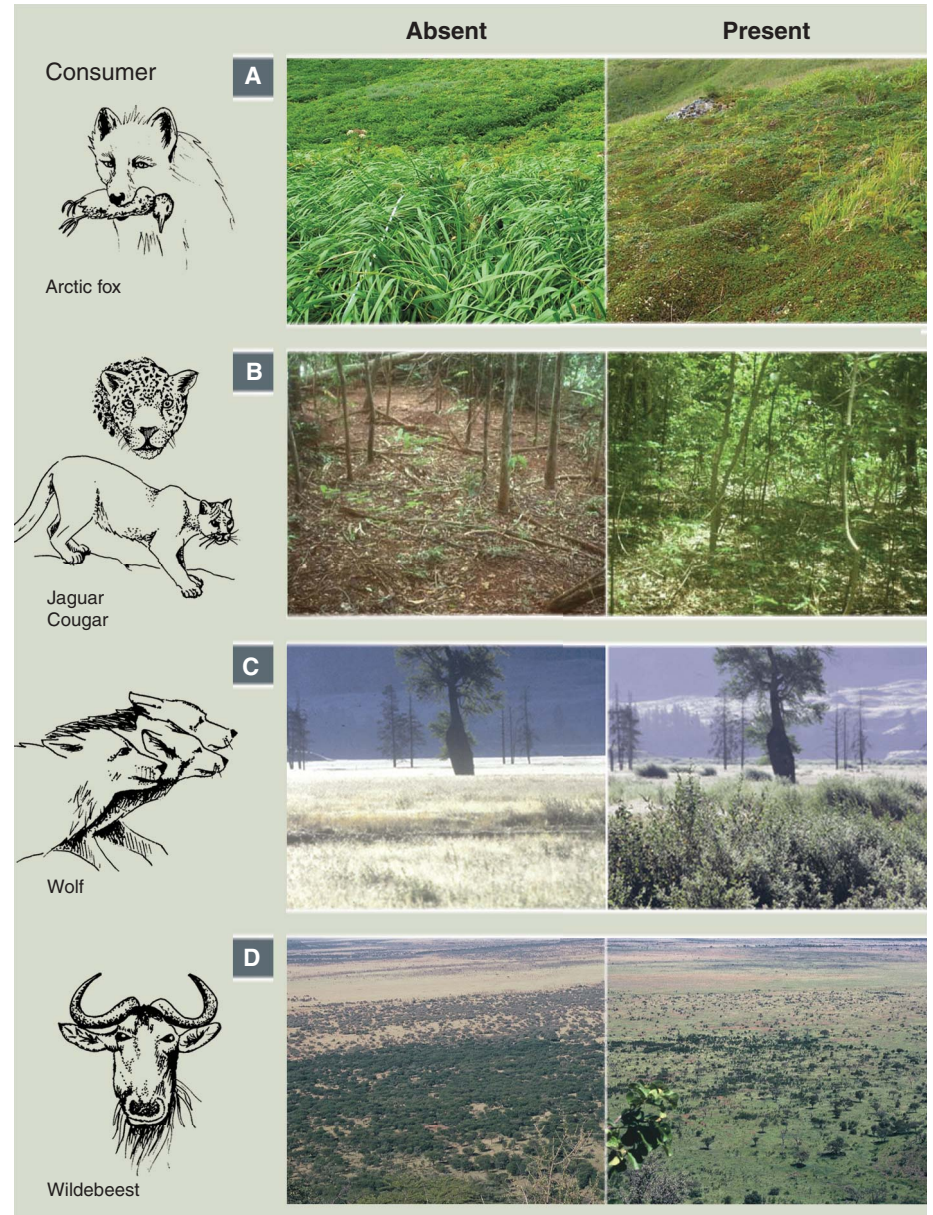


Fig. 2. Landscape-level effects of trophic cascades from four terrestrial ecosystems. **(A)** Upland habitat of islands with (right) and without (left) Arctic foxes in the Aleutian archipelago. Foxes drive terrestrial ecosystems from grasslands to tundra by limiting seabirds and thereby reducing nutrient inputs from sea to land (47). **(B)** Venezuelan forests on small islands of Lago Guri (left: jaguar, cougar, and harpy eagles absent) and mainland forest (right, predators present). A diverse herbivore guild erupted with the loss of predators from the island, thereby reducing plant recruitment and survival (68). **(C)** Riparian habitat near the confluence of Soda Butte Creek with the Lamar River (Yellowstone National Park) illustrating the stature of willow plants during suppression (left, 1997) from long-term elk browsing and their release from elk browsing (right, 2001) after wolf reintroductions of 1995 and 1996 (25). **(D)** Decline of woody vegetation in Serengeti after eradication of rinderpest (by early 1960s) and the recovery of native ungulates (by middle 1980s). Left, 1986; right, 2003 (69).

rise of *Homo sapiens* (4, 27). The apex consumers influence their associated ecosystems through top-down forcing and trophic cascades, which in turn often lead to myriad effects on other species and ecosystem processes (Figs. 3 and 4). Here, we describe some of the known or suspected indirect effects of losing these apex consumers.

Herbivory and wildfire. Wildfires burn up to 500 million ha of the global landscape annually, consuming an estimated 8700 Tg of dry plant biomass, releasing roughly 4000 Tg of carbon to the atmosphere, and costing billions of dollars in fire suppression and property loss (28). The frequency and extent of wildfire have been largely attributed to a warming and drying climate and fuel accumulation from protective wildland management practices. However, the global distribution and biomass of vegetation are poorly predicted by temperature and rainfall (29), and recent analyses suggest that interdependencies among predation (including disease), herbivory, plant communities, and fire may better explain the dynamics of vegetation. Such interdependencies are well illustrated in East Africa, where the introduction of rinderpest in the late 1800s decimated many native ungulate populations, including wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Reductions of these large herbivores caused an increase in plant biomass, which fueled wildfires during the dry season. Rinderpest was eliminated from East Africa in the 1960s through an extensive vaccination and control program. Because of this, wildebeest and buffalo populations had recovered to what was thought to be historically high levels by the early 1980s. The resulting increase in herbivory drove these systems from shrublands to grasslands, thus decreasing the fuel loads and reducing the frequency and intensity of wildfires (30) (Fig. 4). Other examples of the interplay between megafauna and wildfire are the increase in fire frequency after the late Pleistocene/early Holocene decline of megaherbivores in Australia (31) and the north-eastern United States (32).

Disease. The apparent rise of infectious diseases across much of the globe is commonly attributed to climate change, eutrophication, and habitat deterioration. Although these factors are undoubtedly important, links also exist between disease and predation (33). For example, the reduction of lions and leopards from parts of sub-Saharan Africa has led to population outbreaks and changes in behavior of olive baboons (*Papio anubis*). The baboons, in turn, have been drawn into increasing contact with people because of their attraction to crops and other human food resources. The increased baboon densities and their expanded interface with human populations have led to higher rates of intestinal parasites in baboons and the humans who live in close proximity to them (17). A similar result, involving different species and processes, occurred in India, where the decline of vultures also led to increased health risks from rabies and anthrax (34). Further examples of the interplay between predation and disease exist for

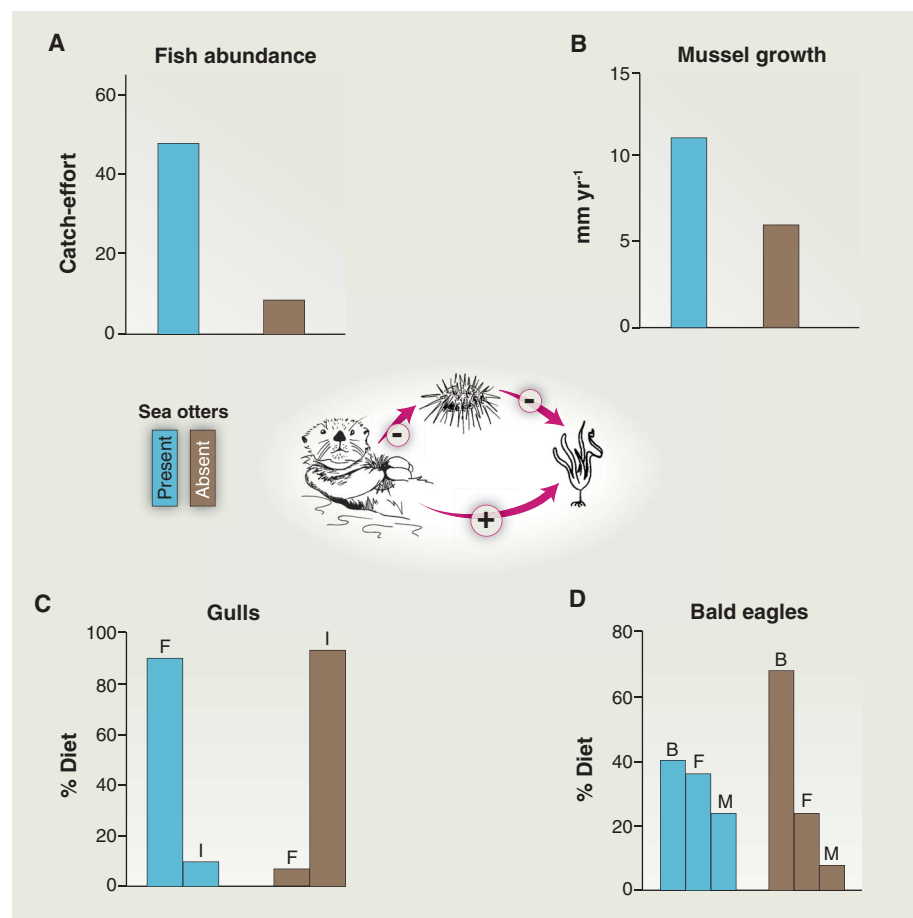


Fig. 3. Trophic cascade from sea otters to sea urchins to kelp (center) has myriad effects on other species and ecological processes. The increase in kelp enhances the abundance of kelp forest fish (A) (70). Enhanced kelp production increases the amount of particulate organic carbon in coastal ocean waters, thus increasing the growth rate of filter-feeding mussels (B) (71). The presence or absence of sea otters influences the diet of other consumers in the coastal ecosystems (C and D). In systems with abundant sea otters, Glaucous winged-gulls (*Larus glaucescens*) consume mostly fish (F), whereas in systems lacking sea otters, gulls consume mostly macroinvertebrates (I) (C) (72). When sea otters were abundant in the Aleutian archipelago, bald eagles (*Haliaeetus leucocephalus*) fed on fish (F), mammals (M), and birds (B) in roughly equal amounts. The loss of sea otters from this system led to a stronger reliance by the eagles on seabirds (D) (73). Blue bars from system with sea otters; brown bars from system without sea otters.

aquatic systems. The establishment of no-take marine reserves in the Channel Islands of southern California led to increases in the size and abundance of spiny lobsters (*Panulirus interruptus*) and declines in population densities of sea urchins, which are preyed on by the lobsters. The reduced urchin densities thwarted the spread of disease among individual sea urchins, which led to a lowered frequency of epidemics of sea urchin wasting disease within the reserves (35) (Fig. 4). In freshwater systems, the localized rise and fall of human malaria is associated with the impacts of predatory fishes on planktivores, which are in turn important consumers of mosquito larvae (36).

Physical and chemical influences. The influences of industrialization and agriculture on Earth's physical environments and geochemical processes are widely known. However, the contributing effects of changes in the distribution and abundance of apex consumers to the physical and chemical nature of our biosphere—the atmosphere,

soils, and water—are understudied and largely unappreciated. Even so, important connections between these entities have become apparent in the few instances where people have looked.

The atmosphere. Linkages between apex consumers and the atmosphere are known or suspected in freshwater, marine, and terrestrial ecosystems. Trophic cascades associated with the presence or absence of apex predatory fishes in lakes can affect phytoplankton density, in turn affecting the rate of primary production, the uptake rate of CO₂, and the direction of carbon flux between lakes and the atmosphere. Where apex predatory fishes are present in sufficient numbers, they reduce the abundance of smaller planktivorous minnows, thus releasing zooplankton from limitation by planktivores and increasing consumption rates of phytoplankton by zooplankton (Fig. 1B). This trophic cascade causes lakes to switch from net sinks for atmospheric CO₂ when predatory fishes are absent to net sources of atmospheric CO₂ when

these fishes are present (37) (Fig. 4). Similar processes occur in the oceans and on land. Industrial whaling during the 20th century transferred some 105 million tons of carbon from great whales to the atmosphere (38), and even today whale feces return various limiting nutrients from the aphotic to photic zones, thereby directly enhancing primary productivity (39, 40) and its influence on carbon flux and sequestration. From land, the demise of Pleistocene megaherbivores may have contributed to or even largely accounted for the reduced atmospheric methane concentration and the resulting abrupt 9°C temperature decline that defines the Younger-Dryas period (41).

Soils. Leaf-eating herbivores profoundly influence soils and their associated biota through altered plant allocation patterns of carbon and nutrients to the roots and rhizosphere, changing the quantity and quality of litter that plants return to the soil. Ungulate herbivores further influence soils through trampling, compaction, and the return of dung and urine. The collective influence of these processes is often an effect on species composition of the vegetation and altered successional pathways (42, 43). Predators of these herbivores and the trophic cascades they set in motion reverse these belowground effects (44). For example, the reintroduction of wolves to Yellowstone National Park has reduced the positive indirect effects of ungulates on soil nitrogen mineralization and potentially the nitrogen supply for plant growth (45). In contrast, introduced rats (46) and arctic foxes (Fig. 4) (47) have reduced soil fertility and plant nutrition on high-latitude islands by disrupting seabirds and their sea-to-land nutrient subsidies, with striking effects on plant community composition.

Water. Large consumers influence the composition and quality of both fresh and salt water through a variety of mechanisms. For example, the collapse of large demersal fish led to a 20% reduction in silica supply to pelagic diatoms in the Baltic Sea (48). In rivers, mass spawning by salmon suspends sediments, thus increasing downstream sediment transport (49) (Fig. 4). This flushing of stream bed sediments by the spawning fish and the increased circulation of fresh water through the gravel interstices of the stream bed have positive feedbacks on salmon populations by increasing oxygen for incubating eggs and fry and decreasing the frequency with which bed-mobilizing floods kill salmon in these early life stages (50). Similarly, in terrestrial systems wolves protect riparian trees and shrubs from overbrowsing by large ungulates, in turn shading and cooling the adjacent streams, reducing stream bank erosion, and providing cover for fish and other aquatic life (51, 52).

Invasive species. A common feature of many successful invasive species is that they have left behind their natural predators and freed themselves from top-down control (53). Likewise, the loss of native predators leaves ecosystems more vulnerable to invasion by nonnative species (54). There are many examples of hypersuccessful invasions due to the absence or loss of top-down

control in aquatic and terrestrial systems. The experimental exclusion of native birds from small areas in Hawaii resulted in an up to 80-fold increase in nonnative spider density (55) (Fig. 4). Other examples include the spread of the invasive brown tree snake (*Boiga irregularis*) on the otherwise vertebrate predator-free island of Guam (56), the facilitating influence of reduced fish predation on the invasion of zebra mussels (*Dreissena polymorpha*) in the Mississippi River (57), and reduced abundance and spread of the introduced European green crab (*Carcinus maenas*) by predation from native blue crabs (*Callinectes sapidus*) in eastern North America (58).

Biodiversity. Earth's biodiversity (defined here as both species diversity and the associated func-

tional diversity) is increasingly confined to formal protected areas. Although the establishment of protected areas mitigates certain threats to biodiversity—habitat loss and fragmentation, overexploitation, and the spread of invasive species—when large apex consumers are missing, protected areas often fail to function as intended. The link between apex consumers and species diversity can occur via a number of interaction pathways, for example, by blocking competitive exclusion [predatory seastars in the rocky intertidal (59)], mesopredator release [coyotes (*Canis latrans*) maintaining small vertebrate species in chaparral habitats (Fig. 4) (60)], and indirect habitat effects [e.g., the loss of small vertebrates from overgrazed and degraded riparian habitats after the

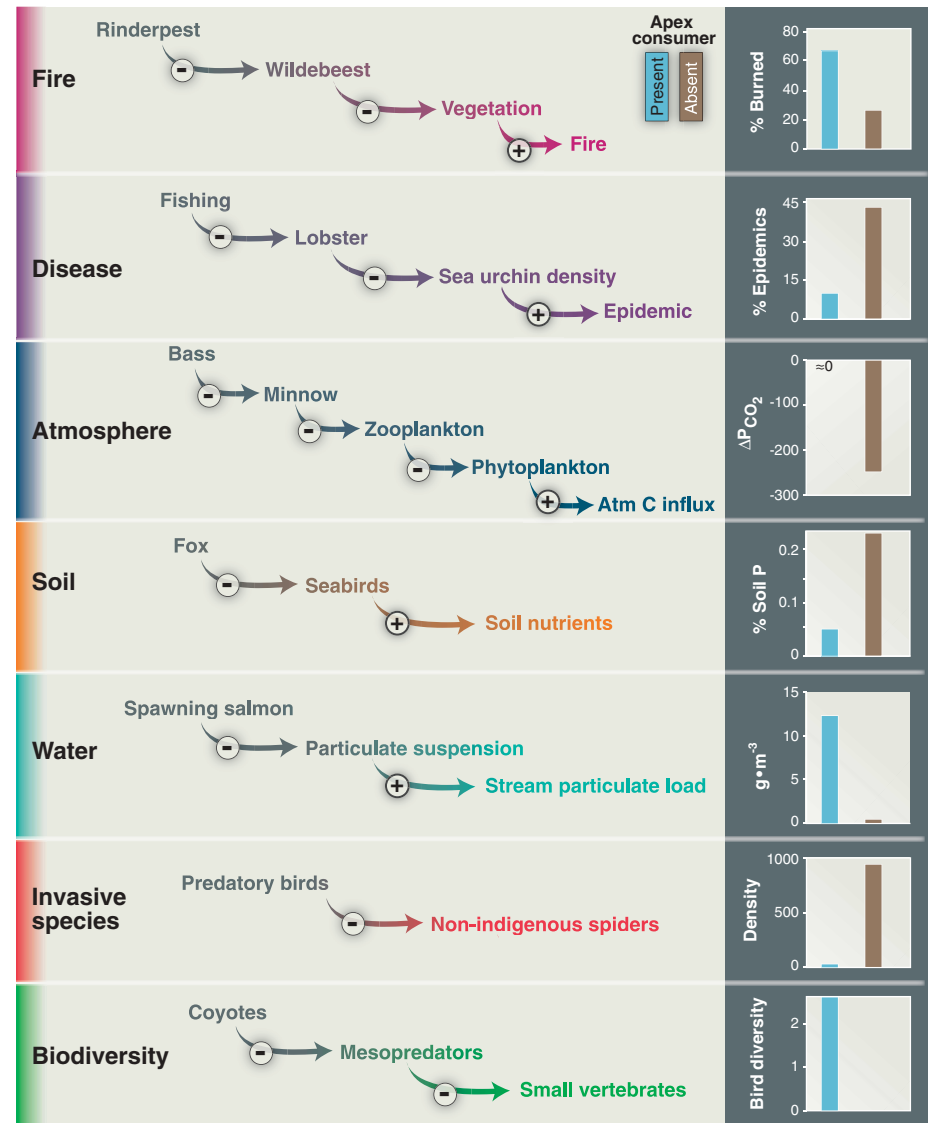


Fig. 4. Examples of the indirect effects of apex consumers and top-down forcing on diverse ecosystem processes, including wildfires (30); disease (35); composition of atmosphere (37), soil (47), and fresh water (49); invadability by exotic species (55); and species diversity (60). Interaction web linkages by which these processes are connected to apex consumers are shown in the center. Magnitude of effect is shown in graphs on right. Blue bars are data from systems containing the apex consumer; brown bars are data from systems lacking the apex consumer. Data replotted from original sources (cited above), except raw data on native bird diversity in chaparral habitats provided by K. Crooks.

loss of cougars (61) or wolves and grizzly bears (*Ursus arctos*) (62) from temperate and boreal forests of western North America].

Tree recruitment failure and the eventual transformation of forests to heaths and grasslands because of increased ungulate herbivory illustrates the influence of large apex consumers on functional diversity. This process is most clearly seen by contrasting areas where apex consumers have been absent for differing lengths of time. In North America, where wolves and other large carnivores were not extirpated until the early 20th century, the effects of their loss on plants is evident only as the recruitment failure of the younger trees. Because of the longevity of adult trees, the older individuals persist in what superficially appears to be a normally functioning forest ecosystem. These effects are best known from various U.S. National Parks, where the loss of large predators a few decades ago has left a characteristic signal of reduced tree growth rate (63) or recruitment failure (64) in the dominant tree species. A longer time horizon can be obtained from the Canadian island of Anticosti, where white-tailed deer (*Odocoileus virginianus*) have persisted in the absence of predators for more than a century, causing the successive elimination of saplings of less and less palatable trees and shrubs and increasing graminoid dominance in the understory (65). The Scottish island of Rùm, from which wolves have been absent for 250 to 500 years, provides a view of the likely final outcome of predator loss and elevated herbivory in many temperate forests. Rùm has transitioned over this same period from a forested environment to a treeless island.

These examples support the conclusion that disruptions of trophic cascades due to the decline of predation constitute a threat to biodiversity from within for which the best management solution is likely the restoration of effective predation regimes.

A Paradigm Shift in Ecology

The accumulation of theoretical and empirical evidence calls for an altered perspective on top-down forcing in ecosystem dynamics. Many practicing ecologists still view large animals in general, and apex consumers in particular, as ecological passengers riding atop the trophic pyramid but having little impact on the structure below. The influences of these animals, although acknowledged in particular cases, are generally regarded as anomalous, occurring in some systems but not in many others. This perception has generally led to the requirement of independent study and confirmation for each species and system before the null hypothesis that they serve no important ecological role can be rejected. We argue that the burden of proof be shifted to show, for any ecosystem, that consumers do (or did) not exert strong cascading effects.

Conclusions

Unanticipated changes in the distribution and abundance of key species have often been attributed in some unspecified manner to the “complexity of nature.” We propose that many of the

ecological surprises that have confronted society over past centuries—pandemics, population collapses of species we value and eruptions of those we do not, major shifts in ecosystem states, and losses of diverse ecosystem services—were caused or facilitated by altered top-down forcing regimes associated with the loss of native apex consumers or the introduction of exotics. Our repeated failure to predict and moderate these events results not only from the complexity of nature but from fundamental misunderstandings of their root causes. Except for controlling predators to enhance fish, wild game, and livestock, resource managers commonly base their actions on the assumption that physical processes are the ultimate driver of ecological change. Bottom-up forces are ubiquitous and fundamental, and they are necessary to account for the responses of ecosystems to perturbations, but they are not sufficient. Top-down forcing must be included in conceptual overviews if there is to be any real hope of understanding and managing the workings of nature.

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Supporting Online Material for

Trophic Downgrading of Planet Earth

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Table S1
References

SOM Table 1. Examples of regime shifts in terrestrial, freshwater, and marine ecosystems resulting from the loss or addition of large-bodied vertebrates. Those based on linkages across 3 or more species are noted with an asterisk

Ecosystem	Perturbation/Location	Response	Reference
<i>Terrestrial</i>			
Arctic tundra	Extinction of megaherbivores/Siberia	Conversion of steppe to tundra	(43)
* Arctic tundra	Introduction of arctic fox/Aleutian Islands	Conversion of grass-land to tundra	(47, 74)
* Boreal forest	Self-introduction of moose/Isle Royale	Reduction of balsam fir	(63)
* Temperate forest	Extirpation of wolf/Yellowstone National Park	Overbrowsing of aspen, cottonwood, willow	(75, 76)
* Temperate forest	Restoration of wolf/ Yellowstone National Park	Recovery of riparian vegetation	(25, 77)

Table 1 (continued)

*Temperate forest	Extirpation of large predators/Europe, Japan, and eastern United States	Eruption of cervid populations, overbrowsing, altered forest composition	(78-80)
*Temperate forest	Loss of cougar/Zion National Park	Eruption of mule deer, loss of riparian vegetation and associated biodiversity, altered channel morphology	(61)
Temperate forest	Introduction of red deer/New Zealand	Overbrowsing, altered composition of forests	(81)
*Tropical forest	Loss of jaguar, cougar, Harpy eagle/Venezuela	Explosion of herbivores, suppression of tree recruitment	(82)
*Tropical forest	Decimation of large birds and mammals by hunting/neotropics	Altered tree recruitment	(83, 84)
*Tropical savanna	Decimation of ungulates by Rinderpest epidemic/Serengeti	Increased extent and frequency of fires	(30, 85)
Tropical savanna	Recovery of white rhino/South Africa	Appearance of grazing lawns, reduced incidence of fire	(86)
Subtropical bush	Predator control of dingo/Australia	Mesopredator release/ proliferation of exotic mesopredators and herbivores/reduced biodiversity	(87)

Table 1 (continued)
Freshwater

*Tropical river	Exclosures and enclosures/Panama	Fishing birds protect algae from grazing catfish	(88, 89)
*Temperate stream	Exclosures and enclosures/Oklahoma	Piscivorous bass protect algae from grazing minnows	(69)
*Temperate stream	Predator introduction/New Zealand	Invasive trout protect algae from grazing insects	(90, 91)
*Boreal stream	Predator introduction/Hokkaido	Invasive trout protect algae from grazing insects	(92)
*Fresh water lake	Remove piscivore trophic level	Reduced water clarity, increase in phytoplankton and primary production, increased N:P ratio, increased response to nutrient inputs, net flux of CO ₂ into the lake	(26, 93)
*Fresh water lake	Introduction of non-native top piscivore	Reorganization of fish community, species loss	(94)

Table 1 (continued)
Marine

*Temperate subtidal	Sea otter recovery	Recovery of kelp forest	(95)
*Temperate subtidal	Overharvest of cod	Urchin outbreak; collapse of kelp forests	(96)
*Temperate estuarine	Decimation of apex sharks	Outbreak of cow-nosed rays, shellfish decline	(19)
Tropical coastal	Reduced grazing by green turtles	Reduced recycling of turtle grass	(97)
*Coral reefs	Overfishing	Reduction in crustose coralline algae resulting in reduced reef calcification,	(98)
*Coral reefs	Overfishing followed by disease	Reef overgrowth by algae	(99)
Continental shelf	Overharvest of cod	Shrimp increases	(100)
*Open ocean (North Pacific)	Pink salmon fluctuation	zooplankton decline, chlorophyll increase	(101)

*Open ocean (North Atlantic)	Overharvest of cod	Planktivorous fish, zooplankton, chlorophyll	(102)
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Table 1 (continued)

*Open ocean (North Atlantic)	Overharvest of cod	Sprat increase, zooplankton decline	(103, 104)
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*Open ocean (North Pacific)	Overharvest of great whales	Killer whale diet shift, pinniped population declines	(105)
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*Open ocean (Southern Ocean)	Overharvest of great whales	Krill increase, adelic penguin diet shift	(106)
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*Open ocean (Black Sea)	Overfishing	Planktivorous fish, gelatinous plankton, zooplankton, phytoplankton	(107)
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Factors Associated with Loss of Brown Bear Cubs in Sweden

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FACTORS ASSOCIATED WITH LOSS OF BROWN BEAR CUBS IN SWEDEN

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Abstract: We documented the loss of brown bear (*Ursus arctos*) cubs-of-the-year (cubs) in 2 Swedish populations for 11 years in the north and 12 years in the south, and made spatial and temporal comparisons to examine whether nutritional, social (sexually selected infanticide), or den disturbance factors best explained the observed variation. Annual cub loss was 0.04 ($n = 78$) in the north and 0.35 ($n = 126$) in the south. The loss of cubs at both levels of comparison was best explained by social factors. Disturbance was only evaluated in the south and explained significant variation. In the north, few adult males died and 3 adult males lost early in the study there were not replaced for many years, presumably due to little immigration of new males. Immigration was probably low due to high illegal mortality around the study area and lack of bear habitat on one side of the study area. In the south, 5 times as many males died annually, and in years with recorded adult male mortality, an average of 20% of the adult males died. The number of adult males remained stable, presumably due to immigration by new males. Illegal mortality appeared to be less in the south, and the study area was surrounded by bear habitat. Number of adult males dying in cub areas (the composite area of all radiomarked females with cubs) 2 years previously was correlated negatively with cub survival in the south. In the north, no factors correlated with temporal patterns of cub loss, but loss of adult males 1–2 years previously was the best variable we tested. We suggest that immigrating males kill cubs, as predicted by the sexually selected infanticide hypothesis. Some other studies have yielded similar results. We recommend that managers assume that loss of adult male bears is compensatory until this question is adequately resolved.

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Key words: brown bear, den disturbance, management, population dynamics, sexually selected infanticide, Sweden, *Ursus arctos*

It was once thought that young bears with their mothers experienced little mortality, but this is now known to be in error (Bunnell and Tait 1985). Survival of cubs-of-the-year (termed “cubs” throughout this paper) has been found to vary temporally within an area (LeCount 1982, Rogers 1987, Miller 1994, Derocher and Stirling 1995, 1996, Swenson et al. 1997a) and spatially among areas (Clark and Smith 1994, Derocher and Taylor 1994, Garshelis 1994, McLellan 1994, Mattson and Reinhart 1995, Swenson et al. 1997a). In a review of the evidence for density-dependent population regulation in North American bears, Taylor (1994) suspected that density-related survival of cubs was the most likely mechanism of density effects, although no such density-dependent effects have yet been documented. Although important in understanding the dynamics of bear populations, the factors influencing cub survival are poorly documented and may vary among species, areas, and years. One reason is, of course, the difficulty of determining the cause of death of small cubs and of separating proximate and ultimate causes. In addition, variables may interact (Derocher and Stirling 1996).

Several factors have been proposed as important for cub survival. They can be grouped into nutritional, social, and disturbance factors. The most direct nutritional factor is food availability to cubs. This has been correlated with cub survival in some studies (Rogers 1987, Derocher and Stirling 1996), although not in others (LeCount 1982, Lindzey et al. 1986, Elowe and Dodge 1989, Clark and Smith 1994, Sellers and Aumiller 1994, Mattson and

Reinhart 1995, Kasbohm et al. 1995). An indirect effect of nutrition is through the condition of the mother. Maternal effects have been suggested by Rogers (1987) and Derocher and Stirling (1996).

The most direct social factor affecting cub survival is intraspecific predation, either by males or females. Lindzey et al. (1986) proposed that adult females might decrease the recruitment of female progeny. However, many others have implicated males in killing cubs (reviews in Garshelis 1994, McLellan 1994). Hrdy (1979) classified the potential reasons for infanticide and concluded that infanticide can benefit the perpetrator if it is linked to competition for limited resources. When these resources are mates, the competition is intrasexual and the infanticide is termed sexually selected. The sexually selected infanticide (SSI) model predicts that infanticide will be directed at offspring unlikely to be direct descendants of the killer, and on average, elimination of the infant increases the infanticidal male's own opportunity to breed, typically by shortening the interval until next ovulation in the mother of the killed infant (Hrdy 1979). According to Miller (1990), some authors have suggested that, because adult males kill cubs, a reduction in the number of adult males should reduce cub mortality. Empirical evidence for this comes from analyses of the Craighead data from the Yellowstone grizzly bear (*Ursus arctos*; McCullough 1981, 1986; Stringham 1983), from comparisons of reproductive potential and proportion of adult males in 6 grizzly bear populations (Stringham 1980), and from a comparison of cub survival and proportion of adult

males in 2 American black bear (*Ursus americanus*) populations (Clark and Smith 1994). Stringham (1983) cautioned against using the results of his and the Yellowstone studies to justify harvesting adult males to increase the production of cubs, because in both data sets, the proportion of adult males and nutrition were correlated, confounding the results. The opposite effect also has been postulated, that increased hunting of adult males can increase cub mortality through SSI by immigrating males (Stringham 1980). The empirical evidence for this comes from 1 population of American black bears and a comparison of 2 populations of brown bears (LeCount 1987, Swenson et al. 1997a). Miller (1990) presented evidence showing that cub mortality remained stable during a period of heavy hunting mortality and declining proportion of adult males in a grizzly bear population that was declining due to overhunting. He also concluded that neither effect of killing adult males described above had been adequately demonstrated at that time. An indirect social factor, which includes the nutritional factor, is that females with cubs may avoid productive habitats in an attempt to avoid potentially infanticidal males. Habitat use by adult female brown bears in North America has been observed that is consistent with this explanation (Wielgus and Bunnell 1994b, 1995).

Disturbance can also be an important mortality factor in some populations. Elowe and Dodge (1989) found that this was the major cause of death for American black bear cubs before emergence from the den in Massachusetts. In central Sweden, human disturbance appeared to be a major cause of den abandonment by brown bears in winter, and pregnant females that changed dens prior to parturition lost young in and near the den significantly more often than those that did not move (Swenson et al. 1997b).

In an earlier paper (Swenson et al. 1997a), we presented circumstantial evidence from 2 Swedish brown bear populations suggesting that SSI by immigrant males, after adult males were killed by hunters, was an important factor influencing cub survival. We present data from 3 additional years for these 2 populations and expand the analysis to evaluate nutritional, social, and disturbance factors to explain the observed temporal and spatial variation in cub survival.

STUDY AREAS

The study areas were in northern Sweden (about 8,000 km²) and central Sweden-southeastern Norway (about 13,000 km²), and are described in Bjärvall and Sandegren (1987). These study areas are about 600 km apart and are near the northern and southern edges of the species' range in Sweden. There are mountains in the north and a rolling landscape in the south. The bears in the north spend

>1 month longer in the den (Sandegren and Swenson 1997), and some categories of bears (yearlings all year and females in the spring) were seen at ungulate carcasses more often there than in the south (Stabell 1999). Both moose (*Alces alces*) and domestic reindeer (*Rangifer tarandus*) were available in the north, but only moose in the south. The study populations belong to separate mitochondrial DNA lineages (Taberlet et al. 1995). However, nuclear DNA analyses have revealed that, although there are differences between the populations, there has been extensive gene flow throughout the Scandinavian brown bear population (Waits et al. 2000). Both populations showed rapid growth, r (exponential rate of increase) = 0.13 in the north and r = 0.15 in the south; environmental variance was statistically different from zero in the south (s_e^2 = 0.003) but not in the north (Sæther et al. 1998).

Bear hunting was generally allowed during the autumn in both areas, but the northern area includes 3 national parks where bear hunting is forbidden. Hunting pressure has increased since 1995 in the southern study area. In the northern area, there is evidence of considerable illegal killing of bears (Swenson and Sandegren 1999). This is less important on the study area than in the surroundings, where it appears to have a major effect on the population. This has been documented through the loss of radiomarked bears, particularly immigrating males leaving the study area, and changes in the distribution of females as determined from the distribution of legally killed female bears (Sandegren and Swenson 1997, Swenson and Sandegren 1999).

METHODS

We documented the disappearance of cubs accompanying radiomarked females during 1988–98 and assumed that cubs that disappeared had died. We observed a family as soon as possible after they left the den, again around the end of the mating season in late June–early July, and again before they entered the den in the autumn. Cubs that died in the den were not considered in this study, but cubs that left the den and disappeared before they were observed were included. In our analyses, we considered a litter that was lost prior to being observed to have consist of 2 cubs, the most common litter size in both areas. We visited dens only in the south to determine if young had been present outside the den, based on tracks or markings from their climbing in nearby trees. The northern study area was inaccessible to vehicles. However, the longer period of snow cover in the north and the less dense forest made it easier to count cubs from the air shortly after they left the den.

We immobilized the bears early in the spring by darting them with a mixture of tiletamine/zolazepam and

medetomidine from a helicopter. We marked captured bears with radio transmitters and weighed them with spring scales. We recaptured growing bears each spring to fit them with a larger collar. We first captured many bears as yearlings, shortly after emerging from their dens with their radiomarked mothers. For bears that were not the yearlings of radiomarked females, we collected a premolar tooth, which we sent to Matson's, Inc. (Milltown, Montana, USA) for age estimation based on the cementum annuli in the tooth root (Craighead et al. 1970). In the north, virtually all bears that we saw were captured and marked. Because the marking season coincided with the mating season and occurred when snow covered the ground, we feel confident that few unmarked adult bears were present on the study area. During 1988–91, 86% of 29 females observed consorting with radiomarked males during the mating season were radiomarked (Swenson et al. 1994); we captured and marked the unmarked females. In the south, the marking season was before the mating season because the snow melted prior to the mating season. Similar observations there in 1988, 1989, and 1993 revealed that 47% of 53 observations were marked females (Swenson et al. 1994, 1995). When we observed marked females with another bear during the breeding season, we recorded whether it was radiomarked. From these observations, we annually estimated the number of breeding adult males in our southern study area with an unbiased Petersen population estimator (Krebs 1989).

As marking occurred only in a short period, we calculated survival rates using the Kaplan-Meier procedure (Kaplan and Meier 1958). We located radiomarked bears generally weekly during the nondenning period. In the south, we located them at least once monthly while denning. We followed most bears over many years, often from the time they were born. Thus, it was possible to accurately determine reproductive parameters such as age of first reproduction and litter interval, among others. We compared these parameters to indirectly assess nutritional status of bears in the 2 areas, because higher reproduction has been found to vary positively with plane of nutrition in populations of brown bears, American black bears and polar bears (*Ursus maritimus*; reviews in Taylor 1994).

Following Garshelis (1994), we used yearling weights as a surrogate measure of food abundance. Yearlings were weighed to the nearest 0.5 kg shortly after den emergence ($n = 53$ in the north, and $n = 66$ in the south). A body mass index for a given year was calculated as the mean of the deviations in body masses for yearlings from the appropriate area, expressed in standard deviation units, from the overall mean for all yearlings for all years for each sex and area. Thus, body masses from both sexes in an area were standardized and could be combined. The pregnant female food index in a year was the yearling body

mass index in that year (when the yearlings emerged, they had lived during the time the females that gave birth that year had been pregnant). The cub food index in that year was the yearling body mass index in the following year, because the cubs emerged the following year and were weighed then as yearlings.

In Sweden, all bears killed by hunters must be shown to the authorities, the exact location of the kill must be reported (and can be verified), and samples from the carcasses must be turned in, including a tooth. The locations where adult males (≥ 5 years old) were known to have died were compared with the locations of radiomarked females with cubs. We produced a composite minimum convex polygon area that included all locations of radiomarked females with cubs for each year. We termed these "cub areas", which varied in size annually, depending on the number and distribution of radiomarked females with cubs. Cub areas averaged 2,488 km² (SE = 550, $n = 11$ years) in the north and 4,108 km² (SE = 924, $n = 12$) in the south. The southern cub areas are *not* comparable to the southern area reported in Swenson et al. (1997a). We used a different method in this analysis to ensure that the males died close to the cubs we were monitoring. We assumed a home range diameter for adult males of 16 km in the north and 18 km in the south, based on home range sizes of 830 km² ($n = 9$) and 1,000 km² ($n = 22$), respectively (B. Dahle, Scandinavian Brown Bear Project, Norwegian University of Science and Technology, Trondheim, Norway, unpublished data). For each cub area, we tallied the number of adult males known to have died within the cub area and within 1 male home-range diameter from it at time lags of 1, 2, and 3 years. We considered all known adult male deaths, not just those due to hunting, as reported earlier (Swenson et al. 1997a). Most males were killed by hunters during the autumn prior to denning, but a few died just after den emergence (marking-induced losses, suspected illegal killing from snowmobiles, killed in traffic). Biologically, the effect on the male social organization was probably the same if a male was killed prior to entering or just after leaving the den. Therefore, we counted deaths in the early spring as occurring in the previous autumn. Also, when we strongly suspect illegal killing of a radiomarked adult male in the north and the male was never recaptured, in spite of our intensive efforts, nor reported as killed legally, we considered it to be dead.

All females with cubs were considered to have been disturbed if they changed den sites or were otherwise known to have been disturbed by people at the den, even if they did not abandon the den. This was recorded only in the southern area.

We analyzed annual variations in cub survival in each study area using a stepwise multiple logistic regression.

The dependent variable was cubs survived or lost, and the independent variables were pregnant female food index, cub food index, number of adult males dying in or near the cub areas for time lags of 1, 2, and 3 years, whether the female had been disturbed during denning (south only), and year, which was a surrogate variable for density in these rapidly growing populations. We entered independent variables into the model and removed by backward elimination using the likelihood ratio statistic for removal (Norušis 1997). Statistical tests were carried out in Statistical Package for the Social Sciences (SPSS) or Statview (Norušis 1997).

RESULTS

Comparison Between Areas (Spatial Scale)

Annual cub loss was 0.35 in the south ($n = 126$) and 0.04 in the north ($n = 78$). This difference was highly significant ($\chi^2_c = 24.51$, 1 df, $P < 0.0001$; Table 1). Among litters that lost cubs during 1987–98, total loss was more common in the south (68%, $n = 34$ litters losing at least 1 cub) than in the north (0%, $n = 3$, Fisher's exact test, $P = 0.034$). Thirty-four cubs (85% of those lost) disappeared during the 2-month breeding season (May–Jun), compared with 6 in the following 4-month period. This was a significantly greater loss during the breeding season than expected from its length (1-way $\chi^2 = 48.27$, 1 df, $P < 0.0001$).

We documented the cause of death for very few cubs, as none were radiomarked. We found a few carcasses, however. In the south, 3 dead cubs from 3 litters were found not far from the den; 1 of these apparently died of

malnutrition. Near another den, we saw the tracks of the female, cubs, and an adult male, judging from the track measurements. These cubs were never observed with the female. In another case, a female that had 4 cubs was observed on 17 May 1996 with only 2 cubs, 1 of which appeared to be injured. An unmarked male followed these bears. Backtracking revealed that 1 cub had been killed and consumed and another was in a tree. The female never returned to the abandoned cub. On 27 May she was with a marked adult male and no cubs. Another cub carcass was found in October 1998; it may have been injured in a traffic accident.

Sex ratios of yearlings marked in the early spring, usually while still with their mothers, were compared in the 2 study areas. The sex ratio of yearlings was the same as for cubs in the north, because annual cub loss there was only 0.04. Captured yearlings were 56% males ($n = 59$) in the north and 49% ($n = 76$) in the south. This difference was not significant ($\chi^2_c = 0.44$, 1 df, $P = 0.51$), suggesting that there was not a sex-specific loss of cubs in the south.

A comparison of reproductive parameters between the 2 areas showed that age of first reproduction and litter interval (all litters) was significantly lower in the south (Table 2). There was no difference in litter size. However, the high cub loss in the south, which particularly affected first-time breeders, resulted in an increased age of first successful reproduction and interval between successful litters. These values did not differ between the areas (Table 2).

A comparison of spring body masses, taken shortly after the bears emerged from their dens, and usually while snow was still present, revealed that the bears in the north grew faster until age 3 years. From age 4 to 6 years, there

Table 1. Loss of cubs-of-the-year with radiomarked female brown bears in the northern and southern study areas in Sweden, 1987–98, with yearling body mass index and number of adult (≥ 5 years) males dying within the cub areas 1, 2, and 3 years previously.

Year	North					South				
	Cub survival (n)	Mass index	Males dying ^a			Cub survival (n)	Mass index	Males dying ^a		
			-1 yr	-2 yr	-3 yr			-1 yr	-2 yr	-3 yr
1987	-	-	0	0	0	0.000 (2)	-	0	0	0
1988	1.000 (5)	-	0	0	0	1.000 (3)	-	0	1	0
1989	1.000 (4)	-0.17	2	0	0	1.000 (5)	-0.39	0	0	3
1990	0.800 (5)	+0.17	0	1	0	1.000 (2)	+0.60	0	0	0
1991	1.000 (5)	+2.07	0	0	1	0.529 (17)	-1.68	1	2	0
1992	1.000 (8)	+0.69	0	0	0	0.625 (8)	-0.46	4	1	2
1993	1.000 (7)	+0.19	0	0	0	0.600 (15)	-0.48	2	4	1
1994	1.000 (7)	-0.28	0	0	0	0.546 (11)	-0.34	0	2	4
1995	1.000 (9)	+0.27	0	0	0	1.000 (15)	-0.21	1	0	2
1996	1.000 (6)	-0.98	0	0	0	0.333 (15)	-0.19	0	1	0
1997	0.833 (12)	-0.47	1	0	0	0.524 (21)	+2.01	3	1	1
1998	1.000 (10)	+0.35	0	1	0	0.571 (21)	+0.41	0	3	0

^a Adult males. Numbers can change when tracked diagonally, because cub areas were different each year.

Table 2. Brown bear reproductive parameters for the northern and southern study areas in Sweden, 1987–98.

Parameter	North	South	Statistical test	
Age, first litter (yr)	5.4 ± 0.15 (11) ^a	4.5 ± 0.15 (17)	$t_{26} = 3.71$	$P < 0.001$
Age, first successful litter (yr)	5.4 ± 0.15 (12)	5.2 ± 0.24 (15)	$t_{25} = 0.72$	$P = 0.48$
Litter size	2.4 ± 0.14 (33)	2.3 ± 0.11 (55)	$t_{86} = 0.51$	$P = 0.61$
Litter interval (yr), all	2.6 ± 0.15 (21)	1.6 ± 0.08 (46)	$t_{65} = 5.90$	$P < 0.001$
Litter interval, successful	2.6 ± 0.14 (18)	2.4 ± 0.12 (23)	$t_{39} = 1.18$	$P = 0.25$

^a Mean ± SE (N)**Table 3.** Comparison of spring body mass of radiomarked brown bears in the northern and southern study areas in Sweden 1987–98.

Age (yr)	Sex	Spring body mass (kg) mean ± SE (n)		Statistical test	
		North	South		
1	M	29.9 ± 1.7 (28)	25.8 ± 1.1 (33)	$t_{59} = 2.10$	$P = 0.04$
	F	24.0 ± 0.9 (25)	21.8 ± 0.8 (33)	$t_{56} = 1.79$	$P = 0.08$
2	M	59.0 ± 3.4 (22)	42.8 ± 1.6 (23)	$t_{30.2} = 4.26^a$	$P < 0.0001$
	F	49.5 ± 2.7 (20)	38.2 ± 1.6 (19)	$t_{30.5} = 2.00^a$	$P = 0.054$
3	M	106.7 ± 11.2 (15)	68.0 ± 2.9 (21)	$t_{15.9} = 3.35^a$	$P = 0.004$
	F	69.9 ± 3.0 (21)	58.8 ± 2.0 (19)	$t_{38} = 3.01$	$P = 0.005$
4	M	114.5 ± 8.4 (11)	104.4 ± 4.8 (17)	$t_{26} = 1.13$	$P = 0.27$
	F	83.1 ± 3.3 (15)	77.2 ± 2.7 (16)	$t_{29} = 1.40$	$P = 0.17$
5	M	137.2 ± 12.0 (6)	137.2 ± 10.4 (10)	$t_{14} = 0.002$	$P = 0.99$
	F	90.9 ± 7.0 (5)	78.9 ± 4.2 (8)	$t_{11} = 1.57$	$P = 0.14$
6	M	172.8 ± 12.4 (6)	149.0 ± 12.0 (8)	$t_{12} = 1.36$	$P = 0.20$
	F	83.8 ± 4.2 (7)	93.0 ± 7.3 (9)	$t_{14} = 1.01$	$P = 0.33$

^a Corrected for unequal variances.

were no differences in spring body masses, although most mean body masses were greater in the north (Table 3). Weights of older bears were not compared by age due to low sample sizes.

Adult males died within the cub areas during 5, 8, and 6 of the 12 years in the south, at time lags of 1, 2, and 3 years, respectively (Table 1). The number that died varied from 1–4 and averaged 2.1 in the years an adult male died and 1.1/year totally. In the north adult males only died during 2 of 11 years, averaging 1.2/year in the years an adult male died and 0.2/year totally. These deaths occurred early and late in the study.

In the north, 2 of the 4 marked adult males died in 1988 and another died while being marked for the first time in early spring 1989. These 3 males were never together within a cub area. Despite our intensive efforts to mark all unmarked bears in the area, we found very few immigrating males, and the number of marked adult males remained stable at a low number during 1989–95. The number increased in 1996 and has remained 3–4 times higher than before (Table 4). This was due primarily to recruitment of locally produced young males into the adult age class. In the south, we were not able and did not attempt to mark all of the bears. Observations of breeding females with other bears suggested that we had marked about 56% of the adult breeding males there (Table 4, marked males divided by the number marked plus the

corrected number of unmarked males). The average number of adult males/year was 9.7 for the 10 years we estimated. There was no temporal trend in the estimated number of adult males present ($r = 0.004$, 8 df, $P = 0.99$). If we combined all the data for all 12 years, a composite estimate was 9.8 males present annually.

These results suggest that there was a greater availability of immigrating males in the south than in the north. This is supported by our data on survival of radiomarked males (Table 5). The probability of a male surviving from den emergence as a yearling through his first year as an adult was 0.223 in the north, including survival of bears that emigrated from the study area. The corresponding value in the south was 0.499, about twice as high, although the differences were not significant for any individual age. In addition, the southern area was surrounded by occupied bear habitat, a potential source of immigrants, whereas the northern area was bounded on the west by mountains above timberline, with few or no bears.

Comparison within Areas (Temporal Scale)

In the southern area, 3 of the factors entered into a multiple stepwise logistic regression (cub food index, number of males dying in and near cub areas 2 years earlier, and whether the female had been disturbed in her den) showed significant negative correlations with cub survival

Table 4. Adult (≥ 5 years old) male brown bears radiomarked on the northern study area in Sweden and point estimates of the total number of adult males consorting with marked females on the southern study area, 1986–98.

Year	North ^a		South ^b			
	Marked adult males	Marked males ^c	Consorting with marked females			Breeding males ^e
			Marked males	Unmarked bears	Total, corrected ^d	
1986	0	2.6	5	0	5	3.6
1987	1	3	3	5	7.4	8.4
1988	4	7	3	5	7.4	16.8
1989	2	10.2	10	3	12.6	13.8
1990	2	4.4	5	5	9.4	9.4
1991	2	3	0	6	5.3	-
1992	2	2	0	6	5.3	-
1993	1	6	15	3	17.6	8.1
1994	2	5	6	3	8.6	8.2
1995	3	6	5	1	5.9	8.0
1996	8	3	3	5	7.4	8.4
1997	6	5	6	8	13	12.0
1998	6	—	—	—	—	—

^a Virtually all adult males were marked.^b Marking all adult males was not attempted.^c Males losing radiocollars were treated as the fraction of the breeding season they were marked. Only males with home ranges overlapping radiomarked adult females were included.^d The number of unmarked males was reduced by 12%, because marked adult females without cubs during the breeding season were seen together in 12% of 72 sightings of marked females.^e Calculated from Krebs (1989:23, eq. 2.2).**Table 5. Survival rates of radiomarked male brown bears ages 1–5 years in the northern and southern study areas in Sweden, 1985–98.**

Age (yr)	North mean \pm SE (n)	South mean \pm SE (n)	Statistical test	
1	0.793 \pm 0.075 (29) ^a	0.938 \pm 0.043 (32)	$z = 1.68$	$P = 0.09$
2	0.857 \pm 0.077 (25)	0.909 \pm 0.062 (25)	$z = 0.64$	$P = 0.52$
3	0.700 \pm 0.115 (18)	0.669 \pm 0.096 (25)	$z = 0.25$	$P = 0.80$
4	0.750 \pm 0.125 (13)	0.954 \pm 0.044 (22)	$z = 1.61$	$P = 0.11$
5	0.625 \pm 0.172 (9)	0.917 \pm 0.080 (19)	$z = 1.64$	$P = 0.10$

Table 6. Results of a stepwise multiple logistic regression with brown bear cub survival in the southern study area in Sweden during 1986–98 as the dependent variable. Independent variables were cub food index, number of adult males dying 1, 2, and 3 years earlier within or adjacent to the cub area, whether the female had been disturbed in the den while pregnant or with cubs, year (surrogate variable for density), and food index in the year the female was pregnant.

Variable	Slope	Wald χ^2	df	P	R ^a
Constant	1.639	15.46	1	0.0001	
Cub food index	-0.887	10.50	1	0.0012	-0.242
Adult males dying 2 years earlier	-0.546	8.33	1	0.0039	-0.209
Den disturbance	-1.767	5.19	1	0.0227	-0.148
Entire model		17.69	3	0.0005	

^a Partial regression coefficient.

(Table 6). When considering only whether an adult male had died in or near the cub area with various time lags, a significant difference was found only with a 2-year time lag, but this difference was highly significant (Table 7).

In the north, there were so few years with dead adult males that another variable, whether an adult male died 1 or 2 years earlier, was included in the stepwise multiple

logistic regression. No significant model was obtained. The last independent variable to be removed from the model was whether an adult male died 1 or 2 years earlier; it was negatively related to the survival of cubs. The last 4 variables to be removed were the 4 variables including males dying within the cub areas. The loss of cubs when an adult male had died 1 or 2 years previously was

Table 7. Loss of brown bear cubs-of-the-year in relation to whether adult (≥ 5 years) males were known to have died within or adjacent to the cub area at various time periods prior to the year the cubs were lost, southern study area, Sweden, 1986-98.

Time lag	Loss after an adult male was known to have died (<i>n</i> cubs)	Loss after no adult male was known to have died	Statistical test	
1 year	0.36 (76)	0.42 (57)	$\chi^2_c = 0.35$	$P = 0.55$
2 years	0.45 (109)	0.08 (24)	$\chi^2_c = 9.66$	$P = 0.002$
3 years	0.32 (75)	0.47 (58)	$\chi^2_c = 2.35$	$P = 0.13$

0.08 ($n = 36$), compared with 0.00 ($n = 42$) if no adult male was known to have died at either time lag. This difference was only marginally significant, however (Fisher's exact test, $P = 0.09$).

DISCUSSION

We found support for the social factor to explain the spatial variation in cub loss. Cub loss was very low in the north (0.04). Few adult males died there and, perhaps more importantly, there appeared to be an extremely low immigration rate. This low immigration rate would explain why the number of males on the northern study area remained low for 7 years, although the area supported more adult males both before and after this period. The reason for a low number of immigrants appears to be the high rate of illegal killing of bears around much of the study area and the lack of bear habitat on one side of the study area. In the south, cubs had a significantly higher loss rate and 5.5 times more adult males died annually than in the north. Subadult male survival was much higher in the south and the study area was surrounded by bear habitat. There, immigration was apparently adequate to maintain a relatively constant number of adult males on the study area, despite the higher loss of adult males.

Loss of entire litters, a phenomenon predicted by the SSI hypothesis, was significantly more common in the south than in the north. However, we did not consider whether males were successful in apparent attempts at infanticide and subsequent mating with the mother. We based our analyses on loss of all cubs, not just loss of entire litters, because we were interested in trying to identify the cause of the loss of cubs, among many potential causes, and the effect of this loss. When males kill cubs, they are not necessarily successful in killing all the cubs in the litter. We observed incomplete loss of a litter due to male predation, as have others (Olson 1993, Hessing and Aumiller 1994), and mothers can successfully defend their young from males (Olson 1993, Hessing and Aumiller 1994). We have not recorded scarring of adult females in our study areas, but we would expect more scarring where there is a higher loss of cubs, if infanticide is an important factor. We will begin recording scarring when we capture females.

Social factors also helped explain much of the temporal variation in cub loss in the south. Cub survival was negatively correlated with the number of adult males dying 2 years earlier in a multivariate analysis, corrected for den disturbance and cub food index. Also, a highly significant difference in cub survival was found when comparing whether any adult male died in or near the cub area 2 years earlier. No factor explained a significant amount of the temporal variation in cub loss in the north, which is probably not surprising, given the low amount of variation in cub loss there. But of all factors examined, whether an adult male had died 1–2 years earlier best explained the observed variation and was marginally significant.

The disturbance factor was also important in explaining the temporal variation in cub loss in the south. We did not examine this factor in the north.

Little support for a nutritional effect was found. Both populations increased at the highest rates reported for brown bears, and the southern population was increasing faster than the northern population, despite the higher cub loss (Sæther et al. 1998). Southern bears had an earlier age of first reproduction and shorter litter intervals than those in the north, although the difference disappeared when only successful litters were considered.

Northern bears were generally heavier than southern bears, but this was only statistically significant for young bears. In the south, the cub food index correlated best with cub survival of all the factors examined, but the relationship was negative with higher survival when cubs were lighter at emergence the following spring. This was counter-intuitive, based on the literature and logic. Perhaps the lightest cubs died consistently, resulting in a lower mean weight following years of higher survival. This seems to be a poor explanation, and it is not consistent with the heavier yearling males and marginally heavier females in the north, where survival was consistently high. There was no significant relationship in the north.

We found a negative correlation earlier between cub survival and spring body mass of adult females in the south (Swenson et al. 1997a). Thus, we do not consider nutrition to be an important factor in explaining cub loss either at the temporal or spatial scale. Opseth (1998) found that the bears' use of major food items in the south varied little during 1994–96, a period with great variation in cub sur-

vival (Table 1). Although the faster growth in the north could be explained by a higher availability of protein through ungulate carcasses (Stabell 1999), bears in the south also had a high availability of protein in the form of ants (30–38 tons/bear; Swenson et al. 1999). An alternate explanation is that northern bears prioritized growth to be able to store more fat (Lindstedt and Boyce 1985), which they needed for the >1-month longer hibernation period (Sandegren and Swenson 1997). Growth may have been prioritized over early reproduction.

The social factor best explained spatial and temporal variations in cub survival in the 2 Swedish brown bear populations. We stress that this is a correlative study, and the results must be viewed accordingly. However, we arrived at the same conclusion earlier (Swenson et al. 1997a), although we now analyzed the data quite differently, adding adult males that were not killed by hunters, examining the location of death at a more local, and appropriate, level in relation to the observed cubs, and more fully examining alternative explanations. We could not determine whether the presumed primary mechanism was direct infanticide (LeCount 1987) or indirect, through female avoidance of productive habitats to avoid potentially infanticidal males (Wielgus and Bunnell 1994b, 1995). We often located females with cubs in the alpine zone, where adult males are rarely located, during the breeding season in the north. There is virtually no alpine zone present in the south.

Our results suggest that the key factor was immigration of subadult(s) following the death of 1 or more established adult males. The density of subadult males apparently increases in an area following the death of many adult males, as shown by Young and Ruff (1982) for American black bears. We suggest that resident adult males were not an important factor in the loss of cubs, because (1) cub survival was high in the northern study area, with little adult male mortality and little immigration, (2) cub survival was high in the southern study area when no adult males had died 2 years earlier, and (3) cub survival was low when adult males died 2 years earlier. Thus, we suggest that it is the loss of adult males and the ensuing immigration of new males, not the presence or abundance of adult males *per se*, that is important. We documented that males were recruited into the adult male category during the last few years in the north, but this was not associated with elevated cub loss (Table 1). Most of these males grew up on the study area, which may have influenced infanticidal behavior. Also, preliminary data from genetic fingerprinting suggests these males were able to first breed successfully as 3-year-olds, compared to 5 years in the south (L. Waits, Scandinavian Brown Bear Research Project, University of Idaho, Moscow, Idaho, USA, unpublished data). Such young males may have difficulty

killing cubs defended by their mother.

LeCount (1987) found high cub mortality, caused primarily by other bears, in a heavily hunted black bear population with few adult males and many presumably immigrating young males. In a comparison of 2 populations of grizzly bears, Wielgus and Bunnell (2000) reported lower reproduction in the population with higher adult male mortality and higher subadult male immigration. They concluded that the lower reproductive rate was not caused by higher cub mortality, but because adult females avoided food-rich habitats used by the potentially infanticidal immigrant males.

The conclusion that SSI occurs in bear populations is considered controversial by some wildlife management agencies and researchers (Wielgus and Bunnell 2000). Our discussions with bear biologists about these results have centered on 2 points: (1) whether it is reasonable that the documented loss of adult males could have such an effect of cub survival, and (2) whether bears should be expected to behave in a manner consistent with the SSI hypothesis, because it is commonly associated with social mammals.

In the southern study area, we estimated an adult male breeding population of 9.8 males, which was constant during the study period. In the years adult males died, the mean loss was 2.1. This is about 20% of the breeding adult males and should be sufficient to disturb the social organization of adult males. The cub areas averaged 4,000 km² in size, and adult male home ranges there are about 1,000 km² in size (median of both 95% fixed kernel and 95% minimum convex polygon methods), or 1,400–2,400 km², if the median and mean, respectively, of 100% minimum convex polygons are used (B. Dahle, Scandinavian Brown Bear Research Project, Norwegian University of Science and Technology, Trondheim, Norway, unpublished data). Using the conservative value implies that the loss of 2 males would affect 25–50% of the cub area, depending on degree of male home range overlap. It is difficult to know which proportion of this area would be affected by settling immigrant males, but we may expect that the number of immigrating males exceeds the number of dying adults (Young and Ruff 1982). Thus, a substantial proportion of females with cubs within a cub area would be affected. The estimated loss of adult males, reported above, is within the 95% confidence limits of the mortality estimated from radiomarked bears. Over the study period in the south, 1.08 adult males were known to have died annually, a rate of 0.110, based on 9.8 males present. Actually, a loss of 0.98, excluding marking-induced mortality, is better to compare with the survival estimate from radiomarked males, which does not include marking-induced mortality. This mortality rate is 0.100. The mortality rate of radiomarked bears, based on 95 bear-years (a bear-year is a bear marked during all or part of a

year), was 0.074 (SE = 0.032), and the 95% confidence interval was 0.011–0.137.

Our results also suggest that the adult male social organization can be disrupted for up to 2 years after the removal of about 20% of the adult males. We suggest that this time lag is not unreasonable for brown bears. Males are generally killed during the autumn, when fattening for winter denning is important. The breeding season starts in the spring not long after den emergence and continues to midsummer. Thus, there is a relatively short time for an immigrating male to become established if he is to participate in breeding the first year after an adult male dies and a vacancy is available.

We do not expect a linear relationship between the loss of adult males and cub mortality due to SSI. It is probable that the per capita effect of removing adult males declines rapidly as the number of males increases, which could account for the stable cub mortality with increasing mortality of adult males reported by Miller (1990). His study did not include a situation where no adult males had been killed. Also, if the mortality of adult and subadult males becomes very high, cub mortality due to SSI might decline if the few immigrating males enter the breeding pool while they are too young to effectively kill defended cubs. We suggested that this happened in the northern study area.

Is it reasonable to expect SSI in a bear population? Infanticide is usually a relatively uncommon event and is most easily observed in social species. Males have been observed killing infants in situations consistent with the predictions of the SSI hypothesis in many social mammals, such as the mountain gorilla (*Gorilla gorilla*, Robbins 1995), Hanuman langur (*Presbytis entellus*, Mohnot 1971), arctic ground squirrel (*Spermophilus parryii*, McLean 1983), Alpine marmot (*Marmota marmota*, Coulon et al. 1995), African lion (*Panthera leo*, Pusey and Packer 1994), red deer (*Cervus elaphus*, Bartos and Madlafousek 1994), hippopotamus (*Hippopotamus amphibius*, Lewison 1998), bottlenose dolphin (*Tursiops truncatus*, Patterson et al. 1998), and in nonsocial mammals, such as the collared lemming (*Dicrostonyx groenlandicus*, Mallory and Brooks 1978), house mouse (*Mus musculus*, vom Saal and Howard 1982) and white-footed mouse (*Peromyscus leucopus*, Wolff and Ciciello 1989). The list also includes birds, such as the barn swallow (*Hirundo rustica*, Crook and Shields 1985; Møller 1988), house wren (*Troglodytes aedon*, Freed 1986), tree swallow (*Tachycineta bicolor*, Robertson and Stutchbury 1988), and house sparrow (*Passer domesticus*, Veiga 1990). Consistent with the SSI hypothesis, female birds can also kill another female's young, such as has been found in two species of polyandrous jacanas (*Jacana spinosa* and *J. jacana*, Stephens 1982, Emlen et al. 1989)

and in the house sparrow (Veiga 1990). Documented infanticide is not always consistent with SSI, but the evidence for SSI has become so numerous as to be very convincing.

But should we really expect to see SSI in a nonsocial carnivore with a promiscuous mating system such as bears? Packer and Pusey (1984) examined the occurrence of SSI in carnivores and state that "...because of their carnivorous habits and because most bear altricial young, carnivores are more likely to exhibit infanticide than any other mammalian order." (Packer and Pusey 1984:31). Although SSI has been best documented in the social lions, they suspected that "infanticide as a male reproductive strategy may be confirmed eventually in many solitary carnivore species where the female's reproduction is accelerated by the death of her young." (Packer and Pusey 1984:42). It has been shown that the death of a female brown bear's young accelerates her reproduction (Swenson et al. 1997a). Female American black bears can breed within 48 hours of losing their cubs (LeCount 1983), and a female brown bear was observed apparently in estrus and with an adult male 4 days after her cubs were killed (Hessing and Aumiller 1994). We have also shown that the cubs in our study died mostly during the breeding season. This does not necessarily support the SSI hypothesis, but it is a requirement for it. In addition, mating with multiple males has been documented in brown bears (Craighead et al. 1995a,b, L. Waits, Scandinavian Brown Bear Research Project, University of Idaho, Moscow, Idaho, USA, unpublished data). Hrdy (1977) proposed that this is an infanticide-avoidance behavior, whereby females mate with likely perpetrators because they are less likely to kill potential offspring. Thus, there is no biological reason to expect that the SSI hypothesis is inappropriate for bears.

MANAGEMENT IMPLICATIONS

Much has been written about the potential effects on the survival of cubs of hunting adult male bears. Miller (1990) has recommended that managers do not assume that the killing of adult males will positively effect cub survivorship, because there is no evidence for such a relationship and such an assumption could lead to overharvest. Wielgus and Bunnell (1994a) went further, and suggested that the hunting of adult males could actually be compensatory. We agree with Wielgus and Bunnell (1994a). Our results suggest that the death of about 20% of the adult males in a local area significantly reduced cub survival. We do not recommend that adult males not be harvested, but we recommend that the potential consequences be considered when modeling the effects of hunting on bear populations and when considering the fate of

problem adult males in control actions in threatened and endangered populations. Our study was correlational, not experimental, and other factors, unexamined or autocorrelated with those we found to be important, may be the true mechanism behind our observed results. Until this question is adequately resolved, managers should act conservatively and assume a population consequence of harvesting adult male bears.

We recommend that other researchers investigate SSI in bear populations. Our results are based on presumed infanticide; we have not marked any cubs and have documented infanticide in only 2 litters. Also, replication is important to determine the generality of the pattern we have observed. In future research, it is important to focus on the loss of adult males and subsequent immigration, not just the proportion of adult males in a population, as was reported in some earlier studies (McCullough 1981, 1986; Stringham 1983; Clark and Smith 1994). We have started an experiment in the southern study area to test the SSI hypothesis. The Swedish Environmental Protection Agency has agreed to keep the harvest level for several years at a constant and high enough level to stop population growth. We predict that cub survival will decrease with the increase in harvest rate, including adult male harvest.

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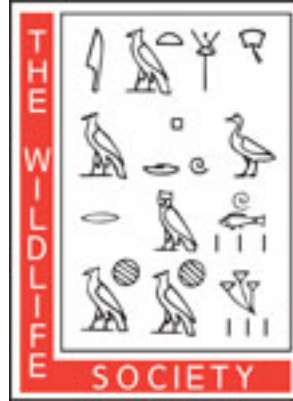
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TESTS OF HYPOTHESES FOR SEXUAL SEGREGATION IN GRIZZLY BEARS

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Abstract: We studied 2 grizzly bear (*Ursus arctos*) populations to test 3 hypotheses of sexual segregation. The “no avoidance” hypothesis predicts that females do not avoid males and male-occupied habitats but simply have different habitats available to them within their home ranges. The “food” hypothesis predicts that subadult and adult females avoid males because of competition or cannibalism by males for food. The “sex” hypothesis predicts that only sexually mature adult females avoid males because of sexually motivated infanticide by nonsire males. Sexually mature females avoided ($P < 0.05$) food-rich, male-occupied habitats in Kananaskis, Alberta, but selected ($P < 0.05$) such habitats in the Selkirk Mountains of Idaho. Sexually immature females selected ($P < 0.05$) food-rich, male-occupied habitats in both areas. Unequal availability of habitat did not explain the pattern of segregation because food-rich habitats were available to all age-sex classes. Competition or cannibalism by males did not explain segregation because only sexually mature females avoided male-occupied habitats in Kananaskis and no females avoided males in the Selkirks. Adult female avoidance of potentially infanticidal, nonsire, immigrant males in Kananaskis appeared to explain the pattern of segregation. High mortality of older males in Kananaskis coincided with an influx of younger, potentially infanticidal, immigrant males, and adult females avoided those males and their favored habitats. No such segregation was observed in the Selkirks where mortality of older males was low and where there were few or no immigrant males. Results are inconsistent with the no avoidance and food hypotheses but consistent with the sex hypothesis of sexual segregation.

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Grizzly bears have disappeared from most of their historic range (Servheen 1990), sometimes by incremental population losses at the edge of the species' range (Wielgus and Bunnell 1994a, Wielgus et al. 1994). Remaining bear populations are classified as threatened in the lower United States (Servheen 1990) and vulnerable in Canada (Banci 1991). We must understand use of habitat and population dynamics in small, peripheral populations to prevent further range contractions and eventual extinction. The 2 populations (Selkirks, Id., and Kananaskis, Alta.) we studied were at the edge of the species' range and at low density (1.4–1.6 bears/100 km²; Wielgus and Bunnell 1994a, Wielgus et al. 1994). Both populations were small with approximately 20 bears in the Selkirks (Knick 1988, Knick and Kasworm 1989) and 38 bears in Kananaskis (Wielgus and Bunnell 1994a), and both were declining (Wielgus and Bunnell 1994a, Wielgus et al. 1994).

Many researchers (Pearson 1975, Wielgus 1986, Darling 1987, Mattson et al. 1987, McLellan and Shackleton 1988) reported that fe-

male grizzly bears, especially those with cubs, used habitats that were less favorable than those used by adult males. They interpreted that as female avoidance of aggressive, cannibalistic males but did not test the hypothesis. Wielgus and Bunnell (1994b) tested and supported the hypothesis of female avoidance of males and suggested that such avoidance could result in food deprivation, reduced cub production or survival, and population decline; however, they did not examine potential reasons for female avoidance of males.

We test 3 competing hypotheses of sexual segregation by examining use of habitat in the 2 grizzly bear populations. The no avoidance hypothesis predicts that females do not avoid adult males and male-occupied habitats but simply have different habitats available to them within their home ranges (Wielgus and Bunnell 1994b). Sexual segregation should not occur in either area if the same habitat is accessible and available to all sex and reproductive classes of bears.

The food hypothesis predicts that females and other subdominants avoid adult males and their

avored habitats because those males compete with and even cannibalize subdominants for food (Hornocker 1962, Egbert and Stokes 1976, McCullough 1981, Stringham 1983). All subdominant classes, including subadult females (Hornocker 1962, Egbert and Stokes 1976), should avoid adult males and male-occupied habitats. Furthermore, Egbert and Stokes (1976) observed competition for food in grizzlies and found that aggression by adult males toward subdominants and avoidance of adult males by subdominants increased with diminishing food supply. Therefore sexual segregation should be more pronounced during seasons of food limitation, not food abundance, and more pronounced in the Selkirks where food supply appeared inferior to that of Kananaskis (Wielgus 1993).

The sex hypothesis predicts that mature females, especially females with offspring, avoid immigrant adult males because they are unlikely to have sired cubs locally and will attack cubs (including cubs in utero) to induce estrus to gain breeding opportunities (Hrdy 1979, Stringham 1980, Hrdy and Hausfater 1984). Vulnerable females that provide reproductive opportunities to nonsire males (e.g., post-estrous ad F) should avoid male-occupied habitats. Other reproductive classes (e.g., sexually immature subad F, subad M) should not avoid these habitats because they offer no such reproductive opportunities. Sexual segregation should thus be more pronounced in Kananaskis where there were a greater number of potentially infanticidal, immigrant males (Wielgus and Bunnell 1994a) than in the Selkirks (Wielgus et al. 1994). Finally, segregation should be more pronounced in Kananaskis during the post-hunting period when there were more immigrant males than during the pre hunting period when immigrant males were rare (Wielgus and Bunnell 1994a).

Wielgus and Bunnell (1994b) pooled radio-location data into sex classes to examine seasonal sexual segregation in Kananaskis. They found that sexual differences in use of habitat increased with increasing numbers of males and male use of the female-occupied area, with females moving out of previously occupied habitats when males moved in. That does not support the no avoidance hypothesis. Wielgus and Bunnell (1994b) also found that sexual segregation was greatest in Kananaskis during the late summer berry season when food was most abundant, and that does not support the food

hypothesis. In this paper we test for sex and reproductive class sexual segregation for individual bears in both areas and test the remaining predictions of the 3 competing hypotheses.

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STUDY AREA

The Kananaskis Provincial Park and Bow Crow Forest encompassed 6,300 km² in southwestern Alberta (50–51°W, 115–116°N). Elevation ranged from 1,300 to 2,700 m in mountainous terrain. Climate was continental with long, cold winters and short, cool summers. Vegetation was in the subalpine fir-Engelmann spruce (*Abies lasiocarpa*-*Picea engelmanni*) forest region (Rowe 1972). Sport hunting of grizzly bears was closed in this area from 1970 to 1981, but was reopened from 1982 to 1988 because the population was believed to be increasing (Carr 1989, Nagy and Gunson 1990). Wiel-

gus and Bunnell (1994a) suggested that the population was decreasing from 1981 to 1984. Density in the 868-km² female composite range was 1.6 bears/100 km² (Wielgus and Bunnell 1994a). The population numbered approximately 38 animals in a 2,315-km² area (Wielgus and Bunnell 1994a).

The U.S. portion of the Selkirk Mountain Grizzly Bear Ecosystem (U.S. SMGBE) covered 3,000 km² in northern Idaho and northeastern Washington (48–49°W, 116–117°N). Physiography was mountainous with elevations from 550 to 2,500 m. Climate was Pacific maritime/Continental with long winters and cool summers. Vegetation was in the subalpine fir-Engelmann spruce and red cedar-western hemlock (*Thuja plicata*-*Tsuga heterophylla*) bigeoclimatic zones (Pojar et al. 1987). Sport hunting of grizzly bears was not allowed in the U.S. portion of the SMGBE under the Endangered Species Act and sport-hunting mortalities did not occur in adjacent British Columbia during research (1985–90). The population was believed stable from 1985 to 1990 (Wielgus et al. 1994) but was probably declining after 1990 because of increased mortalities (Wielgus, unpubl. data). Density in the 815-km² female composite range was 1.4 bears/100 km² (Wielgus et al. 1994). The population numbered approximately 20 animals in the U.S. SMGBE (Knick 1988).

METHODS

Trapping and Habitat Quality

We trapped bears in Kananaskis Park and the U.S. SMGBE using Aldrich leg snares and immobilized them with ketamine HCl and xylazine HCl. We weighed, eartagged, extracted a premolar for aging (Stoneburg and Jonkel 1966), and fitted bears with mortality-sensing radio collars. We handled bears according to protocol of the Canadian Council on Animal Care, University of British Columbia Animal Care Certificate 890105. Details on trapping and monitoring of bears are in Wielgus and Bunnell (1994a,b) and Wielgus et al. (1994).

We trapped and radiocollared bears in Kananaskis in the Highwood trapping zone (HTZ) from 1981 to 1984. The 254-km² HTZ covered a 50-year-old burn in the mountains (1,800 m) and was dominated by soapberry (*Shepherdia canadensis*) shrubfields, whereas surrounding unburned areas were not. We chose the HTZ to maximize trapping success. Bear foods and bear

activity appeared to be more abundant in the HTZ than in surrounding areas (Wielgus and Bunnell 1994a,b). Zager et al. (1983) and Hamer and Herrero (1987) also found that previously burned habitats were more productive for bear foods than were unburned habitats.

During 1985–87 and 1989, we trapped and radiocollared bears in the U.S. SMGBE in the 100-km² Idaho trapping zone (ITZ). The ITZ covered a 20-year-old burn dominated by abundant huckleberry (*Vaccinium globularum*) shrubfields, whereas surrounding unburned areas were not. We chose the ITZ to maximize trapping success. Bear foods and activity were more abundant in the ITZ than in surrounding areas (Knick 1988, Wielgus et al. 1994). For purposes of this study, we define the HTZ and ITZ as superior habitats and surrounding unburned areas as inferior habitats.

Sexual Segregation

We searched for and monitored bears throughout their range using fixed-wing radio telemetry (Whitehouse and Steven 1977) every 1–2 weeks during the nondenning period (early Apr–early Nov) from 1981 to 1984 in Kananaskis and from 1985 to 1990 in the Selkirks. We analyzed use of habitat by 6 reproductive classes: estrous adult females, adult females with cubs, adult females with yearlings, independent subadult females, adult males (≥ 6.5 yr), and independent subadult males (2.5–5.5 yr). We included only bears trapped in the HTZ and ITZ and of known reproductive status. We determined sex during capture and age from known birth dates or by counting cementum annuli (Stoneburg and Jonkel 1966).

We tested for differences in use of HTZ and ITZ habitats to see which, if any, reproductive classes used those superior habitats more or less than did other classes. Because all bears were trapped in the HTZ and ITZ, all bears had equal access to those areas. We tested for differences in percent use of the previously burned habitats between study areas and among age-sex classes (Table 1) using factorial analysis of variance (ANOVA), followed by comparisons of means using Fisher's LSD tests (SYSTAT 1992). The model we tested was percent use = constant + area + age-sex + area·age-sex.

From the no avoidance hypothesis we predicted no differences in use of previously burned areas among age-sex classes in both areas. All age-sex classes should use the HTZ and ITZ

Table 1. Mean percent use of the Highwood trapping zone (HTZ) in Kananaskis, Alberta, 1981–84, and the Idaho trapping zone (ITZ) in the Selkirk Mountains, Idaho, 1985–90, by different age-sex classes of radio-tagged grizzly bears.

Area	Age-sex	\bar{x} use (%) ^a	SE	n
HTZ	Ad M	43	8	7
	Subad M	58	5	8
	Subad F	89	6	2
	Ad F (estrous)	38	16	5
	Ad F ^b	16	9	7
ITZ	Ad M	35	9	3
	Subad M	31	7	5
	Subad F	26	12	3
	Ad F (estrous)	34	6	4
	Ad F ^b	41	10	4

^a Based on percentage of radiolocations in HTZ and ITZ for individual bears.

^b Ad F with offspring (cubs and yearlings).

equally. From the food hypothesis we predicted differences among age-sex classes, but not among areas. Adult males should use the HTZ and ITZ more than other age-sex classes in both areas. From the sex hypothesis we predicted an area by age-sex interaction, whereby adult females with offspring use the HTZ less than do other age-sex classes in Kananaskis, with no differences in use of the ITZ among age-sex classes in the Selkirks.

We then tested for differences in use of habitat by comparing observed and expected number of locations in the HTZ and ITZ for different reproductive phases of each bear. The expected value was calculated from the percentage of a bear's 100% multiannual, minimum area home range (Ackerman et al. 1990) that covered the trapping zone, multiplied by the number of locations for each reproductive phase of that bear. For example, if 20% of a bear's home range were in the trapping zone and if the bear did not select for or against the zone, we would expect 20% of that bear's locations in the zone. We used Chi-square goodness-of-fit (Daniel 1978) to test for third-order selection (selection within home range; Johnson 1980). This method satisfies the assumption of equal availability of habitat because use is compared with availability for each animal.

If bears showed no third-order selection for the HTZ and ITZ, it could be because they already showed second-order selection for the zones (selection of home range; Johnson 1980). We tested for second-order selection by those bears by comparing their percentages of home ranges in the zones with those of bears that

Table 2. Observed and expected number of locations in the Highwood trapping zone (HTZ) of Kananaskis, Alberta, for radio-tagged subadult male and adult male grizzly bears, 1981–84.

Bear no.	Age at capture	Reproductive class	No. locations	Obs. no. locations in HTZ	Expected no. ^a locations in HTZ
S2	3.5	Subad M	21	8	4.8
H6	5.5 ^b	Subad M	11	8	7.3
H10	3.5	Subad M	21	10 + ^c	5.4
H16	3.5	subad M	21	15 +	4.8
H18	3.5	Subad M	20	12 +	3.2
H21	5.5	Subad M	16	9 +	2.4
S1	4.5 ^b	Subad M	26	11 +	1.8
H14	5.5	Ad M	25	7 +	1.7
		Subad M	15	11 +	3.0
H1	12.5 ^b	Ad M	19	10 +	3.8
		Ad M	36	9 +	1.4
H7	15.5 ^b	Ad M	30	18 +	8.7
H19	7.5	Ad M	14	10 +	3.5
H15	15.5	Ad M	6	3	2.4
H17	6.5	Ad M	9	1	0.5

^a Expected no. based on % home range in HTZ.

^b These animals captured during the pre hunting period (1981), all others captured during the post-hunting period (1982–83).

^c + Obs. no. of locations in the HTZ is greater than the expected no. at $P < 0.05$, using Chi-square goodness-of-fit.

showed third-order selection for the zones. If they had larger percentages of their home ranges in zones, we interpreted that as second-order selection for the zones. We used *t*-tests (Zar 1984) and Mann-Whitney *U*-tests (Daniel 1978) to test for differences in mean percentage of home ranges in the zones. This method satisfies the assumption of equal access to habitat because all bears were trapped in the HTZ and ITZ.

RESULTS

Trapping and Monitoring

We trapped and radiomonitored 13 males and 5 females from 1981 to 1984 in the HTZ of Kananaskis (Tables 2 and 3) and 6 males and 7 females from 1985 to 1990 in the ITZ of the Selkirks (Tables 4 and 5). We assumed that all bears using the HTZ and ITZ were trapped and collared (Wielgus and Bunnell 1994a, Wielgus et al. 1994).

In Kananaskis, all 8 subadult males were ≥3.5 years old when captured (Table 2), and none were observed as offspring accompanying resident females, suggesting they were immigrants because males at that age typically emigrate (Glenn and Miller 1980, Blanchard and Knight 1991). Observations suggest that 9 of 13 males monitored may have immigrated to the HTZ after 1981. Increased trapping effort did not

Table 3. Observed and expected number of locations in the Highwood trapping zone (HTZ) of Kananaskis, Alberta, for different reproductive classes of radio-tagged female grizzly bears, 1981–84.

Bear no.	Age at capture	Reproductive class	No. locations	Obs. no. locations in HTZ	Expected no. ^a locations in HTZ
H11	2.5	Subad F	41	34 + ^b	25.8
		Ad F (estrous)	12	8	7.5
H12	2.5	Subad F	16	15 +	9.1
		Ad F (estrous)	22	19 +	12.5
		Ad F (cubs)	12	7	6.8
H9	14.5	Ad F (yearlings) ^c	9	4	4.3
		Ad F (estrous)	25	3 –	12.0
		Ad F (cubs)	19	1 –	9.1
		Ad F (yearlings)	12	1 –	5.8
H13	6.5	Ad F (estrous)	12	2	1.2
		Ad F (cubs)	19	0	1.9
		Ad F (yearlings)	12	0	1.2
H20	10.5	Ad F (estrous)	13	1	1.4
		Ad F (cubs)	12	0	1.3

^a Expected no. based on % home range in HTZ.^b ± Obs. no. of locations in HTZ is less than or greater than the expected no. at $P < 0.05$, using Chi-square goodness-of-fit.^c Data are pre hunting, all other data are post-hunting.

explain increased numbers of captured males after 1981 (Wielgus and Bunnell 1994a).

In the Selkirks, 3 of 5 subadult males (Table 4) were captured and observed as 2.5-year-old offspring of resident females, and all other males were captured during the first year of trapping (1985). Those observations suggest no males immigrated into the ITZ after 1985.

Sexual Segregation

Bears used previously burned areas more in Kananaskis than in the Selkirks (43 vs. 33%; $F = 5.21$; 1, 38 df; $P = 0.03$) but there were no differences in percent use of burned areas among age-sex classes ($F = 1.80$; 4, 38 df; $P = 0.15$). However, there was an area by age-sex interaction for use of the burned areas ($F = 4.05$; 4, 38 df; $P < 0.01$). Adult females with offspring used the HTZ less (LSD, $P < 0.05$) than did

adult males, subadult males, and subadult females in Kananaskis (Table 1). Estrous adult females used the HTZ less than did subadult females ($P < 0.05$), and subadult females used the HTZ more than did adult males ($P < 0.05$). There were no differences ($P > 0.10$) in use of the ITZ among age-sex classes in the Selkirks (Table 1).

In Kananaskis, 9 of 13 males (6 of 8 subad and 5 of 7 ad reproductive phases) used the HTZ more than expected ($\chi^2 > 3.84$, 1 df, $P < 0.05$), indicating third-order selection for the HTZ (Table 2). The remaining 4 males (S2, H6, H15, H17) did not use the HTZ more than expected but, compared with the 9 selective males, 3 of those bears (S2, H6, H15) had a larger mean percentage (43 vs. 18%) of their home ranges in the zone, indicating second-order selection for the HTZ ($t = 2.98$, 10 df, $P = 0.01$; $U = 23.50$,

Table 4. Observed and expected number of locations in the Idaho trapping zone (ITZ) of the Selkirk Mountains, Idaho, for radio-tagged subadult male and adult male grizzly bears, 1985–90.

Bear no.	Age at capture	Reproductive class	No. locations	Obs. no. locations in ITZ	Expected no. ^a locations in ITZ
1091 ^b	2.5	Subad M	28	6 + ^c	1.9
1077 ^b	2.5	Subad M	18	5	3.6
1090 ^b	2.5	Subad M	27	6	5.9
1004	3.5	Subad M	43	11 +	3.4
		Ad M	29	12 +	2.3
962	4.5	Subad M	22	13	10.7
		Ad M	19	9	9.3
1005	6.5	Ad M	38	7 +	2.2

^a Expected no. based on % home range in ITZ.^b Offspring of resident ad F.^c + Obs. no. of locations in the ITZ is greater than the expected no. at $P < 0.05$, using Chi-square goodness-of-fit.

Table 5. Observed and expected number of locations in the Idaho trapping zone (ITZ) of the Selkirk Mountains, Idaho, for different reproductive classes of radio-tagged female grizzly bears, 1985–90.

Bear no.	Age at capture	Reproductive class	No. locations	Obs. no. locations in ITZ	Expected no. ^a locations in ITZ
1089	2.5	Subad F	10	5 + ^b	1.2
1085	2.5	Subad F	6	1	1.9
1042	0.5	Subad F	17	2 –	7.6
867	7.5	Ad F (estrous)	50	26 +	7.0
		Ad F (cubs)	37	18 +	5.1
		Ad F (yearlings)	10	6 +	1.4
1087	8.5	Ad F (estrous)	15	5	2.8
		Ad F (cubs)	21	8 +	3.9
1084	18.5	Ad F (estrous)	23	6 +	2.7
1015	5.5	Ad F (estrous)	34	9	6.4
		Ad F (cubs)	13	2	2.4

^a Expected no. based on % home range in ITZ.
^b ± Obs. no. of locations in the ITZ is less than or greater than the expected no. at $P < 0.05$, using Chi-square goodness-of-fit.

$P = 0.06$). If we include bear H17 in the analysis for second-order selection results are not significant ($t = 1.68$, 11 df, $P = 0.11$; $U = 24.50$, $P = 0.31$) because H17 had a small percentage (6%) of his home range in the HTZ.

Subadult females behaved similarly to males. Subadults (H11 and H12) used the HTZ more than expected ($\chi^2 > 3.84$, 1 df, $P < 0.05$), indicating third-order selection for the HTZ (Table 3). One subadult female (H12) used the HTZ more than expected during her first estrus and used the HTZ as expected when accompanied by her first litter. Adult females behaved differently from males and subadult females. Bear H9 used the HTZ less than expected during all reproductive phases, except prior to the opening of the grizzly bear hunting season when she used the zone as expected (Table 3). The remaining 2 adult females (H13 and H20) did not use the HTZ less than expected but, compared with the 3 other selective females, they had a smaller mean percentage (11 vs. 56%) of their home ranges in the zone, indicating second-order selection against the zone ($t = 8.06$, 3 df, $P = 0.004$; $U = 0.00$, $P = 0.08$). They used the HTZ when estrous and did not use it when with offspring.

In the Selkirks, 3 of 6 males used the ITZ more than expected ($\chi^2 > 3.84$, 1 df, $P < 0.05$) (Table 4). The remaining 3 males (1077, 1090, 962) did not use the ITZ more than expected but, compared with the 3 selective males, they had a larger mean percentage (30 vs. 7%) of their home ranges in the zone, indicating second-order selection ($t = 2.49$, 4 df, $P = 0.06$; $U = 9.00$, $P = 0.05$).

Females behaved similarly to males in the Selkirks. Three of 4 adults and 1 of 3 subadults used the ITZ more than expected ($\chi^2 > 3.84$, 1 df, $P < 0.05$) (Table 5). One adult female (867) selected for the ITZ during all reproductive phases. Another adult female (1087) selected for the ITZ while accompanied by cubs, and another (1084) selected for the ITZ when estrous. Subadult female (1089) selected for and another (1042) against the ITZ. The 3 females (1015, 1085, 1042) that did not use the ITZ more than expected had a larger mean percentage (32 vs. 14%) of their home ranges in the ITZ than the 4 selective females ($t = 2.74$, 5 df, $P = 0.04$; $U = 11.50$, $P = 0.04$).

DISCUSSION

Tests of Sexual Segregation

There was grizzly bear sexual segregation in Kananaskis but not in the Selkirks. Although our sample sizes for bears and locations were small, we are confident in our test results because small sample size will result in decreased power to reject null hypotheses (Roscoe and Byars 1971). Large samples of animals cannot always be obtained, especially when studying threatened populations. We monitored use of habitat for all bears using the HTZ and 18 of 38 estimated bears in Kananaskis (Wielgus and Bunnell 1994a) and all bears using the ITZ and 13 of 20 estimated bears in the Selkirks (Knick 1988, Knick and Kasworm 1989). Those samples compose large proportions of the populations; however, lack of randomization and experimental replication precludes extrapolation to other populations.

Competing Hypotheses of Sexual Segregation

Results are inconsistent with the no avoidance hypothesis because sexual segregation occurred in Kananaskis, despite equal access and availability of the HTZ to all bear sex and reproductive classes. Adult females would not likely choose lower quality unburned areas because of diet preference (Wielgus and Bunnell 1994b). Furthermore, Wielgus and Bunnell (1994b) showed that sexual segregation increased with increasing numbers of males and male use of the female composite range in Kananaskis; females vacated previously occupied habitats when males moved in. Those results also suggest that females avoided males and male-favored habitats in Kananaskis. The presence of roads (McLellan and Shackleton 1988) did not account for adult female avoidance of the HTZ because few existing roads were closed.

Results are inconsistent with the food hypothesis because bears in all subdominant reproductive classes did not avoid adult males in the HTZ, and no bears in sex or reproductive classes avoided adult males in the ITZ. Subadult females selected for the male-occupied HTZ while adult females avoided the HTZ. The 3 other predictions of the food hypothesis also were rejected. Segregation was observed only in Kananaskis despite similar densities in both study areas; density or competition for food did not appear to account for sexual segregation. Second, segregation was greatest in Kananaskis during the late summer berry season when food was most abundant (Wielgus and Bunnell 1994b). Segregation should have been more intense during other seasons of food limitation if competition or cannibalism by males for food were causative (Egbert and Stokes 1976). Finally, segregation occurred in food-rich Kananaskis but not in the food-poor Selkirks (Wielgus 1993). The reverse should have occurred if competition or cannibalism were causative.

Results are consistent with the sex hypothesis (Hrды 1979) because only adult females that offered reproductive opportunities to potentially infanticidal immigrant males avoided the HTZ. Furthermore, segregation was only observed in Kananaskis where there was an abundance of such males (Wielgus and Bunnell 1994a), not in the Selkirks where such males were rare (Wielgus et al. 1994). Finally, H9 did not avoid the HTZ prior to the hunting season

when immigrant males were rare, but she did avoid the HTZ during and after the hunting season when immigrant males were abundant. Her avoidance of the HTZ corresponded with an influx of new immigrant males coincident with increased hunting mortality of older adult males (Wielgus and Bunnell 1994a). One younger (5.5 yr) collared male was shot and 4 males were captured in the HTZ during the pre-hunting period (1980–81). Four older (\bar{x} = 11.7 yr, SE = 2.1) collared males were shot and 9 new males were captured in the HTZ during the post-hunting period (1982–84), suggesting many immigrant males after 1981.

Kemp (1976) and Young and Ruff (1982) also observed an increase in immigrant subadult male black bears (*U. americanus*) after removing adult males. Older adult males may limit immigration of younger males (Bunnell and Tait 1981). Immigrant males are unlikely to have sired cubs and should attempt infanticide to increase their breeding opportunities (Hrды 1979, Hrды and Hausfater 1984, LeCount 1987), so females with offspring are expected to avoid such males. We observed 4 different subadult males consorting with 2 estrous females during the breeding season in 1983 in Kananaskis, suggesting immigrant subadult males were capable of copulation, hence sexually motivated infanticide. Females also bred at 3.5–4.5 years and gave birth at 4.5–5.5 years in Kananaskis (Wielgus and Bunnell 1994a).

In contrast, mortality of older adult males was low in the Selkirks and all males were captured during the first 2 years of trapping, suggesting they were residents (Wielgus et al. 1994). Females with offspring are not expected to avoid resident sires (Hrды 1979, Hrды and Hausfater 1984).

The one apparent inconsistency for female behavior in Kananaskis also fits the sex hypothesis. Unlike adult females (H9, H13, H20), subadult female H12 selected for the HTZ during her first estrus and did not appear to avoid the HTZ after producing her first litter. However, H12 and her new cub moved out of the HTZ during the late summer berry season when large numbers of males arrived (Wielgus and Bunnell 1994b). Unfortunately, she could not be aerielly monitored during that autumn or the following year because aerial telemetry ended. She was, however, radiolocated from the ground that autumn and she was outside the HTZ. Furthermore, she was sighted outside the HTZ by rangers that autumn and the following year and was

not seen again in the HTZ. This suggests she avoided the HTZ when accompanied by offspring.

Reproductive data also corroborate the sex hypothesis; litter size was lower in Kananaskis than in the Selkirks despite abundant food in Kananaskis (Wielgus 1993), but age at first parturition appeared earlier in Kananaskis, corresponding with the pattern of segregation. Sexually immature females did not avoid the male-occupied, food-rich HTZ and that may have enabled them to reach sexual maturity and produce cubs earlier than in the Selkirks (Wielgus 1993). Sexually mature females avoided the HTZ and that may have resulted in food deprivation and production of smaller litters than in the Selkirks.

Whether the sex hypothesis accounts for other instances of sexual segregation in grizzly bears is unknown. This study should be replicated to determine if the sex hypothesis is applicable to other grizzly bear populations and other potentially infanticidal species such as black bears, cougars (*Felis concolor*), lions (*Panthera leo*), and tigers (*P. tigris*).

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BIOLOGICAL CONSEQUENCES OF RELOCATING GRIZZLY BEARS IN THE YELLOWSTONE ECOSYSTEM

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Abstract: Relocating grizzly bears (*Ursus arctos*) from human/bear conflict situations has been a standard management procedure. Using data from Yellowstone National Park, we present components of situations that may affect the outcome of a relocation. Survival rates of transported bears were lower ($I_x = 0.83$) ($P = 0.001$) than those not transported ($I_x = 0.89$). Survival was largely affected by whether the bear returned to the capture site ($P = 0.029$). Return rate was most affected by distance transported ($P = 0.012$) and age-sex group ($P = 0.014$). Return rates decreased at distances ≥ 75 km, and subadult females returned least ($P = 0.050$) often. Because of low survival and high return rates, transporting grizzly bears should be considered a final action to eliminate a conflict situation. However, transporting females must be considered a viable management technique because transports of some individuals have resulted in contributions to the population through successful reproduction.

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Key words: grizzly bear, homing, movements, survival, relocation, transport, *Ursus arctos*, Wyoming, Yellowstone National Park.

Grizzly bears tenuously exist with humans in the lower 48 United States. Management agencies are mandated to protect threatened animals and their habitat. At times, situations arise that potentially endanger lives of humans and/or

bears. Short-term solutions of these immediate crises include transporting the bear to a remote site while the problem creating the conflict is resolved. Transporting a bear is only a short-term management technique with a high return

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The One-Migrant-per-Generation Rule in Conservation and Management

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Abstract: *In the face of continuing habitat fragmentation and isolation, the optimal level of connectivity between populations has become a central issue in conservation biology. A common rule of thumb holds that one migrant per generation into a subpopulation is sufficient to minimize the loss of polymorphism and heterozygosity within subpopulations while allowing for divergence in allele frequencies among subpopulations. The one-migrant-per-generation rule is based on numerous simplifying assumptions that may not hold in natural populations. We examine the conceptual and theoretical basis of the rule and consider both genetic and nongenetic factors that influence the desired level of connectivity among subpopulations. We conclude that one migrant per generation is a desirable minimum, but it may be inadequate for many natural populations. We suggest that a minimum of 1 and a maximum of 10 migrants per generation would be an appropriate general rule of thumb for genetic purposes, bearing in mind that factors other than genetics may further influence the ideal level of connectivity.*

La regla de Un-Migrante-Per-Generación en Conservación y Manejo

Resumen: *Debido a la continua fragmentación y aislamiento de habitats, el nivel óptimo de conectividad entre poblaciones se ha convertido en un tema central en la biología de la conservación. Una regla común sostiene que un amigrante por generación en una subpoblación es suficiente para minimizar la pérdida de polimorfismo y heterocigosidad en las subpoblaciones y al mismo tiempo permite la divergencia de frecuencias alélicas entre subpoblaciones. La regla de un-migrante-por-generación se basa en numerosas suposiciones simplifican que tal vez no sucedan en poblaciones naturales. En este trabajo examinamos las bases conceptuales y teóricas de la regla y consideramos factores genéticos y no genéticos que influyen en el nivel deseado de conectividad entre subpoblaciones. Concluimos que un migrante por generación es un mínimo deseable, pero puede ser inadecuado para muchas poblaciones naturales. Surgerimos que un mínimo de uno y un máximo de diez migrantes por generación sería una regla general apropiada para fines genéticos, sin olvidar que factores no genéticos pueden influir en el nivel ideal de conectividad.*

... evolution depends on a certain balance among its factors. There must be gene mutation, but an excessive rate gives an array of freaks, not evolution; there must be selection, but too severe a process destroys the field of variability, and thus the basis for further advance; prevalence of local inbreeding within a species has extremely important evolutionary consequences, but too close inbreeding leads merely to extinction. A certain amount of

crossbreeding is favorable but not too much. In this dependence on balance the species is like a living organism. At all levels of organization life depends on the maintenance of a certain balance among its factors.

—S. Wright (1932:365)

Introduction

By the 1930s Sewall Wright had clearly established—based on experiments and historical breeding records—

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that inbreeding depression in small, isolated populations typically leads to adaptive decline and extinction (Provine 1986). In Wright's view small amounts of gene flow between partially isolated demes are necessary for long-term persistence. Prompted by Wright's work, the question of how many immigrants ("migrants" in population genetics literature) are needed to prevent population differentiation became the subject of a vast body of theoretical analysis (for review see Slatkin [1985, 1987]). From this analysis emerged a genetic rule of thumb that one migrant individual per local population per generation (OMPG) is sufficient to obscure any disruptive effects of drift (Spieth 1974; see also Kimura and Ohta 1971; Lewontin 1974).

Biologists concerned with population insularization caused by habitat fragmentation began advocating the application of this principle for conservation purposes. Several of the most cited papers advocating, in some sense, the movement of one individual per generation between isolated populations for conservation purposes include Franklin (1980), Frankel and Soulé (1981), and Allendorf (1983). More recently, the OMPG concept has been widely applied by scientists and managers charged with initiating connectivity between potentially isolated populations. For example, Gogan (1990) makes the statement for mammals in general that "Immigration to a subpopulation of only one individual once every five years reduces concerns about inbreeding depression to a negligible level." Triggs et al. (1989) suggest for the critically endangered kakapo (*Strigops habroptilus*) that "In future generations, exchanges of one young kakapo per generation between populations should be made to help maintain genetic variation and reduce inbreeding."

Mace and Lande (1991) have used the OMPG rule as a criterion for fragmentation in defining threatened species categories of the World Conservation Union. In the United States nearly every recovery plan that considers genetic issues and insularization applies the OMPG rule. For example, the black-footed ferret (*Mustela nigripes*) recovery plan states that "If the effective population size is to be maintained among many smaller populations, then exchange of genetic material at the rate of one individual/generation between local populations to ensure random and adaptive divergence among populations is necessary" (U.S. Fish and Wildlife Service 1988:18).

The simplicity of the OMPG—and its widespread adoption—belies confusion over the derivation of the rule, its real generality, and the specifics of implementing it (Varvio et al. 1986). Indeed, immediately after stating that subpopulations would not become fixed for different alleles if there were "an interchange of only one individual every other generation," Wright noted that violations of simplifying assumptions may mean that "... an interchange of the order of thousands of individuals per generation between neighboring subgroups of a widely distributed species might well be insufficient to prevent

a considerable random drifting apart in their genetic compositions" (Wright 1931:128). Thus, from the outset Wright acknowledged the complicating role of the social, ecological, and genetic characteristics of immigrants; these real-world complexities are often neglected in contemporary reference to the OMPG rule.

Human-caused habitat modification is reducing many continuous populations to isolated or semi-isolated fragments (Soulé et al. 1988; Mills 1995). In light of these changes, concerns over the appropriate level of gene flow in fragments are well grounded, both because of the increased potential for demic extinction in isolated populations (Senner 1980; Soulé 1987; Lynch & Gabriel 1990; Mills & Smouse 1994) and because of potential consequences for adaptation to future disturbances (Soulé 1980; Frankel & Soulé 1981). The issue of actually prescribing gene flow in a management context is complicated, however, and it has received little empirical or theoretical consideration.

We describe the OMPG rule, present its theoretical underpinnings, and discuss its application and limitations from a genetics perspective. Finally, we make recommendations that apply both to highly manipulated systems, where managers physically move individuals, as well as to systems in which the movement rate is affected by the size and shape of available habitat or movement corridors.

The One-Migrant-per-Generation Rule

The one-migrant-per-generation rule originated in Wright's analysis of the interplay between genetic drift and gene flow in determining the expected patterns of genetic divergence among a series of subpopulations. Consider a large number of subpopulations in which genetic drift produces genetic divergence among the subpopulations at a rate inversely proportional to the local effective population size (N_e), which is assumed to equal the census size, N . Assume that in each generation a proportion m of the individuals in each subpopulation are migrants from outside that subpopulation and that the allele frequency in migrant individuals is the average allele frequency in all subpopulations. Such migration will limit the amount of divergence that will occur among subpopulations.

This model leads to the surprisingly simple result that at equilibrium the amount of divergence among subpopulations for reasonably small values of m is approximately

$$F_{ST} \approx \frac{1}{4mN + 1}, \quad (1)$$

where F_{ST} is the proportion of total gene diversity (heterozygosity) due to divergence among subpopulations. Note that because m is the proportion of migrants and N is the population size, mN is the actual number of migrants entering a subpopulation each generation.

The amount of divergence among subpopulations as measured by F_{ST} is independent of the total amount of gene diversity in a population (H_T). The F_{ST} can also be thought of as the reduction in heterozygosity within subpopulations (H_S) caused by random genetic drift and divergence among subpopulations. That is,

$$F_{ST} = 1 - \frac{H_S}{H_T}, \quad (2)$$

and F_{ST} is usually called the fixation index. In the case of more than two alleles, each allele may have a different fixation index. Nei (1973) introduced an analogous value (G_{ST} , the coefficient of genetic differentiation) that can be used to describe genetic differentiation for many loci with more than two alleles (Chakraborty & Leimar 1987).

This analysis has two notable results. First, the amount of divergence is dependent only on the number of migrants (mN) and is in a sense independent of population size. For example, we expect the same amount of divergence among subpopulations of size 1000 with 2.5% migration as we do among subpopulations of size 50 with 50% migration; in both cases there are 25 migrants per generation.

The dependence of divergence on the number of migrants, rather than the population size (N) or rate of migration (m), may at first seem counter-intuitive. Divergence, however, results from the opposing effects of migration and genetic drift. The larger the subpopulations, the slower they are diverging through drift; thus, proportionally fewer migrants are needed to counteract the effects of drift. Small subpopulations diverge rapidly through drift, and thus proportionally more migrants are needed to counteract drift.

The second notable aspect of this result is that remarkably small amounts of migration can have powerful genetic consequences on divergence among subpopulations at equilibrium; for example, OMPG is expected to yield an equilibrium F_{ST} of 0.2 (Fig. 1). If we examine the actual distribution of allele frequencies among subpopulations, it is clear that OMPG will also make it unlikely that polymorphism will be lost within subpopulations (Fig. 2; Wright 1931; Fig. 6). With at least one migrant per generation, subpopulations are unlikely to reach equilibrium gene frequencies where one allele or the other is lost (frequency of zero) or "fixed" (frequency of 1.0).

Nevertheless, substantial divergence in allele frequencies across populations is expected with one migrant per generation (Wright 1931, 1969; Allendorf & Phelps 1981). Thus, OMPG provides a desirable balance between drift and gene flow by preventing the loss of alleles and minimizing loss of heterozygosity within subpopulations but allowing genetic divergence to exist among subpopulations. Low amounts of exchange will maintain qualitative similarity among subpopulations and also allow substantial quantitative divergence in allele frequencies.

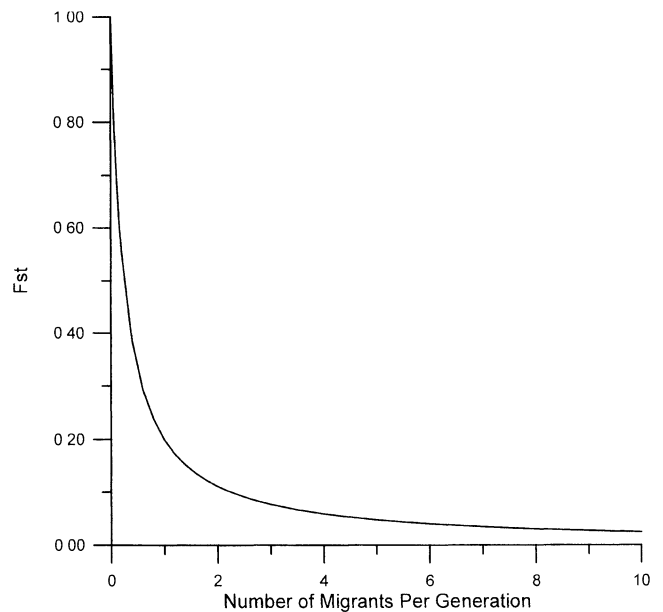


Figure 1. Relationship between number of migrants per generation (mN) and the fixation index (F_{ST}).

We want to emphasize that OMPG is not a discrete quantitative threshold and does not imply panmixia (random mating) among individuals of different populations. Rather, the basis of OMPG originates from a qualitative evaluation of tradeoffs between loss of genetic diversity within populations versus homogenization among populations.

Assumptions of the Rule

The OMPG rule results from a simple model of population structure based upon a host of unrealistic assumptions. We consider the primary assumptions that affect the applications of the results of this basic model to conservation.

(1) *Island model of migration*: A migrant is equally likely to come from any subpopulation so that there is no geographical pattern to gene flow. The assumption is also usually made that there are an infinite number of subpopulations of equal size.

(2) *Selective neutrality and no mutation*: There are no selective differences among genotypes, and no new mutations enter the population. That is, gene-frequency dynamics are determined entirely by the interaction between genetic drift and gene flow.

(3) *Ideal populations*: The subpopulations have the characteristics of an ideal genetic population, so that the census number of individuals equals the effective population size. For general purposes, the ideal population consists of a constant number of N diploid individuals ($N/2$ females and $N/2$ males) in which all parents have

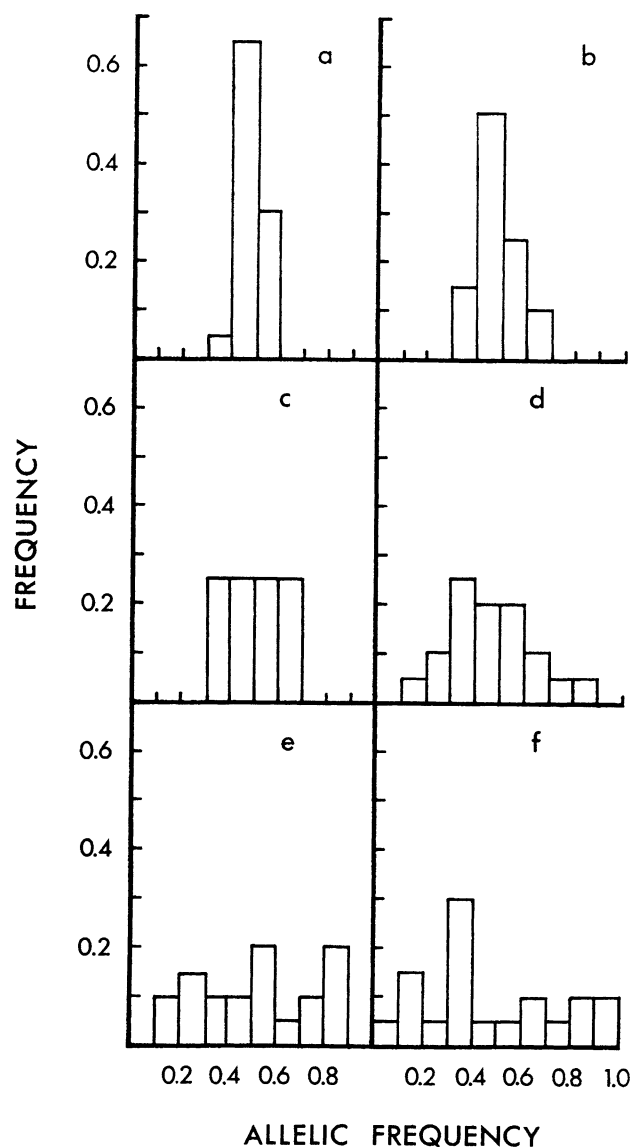


Figure 2. Distribution of allele frequencies in 20 subpopulations ($N = N_e = 200$ each) with different amounts of migration, based upon computer simulations of the island model for two alleles at a single locus (Allendorf & Phelps 1981). For panels a-e, number of migrants per generation decreases and F_{ST} increases, as follows: $mN = 25$, $F_{ST} = 0.0080$ (a); $mN = 10$, $F_{ST} = 0.0175$ (b); $mN = 5$, $F_{ST} = 0.0509$ (c); $mN = 2$, $F_{ST} = 0.1104$ (d); $mN = 1$, $F_{ST} = 0.2513$ (e); and $mN = 0.5$, $F_{ST} = 0.3221$ (f).

equal probability of contributing an offspring to the next generation.

(4) *Demographic equality*: Immigrants have the same demographic attributes, in terms of survival and reproduction probabilities, as resident individuals.

(5) *Equilibrium*: The subpopulations persist long enough to reach steady-state or equilibrium conditions with respect to gene frequencies.

Limitations of the Rule

What are the consequences of violating the simplistic assumptions of the OMPG rule? We consider how population size may affect the predicted effects of OMPG, then evaluate each of its assumptions. In each case we determine whether each complicating factor is expected to increase or decrease the effectiveness of OMPG or whether “it depends.”

Census Population Size

As noted in the derivation of the OMPG rule, one of its interesting and attractive features is that it is independent of population size, as long as gene dynamics are driven entirely by drift and gene flow (mutation and selection play no role). There are, however, at least two caveats to this generalization. First, mN migrants into a small population will represent a larger proportion of the population than if they had entered a larger population; any disruptive social or mating system effects of the immigration will therefore be magnified in smaller populations (Frankel & Soulé 1981; Frankel 1983).

Second, the usual formulation for the loss of genetic variation under drift-migration equilibrium (Eq. 1) is an approximation of the exact equation and holds true only when m (migration rate) is “small” (Wright 1969:291). For a fixed mN , such as one migrant, m becomes large with small population size. For example, when $N = 2$, $m = 0.5$, a large value that leads to less loss in variation (smaller F_{ST}), with the exact equation than expected with the approximation (Fig. 3). We note, however, that the overestimation of F_{ST} with the approximate equation is insignificant with subpopulation sizes large enough to be likely to persist in the face of demographic stochasticity for even relatively short periods of time. For example, for $N = 20$, the exact F_{ST} is 94% of the approximation.

Both of these issues imply that when populations become quite small less migration may be appropriate, both because of possible social disruption and because very small populations are not losing variation as fast as predicted by the F_{ST} approximation. Other factors, such as Allee effects and demographic or environmental stochasticity, lead to the opposite conclusion, with immigrants initiating an important “rescue effect” (Brown & Kodric-Brown 1977).

Island Model: Pattern of Migration

The immigrants in Wright’s infinite island model are randomly chosen from the pool of an infinite number of subpopulations. If individuals in the real world come from nearby populations, their gene frequencies would differ little from the target population, so more immigrants would be necessary to prevent loss of variation

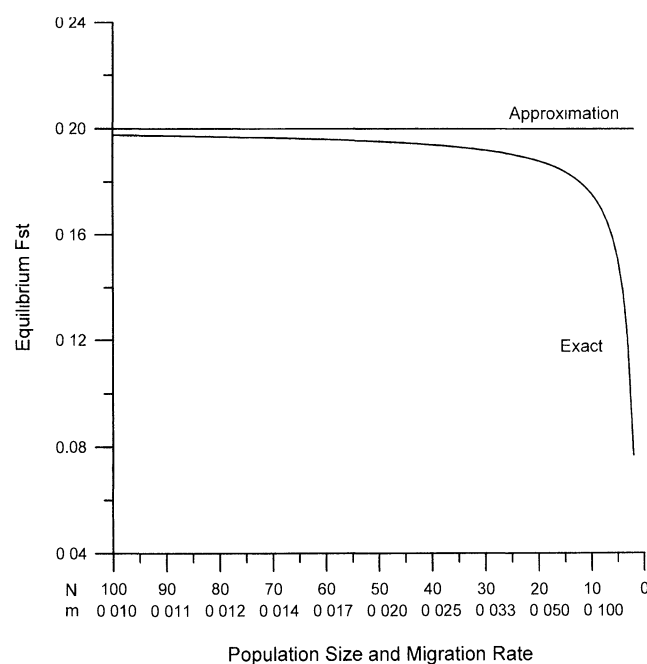


Figure 3. Expected F_{ST} at equilibrium for one migrant per generation ($mN = 1$) using the exact equation (from Eq. 12.2 in Wright 1969) and the commonly used approximation (Eq. 1). Unlike the approximation, which assumes small m , the exact equation changes as m changes.

(Wright 1931; Levin 1988). Crow and Aoki (1984) conclude, however, that unless the number of populations is very large, this neighborhood effect is relatively small; in a finite population model, migrants from neighboring groups are about half as effective in their genetic effects. Kin-structured migration—in which individuals disperse in the company of relatives—will also have the effect of requiring more immigrants for the same effect on genetic drift (Levin 1988).

Directional movement patterns are an important and widespread exception to the assumption of the island migration model. In many situations migrants from a relatively large subpopulation may be moved into a smaller subpopulation that is isolated; this is referred to as a continent-island pattern of migration (Hedrick 1983:278). For example, grizzly bears (*Ursus arctos*) from the Yellowstone National Park region are isolated from other populations. The recovery plan for grizzly bears includes regularly moving bears from more northern populations in Montana that are contiguous with grizzly bear populations in Canada into the Yellowstone region (U.S. Fish and Wildlife Service 1993).

The genetic effects of this type of directional movement pattern are compatible with the OMPG rule. The isolated population can be considered one subpopulation of the island model in which migrants from the larger population represent the migrant pool of the is-

land model. Thus, the predictions of the OMPG rule will be valid as long as the donor population is large so that genetic drift is minimal. Weishampel (1990) cautions that if the donor population has lower genetic variation than the receiving population, migration can actually decrease genetic variation in the population of interest.

Another characteristic of the pattern of migration is the interval between immigrants. In its simplest form the island model assumes that probability of migration per generation is constant. Will 1 migrant per generation have the same effect as 10 migrants every 10 generations? Lacy (1987:153) concludes that sporadic immigration should be just as effective as a steady supplementation, provided that the same long-term average rate is maintained. On the other hand, Levin (1988:645) concludes that “a variable migration rate homogenizes neutral allele frequencies less than a uniform migration rate with the same mean.” This effect is quite small, however, based upon theory (Nagylaki 1979). Experimental work offers no insight into this question. In many cases the driving criteria for the timing of immigrants will probably not be genetic calculations but logistical concerns (transplanting one animal per generation will often be impractical) and behavioral and social considerations whereby groups of immigrants are more likely to experience successful reproduction.

In short, real-world deviations from the simple pattern of migration used to derive the OMPG rule mean that somewhat more than one migrant per generation may be necessary to achieve the desired genetic goals; the necessary increase will depend on particular circumstances, but it is probably small.

Island Model: Number of Subpopulations

The expected value of F_{ST} at equilibrium can be corrected as shown below to take into account a finite number (n) of subpopulations (Slatkin 1995):

$$F_{ST} \approx \frac{1}{4mNa + 1}, \quad (3)$$

where

$$a = \left(\frac{n}{n-1} \right)^2. \quad (4)$$

Total gene diversity (H_T) can be partitioned into within- and between-subpopulation components. Isolation causes a decrease in within-subpopulation variation (H_S), whereas fixation for different alleles maintains total gene diversity (H_T). As long as the subpopulations are connected by gene flow, an allele will eventually be lost from all subpopulations (and therefore the entire population) by genetic drift if there are a finite number of subpopulations. If the subpopulations are isolated, however, then different alleles will drift to fixation in differ-

ent populations, so more alleles will be maintained in the entire population.

There may be merit (Chesser 1983) in maintaining isolated populations so that more alleles can be retained in the entire population. Nevertheless, these benefits must be weighed against increased probability of extinction due to within-population inbreeding depression (Varvio et al. 1986; Mills & Smouse 1994). In short, the tradeoff between within- and among-population variation may dictate more or less migration than the OMPG rule does (Figs. 1 & 2).

Natural Selection and Mutation

The theoretical model upon which the OMPG rule is based assumes selective neutrality—that is, there are no differences in fitness among genotypes. Nevertheless, the OMPG rule itself does take into account natural selection. The OMPG rule was chosen because it is sufficient to avoid the loss of alleles in subpopulations caused by genetic drift but will allow the allele frequencies within subpopulations to respond to local selective pressures.

Even weak natural selection can have a major effect on the amount of genetic divergence among populations (Allendorf 1983). The effects of natural selection will be greater in larger subpopulations because of the reduced effects of drift in larger populations. In general, natural selection will not have a major effect on the distribution of allele frequencies if the selection coefficient (s) is less than the migration rate (m) (Wright 1940). Thus, natural selection will have less effect on allele frequency divergence among subpopulations with smaller subpopulations for the same amount of migration (mN) (Allendorf 1983).

The effect of selection upon the expected amount of divergence with a given amount of gene flow depends upon the pattern of selection. Similar selection in different subpopulations will tend to reduce divergence, whereas different selective conditions will increase divergence among subpopulations (Allendorf 1983). It is likely that both of these patterns of selection will occur at different loci within the same population. Thus, the OMPG rule seems appropriate when we consider the potential effects of natural selection.

Mutation is expected to have little effect on the application of the OMPG rule. The expected amount of divergence at equilibrium for G_{ST} (the multiple-allele form of F_{ST}) is independent of the mutation rate and the number of alleles, as long as the migration rate is much greater than the mutation rate (Hartl & Clark 1989). This condition will be met for all loci in which migration rates are on the order of one per generation ($mN = 1$) or greater.

Ideal Populations and Demographic Equality

The ratio of effective population size to census population size is expected to affect the consequences of vary-

ing migration rates. Wright (1931:128, 1969:292) noted that the smaller N_e is relative to the census N , the larger the number of migrants necessary to minimize differentiation. This is because as N_e decreases below N the population loses variation faster via drift, and a given migrant contributes less to the breeding population, than when N_e equals N . Therefore, populations with highly skewed N_e/N ratios, as is often the case in wild vertebrates (Frankham 1995), may require more than one migrant per generation. How many more are necessary is uncertain; presumably it will depend on why N_e is less than N (for example, because of skewed sex ratio or variance in family size) and on the reproductive characteristics of the immigrants.

Demographic equality also assumes that immigrants are equivalent to residents. To the extent that an immigrant is more or less likely to survive and breed relative to individuals in the target population, it may count as more or less than one migrant. It seems unlikely that immigrants will be demographically equivalent to resident individuals in most situations. In the case in which immigration is imposed by moving captured individuals, there are a variety of reasons to expect immigrants to be less likely to survive and reproduce than residents.

There are also a few situations in which immigrants may be more successful than residents. For example, individuals with rare genotypes have a reproductive advantage in plant species with self-incompatibility systems (Charlesworth 1985). Thus, immigrants from a genetically different subpopulation may have a reproductive advantage in this case.

Because deviations from ideal population structure will tend to compromise the effectiveness of migration relative to expectations, including social structure and taking into account the relative reproductive success of immigrants will mean that more than one migrant per generation may be necessary.

Equilibrium

The OMPG rule is based upon the assumption of equilibrium between the effects of migration and genetic drift. Equilibrium will be reached more quickly with smaller population sizes and higher migration rates (Varvio et al. 1986). Thus, greater migration may be initially desirable with larger subpopulations in order to reach equilibrium more quickly. Equilibrium between gene flow and drift is approached fairly quickly with small population sizes (Table 1; see also Allendorf & Phelps 1981; Table 2).

Before the population reaches equilibrium, the restorative effect of immigration is initially greater for small populations than for large because they have drifted to lower levels of variation (Lacy 1987). This implies that increases above OMPG may well be beneficial when migration is initiated for the first time.

Table 1. Observed and expected genetic divergence among five subpopulations of Leadbeater's opossum connected by gene flow in a simulation study (Lindenmayer & Lacy 1995).*

mN	H_s	Expected F_{ST}	Observed F_{ST}		
			20 yr	50 yr	100 yr
0	0.28	1.000	0.170	0.309	0.509
0.7	0.60	0.186	0.105	0.128	0.130
1.5	0.70	0.096	0.074	0.068	0.079
7.4	0.80	0.021	0.021	0.022	0.024

*The mN values were calculated with the annual migration rate (m) used in the simulations, a generation interval of 3.71 years and an N of 40 based on carrying capacity (see text for discussion of using N versus N_c). H_s values represent observed mean heterozygosity within subpopulations at 100 years. Expected F_{ST} at equilibrium was calculated using Eq. 3 and the actual mN values used in the simulations. Observed F_{ST} values were calculated using Eq. 2.

Implicit in the equilibrium assumption is that populations all persist long enough to reach equilibrium. McCauley (1993) reviews the consequences of relaxing this assumption: incorporating extinction and recolonization dynamics can either increase or decrease genetic differentiation, depending on how high population turnover rates are, where the migrants originate, how many migrants move together, and whether the migrants settle in unoccupied or occupied patches. Extinction and recolonization dynamics tend to accentuate population differentiation most when migrant individuals move into established populations more than colonizing new patches. Therefore, if conspecific attraction (Reed & Dobson 1993) tends to increase the likelihood of a dispenser settling in an already occupied area rather than an unoccupied area in a metapopulation, then those migrants will be less effective at minimizing differentiation in the metapopulation; if they settle more in empty patches, then extinction and recolonization dynamics predict that fewer migrants are needed to prevent differentiation (McCauley 1993).

In general, then, violation of the equilibrium assumption means that somewhat more than one migrant per generation may be beneficial. Extinction and recolonization dynamics could either increase or decrease the desirable number.

Empirical and Simulation Results

What insights can be gained from field studies, laboratory experiments, and comprehensive computer studies of natural populations that violate many of the above assumptions at the same time? Because it is not possible to test the predictions of the OMPG rule within a reasonable time frame for most species of interest, empirical tests will initially come from model genetic species with short generation times.

Little experimental work considers the issue of how many migrants are optimal in natural—or even captive—populations. The most direct experimental work is that of Spielman and Frankham (1992). They found strong and significant increases in reproductive fitness in 10 replicate inbred lines of *Drosophila melanogaster* that received only a single immigrant per generation. On average, OMPG restored nearly 50% of that fitness lost under isolation. Newman (1996) has found similar results with experimental populations of the plant *Brassica campestris*. One migrant per generation among 10 subpopulations had a significantly positive effect for five of six fitness components measured. In contrast to these results, Backus et al. (1995) found no increase in fitness associated with a single immigrant (although higher levels of gene flow did increase fitness) among five subpopulations of the housefly (*Musca domestica*).

Studies that use simulations or analytical approaches incorporating actual life-history information for long-lived species also provide insight into how effective OMPG is expected to be in the face of real-world deviations from the simplifying assumptions. For example, Hedrick (1995) used a variety of theoretical population genetic models to test the validity of the OMPG rule in the case of the Florida panther (*Felis concolor coryi*). The report of a workshop for genetic restoration of the Florida panther recommended an initial influx of 20% of the population, followed by gene flow of one animal per generation. Hedrick's models included various combinations of gene flow and genetic drift. He also examined several violations of the assumptions of the basic model: natural selection, directional gene flow, and nonequilibrium initial conditions. Despite these complicating factors, he concluded that this recommendation was sufficient to eliminate lowered fitness due to inbreeding depression and to retain adaptive alleles in the Florida population.

Allendorf et al. (1991) used simulations with the computer program GAPPs (Harris et al. 1986; Harris & Allendorf 1989) to examine the effects of immigration on effective population size and the rate of loss of genetic variation in an isolated population of grizzly bears in the Rocky Mountains. These simulations used a directional (continent-island) pattern of gene flow in a discrete-time, stochastic computer program that followed each individual bear from birth to death. The estimated effective population size of the isolated population was approximately 30% of the census population size. Their results are in general agreement with those expected with the basic model: the introduction of a few bears per generation greatly reduced the rate of loss of variation in the isolated population. The introduction of males had a greater effect than the introduction of females in the model, but this effect may be outweighed by the reduced likelihood of males being incorporated in the breeding population into which they are introduced be-

cause of the behavioral differences between males and females (Allendorf et al. 1991; U.S. Fish and Wildlife Service 1993).

Dobson et al. (1991) used GAPPS to simulate the viability of isolated populations of black rhinos (*Diceros bicornis*) in Kenya. They used an island-continent pattern of migration and demographic data obtained from black rhino sanctuaries. They also included the effects of inbreeding depression in some of their simulations. They found that one immigrant every 10 years had a major effect on the population size and persistence of isolated populations.

The most realistic test of the OMPG rule using simulations that we are aware of was done by Lindenmayer and Lacy (1995) with Leadbeater's possum (*Gymnobelideus leadbeateri*). They used the computer program VORTEX (Lacy 1993) to model the viability of metapopulations with subpopulations occupying a small number of habitat patches of varying sizes. They used values for life-history parameters drawn from extensive field studies, allowed local subpopulations to become extinct, and included the effects of inbreeding depression. Dramatic effects of migration were observed in their largest metapopulation, which consisted of five subpopulations of 40 individuals each (Table 1).

The results for Leadbeater's possum also can be used to quantitatively test the predictions in a system that violates many of the assumptions upon which the OMPG is based. The observed amount of genetic divergence among the five subpopulations estimated from the data of Lindenmayer and Lacy (1995) is similar to that predicted by the simple equilibrium model (Table 1). As expected, near-equilibrium values were obtained more rapidly with greater amounts of gene flow. Even with $mN = 1.5$, however, the observed F_{ST} value was nearly 75% of that expected at equilibrium after approximately five generations.

Recommendations for Implementing Gene Flow

When connectivity is implemented for genetic purposes, we are interested in finding the middle ground between loss of alleles in local populations (fixation, or loss in heterozygosity) and uniformity of allele frequencies across local populations. One migrant per generation is an appropriate lower limit to the amount of gene flow that is desirable. Nevertheless, sometimes more than an average of one migrant per generation will be necessary because of deviations in real populations from the ideal conditions assumed in developing the OMPG rule.

We hesitate to give "cookbook" prescriptions, but an increase in migration above the mean of one migrant per generation may be desirable under the following conditions: (1) inbreeding depression is thought to be a problem in the local population; (2) migrants are closely related to each other or to the local population; (3) social,

behavioral, or logistical factors prevent single individuals from immigrating, so that movement is in pulses of several animals every several generations; (4) N_e is much less than total population size; (5) migrants are likely to be at a disadvantage in terms of survival and breeding success; (6) the receiving population has been isolated for many generations; and (7) demographic or environmental variation indicates a high danger of extinction without aggressive supplementation.

If one migrant per generation is not enough in many circumstances, then the next question is how much gene flow may be too much to maintain the balance we are seeking. This question is difficult to answer without extensive genetic and demographic information on the population under consideration. Concerns over local adaptation and outbreeding depression dictate that, under some conditions of phenotypic or genotypic dissimilarity, immigration into an isolated population should be minimized (for cogent discussions see Templeton [1986] and Leberg [1990]). Frankel and Soulé (1981) proposed an upper limit of 5 migrants per generation because of concerns with disruptive effects on social structure in small populations. We suggest that up to 10 migrants per generation is not likely to tip the balance too far by causing uniformity of allele frequencies across subpopulations (Fig. 2).

The characteristics of the migrants is as important as the number of migrants. Social, behavioral, and demographic characteristics that affect the likelihood of survival and reproduction of migrants may overwhelm genetic considerations in assessing the "ideal" candidates to recruit as migrants (Kleiman 1989; Stanley-Price 1989; Short et al. 1992). Likewise, considerations of mating system and social structure will affect the genetic impact of an immigrant. Greater numbers of randomly chosen migrants may be necessary to achieve the same genetic effect as fewer migrants chosen to maximize contribution to the effective population size.

Finally, we stress that criteria other than genetic variation will often play pivotal roles in determining the appropriate level of connectivity between semi-isolated fragments. For example, small populations subject to blinking out due to demographic or environmental stochasticity can experience a "rescue effect" (Brown & Kodric-Brown 1977), with immigrants increasing numbers away from the boundary of zero. In this case more migrants increase population persistence, regardless of genetic considerations. On the other hand, contagious diseases have been raised as a factor decreasing the benefits of connectivity (Wilson et al. 1994; Hess 1994).

Conclusions

The OMPG rule has provided much-needed guidance in management and has illuminated the need for genetic

connectivity among isolated populations. Like many theoretical applications in conservation, its utility is strongest when its complexity is appreciated (Doak & Mills 1994). We have seen several compelling real-world factors that suggest more than one migrant per generation may be necessary to achieve genetic goals, and some situations (albeit fewer) in which less connectivity is desirable. One key to practical decision making is to define clearly the desired genetic outcome, as well as other objectives and constraints of the supplementation program (Lacy 1987).

One migrant per generation is an acceptable minimum, but it may be inadequate for many natural populations. Different levels and schedules of supplementation are appropriate under different environmental conditions and with different species. Nevertheless, we suggest that a minimum of 1 and a maximum of 10 migrants per generation would be an appropriate general rule of thumb for genetic purposes.

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Source-Sink Models and the Problem of Habitat Degradation: General Models and Applications to the Yellowstone Grizzly

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Abstract: *I used source-sink population models to explore the consequences of habitat degradation for populations living on good and degraded habitats linked by movement. In particular, I modeled the conversion of land from good habitat quality supporting positive population growth to a degraded condition in which there was population decline. I found that with high rates of movement between good and bad quality areas populations require relatively large amounts of good habitat to remain stable. However, low movement rates resulted in greater sensitivity of population growth to habitat loss. Even small amounts of habitat degradation could result in rapid changes in overall population growth rates depending upon the rates of population increase and decline in the two habitat types. I also developed and simulated an age-structured model for grizzly bears (*Ursus arctos horribilis*) existing in good and degraded habitats and fit this model to data from the Yellowstone grizzly population. I used this model to predict the ability to detect crucial amounts of habitat degradation from census data and found that when degradation is slow (e.g., 1% conversion of good to poor habitat per year), more than a decade may pass between crucial amounts of degradation—beyond which populations begin long-term decline—and its detection, even if census data were unrealistically good. Thus these simple models indicate that, at least in some circumstances, habitat degradation can have rapid and severe impacts on population dynamics and traditional monitoring programs may not be adequate to detect the consequences of degradation.*

Los modelos de fuente-sumidero y el problema de la degradación del hábitat: Modelos generales y aplicaciones al oso gris de Yellowstone.

Resumen: *En el presente estudio se utilizaron modelos a les poblacion fuente-sumidero para explorar las consecuencias de la degradación del hábitat en las poblaciones que viven en hábitats buenos y en hábitats degradados conectados por el movimiento de individuos. En particular, modelé la conversión de tierras que pasaron de ser hábitats de buena calidad, que sustentaban un crecimiento poblacional positivo, a ser hábitats degradados en los cuales existía una declinación poblacional. Encontré que con altas tasas de movimiento entre áreas buenas y malas, las poblaciones requieren altas cantidades relativamente de hábitats buenos para permanecer estables. Sin embargo, tasas de movimiento bajas resultaron en una mayor sensibilidad del crecimiento poblacional a la pérdida del hábitat. Una degradación limitada del hábitat puede conducir a rápidos cambios en la tasa de crecimiento poblacional total dependiendo de las tasas de crecimiento poblacional y de la declinación en los dos tipos de hábitat. También desarrollé y simulé un modelo estructurado por edades para osos grises (*Ursus arctos horribilis*) residentes de los hábitats buenos y degradados y ajusté este modelo a datos obtenidos de la población de osos grises de Yellowstone. Usé este modelo para predecir la capacidad de detectar cantidades cruciales de degradación del hábitat a partir de datos censales y encontré que cuando la degradación es baja (por ejemplo una conversión de los hábitats buenos a pobres de un 1% por año) puede pasar más de una década entre el momento en que las cantidades cruciales de degra-*

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dación (por encima de las cuales las poblaciones comienzan una declinación a largo plazo) se hacen presentes y el momento en que son detectadas, aún si los datos sensales son, en un sentido irreal, buenos. Por consiguiente estos simples modelos indican que por lo menos en ciertas circunstancias la degradación del hábitat puede tener efectos rápidos y severos sobre la dinámica poblacional y que los programas tradicionales de monitoreo pueden no ser adecuados para detectar las consecuencias de la degradación.

Introduction

Habitat destruction and degradation are often cited as the most important causes of species endangerment and extinction. Although habitat destruction is a far more dramatic conservation problem, the degradation of habitat, an often slow transformation from optimal to suboptimal to unsuitable conditions for a species' survival and reproduction, is perhaps the more serious conservation concern in many areas today. Throughout North America and in many other parts of the world, large amounts of natural or semi-natural habitat already are protected at least at some level but are still subject to widespread and ongoing degradation (e.g., national forests and Bureau of Land Management lands). In spite of its prevalence the problem of habitat degradation has proven difficult to address; degradation is usually diffuse and often occurs very gradually through time, thus being quite difficult to measure.

The simplest demographic models linking habitats of differing quality are source-sink difference equations (Pulliam 1988). These models have included birth, death, and movement rates for a source population (in good habitat) and a sink population (in poor habitat). Both Pulliam (1988) and others (Pulliam & Danielson 1991; Howe et al. 1991; Davis & Howe 1992; Wootton & Bell 1992) use source-sink models to illustrate the possible importance of marginal habitats in maintaining overall population numbers and hence long-term viability. However, this simple model structure has not to my knowledge been used to address the dangers gradual habitat degradation poses.

I address the general demographic changes that occur in isolated populations living in two linked or adjoining types of habitat: good habitat and poor or degraded habitat. In particular, I ask how habitat conversion (from good to poor) changes the population growth rate of a species and how difficult it is to detect the effects of conversion on population viability. I first use a general model to explore how movement rates between the two habitat types and the rates of population growth and decline in the good and bad habitats (i.e., the severity of habitat degradation) will affect population responses to degradation. To make this exploration less abstract I then fit a simple age-structured version of the model to data on the Yellowstone grizzly bear (*Ursus arctos horribilis*) population. The Yellowstone grizzlies have been the

subject of extensive field investigations (Mattson et al. 1987; Craighead et al. 1988; Knight et al. 1988; Blanchard & Knight 1991; Mattson & Knight 1991a), modeling efforts (Shaffer 1983; Knight & Eberhardt 1984, 1985; Shaffer & Samson 1985; Dennis et al. 1991; Eberhardt et al. 1994) and a recently released recovery plan (U. S. Fish and Wildlife Service 1993). Further, the ways in which human use decreases the quality of grizzly habitat are relatively well-understood (Knight et al. 1988; Mattson & Knight 1991b; Mattson & Reid 1991). Thus, this is a good population for which to examine the effects of habitat degradation on population health.

A Simple Model of Habitat Degradation

Structure

The simplest model of the effects of habitat degradation on the demography of a species involves only two types of habitat, good and bad, and assumes that the total habitat area remains constant. Therefore, the amount of good and bad habitat can be expressed as fractions of the total habitat area. This scenario corresponds to an isolated habitat patch, such as a national forest, in which some of the area is degraded and hence of lower quality to the species in question, and the rest is still relatively pristine and hence of high habitat quality.

To create the simplest model possible to show the effects of habitat degradation, I assumed that population growth is density independent in good and bad habitat areas and that neither population growth nor movement rates have stochastic variance. Inclusion of these or myriad other complexities could, of course, result in significant quantitative changes in the model results. However, I choose to make these simplifying assumptions because my goal is not to make accurate long-term predictions but rather to provide an initial exploration of the short-term, qualitative effects of degradation.

Two different equations describe the populations living in the two habitat areas:

$$N_g(t+1) = \lambda_g \left[N_g(t) + \frac{M}{2} \left(\frac{N_b(t)}{(1-p)A} - \frac{N_g(t)}{pA} \right) \right] \quad (1)$$

$$N_b(t+1) = \lambda_b \left[N_b(t) + \frac{M}{2} \left(\frac{N_g(t)}{pA} - \frac{N_b(t)}{(1-p)A} \right) \right] \quad (2)$$

Here, $N_g(t)$ and $N_b(t)$ represent the population sizes in the good (g) and bad (b) habitats in year t , and, similarly, λ_g and λ_b are the annual multiplication rates of the population in the good and bad habitats, respectively. The total area of all habitat types is A , and the fraction of this area that is good habitat is equal to p .

The last parameter, the movement coefficient M , requires more explanation. This parameter scales the rate of net movement between the good and bad habitats. The model allows individuals to move in either direction between the habitat types, although if $\lambda_g > 1$ and $\lambda_b < 1$ as in the results I present, net flow will always be out of the good habitat type. The terms N_g/pA and $N_b/(1-p)A$ are the population densities in the good and bad habitats, and thus one-half their difference is the amount by which both densities would have to change in order to be equal. Looked at another way, this difference, $0.5(N_g/pA - N_b/(1-p)A)$, is the density "pressure" that exists between the two habitat types. The movement coefficient is thus a parameter that determines the ease with which movement occurs as a result of this pressure. At a minimum, $M = 0$ and the two habitat types are completely isolated (no movement), and at a maximum, $M = 2Ap(1-p)$ (the movement in each year is exactly enough to equalize the densities in the two habitat types). Between these two extremes the value of M determines the relative ease of movement between the two habitat types, with the absolute amount of movement also being determined by the two densities. The movement coefficient M can also be thought of as the amount of area in each habitat in which the population density will equalize each year with the population in the same amount of area of the other habitat, thus making it the amount of area over which effective movement occurs near to the boundary of the two habitat types.

Importantly, I assumed in this model that individuals do not perceive differences in habitat quality and thus move solely on the basis of relative densities in the two habitat types. This is quite different from the assumptions made in constructing previous source-sink models (Pulliam 1988; Davis & Howe 1992) but is consistent with the dispersal and movement behavior of many species encountering human-altered habitats. Habitat degradation usually results from factors such as mortality on highways, eggshell thinning from pesticide residues, or mortality from shooting, the dangers of which are not adequately perceived or avoided by many species (e.g. grizzly bears [Mattson 1990; Mattson & Reid 1991] and Northern Spotted Owls *Strix occidentalis caurina* [Thomas et al. 1991]). Thus it is reasonable to assume in this simple model that individuals do not perceive degraded areas as such and therefore do not actively avoid these

areas as they naturally would poor habitats. Additionally, the model does not incorporate the effects of boundary/area ratios on movement rates, which drive the behavior of diffusion models for minimum patch size (Okubo 1980).

Interpretation and Results

Because equations (1) and (2) describe a set of simple linear difference equations, constant overall population growth rates (λ_T) exist for the total population for any set of parameter values. Figure 1 shows the effects of movement rate (determined by different values of the movement coefficient, M) on the relationship between the fraction of good habitat and overall population growth and decline for different combinations of λ_g and λ_b and for three different movement coefficients ($M = 160, 40$, or 10). I varied the rates of population change from 2.5 to 10% increase or decline per year to simulate low to high rates of population growth in the good habitats and large to small degrees of habitat degradation in the bad habitats.

Overall population growth is strongly influenced by both the absolute and relative rates of growth and decline in good and bad habitat areas (Fig. 1). The larger the values of λ_g and λ_b , the smaller the fraction of good habitat (p) needed for overall population stability ($\lambda_T = 1$). I refer to this value of p as the critical amount of good habitat. Conversely, when λ_g and λ_b are both small, ($\lambda_g = 1.025$ and $\lambda_b = 0.90$), p must be large in order for a population to remain stable. A more interesting result is that the values of λ_g and λ_b strongly determine the shape of the relationship between λ_T and p . High rates of population growth in good habitat and rapid rates of population decline in bad habitat ($\lambda_g = 1.10$ and $\lambda_b = 0.90$) lead to extreme sensitivity of λ_T to changes in p , with small changes in p translating into large differences in overall population growth. Conversely, slow rates of growth and decline in the two habitats result in a weak dependence of λ_T on changing amounts of good habitat ($\lambda_g = 1.025$ and $\lambda_b = 0.975$).

To clarify the effects of λ_g and λ_b on population growth I plotted λ_T versus p for three combinations of λ_g and λ_b , holding $m = 40$ (Fig. 2). For all three pairs of λ_g and λ_b values plotted the mean of λ_g and λ_b is approximately 1. That is to say, if $p = 0.50$ and mixing between the two habitat types were complete each year, these pairs of λ_g and λ_b values would all result in stable population sizes ($\lambda_T = 1$), although they vary in the magnitude of the difference between growth and decline in the two habitat types. Large differences between λ_g and λ_b result in lower, critical values of p but also in greater sensitivity of λ_T to changes in p . Conversely, when λ_g and λ_b are both near 1, critical values of p are high but sensitivity of λ_T to changing amount of good habitat is fairly low.

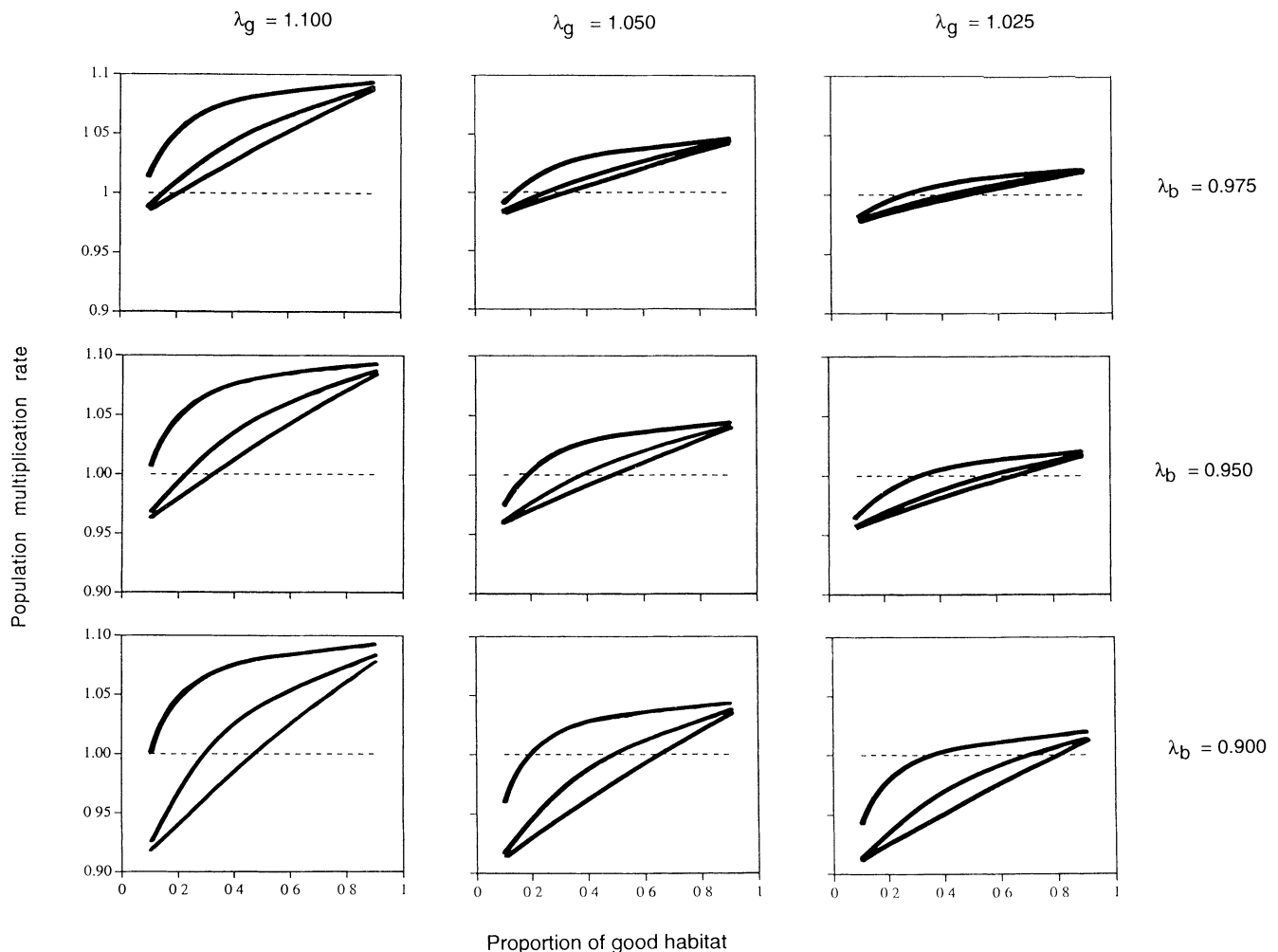


Figure 1. Annual population growth rates plotted as functions of the proportion of good habitat. Each graph shows results for one combination of good and bad habitat qualities (λ_g , good habitat growth rate; λ_b , bad habitat growth rate). In each graph the lowest curve corresponds to the highest movement coefficient (160) and the highest curve to the lowest movement coefficient (10). The middle curve corresponds to a movement coefficient of 10. (If the proportion of good habitat is 0.20, the highest movement coefficient 160, completely equalizes population density in the good and bad habitats each year.) The horizontal, dashed lines indicate a growth rate of one, equivalent to a stable population size. Total area is always equal to 500.

Movement rate, determined by the movement coefficient, has two striking effects on population growth (Fig. 1). First, high movement rates raise the critical value of p , at which overall population growth changes to population decline. This is not surprising because higher movement rates result in faster leakage of individuals from the good into the bad habitat, essentially reducing population growth in the good habitat. The strength of this effect varies with λ_g and λ_b , with the critical values of p being most sensitive to movement when population growth in good habitat is low and population decline in bad habitat is rapid (e.g. $\lambda_g = 1.025$ and $\lambda_b = 0.90$). However, movement exerts a significant effect over all values of λ_g and λ_b shown—the strength of this effect is worth noting if only because accurate knowledge of movement rates is extremely rare.

More interesting is the effect of movement on the shape of the relationship between population growth and the fraction of good habitat. When the movement rate is high, overall population growth is an approximately linear function of p , the fraction of good habitat. However, with lower movement rates this relationship becomes convex and rapid changes in population growth result from small changes in p . This effect is particularly strong when the degraded habitat is quite inhospitable and population growth is rapid in good habitat, although it occurs for all combinations of λ_g and λ_b (Fig. 1).

The important point for conservation that emerges from this simple model is that very small amounts of habitat degradation can lead to dramatic changes in population growth rate, depending upon the severity of degradation and the ease or rate of movement between de-

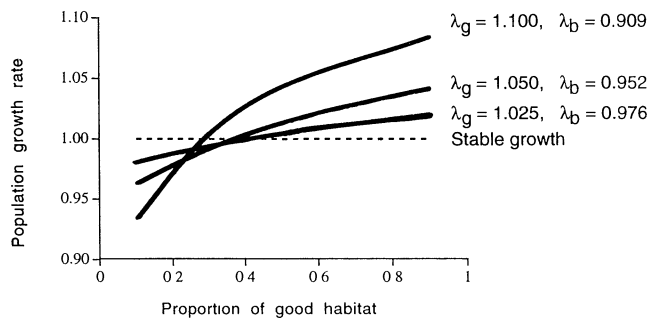


Figure 2. Annual population growth rates for three combinations of good and bad habitat qualities (λ_g , good habitat growth rate; λ_b , bad habitat growth rate) in relation to proportion of good habitat. For all curves plotted the movement coefficient (M) is 40.

graded and undisturbed habitat areas. For example, the additional conversion of 15% of an area from good habitat to bad can shift a population from stability to a 4% annual decline ($\lambda_g = 1.10$, $\lambda_b = 0.90$, $M = 40$). This result raises serious questions about our ability to predict the consequences of habitat degradation. The magnitude of differences between λ_g and λ_b and the absolute values of p and M modeled here are in practice very difficult to resolve with field data. Thus, even what is seen as very mild and incremental degradation (e.g., the building of roads or selective forestry) must be viewed with caution and with the knowledge that severe consequences could result from incremental changes in the proportion of good and bad habitat. Although this concept is not new, my results quantify the risks posed by degradation and emphasize that arguably insignificant changes may have serious results.

A Stage-Structured Model for Grizzlies

To illustrate how this modeling approach can be used to address real species and cases of habitat degradation, I present an age-structured version of the model for a species living in good and bad habitats and fit the model with parameters for grizzly bears inhabiting the Greater Yellowstone Ecosystem (GYE). Although Yellowstone grizzly populations have been modeled in several ways (Shaffer 1983; Knight & Eberhardt 1984, 1985; Shaffer & Samson 1985; Dennis et al. 1991; Eberhardt et al. 1994), previous models have not explicitly linked human degradation of habitat to changes in the population's health. For grizzlies degradation is largely the result of human access to bear habitat, which in turn leads to greatly increased mortality rates due to increased human-bear encounters; this mortality is due both to deliberate (shooting deaths) and accidental (road kills) human action (Knight et al. 1988; Mattson & Knight 1991b; Mattson & Reid 1991).

As with the first model, I take the approach of developing the simplest possible formulation needed to describe the species and its habitat conditions and hence ignore many aspects of bear biology, habitat geometry, and specific threats to bears in the Yellowstone area. Given that the grizzly is a highly intelligent species with diverse and flexible habitat needs and behaviors, the model presented here is best thought of as a cartoon of grizzly populations. This is not to say that the model is useless but rather an extremely simplified depiction of a complicated situation; like other simple models, it can provide insight into reality but should not be interpreted as providing quantitatively robust answers to the concerns it addresses.

The age-structured model is a direct extrapolation of my general model. Again, there are two habitat types linked by movement. In each habitat individuals are now divided into 8 age classes, all of which except the last are one-year age classes (the last class lumps together all individuals 13 or more years of age). The model includes only female bears. In presenting the equations that describe the population the net movement from the good to the bad habitat for a class i is conveniently defined as:

$$m_i(t) = \frac{M}{2} \left(\frac{N_{g,i}(t)}{pA} - \frac{N_{b,i}(t)}{(1-p)A} \right) \quad (3)$$

where $N_{g,i}(t)$ and $N_{b,i}(t)$ are the number of age i bears in year t in the good and bad habitat types, respectively. As in the simple model, A is the total area of habitat, p is the fraction of good habitat, and M is the movement coefficient. From this definition the population in each year is determined by three equations for each type of habitat.

For the good habitat:

(1) age 0 (cubs)

$$N_{g,0}(t+1) = \sum_{i=1}^{13} f_{g,i} s_{g,i-1} [N_{g,i-1}(t) - m_{i-1}(t)]$$

(2) ages $j = 1$ to 12

$$N_{g,j}(t+1) = s_{g,j-1} [N_{g,j-1}(t) - m_{j-1}(t)]$$

(3) ages ≥ 13

$$N_{g,13}(t+1) = s_{g,12} [N_{g,12}(t) - m_{12}(t)] + s_{g,13} [N_{g,13}(t) - m_{13}(t)]$$

For bad habitat:

(1) age 0 (cubs)

$$N_{b,0}(t+1) = \sum_{i=1}^{13} f_{b,i} s_{b,i-1} [N_{b,i-1}(t) + m_{i-1}(t)]$$

(2) ages $j = 1$ to 12

$$N_{b,j}(t+1) = s_{b,j-1} [N_{b,j-1}(t) + m_{j-1}(t)]$$

(3) ages ≥ 13

$$N_{b,13}(t+1) = s_{b,12} [N_{b,12}(t) + m_{12}(t)] + s_{b,13} [N_{b,13}(t) + m_{13}(t)].$$

Here, $s_{g,i}$ and $s_{b,i}$ are the annual survival probabilities from age class i to age class $i+1$ in the good and bad habitats, respectively. Similarly, $f_{g,i}$ and $f_{b,i}$ are the annual fecundities (average number of female offspring) for females in the good and bad habitat areas, respectively.

These equations describe a population divided between two habitats, good and bad. They assume that in each year movement occurs first, followed by survival, growth, and reproduction and then by censusing. I also assumed that only the densities of a given age class determined the movement rate between habitat areas for that age class; that is, that individuals only move in response to densities of bears in their own age class rather than the total densities of bears in the good and bad habitats. Although this assumption is clearly unrealistic (Mattson 1990; Mattson et al. 1987, 1992) because of other assumptions I make in using the model (equal movement rates for all ages and no density dependence in survival and reproduction), it is equivalent, with rescaling, to the assumption that density effects are felt across all age classes. As with the more general model, these equations are linear and hence yield exponential growth or decline for the population as a whole.

Parameter Estimates

I use empirical data from three primary sources to parameterize the model for Yellowstone Grizzlies. First, Knight et al. (1991) provide estimates for natality rates. Second, Knight et al. (1993 and cited in U. S. Fish and Wildlife Service 1993 Appendix D) provide a complete set of survival rate estimates calculated for the entire Yellowstone grizzly population (Table 1). Third, to use these survival data in the model I derive separate estimates of demographic rates for good (undisturbed) and bad (degraded or disturbed) habitats using information in Mattson and Knight (1991b). The first step in this process is the definition of good and bad areas. Various authors (Knight et al. 1988; Mattson & Knight 1991b) argue that otherwise suitable habitats that are close to roads or developments are sinks for grizzlies because of increased human encounters and hence increased mortality rates. I use the classification of disturbance types presented in Mattson and Knight (1991b) who define bad habitat as those areas within 6 km of developments, 3 km of primary roads, or 1.5 km of secondary roads. These areas account for 32.9% of the area of the GYE

(Mattson & Knight 1991b) but from 1983 to 1990 account for 70.3% of all known mortalities occurring in the GYE. In calculating demographic rates for the model I lump together these three types of area as bad habitat and consider all other areas (the backcountries of all national forests and national parks in GYE) as good habitat.

Mattson et al. (1992) provide data showing no or relatively small differences in the densities of grizzlies in areas adjacent to or far from roads and human developments (but see this paper and Mattson et al. 1987 and 1992 for evidence that some density differences do arise from human impacts). Based upon this analysis I assume that the relative areas of good and bad habitat reflect the numbers of bears in these habitats. Given this assumption Mattson and Knight's (1991b) data on the fraction of good and bad habitat (0.329 and 0.671, respectively)—or equivalently the fraction of the total bear population in each habitat type—can be used with the fraction of known mortalities that occurred in good and bad habitats (0.703 and 0.297, respectively) to calculate that the per capita mortality rate in bad habitat is 4.83 times the mortality rate in good habitat. Total mortality should equal the average of the mortality rates in the two habitat types, weighted by area, or $m_t = p_g m_g + (1 - p_g) m_b$. Here m_t is the total mortality rate for an age class throughout the GYE, p_g is the fraction of the ecosystem that is good habitat, and m_g and m_b are the mortality rates in the good and bad habitats, respectively. By substituting in the ratio of mortality rates and using the total annual mortality rates calculated from the total survivorship data (mortality = 1 - survivorship), one can calculate habitat-specific mortality, and hence survivorship, values for the good and bad habitat areas for each age class. Table 1 provides the survival estimates based upon this procedure. I assume that reproductive rates are identical everywhere.

I emphasize that the demographic rates calculated here may not be highly accurate because they are based on a series of simplistic assumptions. However, I am us-

Table 1. Parameters used in simulations of Yellowstone grizzly bears living far from and near roads and developments.^a

Age class (years)	Annual survival rates ^b			Female cubs produced per year ^c
	Observed	Far	Near	
0	0.89	0.95	0.76	0
1	0.85	0.93	0.68	0
2	0.83	0.92	0.64	0
3	0.88	0.95	0.74	0
4	0.88	0.95	0.74	0
5-12	0.93	0.97	0.85	0.41
13 and up	0.90	0.96	0.79	0.41

^aTotal area (A) = 23,000 km and movement coefficient (M) = 4140, 2070, 1035, and 517.5 km.

^bSurvival rates from Knight et al. (1993) for females only. Because of sample sizes, the average survival rates for females ages 5 through 12 years and for all bears of 13 years and older are used.

^cReproductive rates from Knight et al. (1991) for 1981-1990.

ing data for the Yellowstone grizzly to reach general conclusions about the ways in which bears will respond to habitat degradation; somewhat different sets of demographic data will not change the general conclusions, provided that bears on average replace themselves in good habitat and do not do so in bad habitat. I expect my results to be quite optimistic because they rely on very recent demographic estimates that show far higher survival rates, and hence population growth rates, than do slightly older summaries of data for Yellowstone grizzlies (e.g., Knight & Eberhardt 1984).

I found no data that could be used to estimate the movement coefficients for each age class of bears. For bears in the GYE these values reflect both the rate at which bears may change their home ranges on a large scale to overlap with or avoid areas close to humans and more subtle behavioral changes leading to avoidance or attraction to human-impacted areas. A better understanding of the ways in which habituation behavior operates in bears of different ages and sexes would be essential to realistically estimate movement rates and how they vary with density. However, in my model all these effects are lumped into a simple density-driven rate of movement. Data on home range sizes and locations indicate that most bears may regularly travel near roads and developments (Knight et al. 1988), translating into very high movement coefficients in the model. Lacking any quantitative estimates for the movement coefficients, I elected to, first, assume that movement coefficients are identical for bears of all ages and, second, to examine model results under a range of plausible movement coefficients (Table 1). The highest value I used ($M = 4140$) corresponds to complete equalization of densities each year when 10% of the total area is good habitat and when the total area of the GYE is 23,000 km.

Predicting Population Response to Human Encroachment

If no movement were possible between the good and bad habitat areas, given current survival and reproductive rates annual population growth would be 1.123 in the good area and 0.920 in the bad habitat. If one assumes a static landscape with a range of movement rates, this stage-structured model makes similar predictions to that of the simple model (Fig. 3). In particular, lower movement rates allow population stability or growth with smaller fractions of good habitat, but lower movement rates also lead to nonlinear responses of population growth to decreasing amounts of good habitat near the critical point at which annual growth changes into annual decline.

The model can also be used to examine population change in a varying landscape and in particular the ability of population size to indicate long-term population health when habitat degradation is ongoing. I choose to look at the two intermediate movement rates ($M = 1035$

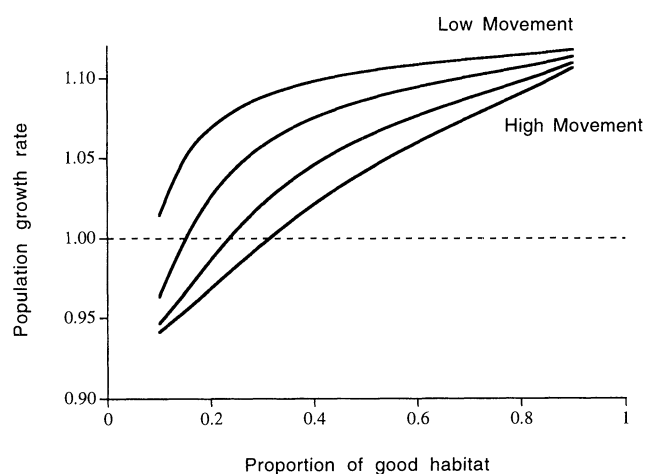


Figure 3. Population growth rates for simulated grizzly bear populations living in connected good and degraded habitat areas. Each curve indicates population growth rates for one movement coefficient value, with curves for four movement coefficients shown ($M = 4140, 2070, 1035$, and 517.5). The dashed line indicates a growth rate of one, equivalent to a stable population size. See Table 1 for parameter values.

and 2070) and at two rates of habitat degradation: conversion of either 0.5% or of 1% of the total area from good to bad habitat per year. For the lower movement rate the population is in equilibrium when $p = 0.152$, and for the higher rate the population is stable when $p = 0.235$. I started simulations with 1000 total bears (arrayed between habitats and ages in a stable distribution) and with slightly more good habitat than needed for population stability (0.162 and 0.245 for the lower and higher movement rates, respectively).

Figure 4 shows the results of these simulations. As expected, ongoing habitat degradation leads to accelerating declines in population size, even though degradation rates are constant in these simulations. Thus, even very slow rates of degradation—conversion of only 0.5% of the total habitat per year—can lead to rapidly worsening population dynamics.

Compounding this problem is what the results imply about the ability to detect changing population health under conditions of slow habitat degradation. Because directly measuring habitat degradation or its immediate effects on individual animals is difficult, most studies gauge the health of populations impacted by habitat degradation by monitoring trends in total population size. This is particularly the case with grizzlies; the recovery plan (U. S. Fish and Wildlife Service 1993) uses measure of population size (unrepeated adult females with cubs) as its primary metric of population health. Therefore, using the model to predict the usefulness of census data in measuring the effects of ongoing habitat degradation is interesting.

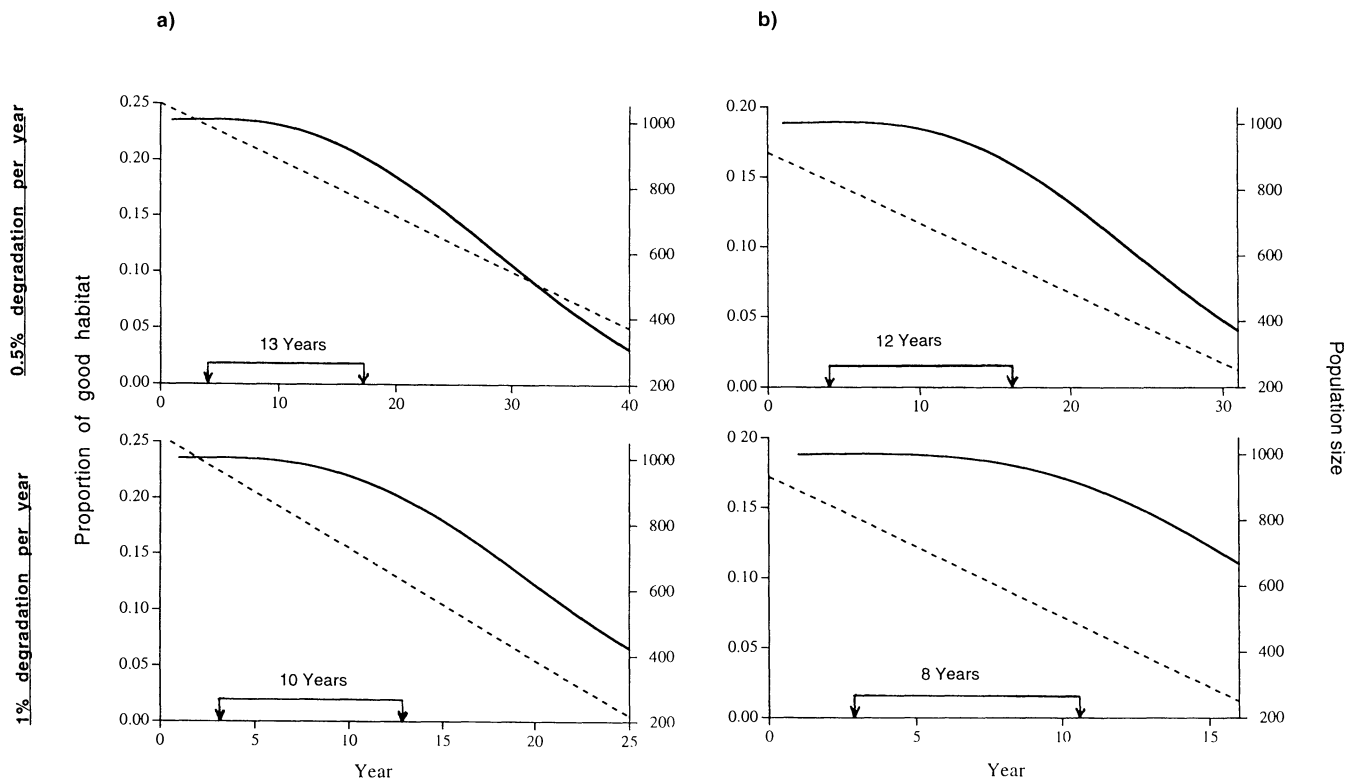


Figure 4. Population trajectories for simulated bear populations subjected to ongoing habitat degradation. Each plot shows population size (solid curve) and the proportion of good habitat remaining (dashed line) through time. Trajectories are shown for 0.5 and 1% rates of habitat conversion per year and for movement coefficients of $M = 2070$ (a) and $M = 1035$ (b). Connected arrows indicate the year when the amount of good habitat first falls below that necessary to maintain a stable population and the year in which population size first falls below 900, a 10% decrease from the starting populations of 1000.

Consider the situation in which a 10% change in population size can be detected from field census data. For species that can be very accurately censused, detecting a 10% decrease in population size may sometimes be possible; it is highly unlikely that so small a change in a grizzly population could ever be detected. Therefore, this detection criterion will give quite optimistic predictions for the particular case of the grizzly. In each graph in Fig. 4 the pair of connected arrows indicate the year in which p is first below that needed for a stable population and the year in which the population size has declined to 90% of its initial value. The difference between the two arrows indicates the lag time between the crucial point in degradation from which population decline will begin and when degradation effects might first be detected. For the four scenarios simulated this lag time ranges from 8 to 13 years. By the time population decline would be detectable, the remaining amount of good habitat—even if no more degradation occurred past that point—would result in annual declines of from 3 to 6%. Thus, the general conclusion is that census data may provide extremely poor measures of population safety or health under conditions of ongoing habitat degradation. As Taylor and Gerrodette (1993) forcefully argue,

statistical problems will often make detection of population declines from census data very unlikely. My results extend their argument by showing that by the time declines are detected, it will probably be too late to prevent critical amounts of habitat degradation from occurring.

Note that the model assumptions I make are biased against finding lag effects in population response to degradation. In particular, assuming that bears of all age classes move between habitats at the same rate reduces time lag effects because of the delayed reproduction. Further, the very slow rates of habitat degradation I simulate here allow the population to track the changing proportions of good and bad habitat. Thus, even species with quite different life history characteristics from bears will probably show similar population level responses to slow degradation.

I emphasize that while generalizations about the sensitivity of population growth to habitat loss and about the timelags expected in our detection degradation of effects are quite robust for different parameter estimates, the absolute value of the critical amount of good habitat is not. In particular, use of other estimates of demographic rates (e.g. Knight & Eberhardt 1985) leads to very different estimates of the minimum amount of good habitat

needed to sustain a grizzly population. Thus, given that demographic estimates for Yellowstone grizzlies have changed considerably over the past three decades and that all estimates come from very small sample sizes, the particular critical amounts of good habitat derived from the analyses I show here should not form the basis of any conclusions about how much absolute amount of degradation is in fact safe.

Discussion

This exercise in simple modeling provides several insights into the phenomenon of habitat degradation in general and the current management of grizzly bears in particular. First, habitat degradation can have highly nonlinear effects on population growth rates, with small amounts of degradation leading to large decreases in overall population growth. Thus to assume the safety of incremental degradation is not possible, very small losses could result in rapid declines of previously stable populations.

Second, our ability to detect crucial degrees of habitat degradation are imperfect at best (Taylor & Gerrodette 1993). The usual test of population health is change in numbers, and political compromises over human development (habitat degradation and loss) often result in ongoing degradation with monitoring of population sizes to gauge effects on threatened species. The statistical power of monitoring to detect population declines is often weak and thus provides little safety for threatened populations (Taylor & Gerrodette 1993). My results show another fallacy of this approach: If degradation is slow, long lag times can exist between critical levels of habitat degradation and any detectable change in population sizes, even when monitoring data are excellent. This point has also been made in the case of habitat destruction for the Northern Spotted Owl (Thomas et al. 1990; Lamberson et al. 1992). Thus, an assurance of even rigorous population monitoring while degradation continues is not a justifiable substitute for an *a priori* analysis of the probable consequences of development.

Third, the models point out that movement rates and habitat-specific demographic rates are crucial variables to understand and measure if we are to predict the critical amounts of degradation that a population can tolerate. These data are rarely available; the model therefore suggests a very conservative approach in assessing the dangers of habitat degradation. This result is particularly relevant to the management of the remaining grizzly populations of the lower 48 States. The Recovery Plan (U. S. Fish and Wildlife 1993) sets criteria that are either indirectly based on population numbers (e.g., number of females with cubs seen per year) or rely on population size estimates (i.e., human-caused mortality as a percent-

age of estimated population size) and uses census data as the primary measures of continuing population health (Shaffer 1992). Although the plan is careful to state that the recovery criteria are not explicitly population number goals, all the criteria are in fact directly related to population size. At the same time, no clear plans are set forth to assess the impacts on bear populations of further development in the national parks and forests that comprise most of the grizzly ecosystems in the lower 48 states. Thus, population monitoring data appear to be the only measures of the continuing, incremental effects of road building for mineral exploration, logging, and tourism.

My analysis indicates that the planned data collection will not adequately safeguard bear populations from this habitat degradation. Rather, analyses of how much degradation is too much and how best to monitor for degradation effects must be completed before degradation proceeds. These analyses could consist of behavioral and demographic modeling of bear populations living in complex sets of interspersed habitat types, similar to the spatially explicit models that have been used to assess the health of Northern Spotted Owl populations (Thomas et al. 1990; Lamberson et al. 1992). In the case of grizzlies and many other species changes in population densities in particular habitat types or change in specific demographic rates may be more effective measures of population status than are overall population numbers. Specific analyses are necessary to determine the most effective monitoring strategy for each species and situation.

By demonstrating the great effects that slow degradation can have on threatened populations and the difficulty in accurately detecting these effects with simple population monitoring, my results bolster the concerns about continuing habitat loss and degradation. Nevertheless, many management plans still rely exclusively on census data to measure effects of ongoing human impacts, even in cases where degradation is essentially irreversible. Little evidence exists to justify such a wait-and-see approach, especially for species such as the grizzly for which relatively complete demographic and behavioral data are already available. Rather, careful analyses to predict future viability should be carried out before allowing habitat degradation and loss to continue and certainly before populations can justifiably be declared recovered.

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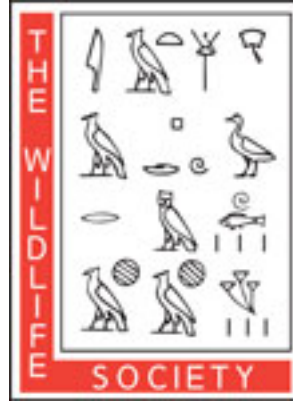
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SEXUAL SEGREGATION AND FEMALE GRIZZLY BEAR AVOIDANCE OF MALES

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Abstract: We examined seasonal use of habitat for 14 male and 5 female grizzly bears (*Ursus arctos*) in southwestern Alberta, 1981–84, to test 2 competing hypotheses regarding segregation of the sexes. The male avoidance hypothesis predicts increasing differences in use of habitat with increasing male use of female-occupied areas because of female avoidance of males. The no avoidance hypothesis predicts decreasing differences in use of habitat with increasing male use of female-occupied areas because of increasing similarity of available habitat. Differences in use of habitat were greatest during late summer, when many males concentrated in the female-occupied area, and they were less during other seasons when few males were in the female-occupied area. Three of 4 habitat variables differed ($P \leq 0.10$) between the sexes during late summer, whereas 2, 1, and 2 variables differed during spring, early summer, and autumn, respectively. Grizzly bear females segregated from males and data support the hypothesis that females avoid males. If females avoid males and male-occupied habitats, reproduction could decline because of nutritional deprivation and survival could decline because of their increased use of human-occupied areas.

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Key words: Alberta, grizzly bear, habitat, sexual segregation, *Ursus arctos*.

Grizzly bears have disappeared from most of their historic range, largely by incremental population and habitat losses at the contracting edges of the species' range (Servheen 1990). In Al-

berta, there were an estimated 780 grizzly bears in 1990, and numbers were declining (Servheen 1990). Nagy and Gunson (1990) estimated 62 grizzly bears in southwestern Alberta, the edge of the species' range. In this study, we radio-monitored 19 of 38 bears in a declining population of Kananaskis Park and Bow Crow Forest, southwestern Alberta (Wielgus and Bunnell 1994). We must understand use of habitat and

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population dynamics in small peripheral populations to prevent further range contractions and eventual extinction of the grizzly bear. The sparse nature or small size of these populations, however, makes large samples impossible and impedes understanding of contracting populations.

Most studies of grizzly bear use of habitat have not examined seasonal differences between the sexes. The sexes often are not identified (Hamer and Herrero 1987a,b; Phillips 1987), are analyzed together (Blanchard 1983, Zager et al. 1983), or only one sex is studied (Hamilton and Bunnell 1987). Some researchers have examined family and single bear use of habitat (Atwell et al. 1980, Darling 1987) but did not discriminate between habitats used by females and those used by males. Only a few studies examined sex-specific seasonal use of habitat. Berns et al. (1980) found little difference between male and female use of habitat. Russell et al. (1979) found that females in Jasper National Park, Alberta, tended to use higher elevations more than did males, especially during spring. Nagy et al. (1983a) reported elevation differences in use of habitat between males and females in the Arctic Mountains but reported no sexual segregation in the Tuktoyaktuk Peninsula (Nagy et al. 1983b). Mattson et al. (1987) and MacLellan and Shackleton (1988) found that females used habitats nearer to roads more than did males. These findings indicate that sexual segregation may occur in some populations but not in others.

When sexual segregation has been observed in grizzly bears, it usually has been interpreted as female avoidance of aggressive or cannibalistic males (Russell et al. 1979, Nagy et al. 1983a, Mattson et al. 1987, McLellan and Shackleton 1988), but that inference has not been tested. This male-avoidance hypothesis predicts that sexual differences in use of habitat should increase with increasing male use of female-occupied areas; that is, females should shift their activity away from males when males move into their areas.

An alternative, no-avoidance hypothesis is that differences in use of habitat result from seasonal differences in habitat availability or diet. For example, males may have different habitats available to them because of their larger home ranges (LeFranc et al. 1987). In this case, differences in use of habitat should decrease with increasing male use of female-occupied areas because of increasing similarity of available

habitat. Differences in use of habitat also may result from females with offspring having reduced mobility and hence reduced access to various habitats. In this case, differences should be greatest early in the year when cubs are most sedentary. Finally, differences in use of habitat may result from sexual differences in dietary preference. In this case, differences should decrease as similarity in diet increases.

We use data collected during a study of grizzly bear use of habitat, movements, and food habits (Wielgus 1986) to determine if sexual segregation occurred and to evaluate consequences predicted by the male-avoidance and no-avoidance hypotheses of such segregation. The biological and behavioral reasons for female avoidance of males were addressed elsewhere (Wielgus 1993, Wielgus and Bunnell 1994).

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STUDY AREA

The study area covered 6,286 km² in Kananaskis Provincial Park and Bow Crow Forest, southwestern Alberta (50–51°N, 115–116°W). Elevation ranged from 1,300 to 2,700 m in mountainous terrain. Climate was continental with long, cold winters and short, cool summers. Vegetation was in the subalpine fir-Engelmann spruce (*Abies lasiocarpa*-*Picea engelmanni*) forest region (Rowe 1972). Forests comprised lodgepole pine (*Pinus contorta*), Engelmann spruce, and subalpine fir. Details of the study

area are given in Wielgus (1986) and Wielgus and Bunnell (1994).

Sport hunting of grizzly bears was closed in the study area from 1970 to 1981 but was reopened from 1982 to 1987. The study population showed high mortality of older adult males and a corresponding high immigration of younger males after 1981 (Wielgus and Bunnell 1994). The small population appeared to be declining from 1981 to 1984 (Wielgus and Bunnell 1994) and was designated as vulnerable by the Committee on the Status of Endangered Wildlife in Canada.

METHODS

Trapping

We trapped grizzly bears from 1980 to 1984 using Aldrich leg snares and immobilized them with ketamine HCl and xylazine HCl in a 1:1 ratio at a dosage of 6.5–10.0 mg/kg body mass. We weighed, eartagged, and aged bears by extracting a premolar (Stoneburg and Jonkel 1966). We then fitted them with activity-sensing radio collars. We trapped and radiocollared bears in the 254-km² Highwood trapping zone, which covered a 50-year-old burn in the mountains (1,800 m elevation) and was dominated by soapberry (*Shepherdia canadensis*) shrubfields. Surrounding areas were unburned and appeared to have comparatively little berry production (Wielgus 1986, 1993).

Seasonal Habitat Use

We monitored radioed bears (14 M, 5 F) from fixed-wing aircraft once every 1–2 weeks during the nondenning period (15 Apr–1 Dec), 1981–84. We estimated bear locations from the aircraft (Whitehouse and Steven 1977) and marked them on 1:50,000 topographic maps. We estimated radiolocation accuracy by noting signal strength when bears were sighted, then used signal strength for determining nonvisual locations. We visually confirmed 81 of 451 locations (18%). We only used locations judged to be accurate within 1 ha and within 1 habitat type (451 of 526 locations, 86%) in habitat analyses. The ratio of radiolocation error (1 ha) to mean forest stand size for a representative map-sheet (28.4 ha, SE = 7.8 ha, $n = 335$) was low, indicating little potential for error (White and Garrot 1986). Only 5% of forest stands had areas ≤ 1 ha. A self-developing photograph was taken and marked to indicate bear location within the

vegetational mosaic. We later transferred locations from topographic maps and photos to corresponding forest habitat maps.

Habitat variables for each location were forest type and age, elevation, aspect, and slope. We assumed those variables to be related to grizzly bear food and cover requirements (McCrory and Herrero 1981, 1983a,b; Zager et al. 1983; Holcroft and Herrero 1984), and they were already mapped and used for forest management. Habitat variables and criteria for designating them were determined in advance by the Alberta Forest Service. Prior to analysis, we reduced the number of forest types to facilitate statistical testing by combining similar classes into broader types on the basis of type and openness of vegetation. Our forest types were alpine (grassy meadows, alpine tundra, barren soil, rock), shrubfield (avalanche chutes, burns, clear-cuts, brushfields), pine-dominated forests (*Pinus* spp.), and spruce-dominated forests (*Picea* spp.). We recorded elevation, aspect, and slope from topographic maps.

We defined seasons by changes in plant phenology and corresponding shift in food habits as determined by scat analyses (Wielgus 1986). We identified 4 seasons: spring (15 Apr–11 Jul, pre-berry season), early summer (12 Jul–15 Aug, onset of berry season), late summer (16 Aug–17 Sep, peak of berry season), and autumn (18 Sep–1 Dec, end of berry season).

Data Analysis

We tested for sexual differences in seasonal use of habitat by comparing seasonal counts of male and female locations using the Chi-square test of homogeneity (Daniel 1978, Wilkinson et al. 1992). We pooled radiolocations of bears into male and female sex classes and across years (1981–84) into seasons, in a modified type-2 design (Thomas and Taylor 1990). Pooling of data allowed adequate sample sizes for tests of seasonal habitat segregation (Roscoe and Byars 1971), assuming no effect of years.

We ensured that our pooled sex-seasonal datasets were not biased toward individual bears or reproductive classes by balancing our radiotelemetry effort across individuals and classes. Data were not biased toward particular individuals because each bear contributed an approximately equal number of locations (Wielgus 1986). Pooled data were representative of individual bears and years because annual use of habitat did not vary among individual bears or

Table 1. Percent use and Chi-square tests (5 df) for homogeneity of forest age types used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84.

Forest type (age in yr)	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
Alpine	17	29	15	12	16	21	10	25
Shrubfield	5	14	10	19	10	23	3	14
Pine (5–50)	22	27	36	42	51	41	18	39
Pine (>50)	31	14	21	15	12	7	33	4
Spruce (5–50)	5	2	4	6	0	4	4	0
Spruce (>50)	20	14	14	6	11	4	32	18
n locations	64	63	51	53	61	43	67	49
n bears	11	5	14	5	14	5	12	5
χ ²	10.87		4.37		8.65		28.81	
P	0.05		0.49		0.12		<0.01	

years, except between subadult and adult females (Wielgus 1993). We assumed data to be independent because all bears traveled alone and radiolocations were obtained at weekly or biweekly intervals (Swihart and Slade 1985). Analyses of annual, not seasonal, use of habitat by individual bears by year were treated elsewhere (Wielgus 1993).

We used log-linear models (Feinberg 1980, Wilkinson et al. 1992) to test if male locations for a given season were obtained during some years and female locations for the same season were obtained during other years. Any such findings would constitute a sex by season by year interaction and would invalidate our test of female seasonal avoidance of males. This analysis comprised 2 sexes, 4 years, and 4 seasons, for a total of 32 cells. Sample sizes and expected values were adequate (<20% of cells with expected values <5) for testing (Wilkinson et al. 1992).

We tested hypotheses of sexual segregation by determining seasonal numbers of individual male bears and percentage of male locations within the female 97.5% multi-annual, composite range of 868 km² (Ackerman et al. 1990). The female composite range was centered on the Highwood trapping zone. Most bears using that zone were believed to be captured and collared (Wielgus and Bunnell 1994). If differences ($P \leq 0.10$) between the sexes occurred for use of habitat variables during late summer, when many males concentrated in the female-occupied area, we interpreted that as support for the male-avoidance hypothesis. If differences were not significant ($P > 0.10$), or if differences were less during the late summer, we interpreted that as support for the no-avoidance hypothesis.

RESULTS

Structure of Pooled Data

Mean number of locations/bear/season was 10.4 (SE = 0.8, $n = 20$) for females and 4.7 (SE = 0.4, $n = 51$) for males (Table 1). Male bears had fewer locations than did females because they suffered higher mortality (Wielgus and Bunnell 1994). Data were not biased toward particular age classes. Single adults (>5.5 yr, $n = 4$) contributed 35%, adults with offspring ($n = 4$) 42%, and subadults (2.5–5.5 yr, $n = 2$) 23% to the female radiolocation data. Adults (>5.5 yr, $n = 7$) contributed 46% and subadults (2.5–5.5 yr, $n = 9$) 54% to male location data.

Sample size or number of locations per cell in the log-linear model varied with sex, year, season, and 2 of their interactions. The most parsimonious log-linear model that fit our data was sex + season + year + sex by year + season by year ($\chi^2 = 13.23$, 12 df, $P = 0.35$). The sex main effect reflected differences between the sexes (M had 54% of locations, F had 46%). The year main effect reflected differences among years. Most data were obtained from 1982 to 1984 (6% of locations were in 1981, 29% in 1982, 48% in 1983, and 17% in 1984). One female was monitored in 1981, 4 in 1982, 5 in 1983, and 5 in 1984. There were 3 males in 1981, 6 in 1982, 10 in 1983, and 5 in 1984. The season main effect was included to account for the seasonal term of a significant year by season interaction. Percents of locations among seasons were similar (28% in spring, 23% in early summer, 23% in late summer, and 26% in autumn). The sex by year interaction reflected occurrence of proportionately more male locations in 1981 and more female locations in 1984. Percents of total

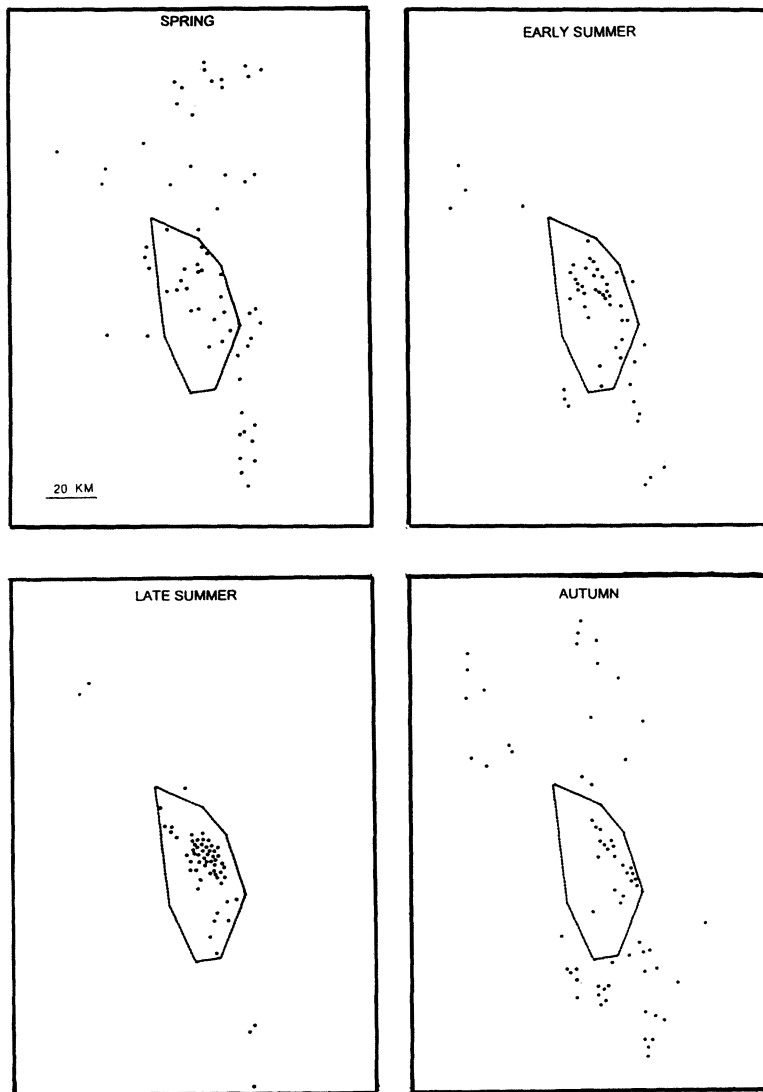


Fig. 1. Seasonal (spring = 15 Apr–11 Jul, early summer = 12 Jul–15 Aug, late summer = 16 Aug–17 Sep, autumn = 18 Sep–1 Dec) distribution of male grizzly bear radiolocations (dots) in relation to 97.5% multi-annual composite home range of female grizzly bears (polygon) in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84.

female locations distributed across years were 3, 27, 43, and 27% for 1981–84, respectively. Percents of total male locations distributed across years were 9, 30, 53, and 8% for 1981–84, respectively. The year by season interaction reflected scarcity of locations in spring and early summer 1981 and autumn 1984, because monitoring began in 1981 and ended in 1984.

Adding more interactions (e.g., sex by season or sex by season by year) to the model did not improve fit of the data ($\chi^2 = 1.1$, 3 df, $P > 0.10$). Therefore, seasonal data were not biased by the

uneven distribution of the sexes' locations among years.

Seasonal Segregation

Data on use of habitat (Tables 1–4) were presented as percentages rather than counts to facilitate comparisons (Hellgren et al. 1991, Wilkinson et al. 1992). During spring, overlap between males and females was low (Fig. 1). We observed 8 male bears and 20 of 64 male locations (31%) in the female composite range.

Table 2. Percent use and Chi-square tests (4 df) for homogeneity of elevation zones used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84. Sample sizes are as in Table 1.

Elevation (m)	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
<1,680	22	5	13	10	7	0	28	2
1,680–1,830	25	22	22	25	36	16	18	22
1,831–1,980	22	33	41	36	32	45	32	27
1,981–2,130	22	21	17	14	20	25	15	25
>2,130	9	19	7	15	5	14	7	24
χ^2	10.68		2.89		10.01		18.85	
P	0.03		0.57		0.04		<0.01	

Use of habitat differed between the sexes for forest age (Table 1) and elevation (Table 2).

In early summer, males began to converge on the female range (Fig. 1). We observed 9 males and 34 of 51 male locations (67%) in the female composite range. Use of aspect differed (Table 3) between the sexes.

During the late summer berry season, geographical overlap between sexes was most pronounced (Fig. 1), when we observed 11 male bears and 55 of 61 male locations (90%) in the female range. Sexual differences for use of habitat variables were greatest during late summer despite concentration of males and females in the same area. Three of 4 habitat variables differed: elevation, aspect, and slope. Location of females shifted to higher elevations (Table 2), different aspects (Table 3), and steeper slopes (Table 4) when males moved into the female area.

During autumn, overlap between the sexes declined as males moved out of the female range (Fig. 1). We observed 8 males and 20 of 67 male

locations (30%) in the female range. Use of 2 variables differed: forest age (Table 1) and elevation (Table 2).

DISCUSSION

Our results show differences between seasonal male and female use of habitat, so we reject the hypothesis that male and female bears used the same habitats. We are confident in our test results despite small sample size, because small sample sizes decrease statistical power, making rejection of null hypotheses more difficult (Allredge and Ratti 1986). Although large samples are desirable they cannot always be obtained, especially when studying small populations (Wielgus and Bunnell 1994).

Sexual differences in grizzly bear use of habitat were greatest during the late summer berry season when the most spatial overlap between the sexes occurred. Sexual difference in diet was unlikely to account for habitat segregation in late summer because of hyperphagia (Nelson et al. 1983) by both sexes on soapberries (McCrory

Table 3. Percent use and Chi-square tests of homogeneity (8 df) for aspects used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84. Sample sizes are as in Table 1.

Aspect	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
Flat	17	11	19	30	18	11	16	8
Northwest	14	10	2	6	1	16	6	12
North	9	3	15	9	10	5	10	10
Northeast	0	10	9	6	15	7	25	16
East	17	22	26	4	13	14	17	23
Southeast	9	6	4	9	7	9	7	4
South	9	12	9	9	5	9	5	2
Southwest	6	10	5	4	13	2	3	10
West	19	16	11	23	18	27	11	15
χ^2	10.79		16.34		14.95		8.21	
P	0.21		0.03		0.06		0.41	

Table 4. Percent use and Chi-square tests of homogeneity (3 df) for slope categories used seasonally by male and female grizzly bears in Kananaskis Park and Bow Crow Forest, Alberta, 1981–84. Sample sizes are as in Table 1.

Slope (°)	Spring 15 Apr–11 Jul		Early summer 12 Jul–15 Aug		Late summer 16 Aug–17 Sep		Autumn 18 Sep–1 Dec	
	M	F	M	F	M	F	M	F
≤10	56	44	52	55	56	34	48	35
11–20	19	19	24	17	15	30	29	41
21–30	23	27	19	25	28	21	21	22
>30	2	10	5	3	1	15	2	2
χ ²	4.68		1.14		13.30		2.74	
P	0.19		0.76		<0.01		0.43	

and Herrero 1983a,b; Wielgus 1986; Hamer and Herrero 1987a,b). Low cub mobility was unlikely to account for habitat segregation in late summer because cubs are mobile relative to earlier seasons. These results lead us to reject the no-avoidance hypothesis and accept the male-avoidance hypothesis of habitat segregation.

Males converged on the female composite range in late summer and concentrated in burned-over, young (5–50 yr) pine forests at low to mid-elevations (1,680–2,130 m), on northeasterly aspects, and on shallow (≤10°) slopes. These sites contained the best soapberry patches in our study area (McCrary and Herrero 1981, 1983a,b; Hamer and Herrero 1987a,b). Females also concentrated in young pine forests and shrubfields during the early summer onset of berry season, but they shifted to higher, drier, steeper, and apparently poorer sites (McCrary and Herrero 1981, 1983a,b; Hamer and Herrero 1987a,b) when males arrived in late summer. We feel it is unlikely that females would select for poorer quality berry patches if males had not arrived.

Females also may have avoided old forests in spring and autumn because of the likelihood of encountering male bears there (Table 1). Wielgus (1986) suggested that males may have used those forests for predation and consumption of elk (*Cervus elaphus*) calves during the spring calving season and elk bulls during the autumn rut and hunting season.

Hornocker (1962), Egbert and Stokes (1976), McCullough (1981), and Stringham (1983) hypothesized that female bears and other subdominants avoid adult males because males compete with, behave aggressively toward, and even kill subdominants for food. Stringham (1980), Wielgus (1986), and LeCount (1987) hypothesized that adult females, especially females with offspring, avoid non-sire, immigrant males because

those males may kill cubs to induce estrus and gain a breeding opportunity (Hrdy and Hausfater 1984). The only tests of those hypotheses were conducted by Wielgus (1993), and results supported the latter hypothesis. Hunting of older adult males resulted in an influx of younger immigrant males (Wielgus and Bunnell 1994) and subsequent female avoidance of those males.

MANAGEMENT IMPLICATIONS

If female grizzly bears use food-poor habitats to avoid males, identification and protection of only food-rich habitats (Mace and Bissell 1986, McCrary et al. 1986) could leave essential habitats for females unidentified and unprotected. That could result in dangerous conflicts between humans and female bears if humans venture unaware into such unidentified female-occupied areas (Herrero 1985). Avoidance of food-rich, male-occupied habitats by females also could slow or stop population growth because of increased female mortality or reduced female reproduction. For example, Mattson et al. (1987) suggested that females avoided males by using habitats close to roads and this led to increased deaths of female grizzly bears by humans. In small populations, the loss of even a few females can cause population declines (Bunnell and Tait 1981, Eberhardt 1990). Wielgus (1993) found that females avoided food-rich habitats occupied by immigrant males and that female reproduction suffered, contributing to population decline. We recommend that other researchers replicate our tests and examine these phenomena to see if results are applicable elsewhere.

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December 7, 2015

Daniel M. Ashe, Director
U.S. Fish and Wildlife Service
1849 C Street NW, Room 3331
Washington, District of Columbia, 20240

Dear Director Ashe:

On August 28, 2015, we wrote you regarding the overdue re-designation and delisting of the Greater Yellowstone Grizzly Bear Distinct Population Segment (DPS). We appreciate the progress and agreements we achieved during our discussions in Tucson on September 14th and your subsequent letter dated September 25, 2015 memorializing those discussions. Since then, our agencies have had several discussions with the U.S. Fish and Wildlife Service (Service) as to documentation for the delisting rulemaking process.


The Ninth Circuit determined that adequate regulatory mechanisms were in place at the time of the prior rule designating and delisting the Greater Yellowstone DPS in 2007. The regulatory mechanisms that the Ninth Circuit found adequate remain in effect today. The Interagency Grizzly Bear Study Team published findings that resolved the single deficiency found by the Ninth Circuit in the 2007 rule, and best available science continues to demonstrate the GYA population consistently exceeds recovery criteria.

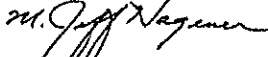
Nevertheless, we agree that additional documentation as to regulatory mechanisms will provide clarity and transparency as to how the states will coordinate with each other and federal land managers to ensure maintenance of the recovered bear population. Various signatory agencies have discussed appropriate updates to the 2007 Interagency Conservation Strategy.

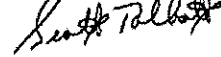
We have also enclosed a draft memorandum of agreement (MOA) among the states that we will recommend to our respective commissions for approval at meetings in the next few months following public notice. Although not necessary for delisting, this MOA memorializes how the three states will coordinate with each other, as well as with federal land managers, regarding bear management and allocation of discretionary mortality. An attachment to the MOA summarizes individual state regulatory mechanisms to manage, monitor, restrict, and adjust bear mortality. We will keep the Service apprised as to our respective commissions' approval of the MOA.

We look forward to continuing to work with you and your staff to finalize all steps necessary to delist. As we stated in our prior letter, delisting delay is needlessly straining relationships vital to responsible grizzly bear management. It is critically important that we capitalize on our tremendous progress and momentum by fulfilling the purpose of the ESA by proceeding with long overdue delisting.

Sincerely,


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Enclosure

FINAL DRAFT 12-4-2015

MEMORANDUM OF AGREEMENT REGARDING THE MANAGEMENT AND ALLOCATION OF DISCRETIONARY MORTALITY OF GRIZZLY BEARS IN THE GREATER YELLOWSTONE AREA

Among

**Wyoming Game and Fish Commission, Wyoming Game and Fish Department,
Montana Fish and Wildlife Commission, Montana Fish, Wildlife and Parks,
Idaho Fish and Game Commission, and Idaho Department of Fish and Game**

This Memorandum of Agreement (MOA) is made and entered into by and among the Wyoming Game and Fish Commission and the Wyoming Game and Fish Department (collectively WGFD), the Montana Fish and Wildlife Commission and Montana Fish, Wildlife and Parks (collectively MFWP), and the Idaho Fish and Game Commission and the Idaho Department of Fish and Game (collectively IDFG), collectively referred to as the Parties.

I. Purpose

The purpose of this MOA is to define the process by which the Parties will coordinate the management and allocation of discretionary mortality of grizzly bears in the Greater Yellowstone Area (GYA). The Parties enter into this MOA in support of the re-designation of the Distinct Population Segment (DPS) of GYA grizzly bears and delisting of this DPS under the federal Endangered Species Act. The Parties intend this MOA to be consistent with the 2007 interagency *Final Conservation Strategy for the Grizzly Bear in the Greater Yellowstone Area* (Strategy) and individual state management plans, and with revisions to these documents made in conjunction with the delisting process.

II. Background

The Interagency Conservation Strategy Team, with the participation of the Parties and various federal agencies, developed the Strategy to implement regulatory mechanisms, interagency cooperation, and population and habitat management and monitoring, and other actions to ensure continued recovery of the GYA grizzly bear. The Strategy was subject to public comment and scientific peer review. The Strategy's key mechanisms for maintaining a recovered GYA grizzly population are its population and habitat standards, which are based on the recovery criteria originally set forth in the USFWS Recovery Plan. The Strategy incorporated the Parties' individual state management plans that have different, but compatible, management objectives.

On March 21, 2013, USFWS published for public comment a draft Supplement to Demographic Recovery Criteria, but USFWS has not yet finalized any such Supplement. For purposes of this MOA, the Parties assume adoption of the Demographic Monitoring Area (DMA) identified in the 2013 draft Supplement as the geographic area used to monitor continued achievement of GYA population and distribution objectives. The Interagency Grizzly Bear Study Team (IGBST) and the Yellowstone Ecosystem

Subcommittee (YES) of the Interagency Grizzly Bear Committee (IGBC) have recommended the use of the DMA for population monitoring, including mortality monitoring.

USFWS' draft 2013 Supplement kept in place the recovery criterion for a conservative total population size of at least 500 GYA bears. This minimum population size includes a conservative buffer in addition to the recommendation of Miller and Waits (2003) for a minimum population size of at least 400 bears to adequately mitigate the potential effects of genetic drift and inbreeding depression in light of the relative isolation of the GYA population. For purposes of this MOA, the Parties assume the conservative criterion for minimum population size will remain in place.

USFWS' draft 2013 Supplement also kept in place the conservative criterion for female occupancy standards in the Primary Conservation Area (PCA). For purposes of this MOA, the Parties assume this conservative criterion will remain in place.

The demographics and vital rates of the GYA population have changed over time. USFWS' draft 2013 Supplement proposed a revision to mortality standards to reflect changes in these rates to ensure a total GYA population of at least 500 bears and to meet the occupancy standard for female bears. For purposes of this MOA, the Parties identified adjustable mortality rates (see Paragraph IV. 2) to manage human-caused mortality within the DMA to levels that will sustain a population range based on the 2002-2014 Chao2 average population estimate of 674 grizzly bears within the DMA.

Adjustable mortality levels allow for higher or lower mortality rates and correspond to the upper and lower 95% confidence intervals of the 2002-2014 Chao2 average population point estimate. Adjustable mortality rates enable the Parties to address higher human-bear conflict levels that may occur when the bear population is well above the population recovery criterion. They also ensure the population stays above the recovery criterion of a minimum population size of 500 animals in the GYA. The Parties will review the population vital rates and demographics (compiled by IGBST) a minimum of every 5 years to recommend appropriate adjustments to mortality rates.

From 2002 to the present, the IGBST has used the Chao2 estimator and model averaging process to calculate population size on an annual basis. As the bear population has grown, Chao2-based estimates have become increasingly conservative (i.e., prone to underestimation). The IGBST has also made population estimates more recently using a mark-resight based technique (IGBST Report, 2012). The mark-resight approach has no known density-associated bias, and should better reflect actual bear abundance; however, current implementation of the approach is less precise than Chao2 at tracking population trend. For purposes of this MOA, the Parties assume that USFWS will, as a matter of best available science and appropriate conservatism, rely on the Chao2 estimate for assessing the population size for the post-delisting monitoring period. The Parties recognize that methods for population estimation may change in the future as circumstances warrant and new methods are scientifically vetted and accepted.

III. Definitions

1. "Discretionary mortality" is the amount of human-caused grizzly bear mortality over which agencies have discretionary authority, such as management removals and regulated harvest.
2. "Non-Discretionary mortality" is documented loss over which agencies do not have discretionary authority, such as naturally occurring mortality or human-caused mortality such as illegal shootings, defense-of-human-life shootings, and vehicle collisions.
3. "Greater Yellowstone Area" (GYA) is defined as that portion of Idaho that is east of Interstate Highway 15 and north of U.S. Highway 30; that portion of Montana that is east of Interstate Highway 15 and south of Interstate Highway 90; that portion of Wyoming south of Interstate Highway 90, west of Interstate Highway 25, Wyoming State Highway 220, and U.S. Highway 287 south of Three Forks (at the 220 and 287 intersection), and north of Interstate Highway 80 and U.S. Highway 30. This definition of GYA was used in the 2007 USFWS rule to designate a distinct population segment (DPS) of grizzly bears under the Endangered Species Act, and to delist that DPS; in 2010 USFWS vacated this rule in response to a court decision. The Parties assume USFWS will re-designate a grizzly bear DPS for the GYA geographic area as defined herein.
4. "The Recovery Zone," also known as the "Primary Conservation Area" (PCA), is the area whose boundaries are approximately depicted on the map attached hereto as Attachment A; the Recovery Zone is divided into 18 Bear Management Units.
5. "Demographic Monitoring Area" (DMA) is the area that includes the Recovery Area and an additional area surrounding the Recovery Area, approximately 19,279 mi² in area and whose boundaries are depicted on the map attached hereto as Attachment A.
6. "Chao2" is the population estimation technique currently used for the GYA population of Grizzly Bears.

IV. Responsibilities

1. The Parties will employ best science and adaptive management approaches to collectively manage grizzly bears within the GYA.
2. To achieve population criteria to support a recovered GYA grizzly bear population, the Parties will:
 - a. Maintain a minimum population size of 500 bears in the GYA.

- i. The Parties agree to achieve this criterion by managing the GYA grizzly bear population within the DMA to at least the 2002-2014 Chao2 average point estimate for total population, with 95% confidence intervals (*i.e.*, 600-747).
- b. Ensure that 16 of the 18 Bear Management Units within the PCA are occupied by at least one female with cubs over a six-year period, with no two adjacent Bear Management Units unoccupied over a six-year period.
- c. Ensure the following total mortality rates are not exceeded within the DMA for three consecutive years for independent males, independent females and dependent young, as set forth in the following table, based on the 2002-2014 Chao2 average point estimate for the total population with 95% confidence intervals (600-747).

	Total Grizzly Bear Population Estimate		
	≤674	675-747	>747
Total mortality rate for independent <u>FEMALES</u> .	7.6%	9%	10%
Total mortality rate for independent <u>MALES</u> .	15%	20%	22%
Total mortality rate for dependent young.	7.6%	9%	10%

- i. The Parties agree to achieve this criterion using an adaptive management framework that will include, but not be limited to, the following:
 - If the population is less than 600, the Parties will not allow discretionary mortality unless necessary to address human safety issues.
 - At any population level greater than 600, if total allowable independent male or female mortality is exceeded, the number exceeding the total allowable mortality will be subtracted from the next year's discretionary mortality available for harvest for that gender.
 - If a state meets any of its allocated regulated harvest limits at any time of the year, the respective state will cease hunting within the DMA.
 - If the total mortality limit for independent males, independent females, or dependent young is exceeded for three consecutive years, the Parties will evaluate alternatives to reduce discretionary mortality and request IGBST biology and monitoring review. The Parties will consider the results of the IGBST review in determining appropriate changes to the management framework.
 - If the distribution of reproductive females does not meet the criterion for Bear Management Unit occupancy, the Parties will request IGBST

biology and monitoring review. The parties will consider the results of the IGBST review in determining appropriate changes to the management framework.

3. The Parties will support the IGBST in the annual monitoring of the GYA grizzly bear population.
4. a. The Parties will meet annually in the month of January to review population monitoring data supplied by IGBST and collectively establish discretionary mortality limits for regulated harvest for each jurisdiction (MT, ID, WY) in the DMA, so DMA thresholds are not exceeded, based upon the following allocation protocol.
 - Begin with DMA Chao2 total population estimate and estimates for independent males, independent females, and dependent young (demographic classes) for the previous calendar year, as reported by the IGBST.
 - Determine the maximum allowable mortality limit for each demographic class based on the mortality rates identified in the table above.
 - Determine total mortality during the previous calendar year for each demographic class.
 - Subtract the previous year's total mortality from the maximum allowable mortality limit for each demographic class. If the difference is negative (*i.e.*, a DMA annual mortality limit is exceeded for any of the three classes), the number of mortalities above the limit will be subtracted from the corresponding DMA discretionary mortality limit for that class for the current year.
 - Allocate discretionary mortality available for regulated harvest for independent males and females to each management jurisdiction as provided in the following table. The Parties may agree to adjust the allocation of discretionary mortality based on management objectives and spatial and temporal circumstances.

Management Jurisdiction*	% of DMA outside NPS lands
WY inside DMA	58%*
MT inside DMA	34%
ID inside DMA	8%

*Four percent (4%) of the DMA outside of National Park System lands in Wyoming is under the jurisdiction of the Joint Business Council of the Eastern Shoshone and Northern Arapaho Tribes of the Wind River Reservation.

- b. The Parties will prohibit hunting of females accompanied by young, and young accompanied by females, and discretionary mortality of such animals will only occur for management removals.
- c. Each party has discretion as to how it applies its allocation of discretionary mortality pursuant to its respective regulatory processes and management plan.
- d. The Parties will coordinate with IGBST to review and make any appropriate adjustments to mortality rates at least every five years.

5. The Parties will confer with the National Park Service (NPS) and United States Forest Service (USFS) annually. The Parties will invite representatives of both GYA National Parks, the NPS regional office and GYA USFS Forest Supervisors to attend the annual meeting.
6. The Parties will monitor mortality throughout the year, and will communicate and coordinate with each other and with federal land management agencies as appropriate to minimize the likelihood of exceeding mortality limits.
7. Each party has discretion to manage grizzly bears within its jurisdiction in areas within the GYA that are outside the DMA pursuant to its respective regulatory processes and state management plan.
8. Each party will designate one representative as a respective Point of Contact for purposes of achieving the objectives of this MOA.

V. Authorities and Regulatory Mechanisms

The Parties enter this MOA pursuant to their respective state authorities as set forth in Title 87 Montana Code Annotated, Title 23 Wyoming Statutes Annotated, and Title 36 Idaho Code.

The Parties have the authority, capability and biological data to implement appropriate hunting restrictions, management relocations and removals, and population management. The Parties will use their respective individual authorities to regulate discretionary mortality as allocated to their jurisdictions under this MOA. The Parties' respective regulatory mechanisms to manage, monitor, restrict, and adjust mortality include, but are not limited to, those identified in Attachment B.

This MOA in no way restricts the Parties from participating in similar activities with other states, agencies, tribes, local governments, or private entities.

VI. No Obligation of Funds

This MOA is neither a fiscal nor a funds obligation document. Any endeavor or transfer of anything of value involving reimbursement or contribution of funds among the Parties will be handled in accordance with applicable laws, regulations, and procedures and such endeavors will be outlined in separate agreements or contracts that shall be made in writing by representatives of the Parties. This MOA does not provide such authority.

VII. Term, Termination and Effective Date

This MOA shall become effective upon the date of signature of all Parties. It shall remain in effect until it is terminated by the Parties. Any party may terminate its participation in

the MOA by providing thirty (30) days written notice to the other Parties, which notice shall be transmitted by hand or other means of delivery confirmation.

VIII. Amendment

The Parties will meet annually to review implementation of the MOA and to recommend any appropriate modifications to the MOA based on changes to the Strategy, state management plans or other pertinent regulatory documents. Any modification to the MOA will only become effective upon the written consent of all Parties.

IX. No Third Party Beneficiary

Nothing contained herein shall be construed as granting, vesting, creating or conferring any right of action or any other right or benefit upon any third party.

X. Severability

Should any portion of this MOA be judicially determined to be illegal or unenforceable, the remainder of the MOA shall continue in full force and effect.

XI. Sovereign Immunity

The states of Wyoming, Montana, and Idaho do not waive their sovereign immunity by entering into this MOA, and each fully retains all immunities and defenses provided by law with respect to any action based on or occurring as a result of this MOA.

In Witness Whereof, the Parties hereto have executed this MOA as of the last written date below.

President, Wyoming Game and Fish Commission

Date

Director, Wyoming Game and Fish Department

Date

Chairman, Montana Fish and Wildlife Commission

Date

Director, Montana Fish, Wildlife and Parks

Date

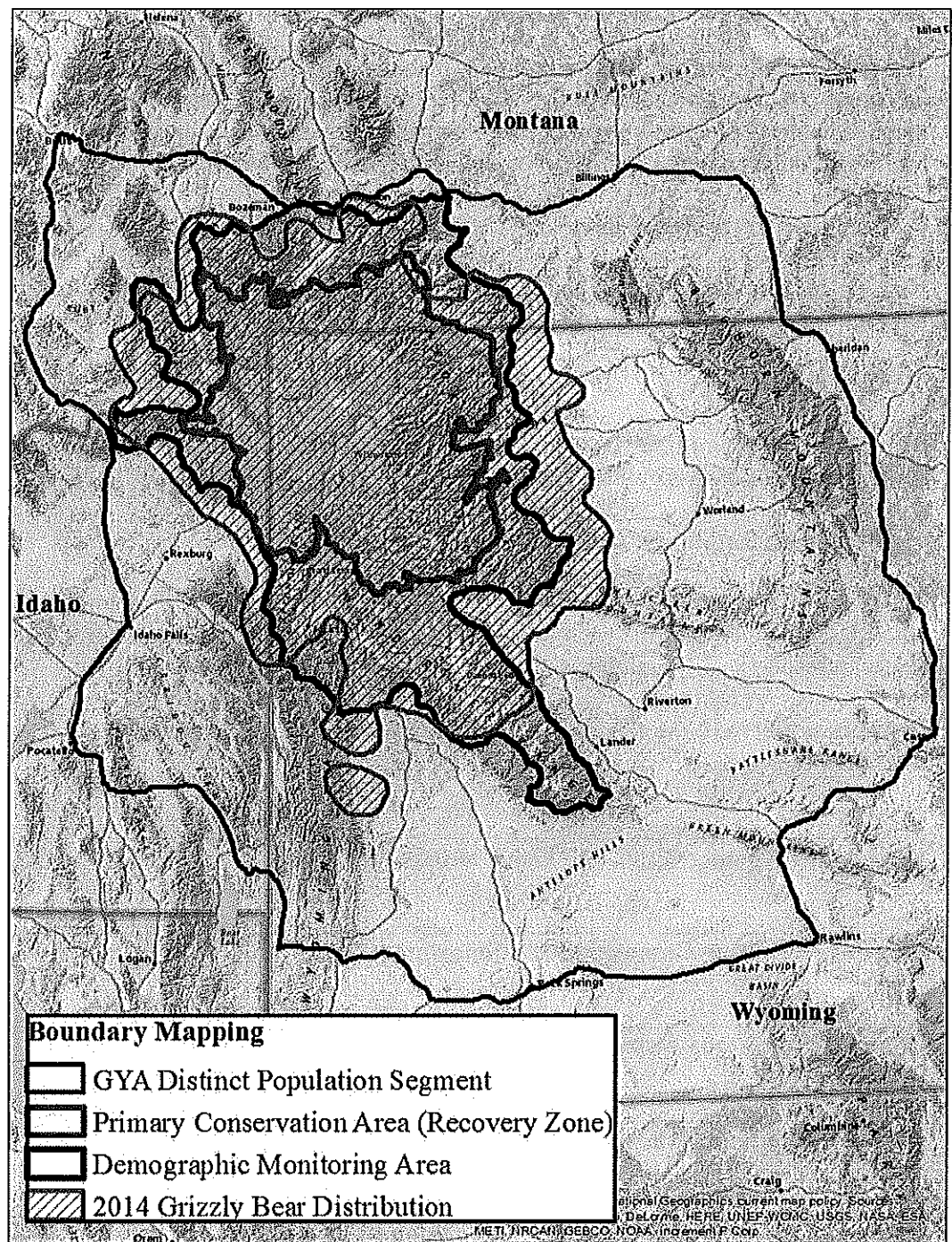
Chairman, Idaho Fish and Game Commission

Date

Director, Idaho Department of Fish and Game

Date

ATTACHMENT A



ATTACHMENT B

	Wyoming WS=Wyoming Statute WGBMP=Wyoming Grizzly Bear Management Plan	Montana MCA= Montana Code Annotated ARM=Admin. Rules of Montana MTFWC – Montana Fish and Wildlife Commission Regulation	Idaho IC=Idaho Code IDAPA=Idaho Admin. Code ISP=Idaho Season Proclamation
Protected Classification	W.S. 23-1-101 (a)(xii)(A) (classified as trophy game animal)	MCA 87-2-101 (4) (classified as a game animal)	IC 36-201 IDAPA 13.01.06.100.01(e) (classified as big game animal)
No Take without Statutory/Commission/Director Authorization	W.S.23-3-102(a)	MCA 87-1-301; MCA 87-1-304; MCA 87-5-302	IC 36-1101(a)
Commission restriction of season, location boundaries, limits, gender, age	W.S. 23-1-302(a)(ii), WGBMP	MCA 87-1-304 (1); MCA 87-5-302	IC 36-104(b)(2) seasons, locations, sex, limits, methods of take; ISP
Commission limit of harvest to automatically close season, including gender-based limits	W.S. 23-1-302(a), WGBMP	MCA 87-1-304; MCA 87-5-302	IC 36-104(b)(2); ISP
Commission authority to restrict hunter effort (e.g., controlled hunts, tag limits)	W.S. 23-1-302(a)(i), WGBMP	MCA 87-1-201(8); MCA 87-1-304 (1); MCA 87-2-702; MCA 87-5-302;	IC 36-104(b)(2) IC 36-104(b)(5) authority to designate controlled hunt IC 36-408(1),(2); ISP
Prohibition against take of females with young present	W.S. 23-1-302(a)	MCA 87-1-304; MCA 87-5-302; MCA 87-5-302	IC 36-104(b)(2) (Commission authority to prohibit in conjunction with season setting); ISP Commission authority to enact through rule (<i>see</i> IDAPA 13.01.08.300)
Requirement for license and tag	W.S. 23-3-102(a)	MCA 87-1-201(8); MCA 87-2-701; MCA 87-2-702; MCA 87 2-814; MCA 87-5-302	IC 36-401 IC 36-409(c)
Mandatory Check/Report to Monitor Harvest	W.S. 23-1-302(a)	MCA 87-1-301; MCA 87-5-302	IC 36-104(b)(3) Commission authority for rules for mandatory check and report requirements (<i>see</i> IDAPA

	Wyoming WS=Wyoming Statute WGBMP=Wyoming Grizzly Bear Management Plan	Montana MCA= Montana Code Annotated ARM=Admin. Rules of Montana MTFWC – Montana Fish and Wildlife Commission Regulation	Idaho IC=Idaho Code IDAPA=Idaho Admin. Code ISP=Idaho Season Proclamation
			13.01.08.420-422 for rules for all big game species open to harvest)
Authority for Emergency Season Closure based on Change in Conditions affecting mortality/habitat	W.S. 16-3-103(b)	MCA 87-1-304 (5); MCA 87-5-302	IC 36-104(b)(3) Commission emergency closure authority IC 36-106(e)(6) Director authority, closure in emergency effective upon written order
Permit required for response to depredation unless self-defense/defense of others/defense of property under threat to human life or domestic animals	W.S. 23-1-302(a)(viii)	MCA 87-1-201(8); MCA 87-1-304(1)(e); ARM 12.9.103(1)(d)	IC 36-1107 (carcass remains property of state)
Mandatory Education	W.S. 23-1-302(a)(xxii)	MCA 87-1-301; MCA 87-1-304 MFWC Black Bear Regulations	IC 36-412(a) Hunter education mandatory for those born after 1/1/1975 IDAPA 13.01.02.100 Recommended additional materials and exam regarding bear identification available on-line.
Penalties	W.S. 23-3-102(d), W.S. 23-6-202, W.S. 23-6-206, W.S. 23-6-208	MCA 87-6-413. (Hunting or killing over limit)	IC 36-1404(c) Misdemeanor IC 36-1404(d) Felony IC 36-1404(e) Revocation of hunting license for certain violations, including for take during closed season, exceeding bag/possession limit IC 36-1404(g): license revocation in Idaho revokes hunting privileges in all 44 states participating in the Interstate Wildlife Violator

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			compact
Civil Penalty	W.S 23-6-204(e)		IC 36-1404(a)(3)
Procedural Aspects of State Regulatory Mechanisms	W.S. 16-3-101, Wyoming Administrative Procedures Act	MCA 2-4-101, et seq, Montana Administrative Procedures Act	IC 74- Open Meeting Requirements, including notice for all meetings of Idaho Fish and Game Commission IC Title 67, Chapter 52 (Idaho Administrative Procedure Act), requirements for public notice and comment, legislative review IC 36-105(3) Public Notice & Publication requirements for season setting

ANIMAL BEHAVIOR **AND** WILDLIFE CONSERVATION



EDITED BY
MARCO FESTA-BIANCHET & MARCO APOLLONIO

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Island Press is the only nonprofit organization in the United States whose principal purpose is the publication of books on environmental issues and natural resource management. We provide solutions-oriented information to professionals, public officials, business and community leaders, and concerned citizens who are shaping responses to environmental problems.

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Animal Behavior **AND Wildlife Conservation**

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EDITED BY
Marco Festa-Bianchet
AND Marco Apollonio

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Preface

The Ettore Majorana Center for Scientific Culture in Erice, Sicily, is known worldwide as a place where important meetings happen, scientific collaborations begin, and new ideas are generated. The unique character of Erice, a walled town perched high upon a hill overlooking the sea, the efficiency and professionalism of the Center's staff, and the great facilities available (from conference rooms to restaurants) combine to provide a wonderfully stimulating atmosphere.

During a 1998 workshop in Erice on vertebrate mating systems, we two editors, Marco Festa-Bianchet and Marco Apollonio, saw the need for more reflection on how the study of animal behavior could facilitate conservation. When Professor Danilo Mainardi, director of the School of Ethology at the Center, asked us to organize another workshop, we said, in unison, "Behavior and conservation," even though we had not previously discussed the idea.

The invitations we extended were met with widespread enthusiasm—many researchers in animal behavior believe their work has useful applications in wildlife conservation. Most of our invited speakers began their scientific career by looking at fundamental questions in the evolution of animal behavior, and then moved to more "applied" research questions. Often, that switch in emphasis was motivated by the realization that animal populations were disappearing as their habitat was being altered by human activities and while many conservation programs continued to ignore the importance of animal behavior, particularly that of individual differences.

We asked all speakers to first review the theoretical foundations of their subject, then explore its implications for wildlife conservation. We also asked all authors to emphasize both the advantages and the limitations of applying knowledge in animal behavior to conservation.

The workshop on Animal Behavior and Conservation was held in Erice in November 2000. All participants provided a chapter for this book, which we rounded out with contributions from researchers who did not take part in the workshop. Financial support for the workshop in Erice was provided by the Erice Center, the Regional Government of Sicily, and the Italian Ministry of University and Scientific Research.

We are very grateful to our colleagues who provided very constructive reviews of earlier drafts of individual chapters: Erin Bayne, Merav Ben-David, David Coltman, Steeve Côté, Tim Coulson, André Desrochers, John Fryxell, Jean-Michel Gaillard, Brendan Godley, Rich Harris, Keith Hobson, Jeff Hutchings, Petr Komers, Wendy King, Gordon Luikart, Sandro Lovari, Dan Mazerolle, Bruce McLellan, Jan Murie, and Bill Sutherland.

Part I

Why Animal Behavior Is Important for Conservation

1.

General Introduction

Marco Festa-Bianchet and Marco Apollonio

Many of the species with whom we share our planet are going extinct because we overexploit them or destroy their habitat (Ehrlich and Wilson 1991, Caughley 1994). Species extinction and habitat destruction have an immediate impact upon many economic and social activities because various uses of wildlife provide income, enjoyment, or recreation for millions of people (Geist 1994). It is therefore not surprising that interest in the conservation of biodiversity is increasing among the general public as well as among behavioral ecologists who study wild animals and their environment.

Two related disciplines, wildlife conservation and wildlife management, use ethological knowledge to limit the impact of humans on ecosystems. Wildlife conservation is concerned with the preservation of species and their habitat in the face of threats from human development. Wildlife management, including fisheries management, seeks sustainable strategies to exploit wild species while ensuring their persistence and availability for future use. Ideally, these strategies should also not damage components of the ecosystem other than the exploited species. Although the distinction between the two disciplines is often blurred, wildlife management is often oriented toward specific objectives for one or a few species of economic interest. The goals of conservation are broader and include the preservation of genetic diversity so

that species will maintain their ability to evolve in response to environmental change. Recently, however, wildlife conservation and management are coalescing into a single discipline. Management is often a component of conservation strategies (for example, limited sport harvest of some high-profile species can be used to generate funds for habitat preservation [Lewis and Alpert 1997]), and the conservation of genetic diversity or interpopulation connectivity is often a goal of wildlife management. For simplicity, we will use the term *management* in this introduction to refer both to situations where wild animals are the subject of some form of exploitative management, and to situations where they are of concern because they are at risk of extinction.

Regardless of how one defines *wildlife management* or *wildlife conservation*, however, practical application of these terms inevitably involves the consideration of both animal and human behavior. This book explores how knowledge of animal behavior can help prevent species extinction and sustainably exploit wildlife populations. It is clear to us, however, that human behavior plays a far greater role than animal behavior in both conservation and management.

The Role of Animal Behavior in Wildlife Management

It is important to define the role that animal behavior can play in wildlife conservation and management. Problems in wildlife management are a subset of the global environmental problems that are of interest to conservation biology. Major ecological problems include the wholesale loss of species through habitat destruction; the pollution of air, soil, and water; the introduction of exotic species (including domestic animals, parasites, and pathogens); and the alteration of global biogeochemical cycles. Knowledge of animal behavior is not the sole key to solving global conservation problems; but then, paradoxically, neither is any branch of ecology or any other science. Indeed, biologists do not make the important decisions that affect species extinction and people's continued ability to benefit from functional ecosystems. Such decisions are the purview of politicians and business leaders, who are primarily interested in political and economic goals and are therefore much more influenced by political and economic processes than by science (Morowitz 1991).

Changes in socioeconomic circumstances are also important. For example, immediately following World War II, agriculture was the main occupation in several southern European countries. People were widely distributed over the countryside. Almost all natural resources were exploited, including lands with low productivity. Following industrialization in the mid-1960s, much of

the land that was either hilly or mountainous was abandoned as people sought a more comfortable lifestyle in cities. Space and resources in the abandoned countryside became available for wildlife. Urbanization may thus explain the recent recovery of wildlife in Europe more than any other economic or biological process. In North America, increased affluence, good rural road networks, and ability to work from home are instead leading to suburbanization of wildlife habitat, with negative consequences for biodiversity, especially of large predators.

Everyone can make “minor” decisions with environmental consequences, from not eating seafood caught with methods causing extensive bycatch of nontarget species, to not building a home on critical habitat, to family planning, to voting patterns in democratic societies. Zoologists, including animal behaviorists, clearly play a major role in the conservation of biodiversity by informing decision makers and the general public about the ecological consequences of human activities. Solving the global conservation problems that threaten our quality of life, and in some cases our very lives, will require scientific knowledge, but first and foremost it will require a better system of economic valuation of goods and services. Economic externalities such as pollution, habitat destruction, and the loss of ecological functions (including those that provide clean air, safe drinking water, and a stable climate) must be incorporated in the evaluation of different activities (Chichilnisky and Heal 1998). Perhaps the greatest contribution that ecologists can make to environmental conservation is to convince decision makers at all levels, from heads of state to individual consumers, to think about the long-term consequences of their decisions.

Behavioral ecologists typically study the long-term evolutionary consequences of different animal behaviors. As a result, when examining the consequences of human actions, they usually consider a longer timescale than the few years to the next election, or this year’s balance sheet, or the time it takes to win one particular court case. It is essential that they transmit such long-term thinking to other sectors of society.

Students of animal behavior can provide an extremely important approach to wildlife conservation because of their tendency to examine individual differences, to emphasize the role of variability, and to think in terms of trade-offs between different behavioral strategies. Such emphasis on the behavior of individuals and the strategies they adopt to maximize fitness plays an important role when a species’ natural behavior can lead to conservation problems in habitats altered by humans. In extreme and rare cases, the best management strategy may be to interfere with a species’ natural behavior.

The study of animal behavior is most usefully applied to the conservation

and management of populations because it both identifies and provides ways to deal with a key characteristic of animals: they are not all alike. Individual differences in age, sex, size, aggressiveness, learning ability, past experience, heterozygosity, and a myriad of other variables can all affect how an animal reacts to a given situation and may determine the success or failure of a management strategy or a conservation initiative. Conservation of animal populations thus often depends on meeting the challenge of how to incorporate individual differences in wildlife management. The importance of individual differences in wildlife conservation is a central theme of this book.

There is a hierarchy of levels of individual heterogeneity, and all are important to wildlife management and conservation. One may start by considering behavioral differences between similar species. For example, two North American canids, the wolf (*Canis lupus*) and the coyote (*C. latrans*) react in opposite ways to urbanization and intensive agriculture: wolves disappear, coyotes prosper (Tremblay, Crête, and Huot 1998; Mladenoff, Sickley, and Wydeven 1999). One may argue that the coyote's greater behavioral adaptability is the key to its success because it allows coexistence with humans, whereas the wolf's behavior leads to its demise: wolves range over a wide area, hunt in packs, and are intolerant of humans. Within the same species, however, there are often behavioral differences between broad geographical areas: wolves in southern Europe coexist with human population densities that are much greater than densities that wolves tolerate in North America (Promberger and Schroeder 1992). The animals belong to the same species, but their behaviors are very different. Southern European wolves resemble North American coyotes in their ability to survive alongside dense human populations. At a smaller geographical scale, variables such as prey type and level of human exploitation can affect pack size, turnover rates, and social structure, which in turn can determine the level of genetic diversity by varying the opportunities for dispersers to recruit into packs. Indeed, it has been suggested that high levels of shooting and trapping in eastern Canada may artificially increase the rate of hybridization of wolves with coyotes (Wilson et al. 2000). Finally, the sex/age composition of each pack, individual preferences, and previous experience may affect variables such as prey selection or space-use patterns, which may in turn affect vulnerability to human harvest or the probability of conflict with humans because of livestock depredation.

Specialist predators that appear to form a "search image" for a particular type of prey are a very good example of how animal behavior can affect wildlife management on a local scale. Marco Festa-Bianchet has studied the ecology and behavior of bighorn sheep (*Ovis canadensis*) in the Sheep River population since 1981 (Festa-Bianchet et al. 1995). From 1982 to 1995, cougars (*Puma concolor*) were studied in the same area. Most cougars in the

Sheep River drainage had radio collars. From 1982 to 1993, they killed only zero to two sheep a year. From 1993 to 1995, one adult female cougar suddenly switched from hunting deer (*Odocoileus* spp.) and wapiti (*Cervus elaphus canadensis*) to preying upon bighorn sheep, and was almost single-handedly responsible for a 20% decline in the bighorn population (Ross, Jalkotzy, and Festa-Bianchet 1997). A similar phenomenon occurred in another study area, Ram Mountain, from 1997 to 1999: again, following a sudden increase in cougar predation, mortality of adult females doubled, mortality of adult males tripled, and the bighorn population declined by almost 50%, although factors other than cougar predation were likely also involved. Almost no cougar predation was recorded at Ram Mountain from 1972 to 1997, but cougar signs were seen in almost every year. In both cases, the increase in predation was apparently due to an individual cougar's specialist behavior. Predation was not associated with increased availability of bighorn sheep as prey or, apparently, a decline in alternate prey.

Because the behavior of bighorn sheep is very different from that of cervids, a cougar must change hunting technique to prey on sheep. Hunting bighorn sheep requires specialized, learned skills that not all cougars have. Indeed, one male cougar attempted to kill a lamb and was itself killed when he and his victim fell off a cliff. From a management viewpoint, the experience both at Sheep River and at Ram Mountain suggests that a generalized predator-control program would have had little effect without removal of the sheep-killing individual (Ernest et al. 2002). Finally, in both cases cougar predation led to an increase in bighorn mortality despite low population density: because the increased predation was due to individual behavior, it was independent of population density.

At about the same time, some cougars in southwestern Alberta started preying on domestic dogs, possibly as a response to increased residential development on cougar range, which is currently a problem in many areas in western North America. Included among the victims were the hounds used to capture cougars at Sheep River from 1985 to 1994. The normal reaction of a cougar pursued by hounds is to climb a tree. It is likely that tree-climbing by cougars has been selected as an adaptive response to pursuit by packs of wolves. Wolves compete with cougars for the same prey and can kill a cougar if they can catch it. Cougars may react to dogs as they would react to wolves. Once a cougar learns that domestic dogs are easily killed, however, it may change its behavior and fight rather than run. Clearly, dog kills lead to rural residents' intolerance of cougars in general. Faced with a difficult social situation, it would be very valuable for managers to know whether the dog-killing behavior is generalized or limited to a few specialist cougars. It would also be very useful to know how to prevent the development of dog-killing

behavior in wild cougars. These examples show how behavior, even the behavior of single individuals, can affect many aspects of wildlife management.

Goals of This Book

Our principal objective in assembling this volume was a simple one: to provide a broad overview of how knowledge of animal behavior can improve our ability to manage wildlife. Most chapters explore how conservation strategies either are or should be affected by animal behavior and how particular aspects of behavior affect the viability and growth of populations. Others explore the limits of animal behavior's contribution to conservation biology. In particular, the book addresses practical aspects of conservation and explores the role of animal behavior in the conservation of various ecosystems. Contributors examine both the importance of general principles and the key role played by specific characteristics of different species. Conservation is not a biological problem, it is a human problem. We do not subscribe to the view that wildlife management must improve natural systems, but rather believe that management actions are required either to remedy environmental damages caused by humans or to lessen the impact of human exploitation on natural systems. Because behavior can affect the reactions of wildlife to different conservation strategies, behavior must be taken into account for both remedial and preventive management. The chapters herein will outline the circumstances in which animal behavior affects conservation biology, and identify which behaviors are particularly important to ensure either the continued survival or the sustainable exploitation of wildlife.

Because conservation biology arises from a need to prevent, or at least lessen, human impact on ecosystems, an exploration of the role of animal behavior in conservation must take into account the diversity of situations that are faced in different areas of the world. Human attitudes, societal orientations, economic diversity, and traditions are all very important aspects of wildlife conservation. Social attitudes also determine what people want to protect or exploit, which wild species have economic or cultural value, and the acceptance of different management strategies. These social and economic factors interplay with animal behavior to affect the consequences of human actions on biodiversity. To partially account for diversity in both biology and culture, we attempted to select contributors interested in different aspects of animal behavior, based in different countries, and with expertise in animal behavior in a variety of geographical and political settings. We were only partially successful, mostly because researchers interested in and able to pursue studies in animal behavior are most often based in Western countries. The contributors bring to bear their own scientific expertise as well

as their personal experience. Just as differences in behavior can affect the success of alternative conservation strategies, differences in societal attitudes are often the main reason why a conservation strategy can work in one human setting and fail in another.

Structure of the Book

The book is organized into five parts. In part I, chapter 1 provides a general introduction. In chapter 2, Morris Gosling explores the main reason why animal behavior is important to conservation: because individuals differ, models attempting to predict population dynamics, genetic variability, and the risk of population extinction can be improved by a consideration of individual behavior.

Part II (chapters 3–7) considers how resource-use strategies affect wildlife conservation. Rosie Woodroffe examines how dispersal behavior, particularly of carnivores, can have both positive and negative implications for conservation. Dispersing individuals can in some situations ensure gene flow and sustain a metapopulation structure, but in other cases dispersal movements bring carnivores into conflict with humans. When most habitat has been destroyed, the chances of successful dispersal are so low that emigration becomes essentially a source of mortality.

Paolo Luschi details the example of marine turtles, which migrate over huge distances over very long periods of time, requiring international coordination of protective measures. For exploited populations there is uncertainty over national “ownership” of different stocks, because individuals traverse the territorial waters of several countries.

André Desrochers considers how different bird species behave near edges of different types of habitat to show how this behavior affects the ability of different species to cope with habitat fragmentation brought about by forest harvesting. This is a very important topic in many boreal forests where forestry activities are expanding, often with unknown consequences for biodiversity.

Isabelle Côté examines fisheries management with and without taking into account details of fish mating systems. Norman Owen-Smith underlines the importance of foraging behavior for the reintroduction of extirpated large herbivores to remaining habitat. Both chapters argue that a knowledge of animal behavior is essential for the success of management programs: availability of suitable habitat is not necessarily all that is needed to guarantee the persistence of some animal populations.

Part III (chapters 8–12) examines practical applications of animal behavior in wildlife management. Jean-Michel Gaillard and coauthors provide an

eloquent illustration of how individual differences, including differences in age/sex composition of ungulate populations, can improve the ability of models to provide a realistic representation of population demography.

Joel Berger and colleagues look at how behavior of individuals affects their reaction to potential predators. Although large predators have been extirpated over large tracts of their historic range, in a few parts of the world this trend has recently been reversed. Successful reintroduction and habitat restoration programs, together with a changing societal attitude toward large carnivores, has allowed the return of bears, wolves, and other large carnivores to areas from which they had been extirpated. Berger and colleagues argue that the impact of recolonizing carnivore populations on prey species is partly a function of how naive prey individuals react to their first encounters with predators.

Marco Apollonio and coauthors examine several recent southern European experiences in the management of large mammals. They point out that animal behavior is often ignored in reintroduction and harvesting programs. Their chapter exposes the problems caused by not taking into account available knowledge of animal behavior, and proposes ways to incorporate behavior into wildlife management in a European context.

The importance of behavioral ecology for exploitative management of carnivores is illustrated by Jon Swenson, who argues that sexually selected infanticide in bears and other large carnivores is a major management concern in cases where adult males are the preferred target of harvesting programs. The traditional view that male bears are “expendable,” given the polygynous mating system of this species, is challenged by suggesting that killing of male bears may increase cub mortality by promoting infanticide committed by surviving males.

Closing this section on the consequences of harvesting programs, Marco Festa-Bianchet suggests that human harvest of wild animals is a major selective force that may shape both the morphology and the reproductive strategies of harvested species. Wildlife managers are interested in the population consequences of sport hunting, but few have considered the possibility that hunting may be a selective pressure. Because hunters select for specific morphology (such as horn or antler size), and because the mortality caused by hunting is very different from natural mortality, hunting could be a very strong agent of evolutionary change.

Part IV (chapters 13–16) explores individual variability in genotype and phenotype. Conservation biologists have long been concerned with heterozygosity and genetic variability because of the negative consequences associated with inbreeding and low genetic variability. Stephen Dobson and Bertram Zinner examine how differences in social structure of mammals can affect

the maintenance of genetic variability in wildlife populations, concentrating on how social structure can affect the difference between census size and effective population size.

Claus Wedekind considers the genetic consequences of mate choice and reproductive skew for conservation programs, particularly for small, free-ranging populations and the management of captive-bred species. Nonrandom mating and reproductive skew are the norm in most wild populations, but within the confines of captivity, or when populations have been reduced to a very small size by human activities, these behaviors are not necessarily to be encouraged by wildlife managers.

Two chapters examine techniques to measure and account for individual differences. Brian Steele and John Hogg offer a detailed look at the uses of Generalized Linear Mixed Models, based on repeated observations of marked individuals. Rather than being affected by the statistical problems of pseudoreplication, these models take advantage of individual heterogeneities to better understand natural variation in different types of behavior, but their use is not for the statistically faint-hearted! In the next chapter, Peter Arcese uses a long-term data set on individually marked song sparrows to search for both a definition and a measure of individual quality. The theme of individual differences is pervasive throughout the book and is picked up again in the last two chapters.

The book's final part is a concluding chapter. Marco Festa-Bianchet provides an overview of the possible future contributions to wildlife management of research in animal behavior. He calls for greater cooperation between managers, researchers, and all people interested in the preservation of biodiversity.

2.

Adaptive Behavior and Population Viability

Leonard Morris Gosling

This chapter focuses on areas where an understanding of adaptive patterns of behavior is important, and sometimes essential, for predicting the demographic and genetic processes that determine population viability. Although many aspects of behavior are important for conservation, I will concentrate on adaptive behavior rather than development or mechanism because it is here that the potential benefits are greatest. The explosion of research in the fields of sociobiology and behavioral ecology over the past 30 years has revolutionized our understanding of animal behavior. But this fundamental understanding has not been fully incorporated into conservation biology, the applied science that aims to provide a scientific underpinning for practical conservation (Clemmons and Buchholz 1997, Caro 1998b, Sutherland and Gosling 2000). Although advances in behavioral ecology are of little use to conservation in the face of wanton overhunting or total habitat destruction, such knowledge is important in circumstances where reason prevails and where careful strategic planning is needed. We are living through an extinction crisis of unprecedented dimensions and must deploy all of the tools at our disposal.

Conservation is concerned principally with the viability of populations, communities, and habitats. All these entities are of daunting complexity, and ecological theorists and practitioners have generally looked for ways to describe and understand their key processes in a relatively tractable fashion. Tractability usually equates with simplicity, and the most obvious way to achieve this is to deal with higher-level processes rather than attempt a reductionist, individual-based approach. This has been the dominant trend in ecology to date and it has achieved considerable success. Thus, in population dynamics, most demographers consider birth rates and death rates of average individuals, or broad patterns of gene–environment interactions rather than dynamics based on the differences between individuals and their interactions.

Increasingly, however, it has become impossible to ignore studies of individual variation on population dynamics, particularly those that address functional issues within behavioral ecology. In addition, many of the problems considered by conservationists involve populations reduced to low levels and in these the behavior of individuals is relatively more important than in larger populations. Estimates suggest that effective population sizes must be at least 5000 to maintain adaptive potential in the face of mutation and random genetic drift (Lande 1995). Many populations or subpopulations of conservation concern are well below this level, and it may only be possible to maintain them under management using detailed information about factors that affect their viability. Many of the models now used for population viability analysis incorporate demographic stochasticity to simulate the sort of chance events that affect individuals within the context of average population values for the main population processes. Only recently have we begun to consider the effect of variation in the mating system and patterns of mate choice in such models (Legendre et al. 1999, Durant 2000a).

Newly developed population models use individual decision rules to derive population processes. Because decisions by individuals have been shaped by selection, an understanding of individual behavior and the incorporation of decision rules into population models should enhance our confidence in predictions about population responses to environmental change (Goss-Custard and Sutherland 1997; Pettifor, Norris, and Rowcliffe 2000; Bradbury et al. 2001). These models also have the advantage that some crucial features, such as frequency-dependent occupation of habitat patches, can be modeled using game theoretic approaches. Individual behavior-based models have had their greatest success in predicting for shorebirds the fitness and demographic consequences of human-caused changes in their foraging environment (Stillman et al. 2000, 2001, West et al. 2002). Although the approach is currently restricted to wintering migratory coastal birds, there is no reason in principle why it should not be applied to a wider range of taxa and habitats.

Such models are likely to be more successful in predicting population changes under novel circumstances than statistically based phenomenological models based on empirical data from a limited time period and a limited range of environmental conditions (Goss-Custard and Sutherland 1997). The approach has also been used to explore carrying capacity in migratory animals and as a guide to habitat management (Goss-Custard et al. 2002).

Perhaps the most compelling reason for believing that incorporating individual behavior into population models enhances our ability to predict population viability is that, under the powerful evolutionary force of sexual selection, the genetic fitness of individuals does not equate with population viability. Indeed, the enhanced fitness of individuals may actually depress the viability of a population and make it more vulnerable to extinction. For example, the evolution of costly display traits may generally be at the expense of other components of fitness, and these may affect population viability (Møller 2000). This argument and others about the negative potential of sexual conflict and intrasexual competition are developed in the following text. When we understand the circumstances under which such phenomena occur, it may become possible to intervene to ameliorate their effect, particularly where their action is conditional on ecological variation. Basic studies of sexual selection can also show where current practice in conservation management may be misguided. Mate choice may allow selection for heritable viability traits or selection against deleterious mutations, particularly where these are expressed in display traits. Where potential mates differ in their heritable viability, the current practice of maximizing outbreeding in conservation breeding programs may thus be an inferior management strategy to one based on free choice (Wedekind 2002a).

Lastly, I will discuss reasons for the failure of advances in behavioral ecology to be used in conservation and conservation biology. The primary issues may be sociological: behavioral ecology is an academic discipline practiced in universities, whereas conservation is a practical discipline that proceeds largely by trial and error in the field. I will debate this proposition and explore ways of reaching a working accommodation.

Density-Dependent Behavior

The best-known link between population density and viability owes its origins to W.C. Allee who observed that many animals suffer a decrease in per capita population growth rate when population density reaches a low level. Under these circumstances, the rate of increase can decline to zero or even to negative values. Although this effect, known as the Allee effect, can easily be mimicked using simple deterministic models (Courchamp et al. 1999), its

occurrence and consequences can only be predicted where details of the mechanism are known and understood. The *Allee effect* is an umbrella term that has limited predictive value until its mechanisms are unraveled. These mechanisms differ between contexts and may not always involve behavior. Genetic inbreeding and forms of demographic stochasticity that do not act on behavior directly (for example, some variation in primary sex ratios) may exert the key effect (Lande 1998a).

Behavioral mechanisms of the Allee effect include the effects of reduced foraging efficiency due to an increased need for vigilance by individuals in small groups and higher rates of predation on such animals. Other behavioral mechanisms are the loss of cooperating individuals (such as nest helpers) and consequences of the mating system or of sexual conflict. For example, males in polygynous mating systems may have to range more widely at low densities to mate with females and may thus be more likely to encounter sit-and-wait predators. In the case of the coypu (*Myocastor coypus*), an environmental pest that was reduced to low densities in a trapping campaign in England, this effect reduced the proportion of males in the adult population to an extent that significantly reduced conceptions and accelerated the population's decline (Gosling and Baker 1989).

Mate choice may also be a key mechanism of the Allee effect. There is considerable empirical support for the involvement of (1) an inability to find a suitable mate, which reduces the frequency of reproduction and (2) poor reproductive success due to differential parental investment by females that do not find suitable or preferred mates (Møller and Legendre 2001). When females are forced to mate with a nonpreferred male, they reproduce at reduced levels. Examples include a reduction of 58% when female zebra finches (*Poephila guttata*) are mated experimentally with nonpreferred males (Burley 1986) and a 35% reduction for female barn swallows (*Hirundo rustica*) (summarized in Møller and Legendre 2001). Models of populations with either random or choosy mating with respect to phenotype show that the probability of population extinction as a function of initial population size was significantly increased with mate choice. Behavioral mate choice is typically ignored in conservation breeding programs, and the high rate of failure to breed species such as giant pandas (*Ailuropoda melanoleuca*) in captivity may be because females do not have the opportunity to choose their mates. In such cases the chances of finding a preferred mate may already be small because of the low numbers available. Reduced reproductive success among females with restricted choice of mates is such that to achieve a given minimum risk of extinction, initial population size must be more than twice as that in the absence of such effects (Møller and Legendre 2001).

There are many consequences for practical conservation from behav-

iorally induced forms of the Allee effect (e.g., Stephens and Sutherland 1999). In the case of the coyote already mentioned, increased male mortality led to more rapid decline than expected and earlier eradication of an unwelcome environmental pest (Gosling and Baker 1989). However, where population growth of an introduced species is slower than expected in its early stages, this may lead to the unwarranted assumption that the species will not thrive and thus to missing the best opportunity for eradication when the population is small and subject to Allee constraints. Failure to recognize Allee effects in exploited populations may also drive them to extinction. This process may have been responsible for the failure of many fisheries operating under the principle of maximum sustainable yield (Liermann and Hilborn 1997). Negative density dependence also affects the critical population size required to manage rare or fragmented populations, including the number required for successful introductions. However, simple adjustments of the number of animals may not be possible (for example when the remaining world population is very low) and in any case may not be necessary. Only when the mechanism of the Allee effect is known can predictions be made and specific corrective action be taken. For example, in the reintroduction of the bush-tailed phascogales (*Phascogales tapoatafa*), a carnivorous marsupial, it is important to allow females to establish territories before releasing males, to prevent the males from dispersing into unoccupied areas (Soderquist 1994).

Behavior under Spatial Constraints

All animals are adapted to particular habitats, and their lives are constrained by the spatial limits of these habitats. Typically, populations are also divided between sub-areas of suitable habitat. The dynamics of such metapopulations becomes partially dependent on the behavioral rules that govern joining and leaving habitat patches and the costs and benefits of moving between patches. In general, the benefit:cost ratio declines as patch size declines and the distance between patches increases—factors that become relevant in networks of protected areas. An understanding of the movements of individuals within and between patches and their population consequences is essential for conservation management. For example, some butterflies are restricted to habitat patches that contain essential larval foods. In each generation a proportion of individuals emigrate from the natal patch and the proportion that leaves depends on the perimeter:patch area ratio. When this ratio is too high, the numbers that leave quickly drive the population to extinction (Thomas and Hanski 1997). Unfortunately, conservation measures are rarely planned using this sort of understanding. More usually we obtain practical information post hoc by observing the consequences of conservation measures

(such as the population viability consequences of adopting particular areas for protected areas) that have been designed without taking into account the natural movements of animals. Thus we tend to measure the decline of populations when they occur in areas that are too small rather than estimating in advance the area required for populations with defined viability criteria.

Often we simply do not know enough about the behavior and ecology of the animals that we seek to conserve. Getting sufficient quantitative information to predict the behavior of individuals and populations under spatial constraints takes time and effort. Putting such information to practical use may be even more difficult. The best example of a system where all these elements have been achieved is in the use of individual behavior-based models in predicting the dynamics of populations of wading birds. Existing models consider patches of habitat within a single estuary with variable resource densities in which birds compete to maximize food intake. An individual bird's access to food patches of varying quality is determined by the bird's own physiological needs, its own foraging efficiency, its dominance status, and the decisions made by its competitors, which in turn depend on their own dominance rankings (Goss-Custard et al. 1995b, Stillman et al. 2000). This sort of model can predict the fitness and population consequences of habitat or demographic changes that have not previously been observed. For example, these models can predict the effect of removing a part of a feeding ground and thus have important relevance to practical conservation, which is often concerned with the loss to habitat to alternative forms of land use. Such approaches have also been extended to entire populations of migratory geese using different wintering sites across large parts of northwestern Europe (Pettifor, Norris, and Rowcliffe 2000).

A major problem for conventional models of animal populations is that it is difficult to estimate density dependence, especially when populations are relatively constant. In addition, any measures of density dependence will tend to apply only to the range of population densities and environmental conditions over which they were measured. These limitations do not apply to individual behavior-based models because the full range of individual experience can be measured and thus included in a model, even when a population is constant. For example, an individual may experience a wide range of local population densities and a wide range of prey densities due to small-scale habitat variation. By combining data from observations of such individuals, the responses of entire populations to similar variation can be simulated (Goss-Custard and Sutherland 1997; Pettifor, Norris, and Rowcliffe 2000). Further, individuals in the models respond flexibly in relation to environmental change, and the demographic consequences of these changes can be used to generate new density-dependent functions. These allow predictions

of future changes of abundance under altered spatial and other environmental constraints, such as different regimes of disturbance (West et al. 2002), that are outside the range of conditions under which the input data were collected (Stillman et al. 2000).

The principles of resource availability and depletion, and frequency-dependent competition based on physiological need, also apply to migratory species. However, in this case, the economic considerations of accumulating nutrient reserves needed to fuel movement between resource patches becomes critical (Piersma and Baker 2000). The costs to individuals of movement between patches are often so large that survival and further movement become critically dependent on adequate resources in a series of patches. Where such staging posts are degraded or destroyed, individuals may starve, become more susceptible to disease, or arrive in such poor condition at the end of migration that they are unable to breed. The conservation of staging posts along migratory routes poses particular problems because often these routes cross several countries, and conservation priorities tend to be agreed upon at a national rather than an international level. There is also inherent instability in a system that depends on a linear series of interconnected events. Even when most staging posts are intact, damage to one essential link could result in population extinction. To date, the number of migratory species that have been lost remains low; but the extinction or near extinction of Eskimo curlews (*Numenius borealis*) over a span of only 30 years, due in part to the destruction of their tallgrass spring staging habitat, is an indication of how vulnerable even very abundant species can be (Piersma and Baker 2000). The slender-billed curlew (*Numenius tenuirostris*) may suffer a similar fate.

The problems of conserving animal populations increase as populations are confined to small protected areas and as species ranges are subdivided and fragmented with intervening human developments that prevent wide-ranging movements or dispersal. Sometimes problems arise when individuals of particular species have very large ranges and are thus likely to wander outside a protected area. Once outside they are at risk from poachers or, more generally, from being in an area with conflicting land-use priorities. A particularly clear analysis of this effect was carried out by Woodroffe and Ginsberg (2000), who show that the probability of extinction of carnivore populations is affected most strongly by an interaction between range size and reserve size. They argue that, although demographic stochasticity may sometimes exert an effect, it is less important than edge effects in understanding and thus trying to prevent carnivore extinctions.

These problems have an additional dimension when combined with sexually selected dispersal. Where one sex disperses more widely than the other,

this sex is likely to die at a faster rate, and in small populations this could potentially lead to Allee effects where the numbers of one sex limit population fecundity. In the case of elephants, there is a further social dimension: males are the dispersing sex, but mortality is biased toward large, socially dominant males because these animals have large tusks and are targeted by poachers. These large males are preferred by females (Poole 1989) and their loss reduces population growth rate and the speed at which populations can recover from overexploitation (Dobson and Poole 1998). The loss of animals with particular genetically determined traits may also select against the trait, and ivory poaching has led to an increase in adults without tusks (Jachmann et al. 1995). The selective loss of males could also lead to unforeseen genetic effects such as the loss of sex-linked genetic variation.

Edge effects may also have less obvious, indirect effects on population viability within the protected area. For example, male lions are often killed by sport hunting outside the Serengeti National Park, leading to a higher takeover rate of prides by coalitions of males. Because males taking over prides often kill existing young to ensure that females invest in their offspring, infanticide may affect population growth (Caro and Durant 1995).

The most general lesson from these examples is the importance of understanding animal movements before planning spatially based conservation measures. This has sometimes been achieved at a population or community level. For example, the modern boundaries of Amboseli National Park, Kenya, were based on a long-term study of the area required by the large mammal community for its year-round food and water supply (Western 1994). The area selected for the park included a dry season food and water reserve and part of the wet season dispersal area. In practice, the wet season dispersal area was so large that the entire area could not be protected, but since this is the least productive part of the range, there have been relatively few conflicts of interest with landowners. Most problems have been caused by elephants when they try to feed on crops outside park boundaries (D. Western, 2002, pers. comm.). Where conflicts of interest are perceived as being too great, an alternative is simply to fence a protected area to eliminate the conflict. However, the demographic costs of fencing an area that does not include all of the seasonal resources needed can be high since flexible movements to limiting resources are crucial adaptations for animals that live in strongly seasonal environments. For example, the fencing of Etosha National Park in Namibia in the 1970s (Berry 1997) was undertaken to prevent animals straying onto farms where they would inevitably have been killed. As a result, seasonal movements to food and water were restricted and there has been a significant reduction in population sizes. Burchell's zebra (*Equus burchelli*) declined from 25,000 to 5000 and gemsbok (*Oryx gazella*) from 5000 to 2200

(Berry 1997). This effect occurred despite the fact that, at more than 22,000 km² in area, Etosha National Park is one of the largest protected areas in the world. When animals suffer in such vast areas, it becomes clear that natural movements of large animals will rarely be possible in fenced areas. Under such circumstances, management intervention may succeed in manipulating movements to some extent (for example, by controlled burning or the provision of artificial water supplies), but reduced carrying capacity is usually unavoidable. This is because movements to seasonally important food resources are individual adaptations that maximize both individual fitness and, generally speaking, population viability.

Very large protected areas would help prevent many of these problems, but the example of Etosha shows that even the largest parks impose spatial constraints on behavior that ultimately limit population size. Often large parks are an impossibility, and, in general, the trend will be to reduce fully protected areas as human populations increase. As protected area size is reduced, population sizes decline and the chance of Allee effects and extinction increases. Data on African parks show that species loss can be predicted from protected area size (Newmark 1996) as would be predicted from relationships between species number and the area of natural islands (Soulé, Wilcox, and Holtby 1979; Cowlshaw 1999). Some form of multiple land use outside protected areas that includes the conservation of dispersing animals may be the only solution. Although it may be possible to negotiate such arrangements with appropriate compensation, as in the case of wolves in parts of Europe or North America, it will often be impossible where the costs of damage are very high, as in the case of African elephants, which sometimes kill people as well as damage crops. Efforts to provide a benefit to people for sharing their land with wild animals (such as the CAMPFIRE scheme in southern Africa) are in their infancy and have had mixed results (Gillingham and Lee 1999; Campbell, Sithole, and Frost 2000; Getz et al. 2000).

Nonrandom Mating and the Maintenance of Genetic Variation

Population viability depends partly on the maintenance of genetic variation. Variation increases the chance that some animals will survive when faced with short-term environmental vicissitudes such as droughts or diseases and also allows the possibility of long-term evolvability; for example, in response to long-term climatic change or the appearance of novel pathogens. Thus behaviors that affect levels of genetic variation may be of vital importance for population viability, particularly when populations are simultaneously

affected by other negative factors such as reduced size. Here I consider the effects of intrasexual competition and mate choice, factors that are rarely considered by conservationists but that may have profound genetic effects on populations. These effects are not simply of theoretical interest because, when they are understood, their effects, or the negative consequences of losing their effects, can potentially be ameliorated by management intervention.

Intrasexual competition and mate choice are the main driving forces of sexual selection. Both sometimes lead to some individuals gaining a disproportionate share of matings and result in strong directional selection on the characteristics of the successful individuals (Andersson 1994). The most dramatic illustration of these effects occurs in lek breeding where a small proportion of males gain most matings. The characteristics of the males chosen include conspicuous displays (e.g., sage grouse [*Centrocercus urophasianus*], Gibson and Bradbury 1985) and display structures (e.g., the peacock's tail) (Petrie, Halliday, and Sanders 1991). Sometimes females choose particular territories in a lek rather than the characteristics of a male, perhaps because the outcome of competition for such territories is a more reliable indicator of fitness than any phenotypic trait. An example is the lek breeding system of topi (*Damaliscis lunatus*) where females strongly favor central lek territories even when a successful male is temporarily replaced by a smaller male (Gosling and Petrie 1990).

Other mating systems are less dramatic but may also result in mating skew. For example, birds in monogamous relationships often show extra-pair copulations, which boost the reproductive success of particular males (Petrie and Kempenaers 1998); female great reed warblers (*Acrocephalus arundinaceus*) choose for extra-pair copulations males who have more elaborate songs than their own male (Catchpole 1986).

Increased mating skew must result in reduced effective population size and, theoretically, reduced genetic variation. Some empirical support for this has come from estimates of variation in neutral genetic markers; for example in ungulates (Apollonio and Hartl 1993). This effect may become extreme in resource defense mating systems where limiting resources are manipulated in protected areas. For example, male springbok (*Antidorcas marsupialis*) can defend highly successful territories next to water holes, resulting in an extreme mating skew (Ritter and Bednekoff 1995). Reduction in effective population size may potentially lead to inbreeding depression. Management intervention to increase the dispersion of the limiting resource may be possible where behavioral observation shows the need.

However, mating skew does not always cause a reduction in genetic variation, particularly where female choice is involved. Female choice is known to be heritable and thus likely to be a character under selection. It appears to

have two main benefits: either females gain for their sons those characteristics that make a male attractive or successful in intrasexual competition, or females gain viability genes for all their offspring (Andersson 1994). “Good gene” arguments are often linked to the evolution of display characters since female choice is often based on the size or elaborateness of male sexual ornaments or the intensity of males’ displays. These are believed to indicate viability or fitness, but how? The most influential idea is that selection favors the evolution of signals that are costly to the signaler because these honestly reflect the signaler’s quality (Zahavi 1975, Grafen 1990). The issue of signal costs will be returned to later in the chapter since the evolution of such “handicaps” may have direct effects on population viability and extinction probabilities. However, the fitness benefits for individuals from mate choice (reviewed by Møller, Christe, and Lux 1999; Jennions and Petrie 2000) are probably concerned principally with the coevolution of parasites and hosts (Hamilton and Zuk 1982). There is currently much interest in choice as it relates to genetic variation in the major histocompatibility complex (MHC), a hypervariable region of the genome concerned with immune function (reviewed by Jordan and Bruford 1998).

Extensive research on mice shows that mates are chosen on the basis of their genetic difference from the subject and that this information is obtained using odors mediated by MHC variation (Potts et al. 1991). The fact that the MHC is a region concerned intimately with immune function suggests that the evolution of dissassortative female choice may be favored by promoting increased disease resistance; for example, through heterozygote advantage. Alternatively MHC variation may simply act as a polymorphic marker to minimize inbreeding (Pusey and Wolf 1996).

A problem for arguments that invoke genetic benefits for female choice is that strong directional selection due to female choice should have depleted any genetic differences among males (as in the case of a reduction in variation due to mating skew, as already outlined). Why is there any genetic variation left among males in the population? This problem, the so-called lek paradox, remains one of the outstanding problems in evolutionary biology and could also have direct consequences for population viability. Theoretically, there should be no additive genetic variance in fitness-related traits (Fisher’s fundamental theorem), and where selection is strong, as it is in sexually selected traits, then additive genetic variance should be lower than in nonsexually selected traits. It is therefore surprising that sexually selected characters show higher levels of additive genetic fitness than characters not under sexual selection (Pomiankowski and Møller 1995). What mechanism involving female choice could promote as well as remove genetic variance in fitness-related traits? The answer has practical as well as theoretical significance if

the variation produced affects population viability. A possible mechanism (M. Petrie, 2002, pers. comm.) is that female choice could support a higher than normal mutation rate if the mutational load can be revealed in a display character. Simulation modeling by G. Roberts and M. Petrie (2002, pers. comm.) suggests that if females can select males who possess beneficial mutations but who carry fewer deleterious mutations, then mutation rates 10 times those under random mating can be sustained. The idea that female choice can maintain mutation rates provides a self-sustaining solution to the lek paradox and predicts a greater level of evolvability in sexual populations.

This has practical consequences for population conservation since the persistence of lek breeding may thus be important for population viability. Lekking in topi is becoming increasingly rare and persists only in the few remaining high-density populations. In the Mara ecosystem in Kenya it exists only where grassland is lightly utilized (as inside the Masai Mara Game Reserve) but not where it is intensively grazed (as outside the reserve with large densities of livestock). The reason may be that leks form where topi cluster in short-grass patches for antipredator advantage (Gosling 1986); this response occurs only where female topi are forced to avoid surrounding long-grass areas during the resting period of the day and not where the sward is uniformly short. If lekking is influenced by such relatively simple habitat features, it may be possible to intervene to help retain this mating system. Of course it would be desirable to do this in any case because such striking behavior as lekking in topi deserves to be conserved in its own right. But it is also possible that such intervention might conserve behavior that selects for high levels of genetic variation, removes deleterious mutations, and thus promotes population viability.

The possibility that patterns of mate choice may confer such important genetic advantages also has general implications for conservation breeding programs. At present most breeding programs of rare animals in captivity simply attempt to maximize outbreeding to retain as much genetic variation as possible. However, for the reasons already discussed here and by Wedekind (2002a) the benefits of allowing natural choice should be given careful consideration. In practice this could be achieved either by allowing females to choose mates or by artificial selection of mates according to the sort of criteria suggested by recent research on mate choice (e.g., using estimates of MHC similarity). Recent research suggests that not only might natural mate choice prevent inbreeding, it might also be driven by genetic compatibility between potential mates that provides resistance against particular pathogens (Wedekind et al. 1996, Rüllicke et al. 1998). Although this latter possibility requires further investigation before its consequences are implemented in conservation breeding programs, there are already grounds for believing that

benefits may be derived from allowing natural mate choice. Thus, where possible, and in species with appropriate mating systems, allowing choice should supersede breeding principles based on maximizing outbreeding since achieving high levels of heterozygosity may not outweigh the costs of accumulating deleterious mutations. The possibility that all potential mates will prefer one individual, thus leading to the prospect of severe inbreeding depression, is unlikely because assortative patterns of mating should generally be more common. Direct natural choice should be used wherever possible, but in intensively managed systems this may not be possible. Examples include small declining wild populations where intervention is essential, or captive populations where the financial cost of providing a natural choice is high. In these cases choice of olfactory signals (particularly scent marks, which can be frozen and shipped among cooperating zoos) provides the greatest promise. These odors provide subtle information about genetic variation in potential mates (reviewed by Gosling and Roberts 2001) and they could provide powerful measures of mate preference if used in properly designed choice assays.

Sexual Selection, Speciation, and Extinction

Some recent thinking about the conservation of biodiversity emphasizes the processes that create biodiversity rather than the pattern that happens to be present today (Mace, Balmford, and Ginsberg 1999). Thus, if we wish to maintain the capacity to create future biodiversity, we need to understand the processes responsible. Although the influence of behavior in reproductive isolating mechanisms has long been recognized, it is only recently that substantial support has emerged for the importance of sexual selection in sympatric speciation. Studies of bird speciation show that sexually selected clades (those with greater sexual dimorphism) are more speciose (Barracough, Harvey, and Nee 1995; Møller and Cuervo 1998). The cichlid species flocks of the African great lakes are the classical example of a group that has shown explosive speciation rates under intense sexual selection (Seehausen 2000).

However, while speciation may proceed rapidly under the influence of sexual selection, the ornamentation or elaborate displays that are generated by male intrasexual competition or female mate preferences may predispose populations that possess them to extinction. Despite the theoretical importance of sexually selected handicaps (Zahavi 1975, Grafen 1990), empirical information on costs is accumulating only slowly. However, signaling intensity and the size of display structures have been shown to have correlated energetic costs in a number of species (e.g., drumming in wolf spiders [Kotiaho et al. 1998]) and to affect life history traits (scent-marking frequency is inversely correlated with growth in mice [Gosling et al. 2000]). The best data

on survival are from experiments on barn swallows showing that survival prospects of males are inversely related to experimentally manipulated tail length (Møller 1994). There is also evidence that males carry ornaments at the expense of their resistance to disease and parasites (Folstad and Karter 1992). Although androgens promote the development of male display structures, they may also suppress immune function. Experimental evidence for a trade-off between the sexually selected trait and immunocompetence is now available in birds, including swallows (Saino and Møller 1996; Saino, Bolzer, and Møller 1997) and domestic fowls (Verhulst et al. 1999). Whatever the costs of display traits, all models of sexual selection predict that the evolution of elaborate display traits involves fitness costs that displace males from their survival optimum (Møller 2000).

Evidence that sexually selected traits affect extinction rates includes data supporting Cope's rule (Cope 1896, Eisenberg 1981), which states that body size tends to increase within evolutionary lineages and that the risk of extinction increases with body size. Although Cope's rule does not apply to all taxa, it probably has some general application (McLain 1993), and since larger body size is selected for under intrasexual competition, this effect may be attributed to sexual selection (Møller 2000). Further evidence comes from the probability of survival of introduced bird populations: McLain, Boulton, and Redfearn (1995) found that sexually dichromatic species were significantly less likely to become established than monochromatic species, perhaps because of the demographic consequences of the more costly sexually selected display features. A separate study of introduction success in New Zealand has been variously explained as a result of the degree of sexual dichromatism (Sorci, Møller, and Clobert 1998) or of demographic stochasticity, influenced by the mating system and female choosiness (Legendre et al. 1999).

The loss of biodiversity through an effect on sexually selected traits may sometimes be inadvertent. For example, the processes of sexual selection that produced the rich diversity of cichlid fishes in Lake Victoria may be disrupted by pollution (Seehausen, van Alphen, and Witte 1997). In these species flocks, reproductive isolation is maintained by mate choice using colorful signals. When these are obscured in turbid water, interbreeding between species increases and biodiversity is reduced. Similar arguments involving natural selection have been made by Endler (1997) about changes in the light environment of forests with consequent effects on the ability of cryptically colored animals to escape predation.

Other examples where individual fitness may conflict with population viability occur in cases of sexual conflict where the outcome may be damaging for one or both sexes and thus for population growth. Male bean weevils (*Callosobruchus maculatus*) damage the genitalia of females during copulation,

perhaps to help prevent other males from mating with the same female and, as a result, female survival is reduced (Crodgington and Siva-Jothy 2000). In evolutionary arms races between the sexes, an adaptation by one sex that gives it an advantage (for example in mating) is generally matched by a counter-adaptation by the other sex. However, the outcome of such races can sometimes favor one sex as revealed in a study of water striders (Heteroptera; Gerridae) (Arnqvist and Rowe 2002). Male water striders attempt to clasp females during mating using clasping genitalia, and since there is a cost to females in being clasped repeatedly after fertilization, females develop counter-adaptations such as abdominal spines. The development of these devices and corresponding behaviors is generally correlated within species, but detailed studies of morphology and reproductive behavior show that the advantage for one sex is greater in some species than in others. This leads to differences in mating rates and thus potentially to differences in population viability.

Sexual conflict is now recognized as being a central process of evolution with the potential to shape both speciation and extinction rates (Parker and Partridge 1998, Arnqvist et al. 2000). Such processes can clearly affect population viability, but are they accessible to conservation intervention? Direct intervention to prevent animals from damaging each other is possible in conservation breeding programs (for example, using advanced reproductive technology) but can anything be done in the wild? In general, it depends on the ecological circumstances and whether they can be manipulated. In the example of polygynous antelopes, there is a potential conflict of interest between males that aim to mate with as many females as possible and females that wish to choose between males. Thus females often try to leave territories and males try to herd them back. The ability of males to monopolize females in this way depends critically on the distribution of resources: where resources are concentrated, males can monopolize more females and female choice is more limited. An example is that of male springbok who defend territories near water holes in arid areas (Ritter and Bednekoff 1995). Such behavior potentially leads to reduced effective population size and inbreeding depression, and could be ameliorated simply by providing more water holes. Intrasexual competition among females may also have a negative effect on population viability. For example, in some cavity-nesting ducks, high levels of brood parasitism may result in lower hatching rates in the population because of inefficient incubation of very large numbers of eggs and disturbance by parasitic females. These effects appear to cause declining populations (Eadie, Sherman, and Semel 1998).

These examples raise the issue of when intervention is ethically acceptable. It is likely to be less acceptable in species in which a sexually selected benefit to one sex is threatening extinction, but more likely to be acceptable

when an additional anthropogenic factor is exacerbating the threat. Thus, if the limited availability of water holes artificially increases the benefit to male springbok at the cost of inbreeding depression, it may be sensible to manipulate the distribution of water to ameliorate this effect.

Conclusions and Recommendations

The adaptive behavior of individual animals is not a peripheral issue that somehow embellishes population processes. Instead, adaptive individual behavior is at the heart of these processes. It is impossible to predict accurately population behavior without an understanding of individually based demographic and genetic effects on population viability. Higher-level processes do not equate with those at an individual level, and they cannot be inferred by simply multiplying the effect of average individuals. Selection at an individual level may work against population survival, as in the case of sexually selected handicaps or sexual conflict. Such effects can never be discovered at a population level but only through studies of individual adaptation. Higher-level descriptions of gene–environment interactions are indirect consequences of these adaptations and so must ultimately be less powerful predictors of population viability. A problem does exist in that the route from individual behavior to population process may be complex and difficult to model, particularly where decision rules are used to structure the model throughout. In contrast, higher-level processes are relatively accessible to analysis, and, when their assumptions are clearly understood, they will often have practical utility. We need a clearer understanding of the circumstances under which models using higher-level processes are a sufficient approximation and those in which they are actively misleading. Further advances in both simulation and mathematical approaches to individually based models seem both inevitable and necessary for conservation applications.

Curiously, behavioral theory has still made little impact on conservation practice. One fundamental issue is that interest in the theory of behavior and in practical conservation belongs to two different cultures with different values. One is essentially academic and the other practical. The two cultures are reinforced by patterns of funding and institutional support: academics work in universities and receive grants from government-funded research councils; conservationists work for government or charities with more restrictively defined programs and receive funding from conservation foundations and charities. The two cultures are mutually suspicious. Academics view practical conservationists as narrow and lacking intellectual rigor; conservationists view academics as putting theory before any benefits for their animal subjects. One conservationist has recently remarked that most behavioral

ecology is “fiddling while Rome burns.” An academic might reply that the rich body of information which is now available for conservation action was achieved by research driven by curiosity, not by practical need. Perhaps most important, practical people whose main focus is on accumulated wisdom through trial and error see science as a radical and disruptive process. In this they are correct, but rather than being a negative attribute, this is the great strength of the scientific process: it is the only mode of investigation that systematically sets out to destroy accepted ideas, and does so because the ideas that survive are generally most useful. But testing ideas to destruction is an uncomfortable process and frequently requires that practice is altered, which is not always popular, particularly in the long and painstaking work that is often required for conservation intervention. However, in the final analysis, practical conservationists and academics interested in animal behavior are both concerned about the conservation of animal diversity, and this goal will suffer until the two cultures reach a working accommodation.

A number of steps can be taken to help achieve this accommodation, but wholesale adoption of a conservation agenda by behavioral ecologists and of behavior studies by conservationists is neither likely nor desirable. Behavioral ecologists are largely curiosity driven and will continue to be curious naturalists, which is in itself important since a fundamental understanding of natural behavior is vital for conservation. Certainly there is no benefit in making good behavioral ecologists into bad conservationists (or vice versa). The body of information that has been, and is being, created is available for use, and the issue is rather one of effective information transfer between the two cultures. This can happen only when the need is recognized, and this is the explicit aim of recent books about behavior’s relevance to conservation (Clemmons and Buchholz 1997, Caro 1998b, Gosling and Sutherland 2000), including this one. Hopefully these books will help conservationists and conservation organizations find ways to use fundamental research for practical purposes.

It is also true that some areas of behavioral ecology that would greatly benefit conservation (notably those with links to population viability) do not receive the attention they deserve from academic researchers. Regrettably, this is partly because most academics work on areas that are funded by government institutions. These tend to favor fundamental research so that strategic research on inbreeding depression and population viability is unlikely to be funded. Work of this kind, which proceeds from basic theory and has clear practical benefits, is too practical for a research council but too theoretical for a conservation trust. This problem could be addressed if organizations that fund basic research took a greater interest in conservation aims: some progress has been made in this respect (such as the Wellcome Trusts’ biodiversity initiative), but such funding schemes are rare. Similarly, conservation

organizations should devote part of their resources to work that aims to understand the basic issues underlying high-priority conservation problems. Last-ditch attempts to save single, highly endangered species are attractive, but they are not enough if we are to make significant strategic advances in the conservation of biodiversity.

Summary

Advances in behavioral ecology have transformed our understanding of animal behavior. Similarly, it has become clear that adaptive individual behavior has consequences for population viability and thus for conservation practice. Individual-based models have made best progress in quantifying the consequences of adaptive individual behavior and in providing techniques that are useful for conservation planning; they have particular utility in providing robust measures of density dependence. Individual behavior becomes particularly important at small population sizes, and mechanisms of the Allee effect, such as failure to find mates, are frequently behavioral. A predictive understanding of behavior is becoming increasingly important as animal populations become fragmented and confined to small protected areas. Sexually selected behavior influences genetic variation within populations and thus the prospects of inbreeding depression and extinction probability. An improved understanding of the genetic consequences of mate choice, particularly in relation to MHC variation, suggest that free choice may be preferable to outbreeding in captive breeding programs. Selection for extravagant displays and evolutionary arms races between the sexes may have negative consequences for population viability. Where these are conditional on environmental variation, conservation intervention may sometimes be possible. Despite these many insights into behavioral effects on population viability, they are rarely used to guide practical conservation. This may be because conservationists and behavioral ecologists belong to different cultures. One is essentially academic and the other practical and these differences are reinforced by patterns of funding and institutional support. Thoughtful changes to funding regimes may be the most realistic means of reaching a working accommodation.

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Part II

Resource-Use Strategies in Space and Time

Most animals are mobile: some are born and die within a few square meters, others have seasonal ranges separated by a few kilometers, still others may walk, fly, or swim tens of thousands of kilometers over their lifetime. Movements are motivated by a variety of needs: finding food or mates, avoiding predation, seeking nesting sites or shelter from rigorous weather. As animals move, they may come into conflict with humans, encounter humanmade barriers, or simply change “legal” status as they cross state or other jurisdictional boundaries. A major preoccupation of conservation biology is to ensure that those movements can proceed unimpeded, and that populations have access to all required seasonal habitats. The study of ranging behavior is therefore a key component of conservation-related research on any animal species, and it is one area where many traditional conservation schemes, based on protecting specific areas, or on management policies that change at political boundaries, simply do not work.

To conserve animal populations, we need to know where individuals go at different times of the year, how far they can disperse, what obstacles they can and cannot cross, how likely they are to locate new and suitable habitat, what they would do if their habitat were altered, and how they would react if reintroduced into former habitat. Some populations are “sinks”: they are not self-sustaining, and they depend on input from “source” populations to persist, but they may play an important role in metapopulation dynamics. Some source populations may be particularly important for supporting a species over a wide geographical area: clearly, such source populations must be identified and protected.

Animal movements underline the need for coordinated conservation actions and management plans over political and jurisdictional boundaries.

Clearly, the first step is to identify those movements: many conservation problems arise because different governments or different sets of people fail to recognize that they are dealing with a “shared” resource, or because animals move outside protected areas. Animal migrations illustrate the need for international agreements for conservation, which present a challenge to human societies. Governments do not like to give up sovereignty, yet that is precisely what is required to foster international conservation. The five chapters that follow explore how animal movements should be taken into account to decrease extinction risk.

3.

Dispersal and Conservation :

A Behavioral Perspective on Metapopulation Persistence

Rosie Woodroffe

The persistence of small, isolated populations has been a major focus of conservation biology since its inception (Soulé 1987). Human activities have fragmented habitats into small, poorly connected “islands” and archipelagos in a sea of modified habitat. The fragmentation process has left many wild populations small and isolated, sometimes doomed to extinction as a result of catastrophes, environmental and demographic stochasticity, loss of genetic diversity, and inbreeding depression. Dispersal of animals between patches, however, has the capacity to remedy these population problems, increasing numbers, replenishing lost genes and genders, and even recolonizing patches vacated by extinct populations (Brown and Kodric-Brown 1977, Hanski and Gilpin 1997). It is hardly surprising, then, that conservation biologists have seized upon dispersal as something approaching a panacea, and metapopulation biology—the study of small populations connected by dispersal—as the area of research most likely to assist future conservation planning (McCullough 1996, Hanski and Gilpin 1997).

Against this backdrop, in this chapter I review the effects of dispersal on the viability of populations and metapopulations. I also consider the effectiveness, in conservation terms, of attempts to manage dispersal behavior, and discuss

the behavioral, ecological, and evolutionary bases of dispersal behavior that may determine why particular management interventions succeed or fail.

Positive and Negative Effects of Dispersal

The fundamental predictions of metapopulation biology are best explained by outlining the “classical” model of Levins (1969). Habitat exists as patches, scattered through a matrix of unsuitable habitat. A proportion, P , of these patches is occupied by subpopulations; thus $(1 - P)$ patches are vacant. Subpopulations become extinct with probability e , and vacant patches are (re)colonized with probability c . P therefore changes over time at rate

$$\frac{dP}{dt} = cP(1 - P) - eP \quad (1)$$

The equilibrium value of P , \hat{P} , is given by

$$\hat{P} = 1 - \frac{e}{c} \quad (2)$$

A metapopulation can persist ($\hat{P} > 0$) only if the probability of colonization exceeds the probability of local extinction. Given a constant extinction rate, therefore, metapopulation persistence may depend upon efficient dispersal between habitat patches. If dispersal is hindered, either because of limited innate dispersal abilities or because patches are too isolated from one another, fragmented populations may be doomed to extinction. Consequently, species that are poor dispersers should be more extinction-prone than other species (e.g., Nee and May 1992).

Colonization processes are expected to occur on a much longer timescale than within-patch population dynamics. Metapopulations may therefore take a long time to reach equilibrium. Many species that appear to be persisting relatively well in fragmented habitats may in fact be declining slowly to extinction; this phenomenon has been termed the extinction debt (Tilman et al. 1994, Hanski 1997).

Failure to colonize suitable patches has indeed undermined the viability of world populations of some species. In 1982 the world population of Seychelles warblers (*Acrocephalus sechellensis*) was limited to the 0.29 km² Cousin Island, even though suitable habitat was available just 1.6 km away on Cousine Island (Komdeur et al. 1995). Translocations of warblers to Cousine and to Aride Island (9 km away) allowed the population to almost double its size (Komdeur et al. 1995), suggesting that the species would have been less vulnerable had it been capable of dispersing to other islands naturally. By contrast, species that are good dispersers may be capable of impressive recoveries from population perturbations. Wolves (*Canis lupus*) were eradicated

from most of western Europe and large tracts of North America but have staged a remarkable recovery, reoccupying many thousands of square kilometers of their former range.

The positive effects of dispersal on recolonization have prompted much research on how to encourage dispersal between patches, including optimal spacing of habitat patches, construction of corridors, “stepping stones,” and artificial translocations. Concerns have likewise been raised about conservation measures such as fences (meant to keep wildlife inside protected areas), which might have some beneficial effects but could also hinder dispersal.

Although dispersal behavior forms an important component of colonization, it may also contribute to local extinctions. Emigration from patches of habitat has the potential to undermine the viability of small, isolated populations, particularly when habitat fragments have high perimeter:area ratios (Stamps, Buechner, and Krishnan 1987).

Emigration from small, isolated patches appears to be an important cause of local extinction in some butterflies (Thomas and Hanski 1997). Thomas and coworkers (unpublished; reported in Thomas and Hanski 1997) modeled the population dynamics of two British butterflies, *Hesperia comma* and *Plebejus argus*, both of which have stringent requirements for habitats that are patchily distributed. They predicted that populations of *H. comma* would collapse in habitat patches below about 0.67 ha because emigration would outstrip breeding. *P. argus*, being less mobile, is less likely to disperse from small patches and should persist in patches down to a minimum of 0.05 ha (Thomas, Baguette, and Lewis 2000). The distribution of the two species across patch sizes gave a good fit to the model predictions.

A similar process operates, on a larger spatial scale, among large mammalian carnivores. For many of these species, which come into conflict with people, “suitable habitat” occurs only inside reserves where they are protected from persecution (Woodroffe and Ginsberg 1998). Animals ranging beyond park borders, however, suffer high mortality due to conflicts with local people, and such mortality has been a major cause of extinction in small, isolated populations (Woodroffe and Ginsberg 1998). Whereas most of this mortality involves resident rather than dispersing animals, mortality of animals dispersing across the inhospitable matrix is likely to be as high or higher, and may effectively halt exchange of animals between reserves.

The Behavioral Ecology of Dispersal

Because dispersal affects both colonization and extinction rates, effective conservation may demand management to encourage or discourage dispersal. Determining whether such management is needed and identifying strategies

most likely to be effective demand information on dispersal behavior. Unfortunately, detailed data are lacking for most species. However, insights into the ecological and social factors that have shaped the evolution of dispersal behavior could help to predict little-known species' responses to habitat fragmentation and to management. This section therefore outlines, and attempts to explain, some variation in dispersal behavior.

WHO DISPERSES?

Successful dispersal has two consequences for an individual's reproductive fate: it may alleviate competition for resources, and it may increase offspring fitness by reducing the probability of inbreeding. These two factors have different effects upon the evolution of dispersal patterns.

Abundant correlational data suggest that dispersal may reduce competition for resources needed to breed. Gray-tailed field voles (*Microtus canicaudus*) that disperse grow more rapidly than those that remain in their natal areas (Davis-Born and Wolff 2000). Likewise, female European badgers (*Meles meles*) breed at an earlier age following dispersal (Woodroffe, Macdonald, and da Silva 1995). In a few social and territorial species, however, dispersal may bring few benefits: female lions (*Panthera leo*) that dispersed bred later and died sooner than females that remained in their natal groups (Pusey and Packer 1987).

If dispersers can escape resource competition, dispersal might be expected to occur most frequently at high population densities. This relationship has been found in some species, especially small mammals (Myers and Krebs 1971). In some social and long-lived species, however, precisely the opposite may be found, with dispersal virtually ceasing at high densities (Komdeur et al. 1995; Woodroffe, Macdonald, and da Silva 1995). In territorial species at high densities the chances of finding an unoccupied territory are so low that individuals who remain at home—with the possibility of inheriting the natal territory (and sometimes, though not always, assisting in the care of their younger relatives)—have higher fitness than those that disperse.

Dispersal reduces the chances that mating partners will be close relatives and thereby helps prevent the reduced reproductive success associated with inbreeding depression (Pusey 1987). Avoidance of inbreeding seems to explain why dispersal is often biased toward one sex. In mammals, females are usually philopatric, whereas males disperse; the opposite pattern occurs in birds (Greenwood 1980). This general pattern, however, hides a wealth of variety. The usual mammalian dispersal roles are reversed in great apes, for example, in which females disperse between groups of philopatric males (Harcourt, Stewart, and Fossey 1976). Dispersal may occur in both sexes

(McNutt 1996), or, exceptionally, in neither (Faulkes, Abbott, and Mellor 1990). The proportion of each sex dispersing, and the distance traveled, may also vary substantially within species (Cheeseman et al. 1988; Woodroffe, Macdonald, and da Silva 1995).

Dispersal behavior may also be influenced by social status. Gese and Crabtree (1996) showed that coyotes (*Canis latrans*) that dispersed tended to be low-ranking group members, whereas higher-ranking siblings remained in the natal territory. Harris and White (1992) showed a similar result for red foxes (*Vulpes vulpes*). Woodroffe, Macdonald, and da Silva (1995), by contrast, found that it was the largest (and presumably most dominant) male European badger cubs that dispersed.

PHASES OF DISPERSAL

In considering the metapopulation implications of dispersal, it is helpful to distinguish the phases involved in colonization of new sites. These are (1) emigration from the natal patch, social group, or area; (2) travel to the new area; and (3) immigration to the new site or social group. Colonization may fail at any of these three stages.

Emigration and immigration may be uncoupled: wolves and coyotes, for example, may spend weeks or months traveling over long distances before establishing new territories (Fuller 1989). This uncoupling reaches its extreme in species such as termites, which can be considered obligate dispersers—reproductive offspring can breed only if they emigrate away from the natal colony, and are morphologically adapted for this dispersal.

Other species are more circumspect in their dispersal decisions. Emigration may be contingent upon immigration, with dispersers moving opportunistically to neighboring territories that have been vacated by breeding competitors (Woodroffe, Macdonald, and da Silva 1995). Some species may make temporary forays away from the natal territory but do not truly emigrate until they locate a breeding opportunity (Waser 1996). Such forays may be prolonged; golden jackals (*Canis aureus*), for example, may return to their natal territories several months after initial dispersal, presumably when they have failed to occupy territories elsewhere (Moehlmann 1987). Similar behavior has been recorded in cougars (*Puma concolor*) occupying highly fragmented landscapes with little available habitat (Maehr 1997).

DISPERSAL DISTANCE

Dispersal distances vary substantially and unpredictably among species. Although Van Vuren (1998) found a general relationship between median dispersal distance and body size, this conceals substantial variation in dispersal

abilities among related species. Gray wolves of both sexes may disperse long distances (median 58 km, maximum 886 km; Fritts 1983, Van Vuren 1998), whereas the closely related (and critically endangered) Ethiopian wolf (*Canis simensis*) shows much more restricted dispersal with all males remaining in the natal territory (Sillero-Zubiri, Gottelli, and Macdonald 1996). Likewise, median dispersal distance for the American badger (*Taxidea taxus*) is 12 km, whereas European badgers disperse over much shorter distances (Waser 1996).

Dispersal distance might also be predictable from ecological insights. For example, Waser (1985) was able to predict dispersal distances for deer mice (*Peromyscus maniculatus*) from measures of intraspecific competition for vacant territories. The same model, however, failed to predict dispersal distances for either male or female great tits (*Parus major*). Clearly, dispersal distance is shaped by a variety of species- and gender-specific factors.

Correlates of Colonization Success and Failure

Population models predict important effects of immigration and emigration, which may lead to differences in the vulnerability of “good” and “poor” dispersers. Definitions of dispersal ability are, however, inconsistent. Population models tend to consider a good disperser to be a species exhibiting a high colonization rate, but, as already discussed, this variable contains elements of emigration probability, dispersal distance, survival during dispersal, and capacity to breed on arrival. In this section I therefore discuss various behavioral traits that characterize “good” and “poor” dispersers, and consider their possible effects upon population dynamics.

WILLINGNESS TO CROSS PHYSICAL BOUNDARIES

Behavioral responses to arriving at the edge of suitable habitats vary between species—some “bounce off” the edge and remain largely in suitable habitat, whereas others readily enter matrix habitats (Desrochers and Hannon 1997, Schultz 1998, Haddad 1999b). Such variation may have important population consequences.

Some species are unable or unwilling to move between patches of suitable habitat. Consequently, such species’ geographic distributions may be limited by comparatively minor physical barriers such as rivers and ranges of hills (Haffer 1997). In natural landscapes and over the very long term, this can promote speciation and may generate high regional biodiversity. In artificially fragmented habitats, however, such cautious behavior can be problematic. For example, dispersing spotted owls (*Strix occidentalis*) may starve at a forest

edge rather than disperse to distant patches of suitable habitat (Arcese, Keller, and Cary 1997). American martens (*Martes americana*) are likewise reluctant to cross gaps in forest cover and are rarely found in even moderately fragmented forest landscapes (Hargis, Bissonette, and Turner 1999).

By contrast, some species appear undeterred by geographical features that might be considered likely barriers to dispersal. Coyotes cross rivers up to 100 m wide (Harrison 1992), and field voles (*Microtus agrestis*) commonly swim up to 620 m to disperse between islands in Finland (Pokki 1981). Seven cougars successfully dispersed across a four-lane highway (Sweanor, Logan, and Hornocker 2000), although two others were killed trying to cross this same road after it had been expanded to six lanes.

Willingness to leave suitable habitat may have negative as well as positive effects. For example, a study of forest songbirds' willingness to cross open areas to investigate call playbacks found that nuthatches (*Sitta canadensis*) were less reluctant than other species to leave forest cover, even when an alternative and only slightly longer route was available through forest cover (Desrochers and Hannon 1997). This willingness to enter unsuitable (and potentially hazardous) habitats could explain why fledglings of the related European nuthatch (*Sitta europaea*) maintain high rates of emigration from habitat fragments, leaving high-quality territories unoccupied (Matthysen 1999). Dispersers appear to suffer high mortality in fragmented habitats, making population persistence unlikely in the absence of immigration from larger source populations (Matthysen and Currie 1996, Matthysen 1999). Willingness to enter unsuitable habitat presumably also underlies the mass emigration from small patches observed in the butterflies studied by Thomas, Baguette, and Lewis (2000).

NATAL PHILOPATRY

In some highly social species, reluctance to leave the natal group can limit colonization in the absence of any obvious habitat boundary. These species are said to exhibit a high degree of natal philopatry. For example, female spotted hyenas (*Crocuta crocuta*) very rarely leave their natal groups; virtually all recorded female dispersals have involved fission of clans to occupy neighboring areas (Holekamp et al. 1993, Waser 1996). Males move only to join groups of females (Frank, Holekamp, and Smale 1995). Probably as a consequence, hyenas are extremely slow to recolonize areas subject to predator control (Smuts 1978) and are unlikely to disperse between habitat patches. By contrast, other species disperse readily from their natal areas or groups and may recolonize vacant habitat rapidly (e.g., wolves, African wild dogs

[*Lycaon pictus*]; Ballard, Whitman, and Gardner 1987; Hayes and Gunson 1995; McNutt 1996; Mills et al. 1998).

DISPERSAL DISTANCE

The distances covered by dispersing animals vary substantially between species and may have a powerful effect upon colonization success. Animals often move rapidly when they are dispersing across unsuitable habitat, and can cover distances greater than they would within their normal home ranges (e.g., Schultz 1998).

Measures of dispersal distance may be biased by both the size of the study area within which dispersers are sought, and the structure of the habitat they occupy. Acorn woodpeckers (*Melanerpes formicivorus*), for example, disperse very short distances within contiguous oak woodland and might be considered to have limited dispersal abilities. Extensive study, however, shows that dispersers can cover up to 200 km and that dispersal between patches occurs relatively frequently in fragmented habitats (Lidicker and Koenig 1996).

In mammalian carnivores, Woodroffe (2001) found no significant relationship between species' dispersal distances and their tendency to become extinct outside protected areas, though the trend suggested that long-distance dispersers might be more, rather than less, vulnerable. Thomas (2000) classified butterflies by a combination of dispersal distances and dispersal probabilities and found that species of moderate dispersal ability were most vulnerable to local extinction. The relationship between dispersal distance and vulnerability appears more complex than that assumed by simple metapopulation models.

INTEGRATION ON ARRIVAL

Colonization will not occur if dispersers fail to survive and breed when they reach new patches of suitable habitat. Such settlement often occurs readily: Seychelles warblers translocated to Aride and Cousine Islands, for example, located suitable habitat and established territories within days (sometimes hours) of arrival (Komdeur et al. 1995). Other species may fail to recognize unoccupied habitat as suitable: this has been documented in dispersing Belding's ground squirrels (*Spermophilus beldingi*) and yellow-bellied marmots (*Marmota flaviventris*) (Van Vuren 1998).

More starkly, human activities may thwart immigration. For example, illegal shooting of immigrating wolves has hindered their recovery in Scandinavia, despite the availability of prey and suitable habitat (Yalden 1993).

Where animals enter patches already occupied by conspecifics, they may experience problems integrating into the local social organization. Aggression

from resident territory-holders appears to be an important cause of mortality among dispersing lions and wolves (Waser 1996). Likewise, black-tailed prairie dogs (*Cynomys ludovicianis*) often fail to immigrate into established colonies because they are driven away by residents (Hoogland 1995).

Many species appear unwilling to disperse without information on where they are dispersing to. Targets for dispersal may be unoccupied patches of suitable habitat, or social vacancies in existing groups. Male European badgers tend to remain in their natal groups until the death or disappearance of a male in a neighboring group creates a breeding vacancy that they can fill (Woodroffe, Macdonald, and da Silva 1995). The need to locate such breeding vacancies may underlie the forays that frequently precede dispersal in a variety of species (Waser 1996).

Managing Dispersal

It is clear that effective conservation often depends upon managing dispersal, though such management may entail limiting or encouraging dispersal, depending on the circumstances. Propensity to disperse—or not—depends upon a complex array of behaviors that are often species-, gender-, or population-specific. In this section, I discuss approaches to population or environmental management that have been used to manage dispersal.

MANAGEMENT TO ENCOURAGE EMIGRATION

A great deal of attention has been paid to promoting dispersal of animals between patches. Indeed, according to Lidicker and Koenig (1996), “The greatest challenge for land managers and conservation biologists is species that are reluctant to venture out of their preferred habitats at any time” (p. 88). Habitat management to overcome animals’ reluctance or inability to disperse includes the construction of corridors and “stepping stones” as well as some other measures.

Corridors

The most widely researched measure for promoting dispersal is the construction of movement corridors. Although corridors have been described as holding “more promise for the conservation of the diversity of life than any other management factor except stabilization of the human population” (p. 493), their value has also been called into question (Simberloff et al. 1992).

Species’ use of corridors varies. Experimental linkage of isolated habitat patches by corridors has been shown to increase interpatch movements for a

variety of butterfly, small mammal, and bird species (Aars and Ims 1999, Haddad 1999a). However, many studies in nonexperimental environments have failed to establish the importance of corridors because they have sought to detect dispersers only in corridors, not in the surrounding matrix (Simberloff et al. 1992). Certainly some species, such as the wood mouse (*Apodemus sylvaticus*), and several butterfly species, will move between patches by crossing the matrix, as well as by using corridors (Zhang and Usher 1991, Haddad 1999b).

Species' use of corridors appears to be related to their responses to habitat edges. Two butterfly species that tended to "bounce" off the edges of forest clearings were found to use corridors to move between clearings, flying straight ahead rather than diverting into the forest matrix (Haddad 1999b). A third species, with less specialist habitat requirements, did not turn back into clearings when encountering forest edges, and left clearings along corridors only at the rate expected by random movement (Haddad 1999b). Responses to habitat edges may therefore be used to assess the likely value of corridors. For example, corridors were dismissed as a management strategy for the Fender's blue butterfly (*Icaricia icarioides fenderi*) because its tendency to "overshoot" habitat edges suggested that its movements might not be effectively directed by construction of corridors (Schultz 1998).

Behavioral responses to habitat edges presumably also influence the effectiveness of different corridor widths in channeling movement between patches. In the study just described, butterflies turned away from forest edges at distances of up to 8 m, and corridors were 32 m wide (Haddad 1999b). Thus half the width of the corridor was "edge," perhaps explaining why butterflies tended to fly straight forward rather than linger in corridors. Relatively wide (3 m) corridors failed to channel root vole (*Microtus oeconomus*) movements effectively between patches because the animals tended to cross the width of the corridor as well as move forward (Andreassen, Halle, and Ims 1996). Narrower (1 m) corridors were much more effective in encouraging dispersal between patches, although voles were reluctant to enter very narrow (0.4 m) corridors (Andreassen, Hall, and Ims 1996).

Corridor use may vary within as well as between species. Experimental corridors constructed between habitat patches increased natal dispersal of female root voles but had no effect upon the (markedly higher) dispersal rates of males (Aars and Ims 1999). Dispersal is generally male-biased in root vole populations, possibly reflecting a higher motivation for dispersal among males. Interestingly, the presence of corridors increased the rate of secondary (postbreeding) dispersal in both sexes (Aars and Ims 1999). Intraspecific variation in corridor use was also found in one of the butterfly species studied by Haddad (1999b). Resident *Phoebis sennae* responded strongly to habitat

edges and tended to leave forest clearings along corridors. Butterflies of the same species studied at a time of year when they were migrating showed similar responses, but the effects were much weaker.

All of these data suggest that, although corridors may sometimes be effective in encouraging movement between patches, their value and optimal design vary substantially within and between species. Crucially, it appears that it would be difficult to predict corridors' likely contribution to the conservation of particular species in the absence of detailed behavioral studies.

Stepping Stones

"Stepping stones," disjointed patches of habitat arranged between larger habitat patches to provide a route for dispersal, have been proposed as an alternative to corridors for more motile species. Stepping-stone arrangements have, for example, been established to protect migratory waterfowl en route between breeding and wintering grounds (Piersma and Baker 2000). Butterflies have naturally recovered by recolonization along stepping stones (Hill, Thomas, and Lewis 1996), and such arrangements have been proposed to link fragments of remaining habitat for other threatened butterfly species (Schultz 1998).

Other Conservation Measures

The widely perceived need to encourage dispersal may also influence decisions concerning other conservation measures. For example, concern was expressed that fencing of Lake Nakuru National Park in Kenya to promote rhino conservation would prevent recolonization by African wild dogs (Frame and Fanshawe 1990).

MANAGEMENT TO LIMIT EMIGRATION

In species where emigration represents a serious threat to the persistence of local populations, management may, paradoxically, be needed to hinder animals' propensity to disperse. Where emigration from isolated patches occurs because patches are small relative to individual home ranges, a simple solution (in theoretical if not in practical terms) is to enlarge the size of habitat patches, or to alter patch geometry to minimize perimeter:area ratios (Stamps, Buechner, and Krishnan 1987; Woodroffe and Ginsberg 1998). For some large-bodied species, fencing may be an effective means of deterring animals from crossing park or habitat borders (Thouless and Sakwa 1995), though the fences needed to enclose large carnivores, in particular, may be

substantial and expensive. More subtle management of habitat boundaries might help to deter emigration of smaller-bodied species.

An alternative to reducing individual emigration from habitat patches is to manage surrounding areas to maximize the chances of dispersal success. Such management might involve measures to limit mortality in the matrix; for example, enforced legal protection of species such as wolves and wild dogs, which suffer persecution in areas occupied by people. Alternatively, suitable habitat patches might be created or protected close to source populations to reduce isolation and “catch” dispersers. Such measures have been planned for black-footed ferrets (*Mustela nigripes*), where optimization procedures (a form of modeling) have been used to investigate how the creation of new habitat patches (through localized cessation of rodenticide use to allow prey populations to recover) can best be structured to encourage growth of ferret numbers (Bever et al. 1997).

Measures to limit emigration may be more direct in some circumstances, especially in the conservation of species that come into conflict with people. Lions, gray wolves, and red wolves (*Canis rufus*) dispersing out of some designated conservation areas have been captured and returned to parks (Stander 1990, Phillips 1995, Phillips and Smith 1996). Such measures have not always resolved conflicts with people but appear to have reduced the numbers of animals having to be killed.

ARTIFICIAL DISPERSAL—TRANSLOCATION

Circumstances may not always permit management to encourage natural dispersal between habitat patches. For example, where patches are very remote from one another, or where they are fenced, measures such as corridors and stepping stones may be inappropriate or uneconomic. In such circumstances, dispersal may have to rely upon artificial translocation. Translocation is widely used to augment populations of game species and is often highly successful (e.g., Castle and Christensen 1990). However, a number of behavioral problems may confound translocation attempts.

Dispersal following Translocation

Release at a new site sometimes seems to elicit elements of natural dispersal behavior. For example, social groups of wolves and African wild dogs translocated together have tended to break up, with animals sometimes moving over thousands of square kilometers following release (Fritts, Paul, and Mech 1984, 1985; Woodroffe and Ginsberg 1999). Translocated wolves settled, on average, 87 km from their release sites (Fritts, Paul, and Mech 1984).

Likewise, about half of the first 37 black-footed ferrets reintroduced to the wild moved rapidly away from their release sites, traveling 4.1 to 17.1 km (Miller, Reading, and Forrest 1996), and translocated sea otters (*Enhydra lutris*) dispersed over 100 km (Estes, Rathbun, and Vanblaricom 1993). Such wide-ranging behavior often involves “homing” to the animal’s original home range: 9 of 32 wolves, and 31 of 139 sea otters “homed” (Fritts, Paul, and Mech 1984; Estes, Rathbun, and Vanblaricom 1993). One captive-bred wolf traveled 280 km back to the breeding colony where she was raised (Henshaw et al. 1979), and a translocated leopard (*Panthera pardus*) traveled 540 km back to its home range (Nowell and Jackson 1996). Similar problems of wide-ranging and homing were encountered in experimental translocations of California ground squirrels (*Spermophilus beecheyi*) (Van Vuren et al. 1997).

Problems of postrelease dispersal have been solved, to some extent, by modification of release procedures. Captive-bred black-footed ferrets given prerelease training in survival skills (including access to realistic habitats and live prey) ranged less widely and were less likely to disperse away from the release site (Miller, Reading, and Forrest 1996). Likewise, wolves and wild dogs held in enclosures at the release site for several months have remained in roughly the intended areas (Phillips and Smith 1996, Woodroffe and Ginsberg 1999). Careful structuring of release groups may also have helped to inhibit dispersal; successful wolf and wild dog reintroductions have mostly involved the release of newly formed groups established in captivity by introducing sexually mature males to females (or groups of female kin) (Phillips and Smith 1996, Woodroffe and Ginsberg 1999).

Failure to Survive or Reproduce on Arrival

Recolonization will fail if translocated animals cannot survive or breed in the target area. Managing this possibility demands a realistic assessment of potential release sites. For example, African wild dogs translocated to Tsavo West National Park in Kenya left the reserve following a series of encounters with lions, major predators of wild dogs, and were subsequently killed by people in the surrounding areas (Kock et al. 1999). These interactions with known threats to wild dog populations suggest that the reintroduction site did not represent suitable habitat (Woodroffe and Ginsberg 1999).

Suitable habitat can be recognized by the presence of a breeding population. Indeed, the purpose of translocation is often to augment existing populations and to promote gene flow between them. Behavior patterns may, however, limit the possibilities for successful translocation, especially for social or territorial species. A tiger (*Panthera tigris*) translocated to the Sundarbans Tiger

Reserve in India was killed by a larger tiger just 20 m from the release cage (Seidensticker et al. 1976). Likewise, survival of translocated leopards is low, partly because resident territory holders respond aggressively to immigrants (Hamilton 1986).

Despite these concerns, one must be cautious in extrapolating from patterns of behavior in undisturbed populations. In unexploited wolf populations, for example, unrelated individuals are rarely accepted into packs, and intraspecific strife is an important cause of mortality (Fritts and Mech 1981). In contrast, in a harvested population 22% of dispersers were able to join established packs (Ballard, Whitman, and Gardner 1987). This raises the possibility that social integration might sometimes be a comparatively minor problem, especially when population density is low. Indeed, rates and causes of mortality were similar among resident and translocated wolves in Minnesota (Fritts, Paul, and Mech 1985).

Problems of intraspecific strife may be limited by careful choice of animals to be translocated. The wild dog population of Hluhluwe-Umfolozi Park was successfully augmented by releasing a group of related females, designed to mimic the natural immigration of a dispersal group (M. Somers, 1997, pers. comm.).

Conclusions and Recommendations

Although dispersal behavior may have a profound effect on (meta)population persistence, this effect is not always a beneficial one. Managers must not, therefore, assume that dispersal is always to be encouraged.

Management may be necessary either to encourage or to discourage individuals to disperse between patches. Unfortunately, dispersal behavior is, at present, somewhat unpredictable. Species and genders vary in their tendencies to emigrate from natal groups or habitat patches, in their dispersal responses to changing population densities, their dispersal distances, their habitat choices during dispersal, and their capacity to survive and breed on arrival at new sites. All of these factors influence whether dispersal needs to be managed, and, if so, what measures are most likely to prove successful. Conservationists must be cautious, therefore, in adopting management approaches, such as construction of corridors, without the support of behavioral evidence to indicate that such measures will be necessary and effective.

Interspecific variation in dispersal behavior also means that measures which are beneficial for one species may be pointless, or even deleterious, for another. For example, optimal spacing of habitat patches for a vagile species may effectively preclude successful dispersal by a sympatric species with more restricted movements.

Insights into natural dispersal behavior may also be important where habitat fragmentation and isolation are so extreme that dispersal must be effected through artificial translocation. Although mimicking some aspects of natural dispersal (e.g., structure of dispersal groups) may increase the success of translocations, other features of natural dispersal (e.g., traveling long distances) may be counterproductive and need to be discouraged.

All of these observations indicate that behavioral research must be a key element of conservation planning for species inhabiting patchy environments. Where possible, studies need to focus on the actual (meta)population to be protected because dispersal behavior may vary substantially in response to different spatial and social environments. Where habitat management is considered to conserve particular species, research should also consider potential negative effects on other species occupying the same landscapes. Clearly, research will be vital if a wide array of species are to be conserved in the world's increasingly fragmented landscapes.

Summary

Dispersal behavior has important effects on animals' population biology. Colonization of vacant patches and the "rescue" of declining or genetically depauperate populations are both brought about by dispersal. In addition, dispersal away from occupied patches may undermine the viability of isolated populations. These positive and negative effects mean that conservation measures may often involve managing dispersal events.

The relationship between dispersal ability and vulnerability to extinction appears more complex than is assumed by simple models. The few empirical attempts to investigate and test this prediction have established no coherent, and certainly no positive, link between the two. Part of the explanation for this may be the coupling of immigration to one patch to emigration from another: the negative effects of emigration may outweigh the positive effects of immigration, especially when dispersers suffer high mortality in the matrix.

Habitat management may be necessary to encourage—or to discourage—dispersal to improve the viability of metapopulations. Such management includes ensuring the optimal size and spacing of habitat patches, construction of corridors, and, in extreme cases, construction of fences. The effectiveness of these approaches depends primarily on individuals' dispersal behavior, particularly their willingness to cross habitat boundaries. Unfortunately, such behavior is not yet predictable, making it difficult to offer general prescriptions for the management of particular groups of species.

In extreme cases, movement of individuals between habitat patches can be

effected only by artificial translocation. Detailed behavioral information may be needed to maximize the success of such translocations, especially for territorial and social species.

All aspects of conservation involving dispersal of animals between habitat patches, from understanding its effects on population viability to recommending the measures most likely to provide effective conservation, require information on the ethology and behavioral ecology of natural dispersal. Unfortunately, there is currently no underlying theory that can reliably predict all aspects of dispersal behavior needed for conservation management, placing a high priority—for the moment—on species- and population-specific research.

4.

Migration and Conservation:

The Case of Sea Turtles

Paolo Luschi

Migration is a widespread behavior by which an animal periodically moves from one region to another that better satisfies the requirements for a phase of its life cycle (Baker 1978, Dingle 1996). Migratory behavior is usually exemplified by animals that regularly shuttle between feeding and breeding areas. Animal migration, however, comprises a broad spectrum of possible patterns, which often makes it difficult to classify a given movement as migratory (Dingle 1996). In this chapter, I use recent research on sea turtles to illustrate the importance of behavior in the conservation of migratory animals.

Migratory movements range from the short-distance changes of habitats of some insects to the spectacular long-distance journeys of some vertebrates. Many migrants moving over large geographical areas traverse a variety of habitats, including some greatly affected by human activities. As a result, migrants are exposed to a number of threats, either along their migratory journey or at their destination, or both. These threats include hunting, habitat loss, and habitat degradation, which can be particularly harmful for migrating animals that are most vulnerable in such physiologically stressful and challenging situations. Migrating birds, for instance, have to meet high energetic demands, often including long stretches of nonstop flight to cross

geographical or ecological barriers such as the open sea, deserts, or mountains. To face these demands, many birds spend long periods foraging to replenish fat deposits in stopover sites along migratory routes (Alerstam and Hedenstrom 1998). Consequently, it is important to protect stopover areas of migratory birds. Because bird migrations usually cross political borders, often spanning immense distances, the protection of en route stopover sites requires coordination between different countries, which is often difficult to achieve. Migration is thus a critical phase in the life cycle of migratory species (Dingle 1996), and any anthropogenic threat can be expected to have particularly deleterious consequences on migrating animals. Conservation measures should therefore take into account the animal's behavior and physiology during migration.

Conservation biologists have long shown special attention to migratory animals. An example of a concrete conservation measure is the 1983 Convention on Migratory Species (also known as the Bonn Convention). That convention, signed by 70 countries, aims to conserve migratory species *throughout their range*, and so highlights the specificity of migrants as animals moving across national boundaries and thus needing conservation on a global scale (Hykle 2000). It places special emphasis on the fact that migrants are to be considered a resource shared by different countries and that protection measures have to be agreed upon internationally. Under the auspices of the Bonn Convention, many conservation and management research activities have been undertaken in favor of migratory species ranging from birds to bats and from cetaceans to marine turtles.

Obviously, suitable conservation measures for a given species need to rely on the scientific knowledge available for that species, and a close interaction between conservationists and scientific research is needed to support any well-planned conservation effort. Scientific research on migratory behavior has greatly benefited conservation of migratory animals. Ethological research on animal migration has a long history and has provided valuable insights on various aspects of animal migrations, such as their general extent and phenology, or the physiology and energetics of migrants (e.g., Berthold 1993, Alerstam and Hedenstrom 1998). The recent advent of satellite telemetry (French 1994) has provided migration researchers with a new and powerful tool that makes it possible to track animals' movements anywhere on Earth and so reconstruct migratory pathways with considerable accuracy. This possibility is most valuable for the conservation of the many migratory species for which the actual geographical areas visited during migration remain poorly known or entirely mysterious. Lack of specific knowledge about the animals' whereabouts prevents the planning of any conservation measure aimed at protecting their habitats. The findings obtained with satellite

telemetry are thus progressively filling a critical gap in the conservation biology of migratory animals.

Marine turtles were one of the first animals to be tracked by satellite (e.g., Stoneburner 1982), and now a large body of satellite tracking data on their migrations is becoming available. These data, however, do not yet provide a complete view of the entire range of movement patterns of sea turtles. Large gaps remain, such as for juveniles or for many populations of adults (see below). Sea turtles are also threatened animals. Some species of sea turtles are near extinction (Limpus 1995, Pritchard 1997), so their conservation has the highest priority. Proper protection of sea turtles must be based on reliable and detailed knowledge of their biology and especially of their movement patterns, which for the most part remain poorly understood. Satellite telemetry now has the potential to elucidate these issues. Indeed, information derived from tracking experiments is often discussed in view of the implications for the conservation of the specific turtle population studied (Morreale et al. 1996, Polovina et al. 2000, Mortimer and Balazs 2000).

Sea Turtles

Marine turtles are truly migratory animals. Some species travel over hundreds or thousands of kilometers while shuttling between nesting and feeding grounds (Carr 1984, Papi and Luschi 1996). Sea turtles travel large distances not only as adults but in nearly all phases of their life cycle, beginning a few hours after hatching.

A generalized life cycle of the seven recognized species of sea turtles (Fig. 4.1) (Carr, Carr, and Meylan 1978; Miller 1997) highlights how turtles move between different, spatially distant, habitats during all stages of their life. Only the flatback turtle (*Natator depressus*), never migrates away from Australian reef areas (Walker and Parmenter 1990).

Females lay eggs in the sand of a tropical or subtropical nesting beach. After 40 to 80 days, the hatchlings emerge from the underground nest and crawl to the sea where they are transported away by sea currents. In this way, they reach their pelagic nursery habitats, which are usually thousands of kilometers away from the nesting area. These nursery habitats are most probably areas in the ocean (such as oceanic frontal systems or convergence areas), where organisms concentrate and therefore food is abundant. Juvenile turtles remain for about 5 to 10 years in their feeding areas. During this long period turtles will not necessarily remain in the same location, as they continue to be transported by large-scale current movements (hatchling developmental migration; Carr 1987). After some time the young turtles, now larger and close to sexual maturity, will leave their pelagic nursery habitat and settle in a

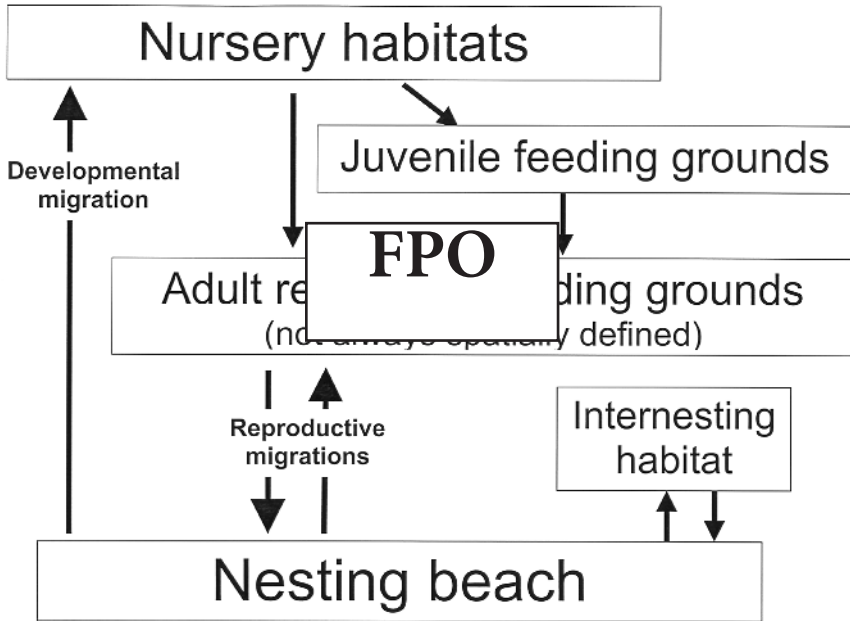


FIG. 4.1. A generalized sea turtle life cycle (modified from Carr, Carr, and Meylan 1978; Miller 1997).

resident feeding ground, which can be either shared with adults or exclusive to juveniles (see Fig. 4.1; Musick and Limpus 1997).

For most species, feeding grounds are specific, spatially defined coastal waters. Leatherback turtles (*Dermochelys coriacea*) and olive ridleys (*Lepidochelys olivacea*), however, have no well-defined feeding areas, and both adults and juveniles simply wander in the open sea without settling in any specific site. At sexual maturity, turtles of both sexes leave the feeding areas and move toward their nesting beach, where females lay eggs several times within a single season, generally every 10 to 14 days. At the end of the reproductive season, both males and females return to the feeding area (see Fig. 4.1). The extent of the reproductive migration can range from a few kilometers (like in many hawksbill turtle [*Eretmochelys imbricata*] populations) to thousands of kilometers, like in green (*Chelonia mydas*) or loggerhead (*Caretta caretta*) turtles. Further short-range movements are made by females between successive egg-layings, when they usually remain in waters close to the nesting beach (internesting habitat). Miller (1997) suggested that some populations also have a specific mating area, but in most cases courtship and mating are thought to occur close to the nesting beaches a few weeks before laying (Godley et al. 2002).

SEA TURTLE CONSERVATION

Many sea turtle populations are critically endangered. Some populations have declined substantially and others have gone extinct (Limpus 1995, Spotila et al. 1996, 2000, Pritchard 1997). Many international conservation organizations have acknowledged this situation. All sea turtle species, excepting the flatback, are regarded as endangered migratory species by the Bonn Convention (listed in Appendix I). They are considered threatened with extinction or endangered by the United States Endangered Species Act and by the Red Book of the World Conservation Union (IUCN). Finally, the Convention on International Trade of Endangered Species (CITES) lists all marine turtles in Appendix I, which prohibits all international trade in turtles or turtle products.

Awareness of the turtles' critical status has led to a number of conservation measures to prevent their decline (Godfrey 1996). These measures have focused on the protection of the nesting areas, which are the only terrestrial habitats used by marine turtles. A series of initiatives have been taken to protect nesting beaches (National Research Council 1990, Lutcavage et al. 1997), including restricted access, especially at night; beach patrols to limit disturbance to nesting turtles (especially natural predation or human harvesting of eggs or adults); and monitoring of egg hatching and hatchling survival, in some cases through the installation of hatcheries where incubation is kept under controlled conditions. All these activities, together with an educational effort to increase awareness of turtle conservation within the local human populations involved, have produced some good results (Hughes 1996; Godley, Broderick, and Hays 2001) and have certainly benefited turtles.

Sea turtles, however, do not live on beaches. Beaches are important for their survival because that is where the delicate and vulnerable nesting activity occurs, but turtles spend the vast majority of their time in the sea. Therefore, any conservation strategy must consider the protection of marine habitats. Beneficial effects of at-sea protection have been recorded, for example for the Ascension Island green turtle population, whose currently favorable status has been attributed to the reduction of harvesting or incidental catch of turtles at their Brazilian feeding areas (Godley, Broderick, and Hays 2001). On a broader perspective, however, little has been done so far, mainly because the scarcity of scientific studies of turtle behavior at sea meant that there was little reliable information about where the different turtle populations stayed after leaving their nesting areas.

Scientists are now filling this gap in our knowledge of turtle behavior. Population genetic studies using molecular markers have joined flipper tagging in providing clues to the geographical origin of turtles found in various locations (Bowen and Karl 1997). Satellite telemetry techniques to monitor

marine animals have provided new insights on the actual turtle movements and behavior between the start and end points of migratory journeys.

EXAMPLES OF SEA TURTLE MIGRATORY JOURNEYS

Satellite telemetry (French 1994) has substantially improved our knowledge of turtle behavior at sea, both in the feeding areas and during migration (Papi and Luschi 1996). In most cases, observations were carried out on females, which can be approached while they are nesting, and satellite-linked transmitters can be attached to their large carapace. Most of the available information therefore regards the postnesting migrations of adult females.

The results of satellite telemetry reveal some variability in the migratory strategy both between and within populations of the same species, but some general patterns in the postnesting movements of marine turtles, can be outlined.

1. Female turtles migrate over very large distances. Their travel routes are often straight and directly oriented toward their destination (Balazs 1994, Luschi et al. 1996, 1998). Males most probably do the same (Beavers and Cassano 1996, Balazs and Ellis 2000, Hays et al. 2001).
2. Although turtles nesting in a given area have similar migratory pathways (Fig. 4.2a) (Balazs 1994, Morreale et al. 1996, Luschi et al. 1998), variations exist even within the same species (Fig. 4.2b) (Luschi et al. 1996, Cheng 2000).
3. After leaving the nesting beach, some species (or possibly populations) move directly toward a specific site, reach it quickly, and remain there, presumably until they are ready to breed again. The herbivorous green turtle is the best example of such a pattern (see Fig. 4.2), which is shared with the hawksbill (which usually makes shorter movements, Mortimer and Balazs 2000) and with many loggerhead populations (Papi et al. 1997).
4. Some turtles continue to wander, probably for the entire interreproductive period, generally in the open sea. This is the case of the olive ridley and, especially, of the leatherback turtle (Fig. 4.2c) (Morreale et al. 1996, Hughes et al. 1998)

It is not only adult turtles that migrate. As I suggested earlier, hatchlings and juveniles also perform migratory movements, often over large distances. Satellite data are limited to movements of juveniles or subadults because it is not yet possible to fit radios on hatchlings, which are only a few centimeters long. Despite the technological challenges, a clearer picture of hatchling movements is beginning to emerge. This is especially true of the loggerheads that hatch in the east coast of Florida. The general course of their developmental

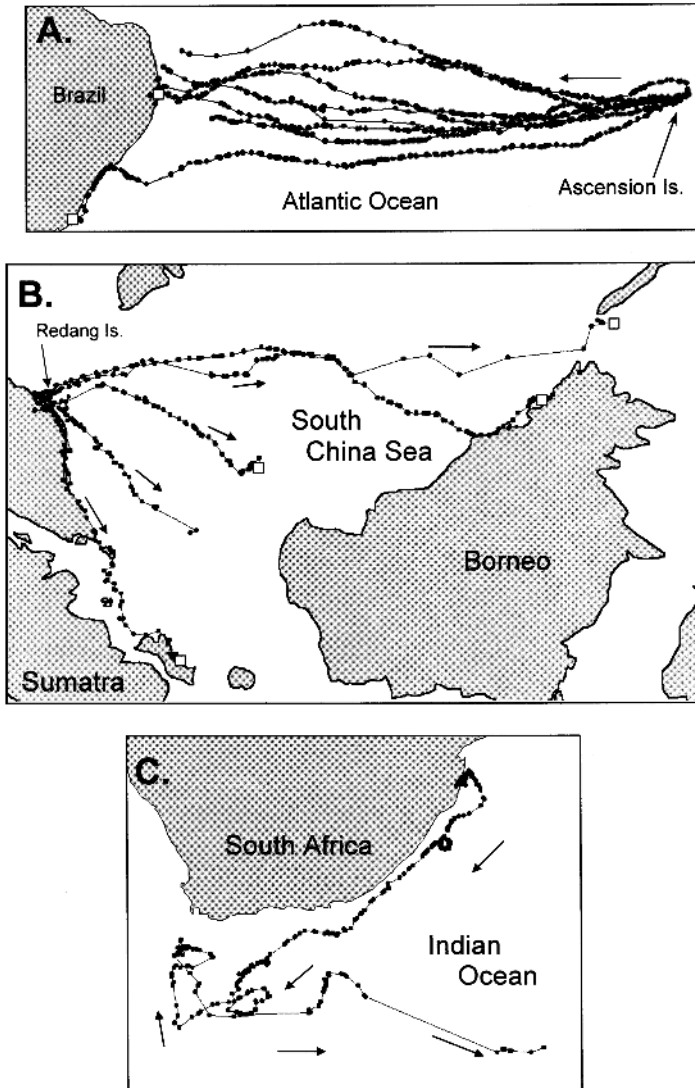


FIG. 4.2. Marine turtle migratory journeys reconstructed by satellite telemetry. (a) Paths of eight green turtles that left nesting beaches at Ascension Island heading for feeding grounds off Brazil (Luschi et al. 1998, Papi et al. 2000). (b) Paths of five Malaysian green turtles dispersing toward different feeding grounds in the South China Sea after nesting on the small Redang Island close to the coast (Luschi et al. 1996). (c) Wandering movements of a leatherback turtle leaving her South African nesting grounds. The journey lasted about 4 months (Hughes et al. 1998). In a and b, white boxes indicate the spatially limited feeding grounds where turtles were localized over a long time.

migration was hypothesized some years ago from hatchling recoveries over many years (Carr 1987), and was recently confirmed by genetic studies (Bolten et al. 1998) and by computer simulations of the hatchling routes (Hays and Marsh 1997). Soon after leaving the Florida shores, these hatchlings enter the Gulf Current, which transports them northeast toward the Azores. From there, other major oceanic currents transport them south toward the Canaries and then westward back onto the Caribbean coasts. It is assumed that the same pattern, including a reliance on oceanic currents to transport the hatchlings and several years of growth in pelagic habitats, also applies to other turtle species and populations (Musick and Limpus 1997). For instance, molecular genetic studies provided evidence that loggerheads born in Japan are transported eastward by oceanic currents to the waters off California, from where they are thought to return to Japan to nest (Bowen et al. 1995).

For older turtles, there are some satellite tracking data available. In most cases, they show slow or wandering movements (e.g., Gitschlag 1996, Polovina et al. 2000, Dellinger and Freitas 2000), with the notable exception of the long-distance movement of a captive loggerhead female of Japanese origin, which was released in Baja California, Mexico, fitted with a radio transmitter, and then tracked while she crossed the entire Pacific Ocean to reach Japan (Nichols et al. 2000). Although this was an adult-sized turtle raised in captivity for years, her journey likely represents a return from her Mexican developmental habitats to her adult feeding grounds in Japanese waters.

SEA TURTLE MIGRATION AND CONSERVATION

These examples demonstrate how research on turtle migration provides a great deal of information about turtles' spatial behavior. The picture emerging from satellite telemetry findings has a number of implications for the conservation of migrating sea turtles.

Turtles move readily across political boundaries; only in rare cases can they be considered the exclusive resource of any one country. On the other hand, their conservation cannot be the responsibility of a single state. The recommendations of the Bonn Convention are therefore particularly appropriate for sea turtles: the conservation of migrating sea turtles must be planned globally, and protective measures have to be agreed on internationally. Our research group already underlined this requirement in 1995 after our first satellite results on Malaysian green turtles (Liew et al. 1995). The IUCN Marine Turtle Specialist Group elaborated in 1995 a global strategy for the conservation and recovery of declining turtle populations. The concept of migrating turtles as a regionally shared natural heritage turned out to be particularly important during a recent legal controversy within the 2000 CITES

Convention of the parties (Richardson 2000). Cuba, supported by Japan, submitted a proposal to reopen the trade in hawksbill shell (downlisting the Caribbean hawksbill from CITES appendix I to II), a proposal that was strongly opposed by many experts in turtle conservation, precisely because hawksbills are migratory animals. Therefore Cuban turtles are not only Cuban, coming from or moving to other Caribbean beaches and waters, as was most clearly demonstrated by a genetic survey of Caribbean hawksbills (Bowen and Karl 1997). These data supported lobbying pressures that led to the rejection of the Cuban proposal, and information on turtle movements substantiated the views of conservationist biologists.

Turtles spend the vast majority of their time at sea, and their movements can be highly variable (see Fig. 4.2b) or totally unpredictable (see Fig. 4.2c). Thus conservation strategies to protect nesting sites are not always effective for migrating turtles and can be used only in specific cases, such as for turtles that migrate to specific, well-defined feeding areas, possibly along similar migratory routes. Satellite telemetry can identify the location of feeding grounds and migratory routes, thus providing the basic information required to substantiate calls for the protection of these important sites. For instance, having identified a migratory corridor in leatherbacks leaving Costa Rican nesting beaches, Morreale et al. (1996) proposed concrete measures to limit fishing activity in that area. More recently, fishing restrictions have been suggested for an oceanic area north of Hawaii that satellite telemetry has shown to be frequented by loggerhead subadults (Polovina et al. 2000). Enforcement of such measures in offshore areas, however, is a challenging task. Finally, satellite telemetry could be used to monitor the fate of turtles caught by fisheries and subsequently released.

The protection of defined geographical areas is not, however, a feasible solution for the protection of turtles that wander over large areas, as is the case of young individuals of most species. Instead, the focus should be less on protection of important sites than on the protection of the turtles themselves. Threats to which turtles are subjected while migrating or staying in the sea must be identified, and their impact must be limited. While at sea, turtles are exposed to many anthropogenic disturbances. The risks of debris ingestion and oil pollution are especially high in the frontal systems that are inhabited by hatchlings for long periods (Eckert 1995, Lutcavage et al. 1997).

The most serious threats, however, are certainly those caused by commercial fisheries (National Research Council 1990, Lutcavage et al. 1997). In particular, shrimp trawling is responsible for about 90% of deaths of adult turtles at sea. A review by American researchers estimated that incidental capture of turtles in shrimp trawls accounted for more deaths than all the other sources of human activities combined. Those researchers estimated that up to 50,000

loggerheads and 5000 ridleys drown every year in shrimp trawls in U.S. waters alone (National Research Council 1990). For the Kemp's ridley (*Lepidochelys kempfi*), estimates of fishing-related mortality exceed the estimated number of nesting females in the world. Pelagic fishing gears such as longlines and gill nets used for swordfish and tuna are also harmful, especially for leatherbacks during pelagic movements (Eckert 1995). Fishing devices can be harmful even when abandoned or lost, because turtles may become entangled in them and drown. The combined effect of incidental exploitation on turtles by fishing can be dramatic, as is clearly illustrated by the leatherback populations nesting in Mexico and Costa Rica. A sharp decline was attributed to high mortality away from the nesting beach, mainly due to pelagic fishing activity (Eckert and Sarti 1997, Spotila et al. 2000). Monitoring through satellite telemetry allowed researchers to identify oceanic areas west of South America where leatherbacks moved to and were incidentally captured after the nesting season (Morreale et al. 1996, Eckert and Sarti 1997).

The attention of turtle conservationists has for a long time focused on the effects of fishing activity and on ways to prevent turtle bycatch. Now some remedies are available or under study, the best known of which is the Turtle Excluder Device (TED), a sort of escape hatch placed in a trawler net that allows turtles to escape (National Research Council 1990). The general idea was first conceived in the 1980s and there are now several models available, which are all inexpensive and thought to reduce turtle mortality by up to 97%. Fishermen, however, tend to dislike TEDs, claiming that they reduce the trawl effectiveness in retaining shrimp, although investigations have recorded only negligible losses of shrimp. TEDs are even thought to have positive effects on fishing efficiency by decreasing the mass of bycatch and reducing the vessel's fuel consumption (National Research Council 1990). In 1989, the United States made the use of certified TEDs mandatory for U.S. shrimp trawlers, thus recognizing that TEDs are effective in protecting turtles without impeding shrimp fishing (Crouse 1999). These regulations were then extended to ban shrimp imports to the United States from nations with an indigenous sea turtle population whose fishing vessels do not install TEDs, an action that was taken in view of the migratory nature of sea turtles. Again, international coordination of the countries fishing in the same area is essential to maximize the positive effects of this device.

Conservation of Migratory Animals

Most of the problems faced by migrating sea turtles are common to other migratory species that use habitats in different geographical areas at different times (Dingle 1996). Migratory marine animals like fishes, pinnipeds, or

cetaceans move in the same environment as sea turtles, and so are affected by specific problems linked to the marine environment, including pollution, habitat degradation, or fishing activity. But any migratory animal, be it a flying bird or butterfly or a walking mammal, is exposed to many of the threats I have outlined for turtles. The very fact that migrants visit many different areas multiplies the possibility of interaction with harmful human activities, from hunting to destructive agricultural practices. Even apparent harmless actions can have detrimental outcomes: dams to supply water to agriculture or for hydroelectric power, for instance, prevent salmon from performing upstream breeding migrations (Dingle 1996).

Most migrants cross national borders, so their conservation in one country might not guarantee them protection. They are linked (sometimes very faithfully) not only to specific breeding and nonbreeding areas, but also to some intermediate transit areas, such as stopover sites. Habitat degradation could affect any of these sites. For migratory animals, each one of these sites is a potential “weak link” in a chain. Lack of protection in one site overrides protection elsewhere. Migrating birds are often disturbed by humans while fueling at stopover sites, for instance, when they are thought to produce crop losses (e.g., in the case of ducks or geese; Greenwood 1993). The detrimental effect of habitat degradation is best exemplified by the migratory populations of monarch butterflies (*Danaus plexippus*), which are now threatened because of adverse climatic changes of anthropogenic origin in the few Mexican forests where they gather to winter after a 3600 km migration from much of North America. Interestingly, nonmigratory populations of the same species are not threatened (Dingle 1996), which shows how migration is a costly behavior even in evolutionary terms.

Conclusions and Recommendations

This chapter has shown how sea turtle migrations provide many examples of fruitful cooperation between fundamental research on migration and conservation biology. Researchers have provided interesting insights into turtle spatial behavior that have been useful in documenting the interaction between sea turtles and human activities such as fishing. The basic knowledge acquired has greatly benefited turtle conservation and facilitated the planning of appropriate protection measures, which should be maintained and possibly increased. Enlarging the number and extent of protected marine areas, including those far from nesting grounds, and enforcing fishing restrictions in different countries (especially making usage of TED mandatory) are two management actions that are likely to greatly improve the conservation status of sea turtles.

Many aspects of the biology and behavior of migrating turtles are still largely unknown, and scientific research has just begun to investigate them. That research should continue because it will increase our knowledge of fundamental turtle biology and provide valuable contributions for planning effective conservation. Studies on the orientation systems underlying the turtles' migratory performances are expected to be of special importance. Knowledge of orientation mechanisms would improve understanding of the navigational machinery that guides turtles during their migratory journeys, by identifying the environmental cues used. Those cues may help us identify other possible, and perhaps unsuspected, threats to migrating turtles. The navigational mechanisms of turtles remain a subject of speculation, with little or no experimental evidence to support or refute various proposed ideas (Papi and Luschi 1996, Lohmann et al. 1997). The availability of reliable telemetry methods to track turtle movements now makes it possible to test these hypotheses explicitly (Papi et al. 2000), and progress in this field is likely in the near future.

A good example of the practical importance of knowing what stimuli are used by turtles to orient their movements comes from studies of the behavior of hatchlings crawling across the beach immediately after emerging from the underground nest (Godfrey 1996). Hatchlings rely on visual stimuli to orient themselves, crawling toward the brightest horizon of the beach, which in natural conditions indicates where the sea is (Lohmann et al. 1997). These basic research findings have been very useful to evaluate the effects of artificial lighting near turtle nesting beaches. Hatchlings orient in the wrong direction if there are lights at the back of the beach: their natural orientation toward the brightest horizon leads them to move away from the surf, with obvious negative consequences (Lutcavage et al. 1997). The identification of this problem prompted greater care in building new human settlements close to sea turtle nesting areas, together with the proposal of simple modifications of artificial lights to reduce beach lighting or at least its negative impact on hatchling orientation (Witherington and Martin 1996, Lutcavage et al. 1997).

This example shows how basic research findings can be extremely useful in answering to conservation needs. Integration between basic research and conservation is the most powerful tool we have at our disposal, if we are to allow turtles and other animals to continue to migrate across our planet.

Summary

Like many other migratory species, marine turtles visit a variety of different habitats during their long-distance movements and are therefore exposed to threats both along the migratory route and at their destinations. Protecting

migrating sea turtles is a challenging task, especially because little is known on turtle behavior at sea. Satellite tracking techniques are progressively filling this gap in our knowledge, and recent findings highlight a number of points of great importance for the conservation of migrating turtles. Turtles usually move across political boundaries and so their protection requires international agreements and global strategies. The turtles' large-scale movements render strategies aimed at preserving specific geographical areas, often successfully used to protect nesting areas, unfeasible or of limited applicability. The most harmful threat to migrating turtles is fishing activity, which, even if it is not targeting turtles, is responsible for the vast majority of turtle deaths at sea. As a tentative countermeasure, actions restricting fishing activity in certain areas or periods have been proposed and sometimes implemented. Specific remedies to limit bycatch captures (especially using modified nets with an escape hatch) are also available, and their use is mandatory in some countries. Also in this case, an international coordination between countries is a key factor to make these solutions most effective. Future conservation efforts should integrate more closely with basic research, which is expected to provide valuable insights on the many poorly known aspects of the biology and behavior of migrating sea turtles.

5.

Bridging the Gap:

Linking Individual Bird Movement and Territory Establishment Rules with Their Patterns of Distribution in Fragmented Forests

André Desrochers

Birds and other terrestrial vertebrates are generally sensitive to habitat changes occurring at the landscape level (Turner, Gardner, and O'Neill 2001). Many papers on landscape management and conservation for birds and other organisms end with a statement on the need to better understand the underlying processes. Yet this message has not elicited much response by ethologists, despite the potential relevance of their work to conservation. Lima and Zollner (1996) illustrated the importance of a “behavioral ecology of landscapes” to provide new ecological insight as well as guidance to landscape managers. In this chapter I examine the potential and realized contribution of ethology toward a theory of habitat fragmentation and, possibly, toward reducing negative effects of habitat fragmentation on wildlife conservation. I define ethology here as the study of animal behavior through direct and detailed observation of individuals. The focus of this essay is forest fragmentation and forest birds, but most issues addressed here should apply to a variety of habitats and organisms.

Forest fragmentation is just one result of the many ways by which humans not only reshape landscapes but also threaten certain wildlife species, regionally or globally. Forest fragmentation is a phenomenon distinct from forest loss; it involves the isolation of habitat patches from one another (Fahrig 1997). In many ways, forest fragmentation is synonymous with forest isolation. Given that birds are among the most vagile terrestrial organisms, they may seem inappropriate models to study in relation to forest fragmentation. There is evidence, however, that woodland animals respond negatively to forest isolation. Most of this evidence takes the form of lower abundance or infrequent occurrence of species in more isolated habitat patches, in species ranging from songbirds (e.g., Opdam, Rijdsdijk, and Hustings 1985) to grouse (Åberg, Swenson, and Andrén 2000) and possibly owls (Redpath 1995). More limited evidence points to lower reproductive performance of birds in isolated forests, through unpaired birds (Gibbs and Faaborg 1990; Villard, Martin, and Drummond 1993; van Horn, Gentry, and Faaborg 1995), lower food availability (Zanette, Doyle, and Trémont 2000), increased nest predation or brood parasitism (Robinson et al. 1995), and, possibly, increased fluctuating asymmetry (Lens et al. 1999). Despite growing evidence on landscape use and associated nesting success, no solid theory has emerged to propose a general picture explaining *how* fragmentation leads to the above patterns. It is increasingly clear that the study of habitat fragmentation will not make significant steps forward unless we understand better how wildlife behaves with regard to various aspects of forest fragmentation.

So far, behavioral studies pertaining to the fragmentation issue mostly addressed dispersal and limitations to movements (reviewed in Desrochers et al. 1999). Despite the emphasis on forest fragmentation as a habitat-isolating process, there is not enough evidence to argue that landscape use is only, or even mainly, a result of movement constraints. Therefore, this chapter focuses not only on isolation; it also briefly reviews the main hypotheses that have been proposed to explain landscape use by birds and presents a broader perspective of how behavioral rules of decision may affect landscape use patterns. Specifically, I address the roles of conspecific attraction on reproduction, habitat edges on reproduction and foraging, and movement constraints on dispersal and the search for territories. Although treated separately, these three aspects are not viewed here as exclusive nor independent; in fact it is likely that they do interact, thus posing additional challenges to our understanding. I conclude with some thoughts on ethologists' role in making wildlife conservation not only solid on scientific grounds but also relevant for those who make or break conservation: landscape managers and the public.

Conspecific Attraction

Habitat selection studies of birds generally consider vegetation as the main, if not the sole, factor of importance, even though conspecifics are recognized as an important part of a bird's habitat. The presence of conspecifics is a critical piece of information for birds, yet it is seldom incorporated in empirical or modeling studies by conservation biologists (Reed and Dobson 1993), especially when fragmentation is the subject matter.

The role of conspecifics is highlighted in situations where nesting birds are found in aggregates. During the breeding season, spatial aggregations of individuals are not limited to so-called colonial species. In "typical" songbirds, aggregations may also occur, with no apparent link to patchy resources per se (Stamps 1988). Spatial aggregations apparently originating from neighbors have been noted as early as the 1930s with song sparrows (*Melospiza melodia*), a territorial, socially monogamous songbird (Nice 1937:73). In a study of landscape use by songbirds, Drolet, Desrochers, and Fortin (1999) provided indirect evidence for clusters of territories of songbirds independent of habitat clusters, but these clusters were treated as a statistical nuisance rather than investigated as the result of a potentially important process. Tarof and Ratcliffe (2000) provided a detailed assessment of relationships among individuals in another socially monogamous species found in clusters, the least flycatcher (*Empidonax minimus*).

Why should we expect social aggregations in apparently monogamous songbirds? It is unlikely that such loose aggregations provide much benefit in terms of nestling survival because of the assumed large surface area of the aggregations relative to search patterns by nest predators. However, loose aggregations may provide opportunities for extra-pair copulations as well as provide useful information about the prospects for nesting success (Desrochers and Magrath 1993, Doligez et al. 1999) or possibly factors linked with adult survivorship.

So far, very few field experiments have attempted to single out the effect of conspecific songbirds on territory settlement (see Alatalo, Lundberg, and Bjorklund 1982 for an experiment based on song recordings to entice birds to establish territories). Furthermore, no study has investigated in detail the possible contribution of conspecific attraction in explaining landscape use by forest songbirds. Recent work highlights the influence of landscape structure to extraterritorial movements by hooded warblers (*Wilsonia citrina*) soliciting extra-pair copulations (Norris and Stutchbury 2001). In that study, male hooded warblers did not include in their "copulation neighborhood" females that inhabited woods separated from their own by open areas more than 500 m wide. Given that extra-pair copulations are the rule rather than the

exception in songbirds (Petrie and Kempenaers 1998), the hooded warbler story may uncover a widespread phenomenon. But to understand the role of interactions among neighbors and how they are affected by habitat fragmentation, we will have to understand not only the nature of the relationships among neighbors but also the spatial extent of bird neighborhoods in a variety of species and landscapes.

If conspecific attraction is an important cause of avoidance of fragmented forests, then one should expect a positive relationship between species' tendencies to establish clusters of territories and their avoidance of fragmented forests. In such a case, management of landscapes for the accommodation of single territories would tend to overestimate the quality of landscapes for certain species. To prevent this problem, a more realistic approach would attempt to reflect a naturally occurring frequency distribution of territory cluster sizes. Managing for territory clusters would entail the preservation of substantially larger habitat patches, even for species with small territories such as the least flycatcher (Tarof and Ratcliffe 2000).

Responses to Habitat Edges

Depending on the degree of forest cover and associated fragmentation, the amount of forest edges will vary enormously (Fig. 5.1). It is difficult to be far from a forest edge in fragmented forests, compared to contiguous forests, and as a result, we need to address the edge issue when addressing the fragmentation issue. Birds and other terrestrial vertebrates often respond to the amount and proximity of forest edges (reviewed by McCollin 1998, Yahner 1988). For decades, forest edges have been considered as positive, or even essential, landscape elements, particularly for game species (Leopold 1933). Seminal papers by Gates and Gysel and Wilcove (1978, 1985, respectively) initiated a new and darker vision of forest edges as ecological traps where naive nesting songbirds suffered high nest depredation levels.

As a result of Wilcove's work and that of many others (including pioneers Gates and Gysel 1978), ecological relationships occurring near forest edges are the most frequently assumed cause of avian responses to forest fragmentation. Response to edge, however, is often confounded with response to forest fragmentation, even though these two processes are very different. According to the edge hypothesis, forest birds will respond to fragmentation because it leads to an increase in exposure to forest edges. Birds may be attracted to (if nest predators) or avoid (if prey) fragmented landscapes where edges tend to be abundant.

Whether forest edges act as ecological traps to which birds respond remains unsure, however, because the vast majority of studies that documented

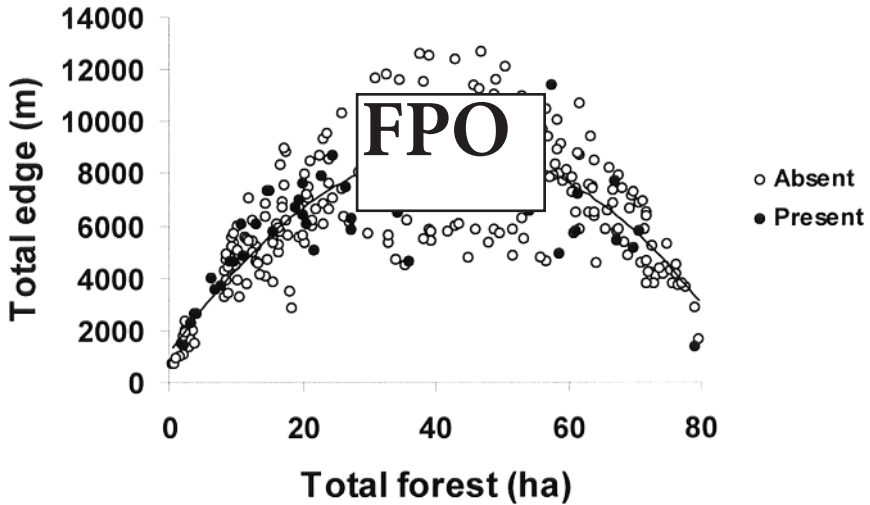


FIG. 5.1. Gray jays are not associated with landscapes dominated by forest edges. Each point represents one 1 km² landscape surrounding a bird point count station (see Drolet, Desrochers, and Fortin 1999 for details). The solid line represents a quadratic curve fit. Points above the line represent point counts made in landscapes with high amount of edge. Open circles: jays present; solid circles: jays absent. Data from J. Ibarzabal and A. Desrochers (unpublished ms).

such effects used artificial nests and therefore had no information relevant to birds' responses to risks associated with forest edges. Even in studies based on real nests, no formal effort has been made to determine whether birds respond to the various threats posed by the proximity of forest edges. We will need input from ethologists and evolutionary ecologists to determine the relative importance of lags in adaptive response and evolutionary trade-offs in explaining how and why forest birds should continue nesting near risky forest edges. Meanwhile, researchers have to contend with broad (and mostly unverified) classifications of species as "edge-associated," "edge-independent," or "forest-interior," as found in Whitcomb et al (1981), all of which are based solely on the pattern of establishment of *territories* relative to forest edges.

These classifications represent almost all we know about bird responses to edges, yet these classifications have to be treated cautiously (Villard 1998) for they are confounded by the diversity of field and analytical methods as well as possible variation in bird responses to edges among localities. Furthermore, these classifications only explore territory settlement patterns, even though responses to edges by songbirds may occur at other scales, such as nest site choice, as illustrated by Kuitunen and Mäkinen (1993).

Rather than seeking unrealistic generalities such as species-wide classifications as “edge-specialists” and the like, we may gain a better theory of avian responses to edges by comparing edge responses among species sharing a similar habitat. But first we must determine whether birds respond adaptively to forest edges and problems associated with them—nest depredation or parasitism, poor foraging habitats, and movement barriers.

Edges as Risky Habitats

According to a large number of studies based on artificial nests, it is clear that forest edges, at least in agricultural landscapes, are risky places in which to place a nest (Paton 1994, Murcia 1995, Hartley and Hunter 1998). Given the importance of nest depredation as a cause of nesting failure (Ricklefs 1969), there has been much attention given to edges as risky nesting habitats. It is usually inferred that nest predators coming from habitats adjacent to forests are the prevailing cause for increases in nest depredation near forest edges (DeGraaf 1995). Nest predators inhabiting forests, however, may also play an important role (Andrén 1995, Hannon and Cotterill 1998). Although the victim side of nest depredation near forest edges is well documented, the nest predator’s side of the process is virtually unknown, as is the response of birds to nest depredation risk near forest edges.

Nest depredation is not the only threat that birds nesting near edges face. Brood parasites such as the brown-headed cowbird (*Molothrus ater*) can travel into forests from their foraging habitats (fields and other nonforested areas) to lay their eggs in nests of forest songbirds. Again, the fact that cowbirds generally live outside the forest means that birds nesting near forest edges will be more exposed to their undesirable effects, as demonstrated in numerous studies, including the detailed study by Donovan et al. (1997). As with nest depredation, our knowledge of forest songbirds’ responses to brood parasitism is incomplete at best. Forest songbirds show a variety of responses to cowbird parasitism (Rothstein 1990), but responses documented to date generally refer to egg, nestling, or adult recognition, rather than the avoidance of particular nest sites, such as those near forest edges. Hobson and Villard’s work (1998) is an interesting exception; they demonstrate that the behavior of adult hosts changes in relation to levels of fragmentation and parasitism risks.

Whether birds respond or not to risks associated with forest edges should affect the way we manage these habitats. Therefore, experimental and observational studies should be designed to (1) determine whether birds prefer to place their nest away from edges (relative to the location of their territory) and (2) determine whether that tendency is modulated by how the risk of either nest depredation or brood parasitism increases near edges.

Edges and Foraging

Interspecific relationships such as those described in the preceding section are not the only reason why birds may avoid forest edges and associated fragmented forests. Food availability has been shown to decrease near forest edges (Jokimäki et al. 1998), and patch size (Burke and Nol 1998; Zanette, Doyle, and Trémont 2000) for certain nesting birds may account for edge avoidance by species such as ovenbirds (*Seiurus aurocapillus*). However, food may be generally more scarce at edges only for certain bird species, depending on their foraging requirements. Furthermore, foraging success has never been shown to decrease near forest edges. The lack of examples showing a decline of foraging success near edges is probably due to the limited research effort to date. However, it is possible that more research will not document such a decline if birds know about and therefore avoid poor foraging areas, such as edges. Again, only experimental, behavioral work can provide strong inference about forest edges as poor foraging habitat.

Can birds determine the potential value of forest edges as foraging habitats? Food hoarding provides interesting opportunities to answer this question. Recently, Brotons et al. conducted an experiment on food hoarding by wintering black-capped chickadees (*Poecile atricapilla*) (Brotons, Desrochers, and Turcotte 2001), with feeders placed near forest edges or in the forest interior. Birds taking food from feeders near edges tended to hoard their seeds further into woodland than birds taking their seeds from the forest-interior feeder. This pattern was especially obvious near edges more exposed to strong winds (Brotons, Desrochers, and Turcotte 2001). This result seems contradictory with Desrochers and Fortin's (2000) finding that wintering chickadees tend to forage near forest edges. However, the latter study was done over 2000 km from Brotons's study area, and was done during clement weather (little or no wind), conditions during which chickadees may not rely as much on food caches. It may thus be that forest edges are suboptimal chickadee foraging habitats only when cached seeds are most needed, such as windy days in late winter (see also Dolby and Grubb 1999).

To conclude with forest edges, it must be noted that associations between forest edges and bird occurrence will come from qualitatively different processes, depending on spatial scale, because of the wide array of spatial scales associated with different bird activities such as nest site choice, foraging, and territory establishment. For example, birds seeking territories may respond to the amount of forest edge within 1 km², while paying little attention to local edges (say, within 100 m) while foraging. The converse can also be true, as we found with family groups of gray jays (*Perisoreus canadensis*). Even though gray jays clearly respond to edges at close range when foraging (Fig.

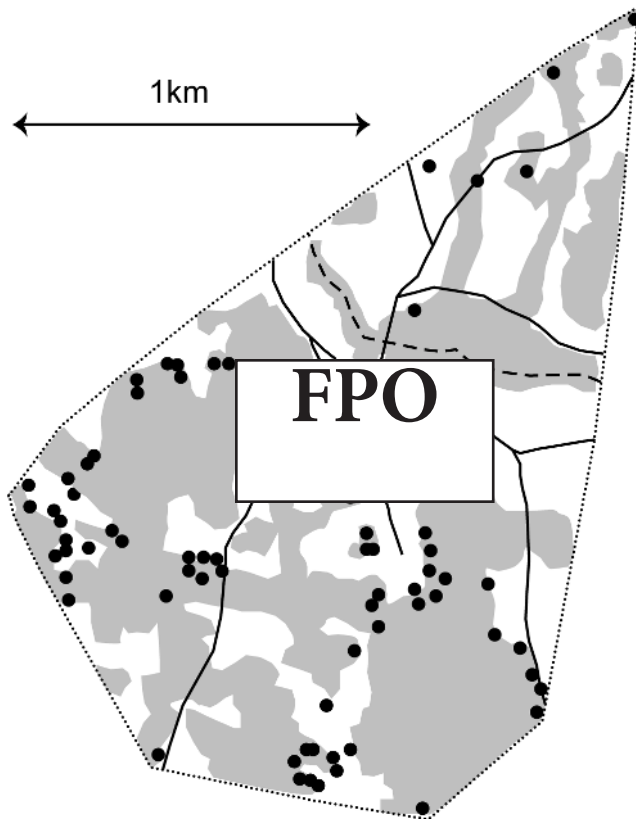


FIG. 5.2. Home range use by a family group of gray jays. Shaded areas represent mature woodland inside the convex polygon delimiting the home range. Data from J. Ibarzabal and A. Desrochers (unpublished ms).

5.2), their response to edges is not observable over whole landscapes of sizes comparable to their home ranges (see Fig. 5.1). This point has major implications, given the abundance of studies adopting a landscape approach, useful for territory establishment patterns but with no fine-grained information on bird movements. Surprising as it may seem, no study has yet attempted to document associations between response to edges at close range versus in the landscape as a whole for given species. It would be useful to test whether species with large home ranges (> 100 ha) are more sensitive to amounts of edge over whole landscapes, and whether species with small home ranges (typically < 10 ha) respond mainly to edges occurring within a few tens of meters. More evidence of the contrast between edge responses at different spatial scales for the same species would force a clearer definition of the term

edge avoidance and remove some of the confusion now prevailing in the literature since the classic work by Whitcomb et al. (1981) was published.

Scaling edge responses would also help provide more specific guidance for forest management, given that abundant edges at one spatial scale do not imply abundant edges at all scales. For example, forests can be managed for large homogeneous patches surrounded by edges convoluted at a small scale (fine-textured edges), thus benefiting species associated with edges at close range, and species avoiding edges at the landscape scale. Conversely, managers could promote a complementary set of bird species by producing a large number of small stands with linear edges, such as in forests harvested in “checkerboard” patterns (small, square clear-cuts).

Constraints to Movements

The hypotheses addressed in the preceding discussion portray landscape use mainly as the result of choices made by birds that had the opportunity to compare many landscape components. However, landscape use may simply stem from birds’ reluctance to venture outside forests when dispersing outside the breeding season, thus missing the opportunity to assess, let alone colonize, isolated forest fragments. If reluctance to enter gaps between forests is important, then forest edges will become barriers. The behavior of birds encountering gaps should therefore contain useful information about movement constraints as a potential process leading to avoidance of fragmented forests. The isolation of a forest fragment may be more important than its size in determining whether it will be used by a given species of bird.

How should we approach the study of constraints to movements across landscapes? The rapid development of movement ecology as a framework to analyze responses of animals to landscape configuration has revived interest in the study of edges, particularly sharp ones (Wiens 1995, Turchin 1998). Modeling tools such as cellular automata (Turchin 1998), and empirical tools such as fractal analysis (Wiens et al. 1995, Desrochers and Fortin 2000) may hold the key to a better understanding of how birds respond to forest edges, and provide an important piece in the puzzle of habitat fragmentation. A major remaining obstacle is the lack of knowledge of the direction (aim) of travel of individual birds through landscapes, as well as the strength of the motivation (Desrochers et al. 1999).

Despite the fact that bird territories or home ranges are sometimes found throughout forested parts of a landscape, irrespective of edges, birds may respond to edges either by “bouncing” on them, following them, or simply passing through them. Forest edges do sometimes act as filters or movement conduits, as has been shown in invertebrates (Wiens, Schooley,

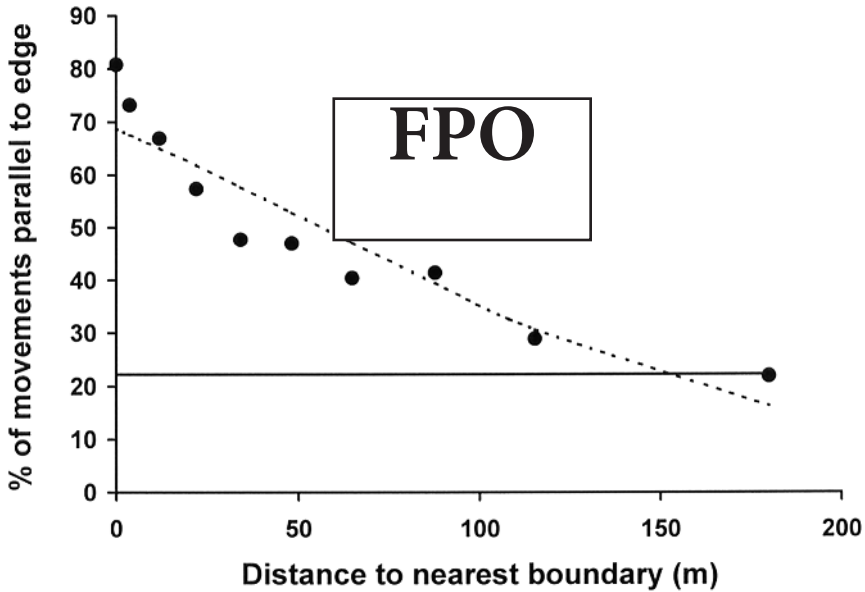


FIG. 5.3. Flocks of black-capped chickadees move parallel to forest edges upon their encounter. Reproduced from Desrochers and Fortin (2000), with permission from Oikos.

and Weeks 1997; Haddad 1999b), mammals (Kozakiewicz 1993), and birds (Machtans, Villard, and Hannon 1996; Desrochers and Fortin 2000). If gaps intervening between forest patches are effective barriers, movements of birds will change abruptly near edges, with consequences in terms of territory settlement as well as dispersal patterns. For example, even though they can be found anywhere in forests, flocks of black-capped chickadees are found disproportionately near edges because when they encounter an edge, flocks tend to move parallel to it rather than reenter the forest or cross a gap (Fig. 5.3). During the dispersal period, when presented with a choice between taking a detour around an open area (field or recent clear-cut), or flying a short distance through the open area, chickadees and other songbirds will often take detours several times longer than the shortcut in the open area, presumably to avoid risks associated with flying into open areas (Desrochers and Hannon 1997). Species-specific responses to forest edges seem to remain fairly stable among seasons, at least for nonmigratory species (Bélisle and Desrochers 2002).

With clear evidence that forest birds avoid traveling into the open, even through distances less than 100 m, one has to ask whether those fine-grained decisions translate into processes operating at the landscape scale. After

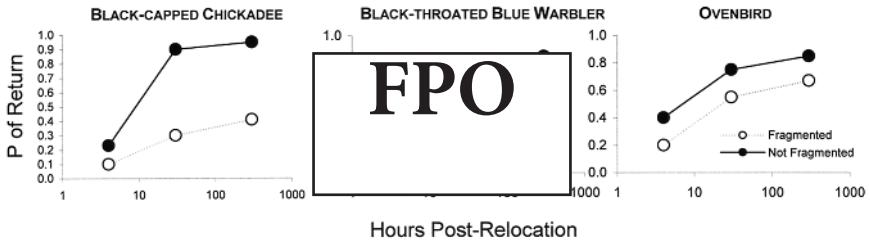


FIG. 5.4. Homing time and success of territorial males of three forest songbird species relocated over distances of 1 to 4 km. Sample sizes of 41, 72, and 92 from left to right. Solid lines: birds relocated across contiguous forests (> 70% forest cover); dashed lines: birds relocated across landscapes with 10 to 30% forest cover.

relocating ~200 territorial forest songbirds over distances of 1 to 4 km, Bélisle, Desrochers, and Fortin (2001) discovered that birds homed back less often, and after longer delays, when forced to traverse fragmented forests, relative to birds homing through contiguous forest (Fig. 5.4). Although several interpretations of this result are possible, they unquestionably show that landscape composition influences bird movements over landscapes. Given the investment made by males to establish a territory (and, presumably, the associated drive to return home), the process behind those results is likely a constraint on movements, such as a cumulative cost of encountering small movement barriers repeatedly.

Predictions of the movement constraint hypothesis would undoubtedly be more specific if empirical work such as already described was incorporated as measured (rather than guessed) parameters in modeling efforts such as those using cellular automata in real landscapes portrayed on geographical information systems (GIS). For example, real forest patch use could be compared to patch use by cellular automata moving under gap-crossing rules such as those measured by Desrochers and Hannon (1997). If constraints to movements are important enough, then birds are expected to settle for less when seeking territories, which means that isolated forest patches will be underutilized. Rarer opportunities to find conspecifics would be another negative effect of movement barriers created by gaps separating habitats, especially for less abundant species.

Conclusion and Recommendations

One of the symposia of the 1998 International Ornithological Congress assessed progress in bridging the gap between pattern and process studies of the consequences of habitat fragmentation (Desrochers et al. 1999). The

emphasis was on how the study of movement could help understand the study of bird occupancy patterns in the landscape. Since then there has been some progress, both empirical and theoretical, but the foregoing discussion makes it clear that wide gaps remain to be bridged between extensive studies seeking patterns, and intensive, behavior-based studies demonstrating (or rejecting) proposed processes.

More behavioral work will undoubtedly show that fragmentation affects not only the mobility of birds but also aspects such as foraging and reproductive strategy, as well as interactions between these factors. For example, because the dispersal of birds from one nesting season to the next is more prominent following nesting failure (Greenwood and Harvey 1982), it is likely that lower nesting success in edge-rich fragmented habitats will only make the impacts of movement constraints greater. We may never understand well the interactions among processes such as nest predation and dispersal, not to mention processes unaddressed here, such as interspecific competition. But perhaps it would be wise to better understand single processes before tackling interactions among processes.

This chapter illustrated some challenges that ethologists could address to bring some order to the current chaos created by ever-increasing amounts of disparate information on landscape use by animals, especially birds. Without unifying hypotheses based on behavior, the mass of information accumulated by landscape ecologists will amount to little more than hearsay that paves the way to useless, unfalsifiable claims such as “birds respond to fragmentation in variable ways in various places.” Worse still, the lack of theory may eventually discredit our efforts toward an understanding of fragmentation effects (and possibly our whole discipline) as an aimless accumulation of information.

How do we work toward unifying hypotheses? One possible answer is the comparative approach, to use rather than dismiss, the variety of responses to habitat fragmentation not only across, but also within, species. Comparative analyses may reveal that species less willing to traverse open areas (to be determined by ethologists) are indeed those that are most sensitive to fragmentation (already determined by landscape ecologists). Also, comparing responses to fragmentation between migrant and resident species may prove fruitful, given their contrasted use of landscapes, at least at certain times of the year. Failing to demonstrate this relationship would be a severe blow to the hypothesis that movement constraints is the key problem. Such a rejection (assuming proper statistical power) would constitute progress in the classic sense of what science is (Quinn and Dunham 1983).

Whatever insights are gained from an effective use of ethology, however, will not necessarily show us the way to effective wildlife conservation. A

greater challenge awaits ethologists as to how much decision makers, not to mention other ecologists, will incorporate recent findings into their agenda. Increasing the public's interest in the problem of forest fragmentation is another major task. Currently, studies of animal behavior sway the opinions of decision makers and the public not only through the solid knowledge they provide, but equally or perhaps more because of the sense of marvel toward wildlife they inspire. Whether this is satisfactory or not is a matter of opinion. However, if ethologists really believe they can contribute to alleviate the effects of forest fragmentation, hypothesized or real, I argue that they will have to exercise their skills on both fronts, aesthetic and scientific. This will be achieved by addressing their work not only to peer-reviewed journals and land managers but also to popular magazines, elementary schools, and the like. These undertakings should not be seen as competing with one another. Indeed, good science often naturally leads to results relevant and appealing to a wide audience (which, ultimately, decides on research funding), and thus aesthetics and science generally have a mutualistic, rather than antagonistic, relationship.

Getting people's attention is a tall order in these busy times, especially given that ethologists often seem reluctant to have their research agendas influenced by public or political opinion. Nevertheless, it is to be hoped that at least some ethologists will choose to embark on the journey to a theory of habitat fragmentation, before their own study areas become the stage for more habitat fragmentation and regional species decline.

Summary

The sensitivity of animals to habitat loss and fragmentation is of major conservation concern. Despite their great ability to move, birds appear sensitive to landscape fragmentation. Hypotheses proposed to explain well-documented distribution patterns of nesting birds in landscapes focus either on choices made by birds seeking territories or on behavioral constraints. Birds may choose particular landscape structures not because of movement constraints through landscapes but because of attributes of habitat patches that are correlated with landscape structure. For example, opportunities for extra-pair fertilizations and information exchange among conspecifics may be too limited in fragmented habitat patches to make those patches attractive even for noncolonial species. Additionally, birds may respond to food abundance, nest depredation, or brood parasitism risk near forest edges in fragmented landscapes. Alternatively, birds may be constrained in their use of landscapes because of their reluctance to cross gaps intervening between habitat patches, for gaps may present increased energy costs or depredation

risk during dispersal and breeding. Although landscape distribution patterns and their hypothesized causes have been well studied in birds, there has been almost no attempt to link these two kinds of evidence formally. I review recent work that addresses fragmentation issues from the standpoint of bird behavioral decisions with respect to dispersal movements, foraging, territory settlement, and reproduction. I propose that comparative analyses should be used to help provide more incisive predictions linking differences in behavior among species with associated differences in their use of landscapes. I conclude by stressing that solid science may not only provide aid to decision making, it may also provide material appealing to the public at large who, ultimately, decide the future of both behavioral research and land management.

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6.

Knowledge of Reproductive Behavior Contributes to Conservation Programs

Isabelle M. Côté

Behavioral studies have contributed relatively little to the multidisciplinary field of conservation biology. The relative isolation of behavior from conservation biology is odd, given the contributions that other branches of the natural sciences, such as population ecology, population genetics, and systematics, have made to conservation (Caro 1999), and the many recent attempts to highlight the potential importance of animal behavior for conservation (Ulfstrand 1996, Clemmons and Buchholz 1997, Caro 1998b, Sutherland 1998, Gosling and Sutherland 2000).

To understand how behavior might affect conservation, it is necessary to define clearly the goal of conservation. Textbooks commonly cite a twofold goal to conservation: (1) to assess the effects of humans on species, communities, and ecosystems; and (2) to mitigate these impacts to prevent species extinction and ultimately reintegrate affected species into functioning ecosystems (e.g., Primack 1998). A common human impact on species is a reduction in population size (or in effective population size). Measures to counter human impacts strive to prevent further declines or, ideally, increase population sizes. Thus, to show the importance of a behavioral approach to

conservation it is crucial to establish a link between individual behavior and population size. There is now a large body of literature that attests to the interaction between individual behavior and population processes (Goss-Custard et al. 1995a, Sutherland 1996, Anholt 1997, Levin et al. 2000).

In this chapter, I focus on a behavior that can influence population size: reproductive behavior. A wealth of data on reproductive behavior, with a well-developed theoretical framework for understanding and predicting the reproductive characteristics of animals, has accumulated over the last few decades. It is difficult to imagine that this information cannot make useful and novel contributions to conservation biology. Reproductive behavior can be linked to changes in population size, and hence to conservation, in two ways. It can be used as a predictor, where inherent differences in behavior lead to different population responses to conservation measures. Alternatively, reproductive behavior may react to conservation actions, with different reproductive responses leading to differences in population sizes. Although insights into behavior can lead, in both cases, to understanding the population consequences of conservation strategies, I believe that the study of animal behavior can make its most significant contribution as a tool for predicting the effectiveness of conservation measures on population sizes. But is this how reproductive behavior is used in conservation? Does ignoring reproductive behavior have an impact on the accuracy of our predictions of the potential effects of conservation actions?

I briefly review the potential role and current use of reproductive behavior as a predictive tool in four areas of conservation biology; namely, predicting (1) the effects of habitat loss, (2) the effects of exploitation, (3) the risk of extinction, and (4) the success of captive breeding, translocations, and reintroductions. I then present two case studies of simulation models to assess how reproductive behavior may affect estimates of population size. Finally, I consider the relative benefits of investing in studies of behavior versus investing in alternative activities to guide conservation action.

Predicting the Effects of Habitat Loss

The problem of predicting the effects of habitat loss and its frequent precursor, habitat fragmentation, on population sizes has been addressed on two scales. At the macrogeographic scale, the metapopulation approach has primarily used behavioral information on ranging and dispersal (Hanski and Gilpin 1997). At the microgeographic scale, behavior-based models have been highly successful in generating testable predictions of the impact of habitat loss on population size (Sutherland and Dolman 1994; Goss-Custard et al. 1995a; Yates, Goss-Custard, and Rispin 1996). These models have relied

so far almost exclusively on detailed studies of foraging behavior. Students of reproductive behavior lag far behind in using their findings to predict the impacts of habitat loss or alteration.

There are, nonetheless, a few remarkable studies of the importance of reproductive behavior in predicting the potential impacts of habitat loss. For example, Smith and colleagues (Smith, Reynolds, and Sutherland 2000; Smith et al. 2000) studied the reproductive behavior of the bitterling (*Rhodeus sericeus*), a European cyprinid fish that lays eggs in the gills of live freshwater mussels and that is threatened over much of its range. Female bitterling avoid mussels that already contain many bitterling eggs (Smith et al. 2000), a behavior that appears adaptive because of high density-dependent mortality of fish embryos in mussels. Using a population model incorporating reproductive behavior and demographic parameters, Smith, Reynolds, and Sutherland (2000) showed that loss of nursery habitat caused by cutting vegetation on riverbanks, a common practice in Europe, would yield a 48% decrease in bitterling population size. However, the accuracy of this prediction, which was validated in the field, depended on the inclusion of reproductive behavior in the model. When avoidance of parasitized mussels by bitterling was excluded from the model, population size was overestimated by 6%. This may seem like a rather small percentage, but it is one-quarter as large as the effect of ignoring predation by perch (*Perca flavescens*) in the model (Smith, Reynolds, and Sutherland 2000). Models of this kind are widely applicable to species, such as many salmonids, for which nesting site quality can be accurately quantified.

Similarly, detailed observations of breeding territory preferences of individual ringed plover (*Charadrius hiaticula*) nesting on beaches in Norfolk, England, revealed that birds settled preferentially on the widest and most vegetated stretches of beach (Liley 2000). This preference appeared related to the lower levels of predation and disturbance associated with wide beaches. By combining a knowledge of breeding territory preferences to potential changes in beach structure resulting from sea-level rise, a serious concern in East Anglia (Boorman, Goss-Custard, and McGrorty 1989), Liley (2000) modeled the impact of various climate change scenarios on plover breeding population size. His model can also be used to manage human disturbance to mitigate the impacts of change in sea level.

More often, however, the links between individual reproductive behavior, habitat quality, and population dynamics are examined without attempting to predict the impact of changes in habitat quality or quantity. For example, when examining the optimal territory selection strategy of individuals recruiting into a breeding population, Boulinier and Danchin (1997) concluded that the best option is to sample several breeding patches before

recruiting, even if this results in a missed breeding opportunity, only if the environment is predictable and contains a low proportion of good patches. Such a model could easily be extended to consider the effects of reducing the availability of suitable breeding habitat.

Predicting the Effects of Exploitation

Exploitation relies on the assumption that there is a yearly surplus of animals that can be culled without causing a long-term decline in population size. However, the removal of this supposed surplus is not usually random, and more often than not, it is biased toward larger and older individuals. Sex-biased culling may distort the sex ratio of surviving animals. Furthermore, the combination of gregarious social systems and specific mate preferences may exacerbate the effects of exploitation. For example, poachers in the past have selected mainly large male elephants (*Loxodonta africana*), which yield the largest tusks. This has resulted in highly skewed sex ratios (up to 74 females per mature male in some areas; Dobson and Poole 1998) which, combined with female gregariousness and preference for larger males (Poole 1989), may now limit conception rates (Dobson and Poole 1998). In contrast, in animals with indeterminate growth, such as fishes, selective harvest of the largest individuals often results in female-biased catches (Coleman, Koenig, and Collins 1996). Because egg number increases allometrically with female body length (Bagenal 1978), fishing can have a disproportionate impact on population productivity by removing the most fertile females. Moreover, the increased mortality generated by exploitation can select within a few generations for earlier ages or sizes at maturity (Rochet 1998, Law 2001). Whether these shifts in life histories are genetic or the result of phenotypic plasticity, they result in concomitant reductions in female fecundity with potential impacts for populations.

Reproductive behaviors can have a massive impact on population responses to harvesting. Some fish migrate to traditional spawning sites, which are highly predictable in space and time (Sadovy 1994). Fish with breeding aggregations are more vulnerable to exploitation than those with less discrete reproductive outbursts. Thus the Nassau grouper (*Epinephelus striatus*, family Serranidae), which once formed spawning aggregations of more than 100,000 individuals throughout the Caribbean (Smith 1972), has seen more than one-third of its aggregations disappear due to fishing and is now a candidate for the U.S. endangered species list (Sadovy and Eklund 1999). Similarly, northern cod (*Gadus morhua*, family Gadidae) off Newfoundland and Labrador were so efficiently harvested by trawlers fishing down spawning aggregations that this stock is no longer commercially exploitable (Hutchings 1996). The effects of exploitation may also vary depending on

patterns of parental care, with species exhibiting care being more vulnerable to fishing than species without parental care (Bruton 1995). If parental care behaviors make parents more susceptible to being captured, the impacts of exploitation will be far greater than catch numbers would suggest because a whole brood fails for each parent removed.

There have been a few attempts to predict the responses of species to exploitation, mainly on the basis of general life-history characteristics (Reynolds et al. 2001). For example, Jennings, Reynolds, and Mills (1998) found that North Atlantic fish stocks that have decreased in abundance in the past century mature at an older age, attain a larger maximum size, and exhibit significantly lower potential rates of population increase than their closest nondeclining relatives. More specific aspects of reproductive behavior have also been linked to specific population responses to harvesting. Greene et al. (1998) showed that mammalian breeding systems could affect how populations responded to hunting. Monogamous and weakly polygynous species are much more susceptible to culling of males than species where a single dominant male typically mates with many females. Other reproductive characteristics, such as infanticide by newly dominant males and reproductive suppression by dominant females, also contribute to reduce a population's ability to withstand exploitation. Studies of animal behavior can thus generate useful rules of thumb to assess the impacts of exploitation.

Finally, data collected on the reproductive behavior of common species for nonapplied purposes may be useful for the management of other species. The breeding success of pied flycatcher *Ficedula hypoleuca*, for example, is highly correlated with the autumn population levels of woodland grouse species, and thus could be used to set bag limits for these game birds the following autumn (Thingstad 1999). It is much easier to estimate breeding parameters for pied flycatcher than population size for grouse.

Predicting the Risk of Extinction

Through exploitation or habitat loss, populations may be reduced to numbers where positive density dependence prevails, a phenomenon known as the Allee effect (Stephens, Sutherland, and Freckleton 1999). If population density decreases further, it may decline past a threshold where the only outcome is extinction. Alternatively, stochasticity in birth and mortality can produce an increased risk of extinction for small populations (Stephens and Sutherland 1999). Can knowledge of reproductive behavior help us predict the susceptibility of species to Allee effects or to stochastic risk of extinction?

Allee effects that arise from impaired social interactions are more likely to be severe when conspecific attraction, for example to breeding grounds, is

strong. Colonially or cooperatively breeding birds are more likely to suffer from Allee effects than solitary nesters (Stephens and Sutherland 1999). Similarly, the fertilization success of marine invertebrates that form spawning aggregations to release their gametes in the sea decreases drastically at low density (Levitan, Sewell, and Chia 1992; Claereboudt 1999).

Mating systems appear to have general and consistent effects on the probability of population extinction. Dobson and Lyles (1989) showed that primate social system influenced threshold population densities below which reproduction would fail. Promiscuous primates, for example, may survive at smaller population densities than solitary or monogamous species. In birds, a similar pattern holds. Legendre et al. (1999) found that the probability of extinction was higher for strictly monogamous birds than for polygynous ones, when population size was small. Modest levels of female choosiness can also lead populations to extinction more quickly than random mating because if preferred males are unavailable, female choice effectively removes from the population females that could otherwise have bred (Legendre et al. 1999). Unfortunately, despite these tantalizing taxon-specific studies, there is still no cross-taxonomic, generalized framework for predicting the likelihood of extinction from reproductive behavior.

Predicting the Success of Captive Breeding, Translocations, and Reintroductions

Behavioral studies are clearly important for *ex situ* conservation by providing information about the most favorable physical, social, and genetic environments for the captive breeding of endangered animals. Similarly, a knowledge of ecological requirements and of basic behavior is required for the successful translocation or reintroduction of individuals into new habitats. But can the likelihood of success of captive breeding, translocations, and reintroductions be predicted from existing knowledge of reproductive behavior?

Some of the problems of captive breeding can be predicted through an understanding of sexual selection. Lack of mate choice imposed on captive females to promote genetic diversity, through exposure to a single mate or artificial insemination, may actually result in an impoverished gene pool. When given a choice among potential mates, a female should choose that which is healthiest, of highest quality, and most compatible with her own genotype (Andersson 1994). Lack of mate choice can result in low offspring survival (Møller and Alatalo 1999) and the spread of undesirable traits within the captive population. In hatchery-reared fish, for example, the random mixing of male and female gametes, stripped manually from adults, has relaxed

sexual selection and resulted in a drastic reduction in male traits associated with sexual competition (Fleming, Jonsson, and Gross 1994).

Sexual selection theory is also helpful for predicting the reproductive characteristics that predispose to successful translocations, reintroductions, or even introductions of exotic species. McLain, Boulton, and Redfearn (1995) found that sexually dichromatic birds introduced to tropical oceanic islands were more likely to go extinct than monochromatic species. Sorci, Møller, and Clobert (1998) found a similar pattern for birds introduced to New Zealand. These results are expected since sexually dichromatic species are generally under sexual selection, and intense male brightness relative to female coloration is correlated with reduced male survival, suggesting a cost of male–male competition (Promislow, Montgomerie, and Martin 1992; Owens and Bennett 1994). Moreover, demographic stochasticity is more likely to bring to extinction small populations in which females are choosy than those where mating is random (Legendre et al. 1999). It thus follows that species under intense sexual selection will require larger effective population sizes for successful introductions, translocations, or reintroductions than those under weaker sexual selection.

What Happens When Reproductive Behavior Is Ignored?

This section uses examples from two fishes to show how alterations of the physical and demographic environments can affect the risk of population extinction. Both cases show how knowledge of reproductive behavior is essential for the conservation of these species.

PREDICTING THE EFFECTS OF HABITAT LOSS ON RIVER BLENNIES

The conservation problems faced by river blennies (*Salaria fluviatilis*, family Blenniidae) are typical of northern Mediterranean fishes that live in small, localized populations. These problems include pollution, the introduction of exotic fish, and habitat loss due to physical alterations of watercourses (Maitland 1995). One relatively common form of waterway alteration, at least on the Iberian Peninsula, is the removal of stones and gravel for the building industry.

Male river blennies establish nests under stones and attract females for spawning. Females deposit a layer of eggs on the underside of the stone, and the male then guards the eggs against predators until they hatch. River blennies from four rivers in three separate drainages showed consistent breeding habitat preferences, with males selecting the largest available stones as nest sites (Côté et al. 1999). We found larger clutches under larger nest

TABLE 6.1. Predictions under different scenarios of river blenny reproductive output before and after a reduction in river stone size from 200 cm² to 50 cm² caused by extraction.

SCENARIO	NEST DENSITY (nests m ⁻²)			EGG PRODUCTIVITY (mm ² of eggs m ⁻²)		
	Before	After	Δ _D	Before	After	Δ _E
A "Reality"	0.15	0.08	-47%	85	342	-75%
B No avoidance of small stones by males	0.16	0.63	+ 294%	368	703	+ 91%
C No preferential spawning by females under large stones	0.15	0.08	-47%	511	266	-48%
B and C	0.16	0.63	+ 294%	549	2195	+ 300%

Δ_D: % change in nest density after stone extraction; Δ_E: % change in egg productivity after stone extraction. "Reality" is a scenario that incorporates knowledge of the reproductive behavior of river blennies.

stones. Combining this knowledge of reproductive ecology with a quantification of stone size distribution at exploited and undisturbed sites, we produced a simulation model that allowed a prediction of the impact of stone removal on blenny nest density and population egg production (Fig. 6.1a and 6.2a). Thus a reduction in mean stone size from 200 cm² to 50 cm², as observed at our Pyrenean study site, should result in a 47% decrease in nest density and a 75% decrease in egg productivity (Table 6.1; Côté et al. 1999).

Rerunning the simulation model without the constraints and assumptions set by a knowledge of reproductive behavior yields very different predictions. Wild males were never observed nesting under stones of less than 96 cm². If male preference for larger stones is ignored and no lower limit of nest stone size suitability is assumed, the relationship between nest density and stone size assumes a decaying exponential shape (Fig. 6.1b). One would then predict higher, rather than lower, nest densities when extraction reduces mean stone size in a river (Table 6.1). Similarly, egg productivity would be predicted to increase substantially (Fig. 6.2b, Table 6.1). If the propensity of females to lay larger clutches under larger stones is removed from the model and an average number of eggs is assigned to all nests regardless of stone size, estimates of nest density are not affected (Table 6.1), but egg production is

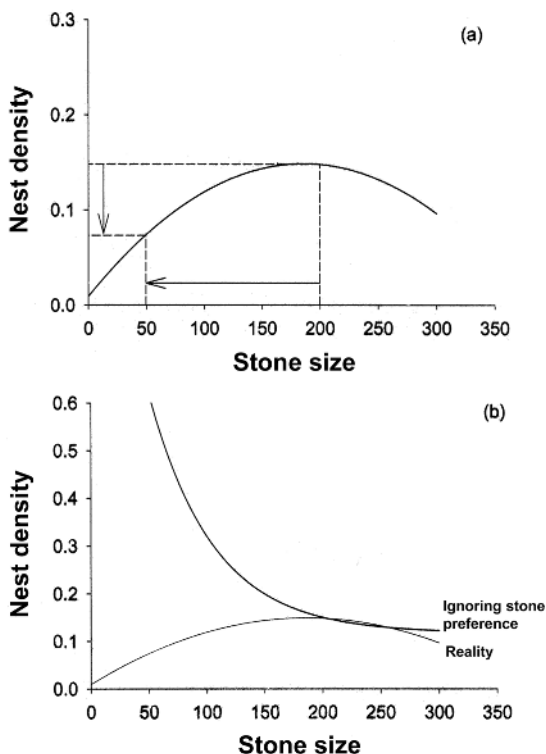


FIG. 6.1. Predicted relationship between nest stone size (cm^2) and river blenny nest density (nests/ m^2), (a) when incorporating male preference for large nest stones and (b) when assuming no male preference, with scenario (a) (= reality) shown in gray for comparison purposes. In (a), the arrows show the concomitant reduction in nest density resulting from a hypothetical reduction in stone size from 200 cm^2 to 50 cm^2 .

predicted to fall less severely than in the more realistic simulation (Fig. 6.2c, Table 6.1). Finally, if both male and female reproductive behaviors are disregarded, both nest density and egg productivity are predicted to show massive increases in response to stone extraction (Fig. 6.2d, Table 6.1). In fact, the densities of river blennies found in extracted sites were even lower than those predicted by the more realistic simulation, and no nests were ever found in disturbed river sections (personal observations).

It is clear that in the case of river blennies, habitat loss in the form of stone extraction would appear not to be detrimental, and on occasion would seem beneficial, if details of the fish's reproductive behavior were omitted from the predictive model.

PREDICTING THE EFFECTS OF EXPLOITATION ON A HERMAPHRODITIC FISH

Hermaphroditism is relatively common in reef fishes, with sex change from female to male (protogyny) occurring in 15 families and from male to female (protandry) in 6 families (Warner 1984). Individual fishes should change sex

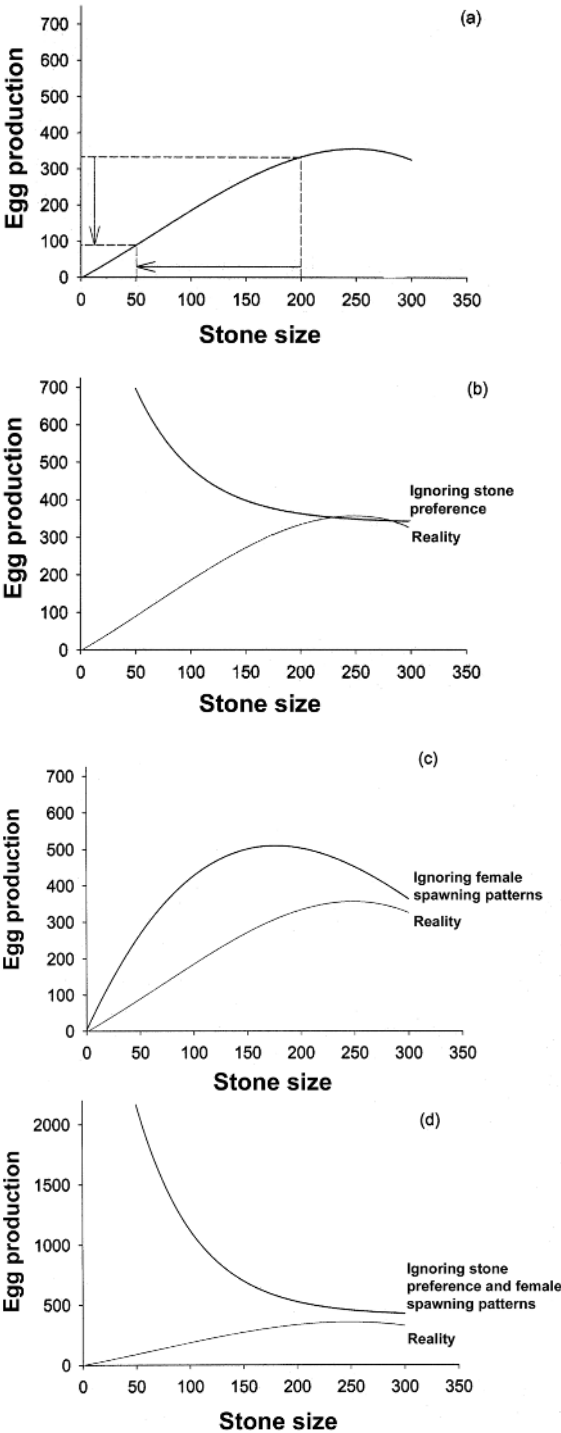


FIG. 6.2. Predicted relationship between nest stone size (cm²) and river blenny egg production (no. eggs produced × 1000) (a) when incorporating male preference for large nest stones, (b) when assuming no male preference for nest stone size, (c) when ignoring female propensity to lay larger clutches under larger stones, and (d) when ignoring both male nest size preference and female spawning pattern. In panels b–d, scenario (a) (= reality) is shown in gray for comparison purposes. In (a), the arrows show the concomitant reduction in egg production resulting from a hypothetical reduction in stone size from 200 cm² to 50 cm².

at a given age or size if sex change increases their reproductive success, compared to not changing sex at all (Warner 1975). The exact trigger for sex change remains unclear, but social and genetic controls have been suggested (Shapiro 1980, Warner 1984). Nevertheless, in sex-changing species, all large individuals tend to be of a single sex.

Current exploitation models (such as dynamic pool models) assume equal growth and fishing mortality for all members of an age or size cohort (Gulland 1977). Species with unorthodox sex determination and sex-specific growth rate, such as hermaphroditic fishes, are therefore overlooked by these models, whose direct application may lead to incorrect estimates of spawning potential or of optimal exploitation levels. Here, I revisit an earlier attempt (Huntsman and Schaaf 1994) to examine the impact of fishing on reproduction of a hermaphroditic grouper, the graysby (*Epinephelus cruentatus*). I ask specifically what are the consequences of ignoring the unusual life history of this species for the assessment of reproductive output.

The graysby is a relatively small (30 cm total length), reef-dwelling, protogynous grouper, ranging from North Carolina through the Caribbean, to Brazil. It is a long-lived, slow-growing species that is fished through most of its range, particularly where larger groupers are now rare. The life history parameters necessary for the simulation model were derived from Nagelkerken (1979). The model itself is based on a simple catch simulation in which the number of individuals alive in each of 10 age/size classes is determined, knowing the initial number in the youngest age class ($N_0 = 1000$) and the total instantaneous mortality rate Z (which is equal to the sum of natural mortality M , initially set at 0.13, and fishing mortality F).

Two sex-change scenarios were investigated: (1) gonochorism, where the number of live individuals in the population were assumed to be mature males or females according to a fixed and nearly even sex ratio (45 males:55 females as found in nature over all age classes; Huntsman and Schaaf 1994), and (2) protogynous hermaphroditism, where the number of mature males and females was determined using the age-specific sex ratios reported by Nagelkerken (1979). For simplicity, I assumed that sex change is under genetic control, occurring at a fixed age/size threshold. The population sex ratio is therefore variable according to the age/size structure of the population.

The reproductive output of the graysby population under each scenario was then approximated as the number of fertilized eggs produced. Egg production was estimated by first relating the number of live, mature females in each age class to biomass, and then female biomass to fecundity using known relationships. The likelihood of fertilization was obtained in two ways: (1) as a ratio of population male biomass to population fecundity (as in Huntsman and Schaaf 1994), which assumes that sperm limitation may occur at low

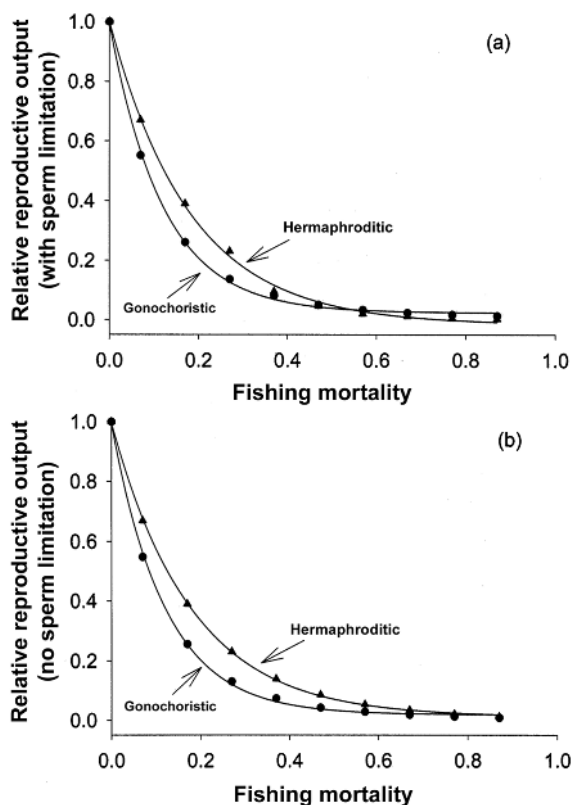


FIG. 6.3. Relative reproductive output of graysby (i.e., fertilized egg production at a given fishing mortality/fertilized egg production at fishing mortality $F = 0$) in relation to fishing mortality for gonochoristic (circles) and hermaphroditic (triangles) stocks when (a) sperm is limited and (b) no sperm limitation occurs.

male numbers; and (2) as a fixed proportion, set at 75%, which reflects recent studies of fertilization rates of hermaphroditic fish in the wild suggesting no evidence for sperm limitation (Petersen et al. 1992). Reproductive output is thus the product of fecundity and likelihood of fertilization, and is expressed relative to reproductive output at $F = 0$.

Not surprisingly, relative reproductive output decreases sharply with increasing fishing intensity (Fig. 6.3). Protogynous graysby tend to lose reproductive capacity more slowly than gonochores at low fishing intensity, but slightly faster at higher fishing mortality. This conclusion depends on whether sperm limitation is assumed to take place (Fig. 6.3a) or not (Fig. 6.3b). In the absence of sperm limitation, hermaphroditic graysby do as well (or as badly) as their gonochoristic counterparts under heavy fishing mortality. These results are largely similar to those of Bannerot, Fox, and Powers (1987), but at odds with those of Huntsman and Schaaf (1994) who suggested that hermaphroditic species lose reproductive capacity more rapidly than gonochores as fishing effort increases and also fail reproductively at lower fishing effort.

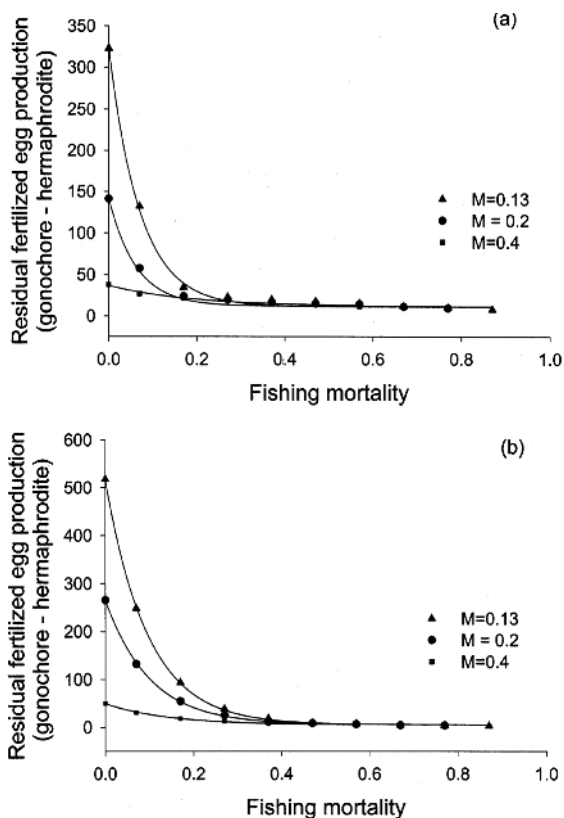


FIG. 6.4. Residual fertilized egg production of graysby (i.e., absolute fertilized egg production of gonochore minus absolute fertilized egg production of hermaphroditic graysby) in relation to fishing mortality at different levels of natural mortality, (a) assuming sperm limitation and (b) assuming no sperm limitation.

The fact that the relative reproductive output of hermaphroditic graysby is generally reduced less than that of gonochoristic graysby is biologically understandable. The exploitation of a gonochoristic fish stock removes from the population large males and large females, with the latter ceasing to contribute disproportionately to egg production. By contrast, exploitation of a hermaphroditic protogynous stock results in the removal of only males from the older size classes. Egg production is therefore not affected to the same extent if sperm depletion does not occur.

Absolute fertilized egg production is predicted to be much higher in the gonochoristic than in the hermaphroditic graysby at low fishing mortalities (Fig. 6.4) because large, very fecund females are assumed to exist under the gonochoristic scenario. However, this effect depends largely on the level of natural mortality: the higher the natural mortality, the lower the apparent initial advantage of gonochores (see Fig. 6.4). Although a relatively low natural mortality ($M = 0.13$) was used throughout these simulations, yearly mortality for species such as graysby may be as high as 0.4 (Pauly 1980, Hoenig 1983).

At high fishing mortalities, absolute egg production for gonochoristic and hermaphroditic stocks converges under all levels of natural mortality (see Fig. 6.4).

Even if gonochores have a higher absolute fertilized egg production most of the time, it is currently impossible to assess whether such an advantage would translate into increased recruitment, which would depend on the strength of density dependence in the survival of eggs and juveniles. Thus, ignoring hermaphroditism when modeling the impact of exploitation on graysby populations will inflate egg production estimates. If density dependence in the grouper's early life stages is weak, then stock size assessment may appear overly optimistic. If density dependence is strong, however, the accuracy of stock size estimates may not be unduly compromised. In fact, weak density dependence is likely to be acting in heavily exploited fish populations because resources are unlikely to be limiting (Lizaso et al. 2000). If so, then heavily exploited hermaphroditic fish stocks, which are most in need of accurate assessment for conservation purposes, will be most inaccurately estimated if sex change is not considered.

Conclusions and Recommendations

Studying reproductive behavior or doing something else: what is best for conservation? This chapter suggests that knowledge of reproductive behavior can, in many cases, alter significantly the predictions made in models of different management strategies. Before jumping to the conclusion that behavioral studies are always essential to conservation, however, we must measure the net benefit of obtaining information on reproductive behavior versus that of engaging in other activities that can also benefit conservation. But how can one compare the value of elucidating the proximate cue for sex change in an exploited hermaphroditic fish and the likely impact that this may have on the predictions on population responses to fishing, to the value of carrying out more field surveys to assess grouper abundance on reefs or in fish markets, or to the value of education programs about coral reef conservation? It may be technically possible to obtain such an answer through sensitivity analyses, but neither behavioral scientists nor conservation managers would deem this a worthy pursuit.

The costs of incorporating behavior into conservation projects can be minimal but the benefits enormous. A lot of the behavioral information necessary to assist in conservation decisions is already available. The details of the mating system or social organization of a rare species in need of conservation intervention may not be known, but often they will be for related species, and behavioral characteristics can be highly conservative. Owens and

Bennett (1995), for example, showed that most of the variability among birds in features such as foraging range and nesting habit occurred at the level of family or above. The behavior of an abundant close relative could therefore be used in lieu of precise knowledge of the behavior of a rare, little-known species to give valuable insights into the latter's requirements.

Several authors have outlined benefits of using a behavioral approach in conservation projects. There are three major advantages:

1. Behavioral scientists generally ask questions about fitness. They therefore identify key factors that affect individual survival and reproduction, and hence population dynamics (Arcese, Keller, and Cary 1997).
2. Behavioral scientists willingly use a predictive approach and have information that makes population models more realistic and more accurate (e.g., Bart 1995).
3. Behavioral scientists simply ask different questions than other members of a conservation team, such as a wildlife manager or even a molecular ecologist (Gavin 1989). They thus offer a different and often valuable perspective on conservation problems.

Given these potential contributions, the question becomes not so much whether behavior should be part of conservation projects but whether conservation projects can afford to ignore a behavioral perspective. As argued by Arcese, Keller, and Cary (1997), when the success of a conservation intervention depends critically on the response of a species to this intervention, the inclusion of a behavioral perspective becomes essential.

My conclusion suggests that the relevance of behavioral studies is limited to conservation projects focused on a single or a few species. This would be a limited sphere of influence indeed, since much of conservation biology today is about identifying and designating areas and ecosystems for protection. As the rate of area preservation slows down, however, issues about the appropriateness of park design in relation to species needs, about edge effects and corridor use, and about human–wildlife conflict management are starting to arise that are fully within the realm of behavioral science. Will behaviorists rise to the challenge of applying their knowledge and perspective to practical purposes? I certainly hope so.

Summary

I review the potential predictive role of reproductive behavior in four aspects of conservation biology: the effects of habitat loss, exploitation and culling, the risk of extinction, and captive breeding, translocations, and reintroductions. Reproductive behavior has the potential to influence the outcome of

most of these conservation actions through a number of mechanisms, including mate choice, social facilitation of reproduction, conspecific attraction to breeding sites, and Allee effects on reproduction, and has been used in a limited number of cases to predict the outcome of conservation measures. To examine specifically the effect of ignoring the minutiae of reproductive behavior, I focus on two case studies. The first involves predicting the effects of habitat loss on river blennies, an endangered European bottom-spawning freshwater fish. Considering nest site preferences of river blennies results in a greater predicted decline in population size than when nest preferences are ignored. The second case study investigates the effect of hermaphroditism in marine fishes subjected to exploitation. I compare the effects of fishing on populations of a tropical grouper, comparing predicted reproductive outputs under assumptions of sex change and gonochorism. In this situation, ignoring the fact that the species under exploitation is a protogynous hermaphrodite would lead to overestimates of stock size when the population is at particularly low levels. The details of reproductive behavior may therefore be important when planning conservation action. There may often be little financial cost involved in incorporating a behavioral approach in conservation projects and great benefits to be derived in terms of insights and predictive power.

Acknowledgments

I thank the many people who patiently discussed the various topics considered in this review: Jenny Gill, Phil Stephens, Bill Sutherland, Dolores Vinyoles, and particularly John Reynolds for explaining fisheries models. I thank Marco Apollonio and Marco Festa-Bianchet for allowing me to submit this chapter even though an unforeseen event prevented me from attending the meeting in Erice. I dedicate this chapter to Catherine, the unforeseen event.

7.

Foraging Behavior, Habitat Suitability, and Translocation Success, with Special Reference to Large Mammalian Herbivores

Norman Owen-Smith

This chapter evaluates how an understanding of foraging behavior might contribute to conservation. It is noteworthy that none of three recent books outlining how ethology has contributed to conservation included a chapter on foraging behavior (Clemmons and Buchholz 1997, Caro 1998b, Gosling and Sutherland 2000). Is food-seeking such a minor aspect of population viability that we can relegate it to academic treatments only? I think not. My view is that understanding how resources are acquired and allocated to maintenance, growth, and reproduction is central not only for theoretical ecology but also for conservation applications.

The specific conservation activity that I address here concerns the translocation of animals to new areas in the wild (Kleiman 1989). These exercises may be reintroductions in the sense that the species formerly occurred in the region (also termed repatriation), or introductions to places where the habitat is deemed suitable although historic records are lacking. The animals

translocated may either be captive-bred specimens being rehabilitated into the wild, or wild-caught animals being moved to a new area.

Despite large investments of time and money, a substantial proportion of such introductions have not led to self-sustaining populations (Griffiths et al. 1989; Wolf et al. 1996; Wolf, Garland, and Griffith 1998; Fischer and Lindenmayer 2000; Komers and Curman 2000). Failures have been associated with shortcomings in habitat “quality” in the release area (Wolf et al. 1996; Wolf, Garland, and Griffith 1998), and in some cases with high losses to predation (Short et al. 1992). It has been recommended that future translocation protocols be based on a rigorous, quantitative assessment of habitat quality (Wolf, Garland, and Griffith 1998). Subjective assessments of habitat conditions as “good” or “poor,” however, are inadequate, given the costs and risks involved. The primary goal of habitat assessments should be to maximize the initial rate of population increase so as to shorten the period during which the population is at risk (Komers and Curman 2000).

Habitat suitability depends fundamentally on the adequacy of food resources. The mere presence of suitable and accessible food is insufficient: the time required to capture this food, and the costs and risks incurred in the process, must be considered. This has been the subject matter of foraging theory since the defining papers of MacArthur and Pianka (1966) and Emlen (1966). For carnivores, potential food items in the form of the bodies of other animals are generally highly nutritious; the problem is how to catch and kill them. For herbivores, vegetation may appear to be available everywhere, but plant species and parts can differ widely in their nutritional value. Decisions about what to eat, and what not to eat, have important consequences for success in meeting physiological demands (Owen-Smith and Novellie 1982), most especially for females that are lactating or in late stages of gestation (Oftedal 1984). Moreover, vegetation growth is usually seasonal, so that the availability and nutritional quality of different food types change widely over time. Foraging behavior must be adapted flexibly to the prevailing circumstances if animals are to meet their nutritional requirements through the seasonal cycle. This encompasses not only diet choice but also food-procuring activities.

Habitat suitability also depends on security from predation and shelter from environmental extremes. The three fundamental habitat requirements—food, shelter, and security—cannot be viewed in isolation. Risk of predation may inhibit animals from using certain areas where suitable food is available, whereas a lack of food in secure habitats may force animals to forage in places that are risky (Sinclair and Arcese 1995a). Animals may avoid extreme cold or heat by forgoing feeding during times when these conditions prevail.

From a wider perspective, the habitat is just one aspect of the ecological niche of a species, its place or “profession” in the environment. The nutritional

benefits of different food types, and time and energy costs incurred in foraging, depend on morphological and physiological adaptations. For large mammalian herbivores, features such as mouth width and the capacity of the digestive system relative to body size crucially influence the rate and conversion efficiencies of ingesting and digesting different plant types, such as grass or browse (Owen-Smith 1982, 1985, Gordon and Illius 1994). Grazers and browsers tend to be distinct not only in features of the digestive tract but also in relative liver and salivary gland size (Hofmann 1989; Robbins, Spalinger, and van Hoven 1995). Among grazers, some species are relatively wide-mouthed, whereas others resemble browsers in having relatively narrow muzzles (Gordon and Illius 1988, Owen-Smith 1982, 1989). Anatomical distinctions lead species to partition food resources based on factors such as nutrient concentrations (Jarman 1974), height above ground (du Toit 1990), and leaf size (Cooper and Owen-Smith 1986). The “fundamental niche” may, however, be further restricted by predation risks, as well as by the effects of interspecific competition. These manifold influences were captured by Hutchinson (1959) in his conceptualization of the niche as the region occupied by a species within a multidimensional hyperspace of resources, conditions, and risks.

But this niche concept is misleadingly static. In the real world, individuals must respond to changing conditions over daily, seasonal, and annual time scales. Phenotypic features can be adjusted to some degree to cope with changing needs and constraints. Although modifications of morphology and life history can occur within individual lifespans, the most plastic aspect of the phenotype is behavior. Learning which food types to eat or avoid is an important component of foraging behavior, but so is knowing where to find such foods. Understanding the basic plasticity of foraging behavior of a particular species, as well as its limits, is important for assessing where and when populations will thrive or expire. Selecting the best food is fine when conditions are favorable, but what do animals do when those food types are no longer available? Here the interaction of innate predisposition, physiological tolerance, and capacity to learn at different stages needs to be understood.

My focus here is specifically on large mammalian herbivores. Conservation agencies face the dilemma of how to respond to small or declining populations of such charismatic species within protected areas, and frequently turn to the option of translocation either into or out of the area of concern. Some reintroductions of large ungulates have been spectacularly successful, notably bison (*Bison bison*) in North America, ibex (*Capra ibex*) in Europe, and white rhinoceros (*Ceratotherium simum*) in Africa (Gordon 1991). Yet there have also been numerous failures, most of these not adequately explained (Novellie and Knight 1994).

How could the success of such repatriation operations be more reliably

guaranteed? How could the suitability of habitats be identified with confidence before a reintroduction is attempted? How could initial problems that may arise following introductions into novel environments be mitigated? How could an understanding of the basic ethology of food-procuring guide such conservation actions? These are some of the questions I address in this overview.

Case Histories

Particularly illuminating are examples where introduced animals initially performed poorly, only to thrive at a later stage. The following are three case histories, outlined in some detail.

SABLE AT PILANESBERG

My personal confrontation with poor population performance following translocation came from setting up a study to establish why the sable antelope (*Hippotragus niger*) introduced into Pilanesberg National Park in South Africa were doing so poorly (Magome 1991). This park had been created in 1979 by moving people out of an area that had great scenic potential for ecotourism. The 530 km² area was then fenced and stocked with almost 6000 animals, representing 17 ungulate species (Anderson 1986). The understanding was that the people would ultimately benefit from the economic spinoffs from the wildlife park. A few species of large mammal still occurred in the park area, but most had to be purchased and brought in at considerable expense. Among the latter were sable antelope. The park was situated close to the type locality for this species in present-day Northwest Province. The habitat conditions and kinds of grasses available were judged to be ideal for the species. Sixty-seven animals were introduced from nearby game ranches in 1982–83, with special care taken to keep social units intact. Five years later, the population still totaled only about 70 animals, a poor gain for a population that should have increased at 20% per year, if most of the calves potentially produced annually had survived.

Our study examined whether food limitation could be a restriction on the population increase of the sable. We recognized that predation on calves by leopards (*Panthera pardus*) or brown hyenas (*Hyaena brunnea*), could also have limited population growth, but predation was difficult to study. No lions (*Panthera leo*) or spotted hyenas (*Crocuta crocuta*) existed in the park at that time. Hence, habit and food selection were investigated for four sable herds at different spatial scales: the landscapes where home ranges had been established, vegetation communities utilized within these ranges at different

stages of the seasonal cycle, and specific grassland types and grass species occurring in feeding sites. However, during the study year most females calved successfully and the population grew to 94 animals, an increase of 34%. By 1991 the sable population totaled 127. Problem solved!

The unexpected outcome of the sable research suggested that 5 years might have been the period required by the sable to establish an effective foraging strategy that enabled them to find nutritionally adequate food throughout the seasonal cycle. However, there were other possible explanations for the delayed population takeoff. The early years postrelease had received below-average rainfall, whereas the study period was a year of high rainfall. The sable depended on green grass regrowth on burns to carry them through the late dry season, and perhaps the prior burning policy had been less effective in making such food available during this critical period.

ORYX IN OMAN

For more enlightenment I turn next to the most thoroughly detailed study of an introduced ungulate population ever undertaken, that of the Arabian oryx (*Oryx leucoryx*) released into the central desert region of Oman in the 1980s (Stanley Price 1990). The species had been completely extirpated in the wild in 1972, the only survivors being animals in zoos. In 1982, 10 captive-raised oryx were released into the wild after a period of acclimation in pens in the chosen area. They were followed by 11 more in 1984. Further releases involved 11 animals in 1988 and 8 in 1989. By 1996 the population had grown to over 300 animals, a shining success. Regretfully, subsequent poaching for live sales of these highly valuable animals has had a severe impact, reducing the wild population to a small remnant (Gorman 1999).

Like the sable, the oryx population grew more slowly during the first few years postrelease than it did subsequently. Over the first 2 to 4 years the inherent rate of population increase, λ , was 1.08 (i.e., 8% per year), estimated from adjusted fecundity and mortality rates for the female segment (Stanley Price 1990); post-1988 it was 1.195 (recalculated from Spalton 1992). There were notable demographic improvements between these two periods: age at first reproduction decreased from 38 months to 24 months, and mortality of calves from birth to 1 month declined from 25% to 14% (Spalton 1992). Although severe drought conditions prevailed during the first 3 years postrelease, animals were supplied with supplementary forage to alleviate the food shortage. Thereafter, supplementary feeding was discontinued so that the oryx had to survive off the natural vegetation alone. Also, one of the dominant males proved to be sterile, which may have reduced the reproductive success of females that associated with him.

Nevertheless, observations revealed fascinating changes in foraging movements as the oryx settled into their new environment. Animals from the first release encountered a habitat devoid of other conspecifics. They made probing movements into new areas following rain, and occupied a sequence of temporary home ranges, each roughly 100 to 300 km² in extent, eventually extending their total range toward nearly 2000 km² (Stanley Price 1990; Tear, Mosley, and Ables 1997). When drought conditions ensued, the animals retreated back to the release area where supplementary forage was available. The second herd was released into drought conditions, and into an environment already occupied by other oryx. They moved less extensively; their total range encompassed 550 km² over 2 years. Observations suggested that individual animals retained a detailed spatial memory of all areas traversed, including the routes that had been followed between different ranges.

Some 6 to 8 years after introduction, oryx in these initial two herds no longer moved widely in response to rain, having apparently established where to find needed resources. In this later stage they made greater use of browse components, including acacia pods as well as leaves and flowers of other tree species, and so became less dependent on the basic *Stipagrostis* grass resource. In contrast, oryx from the two later introductions widened their monthly ranges in response to rain during this same period, just as the previously established herds had done earlier.

Observations indicated how the introduced animals spent additional time and energy getting to know their new environment and the location of resources within it at different times. These animals may have incurred nutritional deficiencies in the process, as evidenced by some mortalities ascribed to botulism due to eating old bones, perhaps to obtain more phosphorus. In later years, animals appeared to exploit the environment more effectively, and the decreased mortality rate, particularly among calves, allowed the population to achieve its full growth potential. If supplementary forage had not been supplied during the initial drought period, the population may have declined. After the first few years, supplementary feeding no longer seemed necessary. However, even after nearly a decade, animals had not located water sources hidden in the foothills on the fringe of the plateau. Although some wolves (*Canis lupus*) and caracals (*Felis caracal*) occurred in the region, predation had no apparent impact on the oryx population.

CARIBOU IN IDAHO

This revealing example involved the translocation from the wild of woodland caribou (*Rangifer tarandus caribou*) of two different ecotypes to augment a remnant native population persisting in the Selkirk Mountains in northern

Idaho (Warren et al. 1996). Animals of the mountain ecotype came from the Canadian extension of the Selkirk range, whereas northern ecotype animals were brought from the Fraser plateau region of British Columbia. Mountain ecotype animals typically depend on arboreal lichens for winter forage, which they can reach because of deep snow accumulations of 2 to 3 m. However, in the plateau habitat inhabited by the northern ecotype, the annual snowfall is much less, permitting animals to access terrestrial lichens by pawing open “craters” in the snow on exposed ridges.

Introduced into the new habitat, the northern animals showed much variability in habitat use during the first year, but only limited dispersal. In contrast, introduced animals of the mountain ecotype showed habitat-use patterns similar to those of the native caribou. The areas that the latter used during fall had more lichen available than those chosen by the northern animals, although by late winter there was no difference. During spring the two ecotypes diverged widely in their habitat choice, with the resident and introduced mountain stock occupying densely forested areas on northern slopes, whereas caribou of northern stock sought open and sparsely forested areas, generally with a southern aspect. Mortality rates over the first 3 years postrelease differed significantly between the two ecotypes, with 64% (14/22) of northern animals dying compared to 33% (6/18) of mountain stock.

In this situation the habitat-use patterns that had been traditional in the original ranges were maintained in the new area, to the disadvantage of one caribou ecotype. However, some modification of habitat selection traditions occurred when animals joined resident caribou and followed the movements of the latter.

OTHER EXAMPLES

In other cases, the initial rate of population increase following introduction was lower than that attained later. Asiatic wild asses (*Equus hemionus*) introduced into the Negev Desert of Israel showed only a 25% overall increase in the breeding female segment (from 12 to 16 animals) over the first 10 years following release (Saltz and Rubenstein 1995; Saltz, Rowen, and Rubenstein 2000). An obvious problem was the male bias in offspring from the prime-age females that predominated among the animals introduced. However, the individual reproductive success of females also remained low during the first 5 years postrelease. This was ascribed to the persistent effects of stress during capture and transport, and a carryover effect from the breeding facility where reproductive performance had been low. However, it is surprising that such effects persisted over 5 years. Foraging problems were not considered.

Similar observations were recorded for Cape mountain zebras (*Equus*

zebra) reintroduced within their former range. Population increase over the first 3 to 5 years postrelease averaged only 0.4% annually, compared with a mean of 9.3% subsequently (Novellie, Millar, and Lloyd 1996). Poor performance was ascribed to insufficient numbers being released, together with capture stress, breakup of family groups, and, vaguely, "adaptation to a new environment." Notably, for two cases where populations showed high initial rates of increase, the release site was close to the source population in the Mountain Zebra National Park, in similar habitat.

As already noted, reintroductions of white rhinoceroses have been widely successful. Nevertheless, mean calving intervals somewhat longer than those exhibited by the source population in the Hluhluwe-Umfolozi Park have been documented in several of the new localities (see Table 8.6 in Owen-Smith 1988).

An interestingly different case history is provided by the establishment of a population of mountain gazelles (*Gazella gazelle*) in the Hawtat Reserve in Saudi Arabia (Dunham 1997). The 71 captive-born animals initially introduced had more than doubled in numbers after 3 years. However, mortality over the first year postrelease was substantially higher for gazelles that were older than 3 years when released than for younger animals (54% vs. 19%), whereas among the older group it was greater for males than for females (73% vs. 38%). The direct cause of most mortality was predation by feral dogs and a lone wolf. However, the question remains why these age/sex classes were especially susceptible to predation, and not younger animals of both sexes.

Follow-up of the long-term case histories of ungulates translocated into South African national parks revealed that 85% (17/20) of attempts were successful, where the habitat was deemed suitable and the locality was within the former range of the species (Novellie and Knight 1994). Where either of these conditions was not met, only 13% (2/16) of translocations succeeded. In most instances, animals were moved into small parks where large predators were absent. Of five species reintroductions into the Kruger National Park, where large predators abound (including two cases subsequent to the period covered by Novellie and Knight 1994), only those of white rhinoceros and black rhinoceros (*Diceros bicornis*) have been successful. Notably, for the latter two species, adults are effectively invulnerable to predation. Lichtenstein's hartebeest (*Alcelaphus lichtensteini*) existed only as a small remnant a few years after release from their holding pen, whereas all introduced oribi (*Ourebia ourebi*) and suni (*Nesotragus moschatus*) have disappeared.

Twelve eland (*Taurotragus oryx*) repatriated to the Umfolozi Game Reserve in 1967 failed to establish a population (Brooks and Macdonald 1983). Although some lions were present, tick infestation rather than predation

seemed to be the prime cause of this failure. In contrast, all 17 ungulate species translocated into the Pilanesberg National Park between 1979 and 1984 have persisted, despite initial concerns about the viability of some populations (Anderson 1986). Notably, lions and spotted hyenas were absent at the time of the introductions, although lions were later introduced. Ungulates of various species have been translocated successfully to stock private wildlife reserves in South Africa on numerous occasions, although summary data are unavailable. Again, larger predators are usually absent or at least suppressed in abundance in such situations. Likewise, reintroductions of wallabies and smaller macropods in Australia have rarely succeeded in the presence of predators such as introduced foxes, feral cats, and dogs (Short et al. 1992).

OVERALL ASSESSMENT

Some notable features emerge from these case histories. Populations of newly introduced ungulates have frequently increased more slowly initially than subsequently, despite being given special care and despite the absence of predation on adults. Moreover, the restricted population growth initially was generally associated with poor reproductive performance by individual females, although small release number and demographic distortions may have contributed. In at least one instance, mature females also survived less well than young females. Strikingly, I could find no records of viable populations of ungulates established from introductions into areas containing abundant large predators, except for megaherbivores that are largely invulnerable to nonhuman predation.

Foraging Behavior

The implication from the preceding examples is that newly introduced animals perform poorly initially in acquiring the nutritional intake needed to realize their reproductive potential. Animals introduced into a new environment must learn new foraging habits, not only what plant types to consume but also where to find these at different times. Mothers may initially guide their offspring toward favorable plant species (Edwards 1977), but after weaning, young animals must extend this learning further, in particular to secure the key resources needed through the critical periods of late winter or the dry season.

Studies reveal that young ungulates have an innate predisposition to feed on certain food plants, which can become modified through experience. Bottle-raised roe deer (*Capreolus capreolus*) observed from birth to 1.5 months of

age discriminated among plant species at first contact, such that more bites were taken from generally preferred than from avoided species (Tixier et al. 1998). Thereafter the naive animals increased their consumption of species that were favored by experienced adults while still eating small amounts of species that wild deer generally rejected, except for two species that produced noxious sensations and potentially toxic consequences. Initial learning appeared to be primarily through taste rather than olfaction, perhaps reinforced by postingestive consequences, but later the fawns apparently learned to avoid the toxic species by odor. By 1 month of age, the fawns distinguished among plant species almost as well as adult deer, despite having had no maternal guidance.

Zoo-bred scimitar-horned oryx (*Oryx dammah*), transferred as adults into an acclimation pen in Tunisia prior to release, approached novel plant species cautiously and smelled the leaves (Gordon 1991). Sometimes the sniffing was followed by tentative nibbling and sometimes by the animals thrashing the bush with their horns. A small woody herb not eaten by sheep or goats was also rejected by the oryx, despite being abundant and green, and a shrub known to be toxic to domestic livestock was also not eaten. Thus food selection was discriminating despite lack of prior experience.

Hand-reared impalas (*Aepyceros melampus*) that had been removed from their mothers when only a few days old accepted without hesitation many of the plant species that were commonly eaten by wild impalas (Frost 1981). Other plant species were ignored, including some that became included in the diet of these animals after they had been released into the Nylsvley study area. During the dry season, our hand-reared kudus (*Tragelaphus strepsiceros*) (also at Nylsvley) expanded their dietary range to incorporate other plant species eaten rarely, or not at all, over the wet season (Owen-Smith and Cooper 1987, 1989). Acceptance ratings for various woody plant species were correlated closely with indices of nutritional value based on relative contents of nutrients, as represented by crude protein, and antinutrients, as represented by condensed tannins (Cooper, Owen-Smith, and Bryant 1988; Owen-Smith 1994). Some forb and shrublet species were never eaten, presumably because they contained unidentified toxins.

Hand-reared lesser kudu (*Tragelaphus imberbis*) and gerenuk (*Litocranius walleri*) likewise showed spontaneous acceptance of certain food species at first presentation, but rejected some species known to be consumed in the wild (Leuthold 1971). Naive white-tailed deer (*Odocoileus virginianus*) fawns selected a diet closely resembling that of experienced fawns and adults in species preference rankings, as well as in bite sizes, biting rates, and intake rate obtained (Spalinger et al. 1997). The notable distinction was for thorny acacia species, for which the bite rate of naive fawns was lower than that of

experienced juveniles. Likewise the bite rate of a naive young impala feeding on *Acacia tortilis* was slower than that of experienced animals feeding on the same species because it caught its lips and tongue on the recurved thorns (Dunham 1980).

Sheep that differed in their early nutritional experience, with food sources ranging from hay in pens through sown pastures to semiarid rangeland communities, showed marked differences in grazing preferences that persisted for more than a year despite attempts to change them (Arnold and Maller 1977). Sheep moved from pastoral areas to sown pastures took longer to adjust to the new food source than sheep transferred in the reverse direction, and adults took longer than lambs to adapt to new forages. Sheep that had been reared on hay grazed for 20% more time while feeding on natural rangeland than did sheep reared on pastures, but obtained 40% less food within this time. These large differences show how skills involved in manipulating food types can depend on early experience, with potential consequences for later food selection.

Observations of domestic sheep and goats show that young animals accept novel foods more readily than adults (Provenza and Balph 1987). Dietary learning is based largely on postingestive consequences, both positive and negative, of eating different kinds of forage (Provenza, Pfister, and Cheney 1992). Physiological adaptation to initially noxious chemicals can also occur. For example, sheep became more tolerant to the cyanogenic compounds sometimes present in clover after having been exposed to these chemicals for a period (Harborne 1988). Consequently, foraging behavior must be sufficiently flexible to allow resampling of food types to accommodate changes in noxious properties that may occur over time.

The capacity to learn to avoid poisonous plants may be underlain by a higher innate tolerance for the toxin in native than in alien populations. This has been most clearly documented for kangaroos and other species with distribution ranges either within or outside the range of highly toxic plant genera containing fluoracetate in western Australia (Twigg and King 1991). Eland likewise have some tolerance for this same toxin in a South African shrub called gifblaar (*Dichapetalum cymosum*; Basson et al. 1982). Neither our hand-reared impalas nor the kudus ate gifblaar at any stage while under observation, although they readily consumed similar-looking plants of other species. Cattle, however, cannot resist consuming gifblaar when it presents tempting new leaves in spring while the grass is still brown, usually with fatal consequences. We were unsure how our study goats would respond until one of them ate gifblaar in the presence of my colleague Susan Cooper. She dosed the goat with cooking oil to prevent the toxin from being absorbed and released the goat back into the study area. A few days later this same animal

again ate gifblaar when no one was around to help, and died. No learning had occurred on this occasion!

In summary, there is ample evidence that young ungulates can learn which food plants are most nutritious, presumably from subsequent physiological consequences. During the dry season or winter when animals must turn to less favorable species, they cannot depend on maternal tutoring. Animals are vulnerable to being poisoned by certain plant species that are highly toxic unless they have some innate tolerance for the toxin. Learning how to manipulate those plant species that require special handling, such as thorny species, appears to be more strongly restricted by early experience than by chemically assessing nutritional value.

Likewise, newly introduced ungulates face similar challenges in learning what not to eat from the novel array of plant species confronting them, and in gaining experience in handling the structural deterrents that many plants possess. Behavioral adjustments and physiological adaptation can take time to become effective, and in the meanwhile animals may be nutritionally disadvantaged.

An animal's performance depends not only on what foods it consumes but also on how efficiently it obtains these foods. We have already noted how efficiency in handling certain food types can affect ingestion rate. Search time is also an important component of foraging behavior. The margin between a daily nutritional intake that is adequate and one that is submaintenance can be quite small. Such differences can be responsible for changing habitat selection over the seasonal cycle.

In the Kruger National Park, kudus used open acacia savanna habitats extensively during the wet season but contracted their foraging range largely to hillslope base regions, or to riparian fringing woodlands, during the dry season (Owen-Smith 1979, du Toit 1995). Foraging efficiency, as assessed by the feeding time obtained per step taken, or more broadly by the proportion of foraging time spent actually feeding, was always higher in the hill base ecotone because of the greater concentration of woody plants in this region. Nevertheless, the greater availability of forbs and creepers, which constitute high-quality food types, in the acacia savanna was probably an attraction. In the dry season, when these plant types became less available and deciduous tree species had mostly shed their leaves, the acacia habitat was largely abandoned by the kudus. Notably, this took place after the feeding time per step had declined to under 2 seconds, and the proportion of foraging time spent feeding to less than 60%.

At Nylsvley, patches of acacia-dominated savanna were likewise favored during the wet season but largely abandoned during the dry season (Owen-Smith 1993). In the Kruger National Park, no resident kudu herds were

encountered within a region of largely umbrella thorn savanna that I traversed almost daily during my study period, although impala and giraffe (*Giraffa camelopardalis*) were regularly seen there. Kudus are absent from Tanzania's Serengeti National Park, although both giraffe and impala are common. What subtle vegetation differences distinguish areas that are suitable habitat for some browsing ungulate species and unsuitable habitat for others?

A modeling assessment indicated that kudus would have obtained a sub-maintenance energy intake had they foraged in the acacia patches during the dry season, largely because of the absence of any evergreen or semi-evergreen browse components to provide forage late in that season (Owen-Smith 2002). Impalas can obtain an adequate food intake rate when browsing fine-leaved thorn-trees because of their smaller size and their ability to graze as well as to browse (Cooper and Owen-Smith 1986). Giraffe have a special ability to strip multiple leaves from thorny branch tips (Pellew 1984), and their large size enables them to travel further and to obtain more nutrition from chemically defended evergreen browse during critical periods (du Toit and Owen-Smith 1989). A modeling exercise confirmed how sensitive the nutritional balance of herbivores can be to small differences in bite size and in forage quality, as influenced by morphological differences in body size and oral dimensions (Owen-Smith 1985).

Food sources that may be quite minor in their overall dietary contribution can be crucially important for bridging the critical period through the late dry season into the start of the new growing season (and presumably through late winter in temperate latitudes). For kudus, these foods included certain fruits that ripened toward the end of the dry season, as well as the flowers and foliage that were produced by certain tree species ahead of the rains (Owen-Smith and Cooper 1989). Notably, the latter included mostly species that were otherwise unpalatable due to the high levels of condensed tannins in their leaves (Cooper, Owen-Smith, and Bryant 1988). These bridging resources enabled our study animals to maintain their metabolizable energy intake no more than 10% below their daily maintenance requirement even during the final critical month of the dry season (Owen-Smith 1994). Without such resources, the animals would have starved more rapidly and may not have survived to the new growing season.

In following our habituated young kudus at Nylsvley, it was apparent that, rather than searching at random, they knew where particular resources occurred within the 215 ha pen to which they were confined. For instance, when nearing a tree producing the large "monkey oranges" that were sought out during the late dry season, it became a race as to which kudu reached the tree subcanopy first to find whether any fruits had fallen since the last visit.

Spatial cognitive aspects of foraging behavior have hardly been studied, at least for wild ungulates (Bailey et al. 1996).

Habitat suitability cannot be judged simply from the presence of edible and acceptable browse or graze during the favorable season. It depends also on how the supply of particular resource types persists over the seasonal cycle, and on the effective rates of food intake that these yield. Particularly important are vegetation components providing alternative or reserve resources through the winter or dry season period. Even unpalatable species offering submaintenance nutrition can play a valuable buffering role. Moreover, the use of particular habitats depends on their mosaic juxtaposition with other habitats within regional landscapes.

The chemical basis for food acceptance may be partly innate and readily modified from experience based on postingestive consequences. Less flexible are techniques of manipulating structurally challenging vegetation components to obtain an adequate rate of food intake. Lack of early experience may have more persistent consequences. Even more crucially important is the opportunity to locate resource types or habitat regions that yield an adequate, or at most marginally submaintenance, nutritional gain through critical bottleneck periods of the seasonal cycle. Without such vegetation components being available, what may seem superficially to be suitable habitat becomes unsuitable habitat in its capacity to support a population year-round.

A Current Conservation Dilemma: Roan Antelope in the Kruger Park

I will now highlight some challenging issues concerning the in situ conservation of South Africa's most threatened antelope species, the roan antelope (*Hippotragus equinos*), within its premier national park range. The roan population inhabiting the Kruger Park has always been small, with numbers varying around 300. Because of its rarity it was given special attention, to the extent of immunizing animals against anthrax by darting them with vaccine from helicopters. Nevertheless, between 1986 and 1993 the park population declined from a peak of 450 to a remnant of 45 (Harrington et al. 1999). The problem was recognized as being associated with excessive provision of artificial waterpoints within the roan habitat in the north of the park, which attracted an influx of zebra. The zebra exacerbated grazing impacts during a prolonged drought period, and led to an increase in lion abundance, heightening predation pressure on the roan.

The park managers acted firmly, if belatedly, by closing all boreholes within the core region of the northern plains habitat in 1994. Remnants of

roan herds that had been reduced to ones and twos were relocated to a 400 ha fenced enclosure offering suitable habitat within this region. Zebras tended to move off the plains following waterpoint closure, and the lions followed, but not completely because of remaining surface water around the edge of this arid region. Despite these measures, roan numbers continued to decline, such that by 2000 only 23 free-ranging roan remained, concentrated in two to three herds in the area of waterpoint closure. Almost all roan elsewhere seem to have disappeared. However, the 8 roan that were placed in the enclosure had increased to a total of 31.

The dilemma now is how to best preserve this small remnant of Kruger's gene pool of roan antelope. Should animals from the enclosure be released to augment the free-ranging population? Should the remaining free-ranging roan be moved to another enclosure elsewhere in the park? Should all of the roan be moved to captivity outside the park so they could multiply in captivity for later reintroduction? Should other roan be purchased at great expense to increase the Kruger population?

These decisions rest crucially on assessments of likely success, taking into account food supplies relative to predation risks. Animals released into the park face a full gamut of predators, from lions downward. The Lichtenstein's hartebeest that were released from the existing enclosure to make way for the roan have declined to a small, probably nonviable, remnant, probably largely through predation. Roan obtained from captive situations will be naive in their responses to predators and will thus inevitably suffer heightened attrition until the survivors gain experience. The park authorities are reluctant to interfere to the extent of culling predators in a large national park intended to promote natural ecological processes. What fraction of genes would be expected to persist were captive-held animals to be released into an aridified environment containing an abundance of predators? The dilemma is acute and unresolved at the time of writing.

A basic question remains: Why are the roan so vulnerable to predation? Their large body size (280 kg) facilitates digesting the poor-quality forage associated with the nutrient-poor savanna regions they commonly inhabit (Heitkonig and Owen-Smith 1998), but it probably makes them somewhat slow in evading a lion attack, compared with smaller grazers like wildebeest (*Connochaetes taurinus*) and tsessebe (*Damaliscus lunatus*). Also, larger species, who have a lowered surface area to volume ratio than smaller species, have greater difficulty dissipating the internal body heat generated during active foraging (Owen-Smith 1988). This could predispose roan to foraging somewhat more at night than during the day, especially during hot times of the year, which could also expose them to heightened predation risks.

Conclusions and Recommendations

Those responsible for translocation operations involving ungulates need to be more deeply aware of the foraging constraints that may restrict the performance of these animals in their new environment, at least for an initial period. Even when sufficient food may seem to be present, animals may not be able to harvest it at an effective rate. To gauge the success of new introductions, managers must consider the oral and digestive morphology and other relevant phenotypic features of the species concerned. Are the resources that are available adequate to support animals throughout the seasonal cycle, even during extreme years? Will the introduced ungulates be able to readily locate the food types needed to bridge crucial periods? An appropriate computational model is needed to address these leading questions. The model should specifically accommodate the adaptive adjustments of the animals to seasonally and annually changing conditions, in behavior, physiology, and life history features. If there is any uncertainty regarding resource security, supplementary forage should be provided during the crucial periods over the initial few years, then be progressively withdrawn.

The presence of any substantial predation risk, especially to adults, may just tip the balance between a situation where the herbivore population has a small but positive rate of increase initially, and one where a negative population growth leads inexorably to extirpation. Intervention may be needed to eliminate, or at least drastically reduce, the predator threat through the initial postrelease period. Once the herbivores are secure in their resource relationship, they are better able to confront the predation challenge.

Follow-up monitoring of animals postrelease is also crucially needed to identify resource inadequacies before they threaten population viability. Behavioral indicators of foraging efficiency, in particular time allocation both over the day and during foraging spells, should be coupled with spatial assessment of habitat-use patterns. In addition, seasonal changes in diet quality should be assessed from fecal analysis.

Summary

There is quite widespread evidence that the reproductive success and population growth rate of introduced ungulates are often poor in the first few years postrelease, but then tend to improve at a later stage in the same habitat. I suggest that this pattern could be due to the time required to learn where to find and how best to exploit the food resources needed at different stages of the seasonal cycle, and hence to initially inefficient foraging behavior. This is conjectural—only for the Arabian oryx introduction have aspects of foraging behavior been studied in any detail. Other factors could also contribute to

the poor population performance initially: physiological adjustments, social disruption, and vulnerability to predation. However, susceptibility to predation can also be heightened by nutritional shortfalls, and inefficient foraging exposes animals to greater predation risks.

Studies of foraging behavior reveal that ungulates are innately predisposed to consume particular plant species but also adjust their diet choice quite rapidly and sensitively to changing resource availability, probably by assessing the postingestive consequences of different forage species. The manipulation techniques initially learned to handle particular food types may be less flexibly altered for mature animals than for younger ones. Animals may require a long time, perhaps several years, to find and efficiently exploit the resources needed to bridge crucial periods of the seasonal cycle. This may result in reduced foraging efficiency and hence curtailed population performance during the first few years in a novel environment. Exactly how managers should cope with such foraging limitations following translocations constitutes the practical conservation dilemma. Recommendations include active intervention through the initial years, in the form of critically assessed food supplementation coupled with predator suppression where necessary.

Part III

Wildlife Management

Most of the chapters in this section are concerned with sport hunting of large mammals, but the problems considered and the ideas proposed here apply to other groups of animals that are harvested by humans. Sport hunting is the prevailing form of exploitative wildlife management in much of the world, and certainly in Europe and North America.

What does the knowledge of animal behavior have to offer to wildlife management? Wildlife managers are mostly interested in the number of animals available and the consequences of alternative harvesting strategies, so they are mostly concerned with population dynamics. Increasingly, however, managers are interested in individual quality, particularly in the case of trophy hunting, and recognize that the inclusion of species-specific behavior can be a powerful tool for choosing among different management strategies.

The importance of individual differences reverberates through all the chapters in this section. First, Jean-Michel Gaillard and coauthors examine how differences in behavior among species affect the reliability of different census techniques. It may seem incredible that a species could be managed without managers knowing its abundance, yet for roe deer all census techniques fail miserably to provide an adequate measure of population density. The only way to count roe deer is to mark most individuals and then apply capture-mark-recapture methods over several years. For other species, the reliability of censuses may vary with population density. In the second part of their chapter, Gaillard et al. examine how the incorporation of details on population structure may help provide more accurate predictive models of population dynamics. Individuals of different sex and age have different reproductive strategies, and so they have different probabilities of contributing to population dynamics by either reproducing or remaining alive. Information on sex/age composition of exploited populations is therefore particularly useful for managers.

The outcome of predator–prey interactions is affected by the behavior of both prey and predator. As large predators regain some of the ground they lost in the past century, particularly in mountainous areas of Europe and North America, they encounter prey individuals that appear to have forgotten what predators are and how to avoid them, sometimes with dramatic consequences. Joel Berger and collaborators explore some of the consequences of changes in community composition due first to the long-term absence of large predators, and then to their reestablishment, either naturally or through reintroduction programs. The importance of behavior in the planning of reintroduction programs was already underscored in chapter 7 and is further emphasized by Marco Apollonio and coauthors, particularly with regard to the reintroduction of large predators. Few such introductions have been attempted, and the ongoing experimental reintroduction of brown bears (together with the natural recolonization by wolves) in the Alps will tell us a lot about whether modern humans are able to coexist with large predators. The behavior of both species is crucial to their return to the Alps.

Unfortunately, just as some moose in Wyoming do not know how to behave toward large predators, humans in the Alps have forgotten how to behave toward bears and wolves. Much of the current behavior of humans in the Alps, particularly several agricultural practices, is incompatible with large predators. Recovering predator populations are rapidly changing the dynamics of many areas where sport hunting of ungulates has gone on for decades in the absence of any predator-induced mortality on adults. In some of these areas, managers are unfamiliar with the behavior of large carnivores, and results from areas where carnivore populations have persisted may not necessarily be an appropriate guide for how to deal with recovering populations.

Recolonizations by large predators are certain to provide many challenges to conservationists and wildlife managers. At a time when conservation biology mostly deals with losses and extinctions, it is refreshing to realize that some management problems are due to increases in biodiversity. Wolves, bears, and lynx are returning to parts of their historic range in the Alps, the Pyrenees, the Rockies, and Scandinavia. In Sweden, bear populations have recovered to the point where sport hunting of bears has increased. Brown bears are also hunted in Canada, Alaska, and Russia. Normally, one would expect that in a polygynous species it should be possible to harvest a considerable proportion of males because one male can breed with several females. Jon Swenson, however, uses his long-term research on bears in Scandinavia and literature on other large carnivores to suggest that in some cases male harvest may have a greater impact on population dynamics than we may suspect. Individual behavior, once again, is at the base of that suggestion: if surviving male bears kill cubs fathered by bears shot by hunters, the killing of an adult

male may have an impact on population growth rate similar to the killing of an adult female.

Managing for sport hunting poses a number of ecological, social, and economic challenges to wildlife biologists. Some of those challenges can only be met by taking animal behavior into account. Inevitably, harvest has a quantitative impact on populations, but over the long term it may also have a qualitative impact. Behavioral ecologists are used to thinking of evolutionary questions, and it may benefit wildlife managers to also think of the potential evolutionary impacts of different harvest strategies, as examined by Marco Festa-Bianchet in the last chapter of this section. Once again, emphasis on individual differences leads one to view the impacts of sport hunting under a broader spectrum than that provided by a simple consideration of numbers counted, numbers shot, and numbers likely to be available next year.

8.

Variation in Life History Traits and Realistic Population Models for Wildlife Management:

The Case of Ungulates

Jean-Michel Gaillard, Anne Loison, and Carole Toïgo

Most populations of large vertebrates are now the target of intensive management or conservation programs (Caughley and Sinclair 1994). These programs usually entail a four-step process (five steps if we include the initial choice of a management goal): (1) assessment of population status using several measurements of population parameters, such as survival and reproductive rates, habitat quality, or animal condition; (2) some measure of population performance to synthesize the different measures performed during the population assessment stage (at this point, managers know whether the population is declining, stable, or increasing); (3) deciding what strategy is most appropriate to attain the goals of a management or conservation plan to balance the observed performance with the desired status of the population; (4) forecasting the population effects of a given management or conservation action so managers can assess the effectiveness of their strategy. At each of these four steps—parameter estimate, population performance assessment,

decision, and forecasting—population models play an important role, and the choice of model may affect the outcome of each step.

For population assessment, field data are usually collected through some sampling procedure. Various models can then be used to estimate population parameters from the field. For example, monthly observations of previously marked animals can be collected from a sampling design stratified according to habitat type. Then a capture–mark–recapture (CMR) model (see Schwarz and Seber 2001 for a review) may be used to estimate habitat-specific population size and/or monthly survival.

To obtain a global measure of population performance, information provided by each of the population parameters during the first step has to be combined. Once again, models are required to perform this task. Returning to our example, habitat-specific estimates of population size can be modeled through linear regressions to assess population growth rate (Lebreton and Millier 1982).

To reach their management goal, managers need to identify the target of management actions. Suppose that the goal was to maintain a stable population, but the population actually grew by 30%. Demographic models could simulate different scenarios and suggest which harvest strategy would stabilize the population. Lastly, simulations of the expected consequences of a management strategy could assess whether it had the desired results.

Intensive monitoring programs generally focus on two broad types of populations for which both analyses and currencies generally differ. First, for endangered populations, Population Viability Analysis (PVA) is the most common type of model used. Extinction risk is thus often the currency (Boyce 1992). Population dynamics are also often performed for exploited populations. Here, the currency is the population growth rate or the natural rate of increase (Tuljapurkar and Caswell 1996). This chapter focuses on ungulates, a group that is intensively managed all over the world (Nowak 1991) and whose population dynamics have been intensively studied, particularly in temperate areas (Gaillard et al. 2000).

Historically, two approaches have been used to manage ungulate populations: time series of population counts, which generally consist of yearly estimates of population size, and demographic models based on yearly estimates of fitness components. After briefly reviewing the basic principles of both approaches, we present case studies to highlight the current limits of the models, and then demonstrate how they can be improved by accounting for life history variation among sex/age classes and among individuals.

Using Population Counts: Principles and Limits

Although several methods are available to estimate population growth rate from a time series of population counts (Lebreton and Millier 1982), regressing yearly estimates of population counts (after log-transformation) on time is the most commonly used procedure: the slope of the regression is the population growth rate. Several problems, however, affect the estimation of yearly population size. Despite many improvements in field techniques, sampling designs, and statistical procedures (Seber 1986; Buckland, Goudie, and Borchers 2000; Schwarz and Seber 2001), counts have generally low precision (the coefficient of variation is seldom less than 20%; Caughley 1977) and low accuracy (Strandgaard 1972), and variation in counts is often difficult to interpret (Morellet et al. 2001). Two case studies will demonstrate the magnitude of such problems in ungulate populations.

COUNTING ROE DEER

The roe deer (*Capreolus capreolus*) is a medium-sized, inconspicuous forest-dwelling species. Given these characteristics, we can expect rather large biases in assessment of population size. Indeed, severely biased estimates of roe deer population size have been reported (Strandgaard 1972, Pielowski 1984). In both of these studies, a total removal of roe deer showed that true population size had been underestimated by a factor of three. These experiments, however, do not provide information about whether field assessments of population size over time tracked the real variation of population size over years.

The intensive, long-term monitoring of the roe deer population in Chizé (West France), provides the opportunity for such a test (Gaillard et al. 1998b). Because about 70% of roe deer have been individually marked since 1979, we can confidently assume that the CMR estimates of the population are accurate (Strandgaard 1967, Gaillard et al. 1993). Therefore, we tested whether indices of yearly population size estimated from road counts at night, a census method commonly used for roe deer (Maillard, Gaultier, and Boisaubert 1999), tracked the yearly population size estimated from CMR. Although roe deer population size varied from about 200 in 1980 to 500 in 1984, yearly variation in the number seen per kilometer was not correlated with the yearly variation in population size (Fig. 8.1), indicating that night counts are useless to monitor temporal variation of roe deer population size. Individual variation in behavior likely affects the detection probability of roe deer (Ellenberg 1978), as do observer differences in the ability to detect roe deer from the road (Delorme 1989, Van Laere et al. 2001).

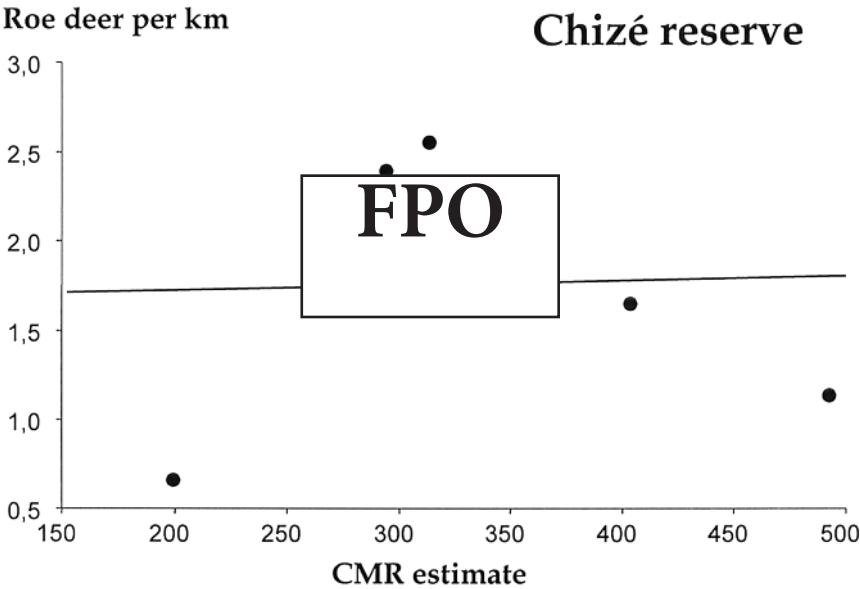


FIG. 8.1. Capture–mark–recapture (CMR) estimates of the size of the Chizé roe deer population (West France) and number of roe deer seen per km of road during night counts over 6 years.

CENSUSING IBEX

Our second example comes from studies of Alpine ibex (*Capra ibex*), a species that contrasts markedly with roe deer: ibex are large, usually live in open mountainous areas, and are very conspicuous (Couturier 1962). Consequently, managers often rely exclusively on ground counts to assess status of ibex populations (Girard 2000). Therefore, we expected ibex counts to be rather accurate. The long-term monitoring of the ibex population of Belledone (France) allowed us to test the reliability of ibex counts. Many ibex at Belledone have been individually marked since 1983, allowing for a CMR estimate of population size. We measured the proportion of underestimation as $(\text{CMR estimate} - \text{number of ibex counted}) / \text{CMR estimate}$ (see Toïgo 1998 for details). Contrary to our expectation, counts consistently underestimated population size by at least 20% (Table 8.1). Moreover, the rate of underestimation increased markedly with population size: less than half the total number of ibex was counted as the population increased beyond 100 (Table 8.1). Differences in ibex behavior according to age and sex class may account for some bias in counts. Thus, although an unbiased count would lead to a

TABLE 8.1. Reliability of total population counts of a colonizing alpine ibex population (Belledone, France).

YEAR	TOTAL COUNT	RATE OF UNDERESTIMATION
1988	39	22
1989	41	37
1990	35	36
1992	35	62
1993	110	43
1994	96	60

Reliability is measured by the rate of underestimation assessed from capture–mark–recapture (CMR) estimates of population size (see Toigo 1998 and text for details).

sighting rate of 1.00 whatever the ibex category, a study in Les Ecrins National Park revealed between-sex differences in sighting rates. In the colonizing population of Champsaur, sighting rates of 0.84 and 0.92 were estimated for males and females, respectively (Spaggiari 2000). Individual heterogeneities in sighting rates may be higher in well-established populations of ibex, where both nursery groups and male groups are large (Gauthier et al. 1994; Toigo, Gaillard, and Michallet 1997), increasing the probability that some individuals will be missed.

The case studies of roe deer and ibex underline severe problems with the use of population counts to manage ungulate populations. It is well known that most counts underestimate population size. Our examples highlight two other major pitfalls of population counts that may invalidate them as management tools: inability to track yearly changes in population size (in roe deer) and increasing rate of underestimation with increasing density (in ibex). The latter problem may render hopeless the search for a correction factor, often used to calibrate population indices. Therefore, the main weaknesses of the approach based on counts occurs at the population assessment step. When population counts are applied to the management of ungulates, another major problem occurs at the third step of the process, when a decision has to be made. Population counts only provide a global measure of performance. Even assuming that counts are reliable, however, population growth rate does not tell us how to reach a management goal, and additional information is required. Demographic models built on field assessment of fitness components provide such information.

Demographic Models: State of the Art and Possible Improvements

Demographic models are usually based on population matrices (see Caswell 2001 for a review). Among such models, the simple Leslie matrix model (Leslie 1945), a deterministic, age-structured, and female-dominated model, is most commonly used to manage ungulate populations (Eberhardt 1991). Leslie matrix models can estimate the asymptotic natural rate of increase (λ), the asymptotic stable age structure and the generation time (the mean weighted age of reproducing females). These models require mean yearly estimates of fitness components, including reproductive parameters such as age of primiparity, age-specific proportions of breeding females, age-specific fertility (average number of females produced per female), juvenile survival from birth to 1 year of age, and age-specific survival of yearlings and adults.

Consider an ungulate population where females first breed at 3 years of age, 95% of females 3 years or older breed every year and produce one offspring (therefore have a fertility of 0.5 assuming an even sex ratio), 65% of newborns survive over their first year, 80% of 1-year-olds survive over their second year, and 90% of adults survive from year to year. That population will have a λ of 1.12 and a generation time of 6.08 years. Leslie matrix models have high heuristic value (Eberhardt 1991) but only account for age variation. Although age is undoubtedly a main structuring factor of vertebrate populations (Charlesworth 1994), life history variation also originates from many other factors. Previous studies have reported that temporal variation generated by density dependence (Fowler 1987) and/or environmental variation (Newton 1998), sex (Short and Baladan 1994), spatial structure (Gilpin and Hanski 1991; Milner-Gulland, Coulson, and Clutton-Brock 2000), phenotypic (Sauer and Slade 1987) or genotypic (Moorcroft et al. 1996, Slate et al. 2000) quality, and infrapopulation structures such as cohort (Albon, Clutton-Brock, and Guinness 1987; Gaillard et al. 1997; Coltman et al. 1999a) and family (Gaillard et al. 1998a) may influence markedly population dynamics of vertebrates. In the following, we will assess whether accounting for environmental variation, cohort variation, and between-sex differences in fitness components will improve our understanding of ungulate population dynamics.

ENVIRONMENTAL VARIATION: ROE DEER AT CHIZÉ

The roe deer population at Chizé has been monitored since 1977. In this fenced forest of 2614 ha, animals were marked either as newborns in May–June or as weaned fawns in January–February, and were thereby of

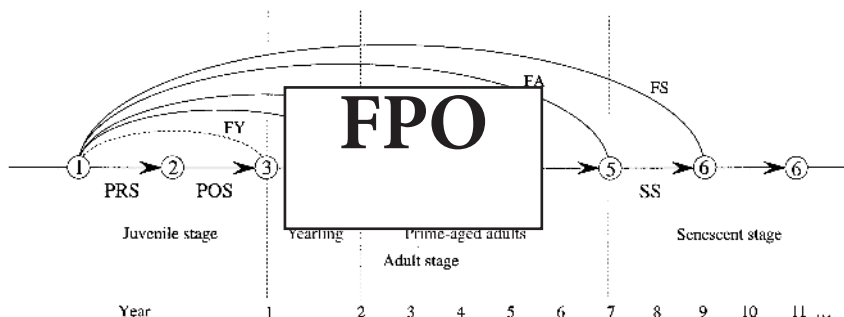


FIG. 8.2. Life cycle of roe deer: (1) newborn, (2) weaned young, (3) yearling, (4) 2-year-olds, (5) prime-aged adults, (6) senescent adults (older than 7 years). Straight lines indicate transitions from one age group to the next, curved lines indicate reproduction. These fitness components describe the development of individuals through the life cycle:

PRS: summer survival of fawns; POS: winter survival of fawns; YS: yearling survival; AS: prime-age adult survival; SS: senescent survival; FY: fecundity of yearlings; F2: fecundity of 2-year-old females; FA: fecundity of prime-aged females; FS: fecundity of senescent females.

known age. Here we use data collected over 15 years (1985–1998) during which more than 70% of the deer were individually marked, providing reliable estimates of required fitness components from CMR modeling (Gaillard et al. 1992, 1993, 1997, 1998b). As is typical for ungulates in temperate areas (Gaillard et al. 2000), the life cycle of roe deer has three main stages (Fig. 8.2): a juvenile stage subdivided into summer (survival from birth to weaning) and winter (survival from weaning to 1 year), a prime-age stage pooling the nonreproductive yearlings with adults aged 2 to 7 years (Gaillard et al. 1993) that reproduce annually (Gaillard et al. 1992), and a senescent stage (beyond 8 years of age) during which both survival and fertility decline (Gaillard et al. 1998b).

Mean estimates of fitness components (Fig. 8.3) were entered in a Leslie matrix model to calculate the natural rate of increase and the mean generation time. The results showed that between 1985 and 1998 the population had a mean natural rate of increase of 1.188. Generation time was 5.37 years. We then performed a sensitivity analysis to determine which fitness component was the most influential for roe deer population dynamics. A prospective analysis of perturbation (*sensu* Caswell 2000) based on elasticity (corresponding to the relative sensitivity, de Kroon et al. 1986) showed that survival of prime-aged females had the highest elasticity (0.698), whereas the breeding

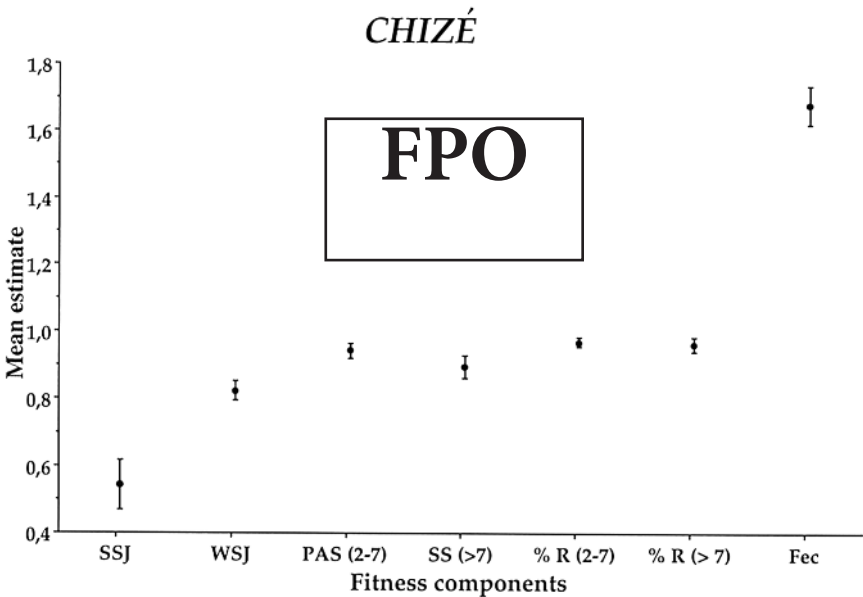


FIG. 8.3. Mean estimate of fitness components obtained from the capture–mark–recapture (CMR) monitoring of the Chizé population (West France) between 1985 and 1998.

proportion of females older than 7 years had the lowest elasticity (0.038). The elasticities of fawn survival (0.191), fertility (0.191), and breeding proportion of prime-aged females (0.111) had intermediate values. These results suggest that the impact of a given variation in survival of prime-aged females on the natural rate of increase is at least 3.65 times higher than the impact of the same variation in any of the recruitment components (juvenile survival, age-specific breeding proportion, and fertility). From the prospective analysis, we may thus conclude that survival of prime-aged females is the critical component of roe deer population dynamics.

Two main limitations are inherent to prospective analyses. First, from a biological viewpoint, the notion that prime-age survival is key to explaining variation in growth of ungulate populations may appear trivial. Indeed, the existence of a “slow–fast continuum” in mammalian life history strategies has been repeatedly demonstrated (Stearns 1983, Gaillard et al. 1989, Read and Harvey 1989, Sæther and Gordon 1994). Ungulates obviously belong to the slow end of the continuum by showing a covariation between large body size, low fertility, and high life expectancy. Therefore, the high elasticity of prime-age survival for population growth of roe deer can be viewed as a simple

TABLE 8.2, Ratios between elasticity of adult survival and elasticity of juvenile survival in ungulate populations.

SPECIES	ELASTICITY RATIO
Pronghorn	8.53
Moose	6.77
Reindeer	6.48
Mountain goat	5.99
Caribou	5.63
Greater kudu	5.30
Red deer	4.81
Mule deer	4.45
Soay sheep	3.83

Ratios indicate by how much more a given change in adult survival will affect the natural rate of increase than the same change in juvenile survival (Gaillard and Yoccoz, unpublished data).

consequence of the covariation between body size and generation time. Supporting this hypothesis, prospective analyses of nine other ungulate species consistently showed that prime-age survival had elasticities between four and nine times higher than those of juvenile survival (Table 8.2). Prospective analyses also have a methodological limit because they do not account for temporal variation in fitness components. Thus the relative importance of fitness components is determined by assuming that all fitness components have a similar level of temporal variation. But is that a reasonable assumption? To answer this question, we used the coefficient of variation (CV) of fitness components calculated from the 15-year time series available at Chizé as a measure of temporal variation. Our results clearly showed large differences of temporal variation among fitness components. Thus summer survival of fawns was highly variable ($CV = 0.529$), whereas age-specific breeding proportions of females ($CV = 0.056$ and $CV = 0.084$ for prime-aged and old females, respectively) and survival of prime-aged females ($CV = 0.094$) varied only little over the years. Winter survival of fawns ($CV = 0.134$), yearly survival of old females ($CV = 0.135$), and fecundity ($CV = 0.131$, all females combined because we found no differences in litter size among age classes; Gaillard et al. unpublished data) had intermediate levels of temporal variation.

There appears to be a negative correlation between elasticity and temporal variation of different fitness components: components with a strong impact on population growth rate tend to have low temporal variability (see Gaillard

et al. 2000 on ungulates, Sæther and Bakke 2000 on birds, Pfister 1998 on a variety of organisms). Thus, in roe deer at Chizé, survival of prime-aged females had high elasticity and low temporal variability, whereas the various components of recruitment showed the opposite covariation of low elasticity and high temporal variability. This demographic pattern seems to be a characteristic feature of ungulates. We previously underlined that demographic analyses of ungulate populations consistently reveal that prime-age survival has the highest elasticity (Table 8.2). Likewise, recruitment parameters typically have high variability (Gaillard et al. 2000). To manage ungulate populations, it is therefore important to account for the differences among fitness components in susceptibility to environmental variation. Retrospective analyses of perturbation (*sensu* Caswell 2000) are designed for such a task. We thus performed a retrospective analysis on the Chizé roe deer population. Retrospective perturbation analysis involves a decomposition of changes in natural rate of population increase (variance $[\lambda]$) according to fitness components into two parts, the elasticity (e), or the potential impact of a given component on population growth and the coefficient of variation (CV), or the observed variation of a given vital rate (Tuljapurkar 1990, Brault and Caswell 1993, Caswell 2000):

$$\text{Variance } (\lambda) = \sum_{\text{fitness components}} (e^2 \times \text{CV}^2) \quad (1)$$

From Equation (1), it is clear that a fitness component with an elasticity of 0.1 and a CV of 0.5 will contribute equally to changes in population growth as a fitness component with an elasticity of 0.5 and a CV of 0.1 (same value for $e^2 \times \text{CV}^2$). Using this method, we can assess whether the differences among fitness components in temporal variation balance the corresponding differences in elasticity. We found that the proportion of variance in roe deer population growth that is accounted for by different fitness components is highly variable. Thus summer survival of fawns accounted for more than 60% of the variation in population growth of Chizé roe deer, whereas adult survival accounted for only 25% of the variation. Other fitness components had a very low influence on roe deer population growth because they had low elasticities and small coefficients of variation. Therefore, retrospective analysis suggests that summer survival of fawns accounts for about 2.37 times more variation in natural rate of increase than what can be accounted for by survival of prime-aged females. Summer survival of fawns is therefore the critical component of roe deer population dynamics in Chizé.

Prospective and retrospective analyses of perturbation therefore appear to provide two very different interpretations of what is driving roe deer population dynamics, because prospective analyses clearly indicate that survival of

prime-aged females is the vital rate with the highest elasticity, but retrospective analyses suggest that fawn summer survival accounts for much of the observed temporal variability in population growth. These contrasting interpretations would likely lead to radically different management strategies.

What should a manager trust: prospective or retrospective analyses? Prospective and retrospective analyses answer different questions (see Caswell 2000 for a detailed discussion). Prospective analyses can identify the fitness component that, if it were to vary, would have the greatest influence on population dynamics. For roe deer, that fitness component is the survival of prime-aged females. If some factor, either artificial or environmental, will lead to changes in survival of prime-aged females, that factor will drive future changes in roe deer population sizes. On the other hand, retrospective analyses quantify the respective influences of fitness components from empirical observations. At Chizé, summer survival of fawns drove changes in roe deer population size, and is likely to remain the main driving force as long as environmental variation remains within the range observed during the study. To manage exploited populations, we suggest that retrospective analyses would be better suited for generating decision rules provided that they were based on a monitoring period long enough to be representative of future ecological conditions.

Because our analysis of roe deer was based upon 15 years of monitoring, we suggest that summer survival of fawns is likely to be much more influential in shaping future variations in population size over time than survival of prime-aged females. In that particular case, accounting for environmental variation markedly changes the management decisions. Of course, managers should always assess whether they monitor populations long enough to obtain a reliable picture of the influence of environmental variation. Detailed long-term studies of populations are required at this stage. If, based upon prospective analyses, managers choose to monitor adult survival of females, they will hardly detect any changes in population dynamics that may occur, and will not be able to track changes in population size. On the other hand, if, based upon retrospective analyses, managers choose to monitor recruitment of fawns in the winter population, they will be able to track changes in population size more closely and adjust hunting quotas according to the observed yearly variation in recruitment. By only monitoring recruitment, however, managers will not detect any changes in predation or human activities that may affect mortality of adult females. Under these exceptional conditions, monitoring recruitment can then lead to overhunting and, possibly, extinction of local populations.

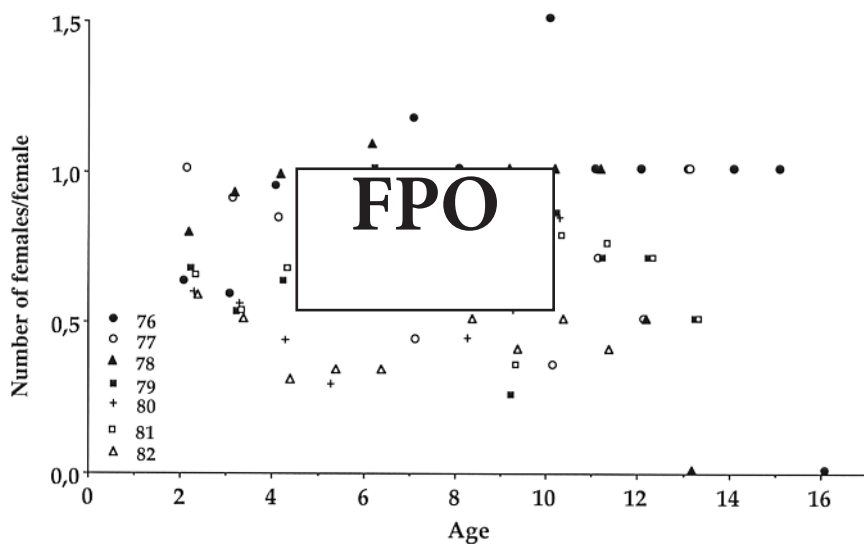
COHORT VARIATION: ROE DEER AT TROIS FONTAINES

Trois Fontaines is an enclosed forest of 1360 ha. Roe deer are marked either as newborn in May–June or as fawns in January–February, and are thereby of known age. The sampling design, based on CMR modeling, provided reliable estimates of all fitness components (Gaillard et al. 1992, 1993, 1997, 1998b). We used data from seven cohorts (1976–1982) of females monitored from 1975 to 1999 because to reliably assess between-cohort differences in natural rate of increase, one should wait until all females from all cohorts have died. To avoid the large variation in first-year survival among cohorts (Gaillard et al. 1997, 1998b), we considered only individual performance from 2 years of age onward.

We first estimated the natural rate of increase of the population by applying a Leslie matrix model to survival and reproductive data for 43 females that survived to the age of first reproduction and were monitored throughout their lifespan. That estimate did not account for between-cohort variation. We then estimated cohort-specific fitness components and built Leslie matrix models to estimate the natural rate of increase for each cohort. Lastly, as a measure of cohort variation, we estimated the cohort-specific population doubling time. Using the mean fitness components of females born between 1976 and 1982, we found that the Trois Fontaines population increased over time. The estimated natural rate of increase of 1.385 is typical of colonizing populations of roe deer (Gaillard et al. 1998a) and is close to the value obtained from transversal age-specific estimates of fitness components ($\lambda = 1.372$; Gaillard 1988). Cohort differences, however, occurred in both age-specific reproductive performance (the number of daughters weaned per female, Fig. 8.4a) and age-specific survivorship (measured by survival curves, e.g., Caughley 1977, Fig. 8.4b). Therefore, natural rates of increase differed sharply among cohorts. Females born in 1977 had the highest λ (1.534), whereas females born in 1982 had the lowest λ (1.265, Table 8.3). Differences in λ , led to marked among-cohort differences in the time required for the population to double (Table 8.3).

It is somewhat surprising that we found evidence for such large cohort variation in λ , because yearly removals maintain the Trois Fontaines roe deer population at low density, simulating a colonizing regime (Gaillard et al. 1993, 1998a). Resources are generally abundant, and very little cohort variation occurs in phenotypic quality (Gaillard et al. 1997). It is likely that cohort-specific growth rates would be much greater in resource-limited populations, such as the one at Chizé, that exhibit strong cohort variation in adult mass (Gaillard et al. 1997, Pettorelli et al. 2002). Therefore, optimal

TROIS FONTAINES



TROIS FONTAINES

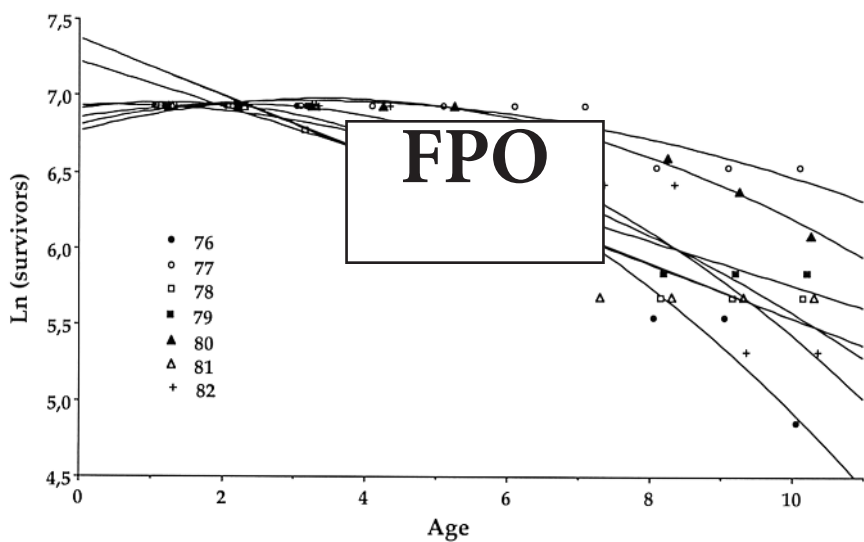


FIG. 8.4. Age-specific (a) reproductive performance and (b) survival curve for seven cohorts of roe deer females monitored from 2 years of age until death at Trois Fontaines (East France, cohorts born in 1976–1982).

TABLE 8.3. Cohort-specific population increase (λ) and cohort-specific time (in years) required for the population to double (TD) for roe deer at Trois Fontaines (East France, see text for details).

COHORT	λ	TD
1976	1.397	2.07
1977	1.534	1.62
1978	1.468	1.81
1979	1.348	2.32
1980	1.347	2.33
1981	1.349	2.32
1982	1.265	2.95

management of roe deer should account for population history and differences in cohort quality.

BETWEEN-SEX DIFFERENCES: RED DEER AT TRONDELAG

To assess whether accounting for between-sex differences in fitness components could make a difference for managers, we used the data collected on red deer (*Cervus elaphus* in Trondelag, Norway, from both monitoring and hunting of known-aged females (Langvatn and Loison 1999). More than 300 deer of each sex (over 600 in total) were individually marked. The red deer data were analyzed by using a CMR design that accounted for yearly differences in both resighting probability and the probability of being shot during the hunting season (Langvatn and Loison 1999). We thus obtained estimates of the fitness components required to estimate the natural rate of increase. We first assessed the potential dynamics of the red deer population by excluding the effects of hunting. Without hunting and irrespective of sex, 75% of fawns survived their first year, 90% of yearlings survived to 2 years, and 93% of females older than 2 years survived each year. Litter size was fixed at one, and 70% of 2-year-old females and 98% of females older than 2 years produced an offspring. A Leslie matrix with these estimates led to λ of 1.191, suggesting that the population was increasing rapidly. As expected for an exploited population, the red deer population at Trondelag had a colonizing demographic regime when hunting was ignored.

We then analyzed the effects of hunting on population demography by using simulations. We set hunting pressure at 10% and estimated the population kinetics over 20 years. The initial population size was set at 1000 red deer. In a first simulation, we accounted for age-structure as previously done for assessing the potential dynamics. The 1000 deer included 160 juveniles,

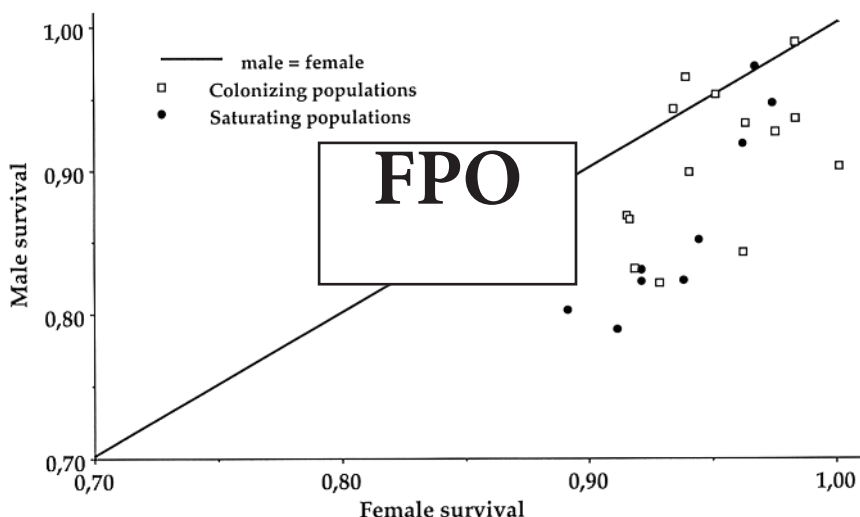
SEX-BIASED SURVIVAL IN UNGULATES

FIG. 8.5. Relationships between adult male survival and adult female survival in ungulate populations. Overall, survival is biased in favor of females because most points are below the line of equal survival between sexes. The magnitude of the sexual differences is higher for populations close to saturation (with density-dependent responses and/or resource-limited, filled points) than for colonizing populations (open squares). Toïgo and Gaillard, unpublished data.

100 yearlings, and 740 adults. We found an asymptotic rate of increase of 1.090 for this red deer population. That first model did not account for between-sex differences, but evidence for sex-biased survival has often been reported in ungulate populations (Clutton-Brock, Guinness, and Albon 1982; Jorgenson et al. 1997; Berger and Gompper 1999).

We obtained mean estimates of sex-specific adult survival in ungulate populations from the literature. Females survived better than males in most populations of polygynous ungulates (Fig. 8.5). Female-biased survival was greater in populations close to saturation than in colonizing populations (Fig. 8.5), suggesting that sex-biased survival is pervasive among populations of polygynous ungulates, especially at high density.

Does sex-biased survival affect management of exploited populations? To simulate the situation where male survival is lower than female survival, we assumed that only 85% of yearling and 80% of adult males survived from 1 year to the next (compared to 90% and 93% in females). The simulation over 20 years with an age- and sex-structured Leslie matrix model

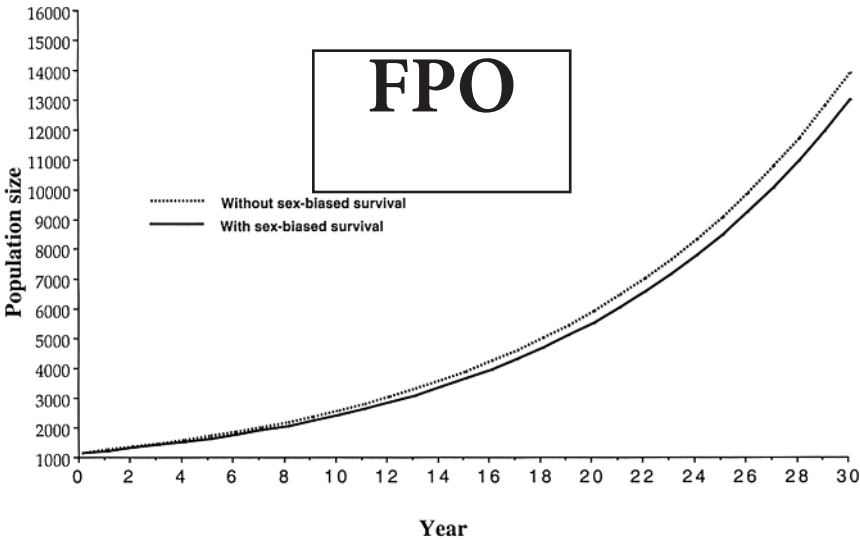


FIG. 8.6. Population kinetics of red deer at Trondelag (Norway) expected under a hunting pressure of 10% with (solid line) and without (dashed line) accounting for between-sex differences in survival (see text for details).

led to exactly the same natural rate of increase of 1.090. Accounting for between-sex differences in survival did not change the estimated population growth, assuming that availability of males does not limit female reproduction (but see Ginsberg and Milner-Gulland 1994). The red deer population estimated from the age- and sex-structured model, however, was consistently lower than that estimated from the age-structured model, the between-model differences increasing over time (Fig. 8.6). Although it did not change the asymptotic λ , low male survival decreased population size and should therefore be accounted for in management decisions. For example, consider a population of 100 deer of each sex with a λ of 1.20 constant over time. Let's assume this population is hunted (with a balanced sex ratio) at the maximum sustainable yield calculated from a model that ignores the lower survival of males. The hunting bag will be 20 individuals of each sex. However, due to higher mortality, male recruitment will not compensate the loss from natural mortality and hunting. The number of males will decrease over time until extinction. The population therefore will go extinct. For species where sex-biased survival is likely to occur, management must be based on sex-structured models to prevent overexploitation.

Conclusions and Recommendations

Our analyses of ungulate case studies highlight three main results that may affect wildlife management. First, although counts appear to be reasonably reliable for monitoring colonizing populations of ungulates, they are most often both inaccurate and imprecise for well-established populations at intermediate and high densities. Many ungulate populations in Europe and North America increased steadily during the last decades (Gill 1990) and are currently at high density (McShea, Underwood, and Rappole 1997; Maillard, Gaultier, and Boisaubert 1999). Consequently, counts can no longer be considered the basic management tool of ungulate populations. Indicators of population performance such as body mass (Gaillard et al. 1996), offspring sex ratio (Kohlmann 1999), browsing pressure (Morellet et al. 2001), or age-dependent survival of radio-tracked animals (Bowden, White, and Bartmann 2000) may be more useful than counts to manage abundant ungulate populations. Measures of population performance such as r or λ are often required by managers, but do not provide sufficient information for efficient management of ungulate populations. A given population growth rate may correspond to different covariation among fitness components and thereby to different population dynamics. For a given population growth rate, environmental variation, cohort variation, and sex-bias in survival all have a strong influence on selecting the optimal management strategy. Indeed, accounting for temporal variation in fitness components often leads to identifying a critical life history stage which differs from that identified by the usual deterministic models. Likewise, cohorts may have markedly different growth rates even in highly productive populations that are rather constant in size over years. Such cohort-specific performance demonstrates that population history plays a determinant role in population dynamics (Coulson et al. 2001) and should be accounted for in management actions. Sampling biases due to cohort effects may bias estimates of population growth rate. Lastly, because most ungulates are polygynous and dimorphic in size (Loison et al. 1999b), males are expected to have lower survival than females, especially in high-density or resource-limited populations. Under such conditions, sex-specific models should be preferred to the female-dominant models that are usually applied. Indeed, even if asymptotic population growth rate is not influenced by low male survival because enough adult males remain to permit females to reproduce yearly (Laurian et al. 2000), lower male survival leads to lower population size in a given year. By neglecting sex-biased survival, managers could therefore overexploit ungulate populations. We conclude confidently that accounting for variation in life history traits

provides a first step toward more realistic models of ungulate populations, which will be relevant to management decisions.

Summary

Wildlife managers need information on temporal trends in the size of exploited populations. To obtain this information, one may either analyze a time series of population counts or build a demographic model to estimate the rate of increase (λ or its antilog, the population growth rate [r]). Inaccurate estimates of population parameters, however, often lead to erroneous assessment of population trends. Total counts generally underestimate population size, especially at high density, and have low precision (CV usually $> 20\%$). Some biases in population counts may result from among-individual differences in sighting probability. Census techniques should thus account for behavioral factors that affect sighting probabilities. In the cases examined here, demographic models are used to estimate population trends and to identify the critical parameters responsible for changes in population size. The age-structured Leslie matrix model cannot provide a satisfactory picture of most ungulate populations because it typically does not account for variation in life history traits arising from factors other than age. After reviewing evidence of environmental variation, cohort effects, and between-sex differences in ungulate populations, we show that (1) when temporal variation in fitness components is accounted for, often the key parameter affecting changes in population size differs from the one identified by using a deterministic model; (2) because cohort-specific growth rates may vary substantially, the growth rate calculated at the population level may be biased by sampling heterogeneities among cohorts; and (3) sex-specific models should be preferred to female-dominated models when survival patterns differ between sexes. We conclude that accounting for environmental variation, cohort variation, and between-sex differences would lead to more realistic models of ungulate populations.

9.

Through the Eyes of Prey:

How the Extinction and Conservation of North America's Large Carnivores Alter Prey Systems and Biodiversity

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J. Ward Testa*

That predators affect the biology of their prey is something that few, if any, people—scientists, writers, naturalists, or laypersons—would dispute. Such processes were obviously recognized by Kipling in describing how prey species shifted in response to Shere Khan's movements.

He has no right, he has no right to change his quarters without due warning. He will frighten every head of game within ten miles.

So said Father Wolf of Shere Khan the tiger, Rudyard Kipling,
Jungle Book, 1894

Aldo Leopold must have believed similarly in 1922, while searching areas of Sonora, Mexico, where jaguars were likely extinct.

We saw neither hide nor hair of him . . . (but) . . . no living beast forgot his presence . . . no deer rounded a bush, or stopped to nibble . . . without a premonitory sniff for el tigre.

And both Kipling and Leopold recognized an ecological role for large carnivores while simultaneously expressing wonderment for how carnivores, as aberrations, may shape prey behavior.

But, to what extent, if any, do large terrestrial carnivores shape prey behavior and ecology? Some evidence may suggest effects are few. Both in southwestern Greenland and on the Svalbard Archipelago (Norway) at 80° north, caribou (*Rangifer tarandus*) have not encountered wolves (*Canis lupus*) for anywhere from 1500 to perhaps 10,000 years, yet it remains uncertain whether group sizes are shaped more by food than by predation (Boving and Post 1997). Where predation once occurred and has subsequently been lost, have antipredator tactics devolved? If so, who really cares other than perhaps a few academics? What can possibly be learned about the role of predation by studying systems where carnivores are now extinct? And, assuming knowledge might be garnered, is it relevant to the biodiversity crossroads that this planet faces? These queries guide this chapter.

Much is already known about this topic, however, and surprises may be few. For example, although confusion exists about mechanisms of possible population-limiting roles of carnivores (Boutin 1992, Krebs 2000), the evidence may often speak for itself. North American bison (*Bison bison*) once numbered in the millions despite coexistence with wolves and grizzly bears. With these carnivores gone from the prairie ecosystem for more than a century, only a neophyte would be shocked to learn that bison in small reserves enjoy rapid population growth when not limited by food. Nor is it surprising that, perhaps due to a small number of founders, the highly inbred population in the Badlands (of South Dakota) contains a high frequency of malformed juveniles; not only do these bison fail to succumb to predation but they survive and may reproduce (Berger and Cunningham 1994). Community-level effects have also arisen as a consequence of the extinction of wolves on North American prairies. In their absence, coyotes (*Canis latrans*) have proliferated (Bekoff 1977, Crabtree and Sheldon 1999). But, where coyotes are reduced by humans, red foxes (*Vulpes vulpes*) have increased (Sargeant, Allen, and Hastings 1987; Sargeant and Allen 1989), and they currently depress the survival of shorebirds and waterfowl (Sargeant, Allen, and Eberhardt 1984). So, on the one hand, although some effects of losing large carnivores appear highly predictable, others are subtle and occur at multiple trophic levels.

This chapter considers questions about interactions between prey species and large terrestrial carnivores, specifically consequences of carnivore loss, maintenance, and restoration. Although these issues can be restricted to prey behavior exclusively, the results in our opinion would be far less interesting if not linked to broader issues involving ecology and conservation. Although

behavior in and of itself is clearly fascinating (Tinbergen 1951, Wilson 1975), in many ways its contribution to conservation may be far stronger when interfaced with population processes and community ecology (Caro 1994, 1998b, Gosling and Sutherland 2000). Therefore, we attempt to offer insights at three levels—behavioral, demographic, and ecosystem—by considering spatial and temporal events for each.

Such queries seem relevant for at least three reasons. Large carnivores are being reduced in many regions: for example, tigers (*Panthera tigris*) in Russia and India, jaguars (*P. onca*) in Latin America, and grizzly bears (*Ursus arctos*) in Canada and the United States. They are also being reintroduced or expanding naturally in others: cheetahs (*Acinonyx jubata*) and lions (*Panthera leo*) in South Africa (Hunter and Skinner 1998), wolves in Italy and the United States (Boyd et al. 1994, Boitani 2000), and brown bears in Europe (Breitenmoser 1998, Swenson et al. 1999). Irrespective of whether extermination or expansion is occurring, knowing something about the possible responses of prey populations and ecosystems will help inform decisions about the use and protection of such regions. In the United States, the reintroduction of wolves into the Greater Yellowstone Ecosystem (GYE) has caused great concern about the short-term viability of some prey populations, particularly elk (*Cervus elaphus*) and moose (*Alces alces*) (Phillips and Smith 1996, Boyce 1999), and any knowledge that contributes to wise decision making is often appreciated. Second, mammalian carnivores, whether terrestrial or aquatic, can contribute significantly to ecosystem processes and the maintenance of biological diversity (Ben-David et al. 1998; Estes, Tinker, and Doak 1998; Crooks and Soulé 1999). Both of these commodities are increasingly being viewed as important to the welfare of the environment, and they tend to have economical impacts on neighboring human communities. Finally, the public, whether urban or rural, Botswanan or British, Mongolian or Mexican, is passionate about wildlife in general and carnivores in particular. Gaining societal support for environmental conservation can come about not only through visiting zoos and watching television but also by the popularization of scientific study. Whatever fuels the public imagination and infuses some sense of curiosity about the natural world must be viewed as positive. Understanding animals is but one of the inspirational ways in which the public becomes interested in science and, hopefully, conservation. It is hoped that the enhancement of knowledge about the effects of the presence and absence of large carnivores on prey systems, behavior(s) included, will improve opportunities for conservation measures.

Berger began work on these issues in 1995, focusing on moose, in Alaska where grizzly bears and wolves are still relatively abundant, and in the southern part of the GYE where these two species had been missing for about 60 to

75 years until recently (details to follow). Why moose? Primarily because their dynamics appeared to be inextricably linked to the distribution of grizzly bears and wolves both in systems where these carnivores still existed and in systems where they were absent. Numerous other North American ungulates, of course, fit the binary criteria of large predators present and absent (e.g., caribou, elk), but study situations involving these other species have usually been less than ideal in that observability might be compromised, or females heavily hunted, or habitats strikingly different. For moose, on the other hand, finer nuances of their interactions with bears and wolves had been studied (Peterson 1977; Ballard, Spraker, and Taylor 1991; Schwartz and Franzmann 1991; Gasaway et al. 1992).

Additionally, in 1994, J. Ward Testa and Terry Bowyer initiated independent studies of Alaskan moose and offered to make either their radio-collared study animals (Testa) or components of their data (Bowyer) available to facilitate Berger's impending efforts. Since then, Berger established control (baseline) values of moose at sites where wolves and grizzly bears have never been extirpated and their densities were not radically modified by humans (Miller et al. 1997; Bowyer et al. 1999a; Testa, Becker, and Lee 2000). Experimental treatments were areas where moose had not encountered wolves and grizzly bears for 60 to 75 years irrespective of the causes underlying carnivore losses.

Demography of Moose in the Absence of Wolves and Grizzly Bears

Although grizzly bears and wolves are often major predators of moose in northern circumpolar systems, as ungulate diversity and the availability of smaller-bodied species increase at more southern latitudes, so does prey switching (Boyd et al. 1994, Weaver 1994, Kunkel et al. 1999), and elk and deer become more favored prey than moose (Craighead, Sumner, and Mitchell 1995; Mattson 1997; Kunkel and Pletscher 1999). A consequence of this shift by carnivores to less formidable prey is that moose may be released from predation.

Accepting assumptions about relaxed predation is very different from knowing whether predation release has truly occurred. If the assumption is wrong, then one may conclude that predation has not shaped a system when the converse may be true. In some systems, small-bodied canids such as red foxes become capable predators of young ungulates, a fact that would have remained unknown in the absence of detailed or comparative study (Aanes and Andersen 1996, Andersen and Linnell 1998). But, ignoring long-term

effects of historically extinct predators also carries a potential liability and may even preclude an accurate understanding of current prey adaptive responses (Csermely 1996). The “ghost effects of predators past” may shape the biology of a prey species even if predators have been extinct for thousands of years (Byers 1997). Understanding whether recent anthropogenic-induced loss of predators results in an immediate relaxation of predation is important from both demographic and behavioral perspectives.

Consider for example the broad array of sites in North America where wolves and grizzly bears are extinct. Potential extant carnivores include black bears (*Ursus americanus*) and cougars (*Puma concolor*), both of which prey on elk and mule and white-tailed deer or their offspring (Linnell, Aanes, and Andersen 1995; Smith and Andersen 1996). At sites where these extant carnivores exist but not wolves or grizzly bears, is it reasonable to assume that moose have become predator-free?

The simple answer is no. The assumption of predation release would have been a poor one because both in the Canadian Rockies and on Alaska’s Kenai Peninsula, respectively, cougars and black bears may be substantial predators of moose calves or yearlings (Schwartz and Franzmann 1991, Ross and Jalkotzy 1996). By contrast, the assumption of relaxed predation is justified in Scandinavia where neither of these two carnivores exist. In their absence an inverse association between juvenile recruitment and large carnivore extinctions is robust (Swenson et al. 1999).

To examine the assumption of predation release in North America, we contrasted neonate recruitment between Alaskan and Wyoming moose populations. Moreover, the comparisons enabled an evaluation of whether meso-carnivores contributed as replacement predators because, despite the loss of grizzly bears and wolves at the Wyoming sites for more than 60 years, black bears and cougars have always been extant. If these latter two carnivora affect neonate recruitment, then differences between Alaska and Wyoming might be less striking than those reported in Scandinavia.

The results of macrogeographical contrasts fail to support this possibility. Juvenile moose survival to 2 months of age was about three times greater in areas of Wyoming than in Alaska or the Yukon (Orians et al. 1997, Berger et al. 1999). Although these results suggest predation may retard recruitment, they fail to account for other possibilities.

Linnell, Aanes, and Andersen (1995), in a provocative analysis, suggested the possibility that the Bambi syndrome (the loss of young cervids to “big bad” predators) has been partially promulgated by socioeconomic concerns about offspring recruitment and the extent to which prey is subsequently available to humans for meat and for trophy. If, however, young are disproportionately fewer in a population irrespective of the presence of larger

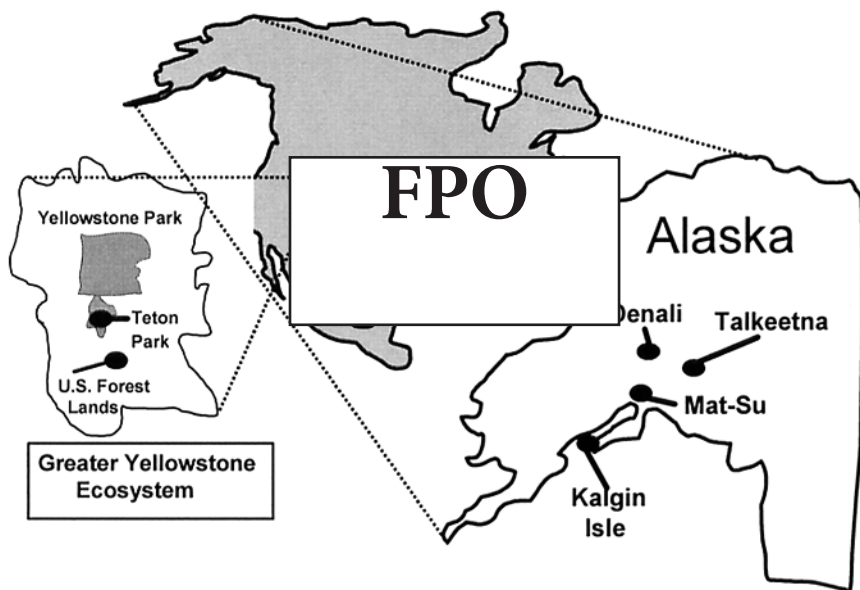


FIG. 9.1. Overview of study areas: carnivores were present at Denali, Talkeetna, and Matunuska-Susitna; carnivores were absent from Teton (until 1990s, brown bears, and 1997, wolves), U.S. Forest Service lands, and Kalgin Island. Brown bears present continuously in Yellowstone Park and a few adjacent (nonpark) areas.

carnivores, the reduction may be due to any number of factors—drowning, light birth mass, low pregnancy rates—some perhaps related to density, others not (Festa-Bianchet 1988b, Gaillard et al. 1993).

To evaluate whether factors other than predation might explain low juvenile recruitment at sites where grizzly bears recently began recolonization (e.g., areas in and adjacent to Grand Teton National Park; Fig. 9.1), we focused on a hypothesis alternative to that of predation—that an inadequate food supply limits fecundity and hence neonate production. This hypothesis is amenable to empirical examination because the noninvasive monitoring of fecal steroid hormones permits an unbiased measure of pregnancy (Monfort, Schwartz, and Wasser 1993). The working assumption is that pregnancy rates in food-limited populations will be lower than those in populations with predation. This prediction is anything but novel, having been confirmed empirically for numerous large herbivores (Clutton-Brock and Albon 1989, Sinclair 1989), including moose (Franzmann and Schwartz 1985, Gasaway et al. 1992). But what is important here is that if diminished juvenile representation in a population is explained by food limitation rather than predation,

then it becomes possible to test hypotheses about the Bambi syndrome, including the effects of relaxed predation on individual behavior and on community structure.

Predators may kill juveniles, but how did prey fecundity vary in the absence of predation? Because methods have been described in detail elsewhere (Testa and Adams 1998, Berger et al. 1999), only a brief summary is offered here. Pregnancy in restrained females was diagnosed by palpation and follow-up observations of calves in the southern GYE (sGYE) or by analyses of ultrasound, hormones, and observations of calves (Tallkeetna Mountains; Testa and Adams 1998; Testa, Becker, and Lee 2000). Assessments in the sGYE were subsequently improved by noninvasive monitoring of fecal progesterone concentration (FPC; Monfort, Schwartz, and Wasser 1993; Schwartz et al. 1995), and with an ecological application involving subsequent births (Berger et al. 1999).

During an approximate 60- to 75-year period, which initially coincided with the local extinction of wolves and grizzly bears, the moose population in the region of Grand Teton National Park experienced exponential growth (Fig. 9.2). During the only period (1963–1966) of this demographic irruption

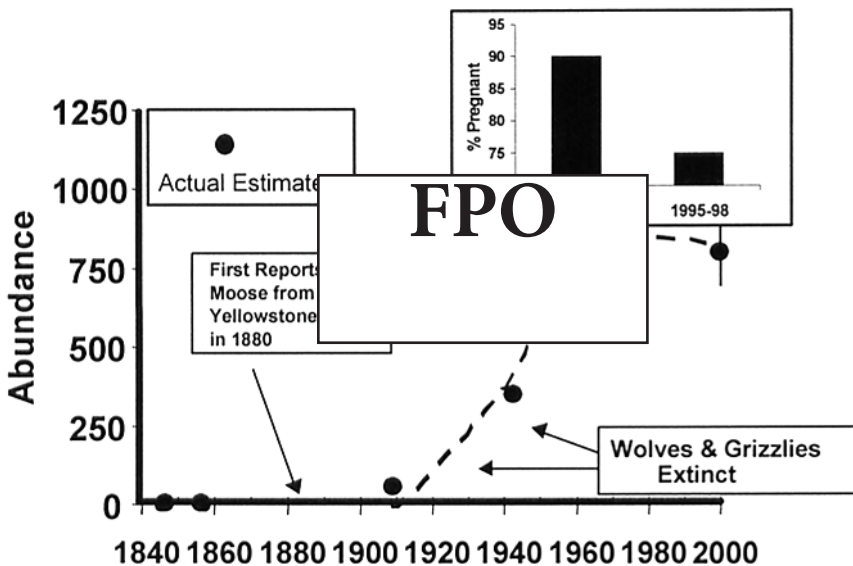


FIG. 9.2. Summary of changes in estimated population size of moose in the Jackson Hole region of the Greater Yellowstone Ecosystem (from Berger et al. 2001). Inset reflects changes in pregnancy rate during the last 30 years (from Berger et al. 1999).

for which data on fecundity were available (Houston 1968), pregnancy rates were 90%, a value consistent with that of other North American populations not limited by food. By 30 years later, pregnancy rates had dropped to 75% (G test for independence; $G_{adj} = 3.36$; $N = 90$; $0.05 < p < 0.10$) during a period in which population growth no longer occurred (Fig. 9.2). These findings are for a population that expanded in an environment free of wolves and essentially free of grizzly bears. The drop in pregnancy rates currently places this population within the lowest fifteenth percentile in North America (Berger et al. 1999).

Although it is unclear how weather, food, or other factors may have contributed to the present relatively low pregnancy rates, populations that are near or below their ecological carrying capacity due to predation (by either natural carnivores or humans) have greater pregnancy rates than those exceeding their food base. Although food quality and availability have not been directly assessed in the sGYE, the decline in pregnancy rates, apparent lack of significant population growth, starvation rate of about 60% (Berger, unpubl.), and general absence of predation on moose are not inconsistent with the possibility of food limitation.

Prey, Scavengers, and Desensitization to Carnivore Loss

Given the marked influence of relaxed predation on demography, to what extent have prey ecology and behavior been affected? In systems that have not experienced predator–prey disequilibria, a major tenet in behavioral ecology is that individuals derive antipredator benefits by group formation, which minimizes an individual's probability of succumbing to an attack (Lima 1987, Dehn 1990). Nevertheless, in a generally asocial, browsing species like moose, it would be difficult to disentangle relative effects of food quality and quantity from those of predation on group formation, especially in the absence of some large-scale field manipulation. An alternative approach to gauge the sensitivity of prey to possible predators is the use of playback experiments, a technique that has proved useful for a variety of taxa (Philips and Alberts 1992, Flowers and Graves 1997, Durant 2000a, 2000b).

Scavengers and carnivores have long held a mutualistic relationship, one that has been conspicuous in the rich folklore of northern boreal zones. Ravens have figured prominently in symbols and culture of the Athabascans (Nelson 1983), and evidence suggests an interdependency involving species such as foxes, bears, wolves, and ravens (Mech 1970, Henry 1986, Heinrich 1989, Peterson 1995). Ravens may be attracted to wolf vocalizations (Harrington 1978). Further south, relationships exist between magpies and predators

(Birkhead 1991), and, perhaps, between prey and scavengers (Stockwell 1991; Genov, Gigantesco, and Massei 1998).

Because scavengers such as ravens are reliant on carnivores to open the carcasses of thick-skinned prey (Heinrich 1989), and are intimately associated with bears and wolves, especially at carcasses (Mech 1970, Mysterud 1973, Craighead 1979), prey species may cue on scavengers to facilitate the early warning or detection of predators. Given the consistent and striking demographic differences in juvenile survival at sites with and without large carnivores (see earlier discussion), we expected deftness in environmental monitoring by prey; that is, vigilance in response to detection of scavengers should be positively associated with predation risk. The converse might also be expected. If recognition of ravens by moose occurs, then following the extinction of grizzly bears and wolves, moose may fail to respond to ravens because the incentive to respond (possible predator detection) is diminished. Neither scenario may, however, be correct. Antipredator responses may be less labile than expected, or the response of moose to the immediate presence of ravens may be independent of the risk of predation.

These possibilities were examined through the use of experimental playback calls in the field. We used six independent study areas, three with intact carnivore communities and three lacking both grizzly bears and wolves (1995–1998). Sites with intact carnivore communities were the Talkeetna Mountains, Denali National Park, and the Matanuska-Susitna Valley regions, areas geographically separated from each other by at least 150 km (see Fig. 9.1). Areas lacking grizzly bears and wolves were Grand Teton National Park and Bridger-Teton National Forest in northwestern Wyoming (each separated by 10–75 km) and Kalgin Island in Alaska's Cook Inlet (a site where moose were transplanted in the late 1950s; Bowyer et al. 1999b). Neither grizzly bears nor wolves occur on the 20 km² island, probably due to strong marine undercurrents or a lack of food.

Responses of adult females were assessed during experimental playback of sounds and postplayback periods (Berger 1999). Briefly, sounds were played to adult female moose under four conditions: (1) control (= baseline; no overt or experimental disturbance), and 25 sec playbacks of (2) raven and (3) red-tailed hawk vocalizations, and (4) a dummy sound (running water). Distances between the subject and sounds from a JBL Pro-III speaker connected to a 40 w Kenwood amplifier and powered by a 12 v battery averaged 145 m (SEm = 6.90; $N = 203$, range 30–800 m). All experiments were on calm days. The response variable was the proportion of time an individual either foraged or was vigilant per 180 sec bout. General linear models were employed for statistical analyses using appropriate transformation (Berger 1999), but data are summarized here as means.

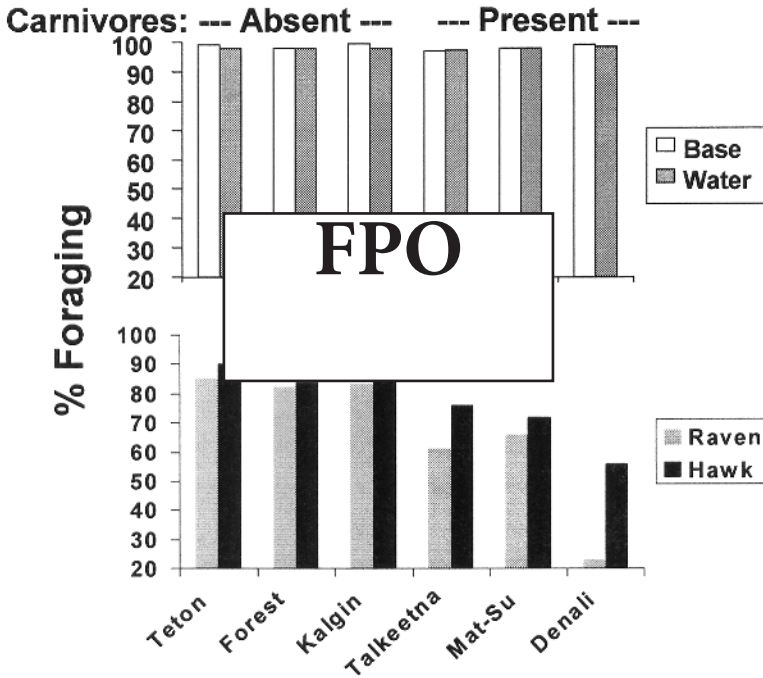


FIG. 9.3. Mean foraging rates (per 180 sec bouts) of adult female moose at sites with and without wolves during two types of auditory playbacks. Sample sizes/site (respectively) are 105, 23, 12, 22, 22, and 25 (modified from Berger 1999).

If predation pressure shaped patterns of foraging, moose from sites with wolves and grizzly bears should feed at greater per capita rates than moose from sites free of wolves and bears. Contrasts among nondisturbed adult female moose involving the six study areas categorized by predation treatment revealed little detectable variation in foraging, nor were differences evident when the sounds of running water were used as a control sound (Fig. 9.3). Therefore, in the absence of disturbance and with exposure to a familiar neutral sound, foraging is independent of predation regime. Hence, observational measures lacking contextual cues associated with predation risk produced no detectable site-specific variation in behavior. If prey foraging was used to assess potential predation risk, then the assumption that differential behavior reflects predation risk would be flawed. Playbacks of familiar sounds of red-tailed hawks and ravens, however, resulted in striking between-site differences that varied by predation pressure. Under relaxed predation, females responded only weakly to hawks or ravens (Fig. 9.3), but at predator-rich sites decreases in foraging were large (both $p < 0.0001$), and greater for ravens than red-tails.

Four additional findings were consistent with the hypothesis that prey were more responsive to scavengers at sites with active predation than at sites with no predators. First, whereas group size had no effect, foraging was less for mothers with calves at sites with predation, a relationship that suggests mothers were more apt to trade-off feeding to survey environments where they coexist with grizzly bears and wolves ($p = 0.034$). Second, distance to the sounds of surrogate predators resulted in differences in moose foraging rates, and these varied by predation treatment but were significant only for ravens ($p = 0.048$); at predator-free sites, the distance of avian sounds had no effect on feeding. Third, vigilance was not related to distance to canopy during raven or hawk vocalizations at predator-free sites but it was in areas with large carnivores, and these relationships differed between predation regime ($p = 0.03$). Finally, patterns of postplayback feeding differed between predator-free and predator-rich sites. With the effects of other variables removed, both ravens and hawks elicited greater reductions in feeding in areas where grizzly bears and wolves still existed (both $p < 0.0001$). These findings affirm not only the recent existence of geographical variation in how mammalian prey rely on cues from aerial scavengers to detect predators, but also that the variation is a consequence of recent ecological instability, namely the extinction of wolves and grizzly bears by humans.

An Experiment: Carnivore Restoration and Reinstillation of Antipredator Behavior

Here we consider how the expansion of grizzly bears and wolves into areas that had been predator-free for many decades may have altered moose antipredator behavior. First it is necessary to frame the ecological context in which carnivore restoration in the GYE has occurred.

In the contiguous United States, both wolves and grizzly bears receive special protection under the Endangered Species Act (ESA). An ultimate goal of the ESA is demographic restoration such that species can be “de-listed” from federal protection once their viability is no longer jeopardized. Although grizzly bears were never extirpated from Yellowstone National Park’s 8900 km², they were extinct in much of the 100,000 km² that constitute the GYE, including areas south of the park. Beginning around 1990 and still continuing, perhaps as a consequence of the 1988 fires that burned nearly half of Yellowstone Park, grizzly bears naturally recolonized portions of the northern Tetons and areas to the east and southeast. Unlike grizzly bears, wolves were extirpated from all of the Rocky Mountain regions during most of the twentieth century. Immigrant wolves from Canada have recently moved into

northern Montana (Boyd et al. 1994) but not in the GYE. The U.S. Fish and Wildlife Service restored wolves to Yellowstone Park in 1995, and the first dispersing wolves from there arrived in the Tetons in late 1997.

Between 1996 and 2001, grizzly bears killed at least 12 adult moose in and adjacent to the Tetons, and in March and April 1999 wolves were responsible for the loss of at least eight 9- to 10-month-old moose calves. Some level of predation by both bears and wolves has been restored in a system where it had been lacking for 60 to 75 years. If previously predator-naïve moose are quick to learn about predators, it may not be unexpected that they too learn to associate ravens with carnivores, as has occurred in Alaska (see Fig. 9.3).

One model of learning posits the rapid development of predator recognition through individual experience. To examine whether Teton moose who were initially free from predation changed their responsiveness both to wolves directly and to ravens, we contrasted mothers whose calves were killed by wolves and those who did not lose calves (both in the sGYE), and then compared these to Alaskan females (Fig. 9.4).

The responses of sGYE females to the calls of ravens did not vary temporarily with respect to predation events or by maternal status (e.g., whether calves survived or not; see Fig. 9.4). These findings indicate that over short periods of time, moose mothers either fail to associate ravens with carnivores

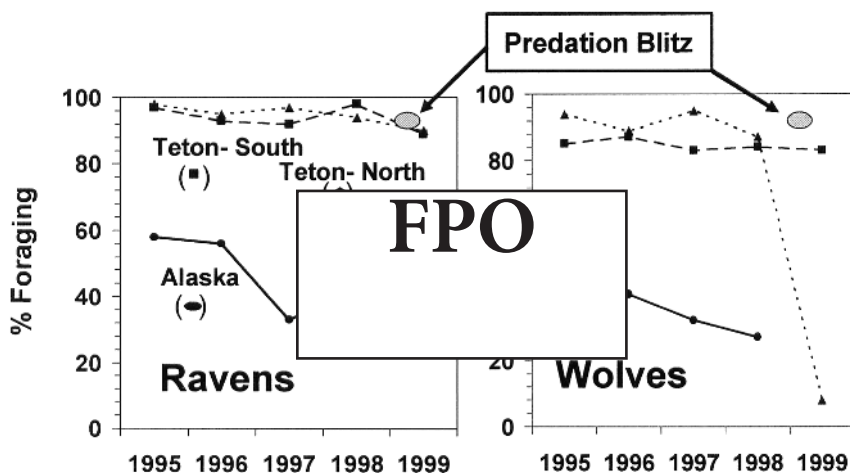


FIG. 9.4. Summary of comparative mean annual postplayback foraging responses of adult female moose to calls of ravens and wolves. The “predation blitz” occurred in early 1999 only in the Teton-South region of Grand Teton National Park (Wyoming). Females of Teton-South that lost their young to wolves had heightened responses in contrast to Teton-North females ($F = 24.625$; $p < 0.0001$). Sample sizes for wolf playbacks are as follows: Tetons–215; Alaska–82.

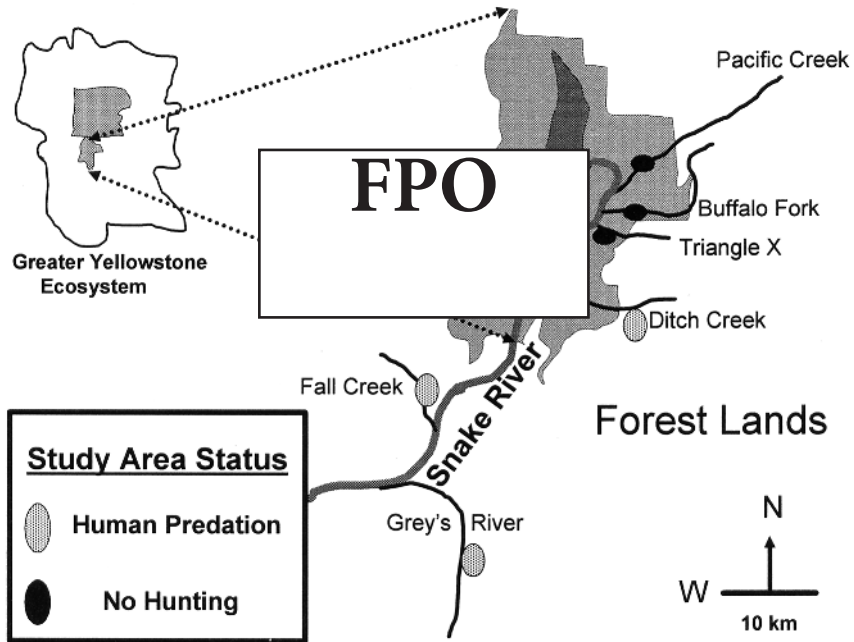


FIG. 9.5. Locations of riparian sites for studies of vegetation and bird diversity within and adjacent to Grand Teton National Park (no hunting—moose at high density) and on adjacent Bridger-Teton National Forest.

or, if they do, they fail to respond. Unlike Alaskan mothers, moose in environments that have been predator-free for 60 to 75 years are less wary of ravens even when predation on their offspring has occurred.

Wolf howls, in contrast, produced massive changes in the behavior of mothers who lost calves. They decreased feeding rates by a magnitude of five, and their reduction in feeding became similar to that of Alaskan moose (Fig. 9.5) only after the predation blitz ($F_{1, 89} = 32.516$, $p < 0.0001$). That such dramatic changes were caused by wolf predation per se, rather than other factors, is supported by two comparative analyses (Berger, Swenson, and Lill-Persson 2001): mothers whose calves died due to starvation or vehicles ($N = 3$) had greater feeding rates per bout ($x = 71\%$) during playbacks of wolf howls than mothers with wolf experience ($x = 8\%$) ($F_{1, 16} = 24.625$, $p < 0.0001$), and differences between these “control” mothers (who had not lost offspring to wolves) and mothers in areas without wolves ($x = 83\%$) were not detectable ($p = 0.772$).

These findings are important because they (1) suggest that variation in behavior can occur rapidly, in this case in less than a single generation;

(2) demonstrate heightened sensitivity by mothers who lost calves to predators; (3) support the idea of a developmental hierarchy of predator-detection cues in which prey learn about carnivores; and (4) indicate that mothers developed greater response sensitivity to wolves than to ravens. Although it is well known that varied mammalian taxa learn about, or retain memory of, possible predators (Blumstein et al. 2000) and can differentiate among them (Cheney and Seyfarth 1990), what differs about the moose–wolf–bear–raven system is the rapid pace at which receptivity is lost and may be regained. In ground squirrels (*Spermophilus beechei*), for instance, antisnake behavior may persist for hundreds or more generations despite the loss of some predators (Coss 1991).

Whether moose can serve as a general model for other asocial species, or social ones such as elk and bison, wildebeest (*Connochaetes taurinus*) or gazelle (*Gazella* spp.), is uncertain. Among factors that will inevitably shape prey responsiveness to predators will be the length of time of exposure as well as the intensity of predation. But, in today's fragmented, alien-laden, and less biologically diverse world, the emergent issues that will continue to shape and diminish potential prey populations will also be the degree of familiarity to potential selective agents. Already the evidence is strong that alien species, whether dingoes (*Canis lupus*) or foxes into Australia or cats onto islands, have a relative easier time dispatching prey than in coevolved systems. Although for moose, it is now evident that antipredator behavior is relatively labile, at least under some conditions, it remains unclear if the restoration of native carnivores into many of the other systems where they have been extirpated will elicit a similar return of "normalized" antipredator behavior. Only studies in those specific systems will produce answers.

Possible Apex Carnivores and Community Interactions

The preceding findings indicate that the loss of large carnivores has had dramatic effects on the demography and behavior of one species of prey, including alterations of (1) rates of adult pregnancy, (2) patterns of juvenile survival, (3) reactions to scavengers, and (4) learning about predators. Additionally, the release of predation in the sGYE has resulted in a moose population that must hover near to or beyond the food ceiling because population growth has ceased and pregnancy rates have declined (see Fig. 9.2).

The implications of removing large carnivores is relevant for many ecosystems in areas of Europe and Asia and, indeed, globally, where ecological communities are either missing dominant selective forces or have new ones dependent upon humans. These large-scale manipulations offer unique opportunities to investigate how the loss of large carnivores affects community

dynamics, particularly the possibility that interactions may be influenced at multiple trophic levels.

How important are carnivores in terrestrial ecosystems? In the neotropics, sites that otherwise appear virtually intact have been referred to as empty forests due to the depletion of game (Redford 1992). Not only may these areas be lacking in wildlife that is consumable by humans, but, because humans and big cats (jaguars and cougars) compete for the same food, these nonhuman carnivores may also be lacking (Jorgensen and Redford 1993), and the system's past equilibria become radically changed (Novaro, Funes, and Walker 2000). Not dissimilarly, in western North America and montane regions of Europe, some lands that look as if they are "wilderness" also lack brown bears and wolves. But the mere loss of large carnivores from ecosystems says little about their role as apex organisms or the scale at which predator-prey disequilibria operate. These losses do, however, create opportunities to learn more about ecological processes and may shed light on the longstanding debate over the role of top carnivores in regulation of prey populations (Terborgh 1987; Wright, Gompper, and De Leon 1994), and whether top-down or bottom-up effects play a larger role in biological organization (Paine 1966, Polis and Strong 1996). Although most research on trophic cascades has focused on aquatic or marine systems (Power 1992; Estes, Tinker, and Doak 1998) and involved heterotherms and invertebrates (Spiller and Schoener 1994, Carter and Rypstra 1995), the recent losses of large vertebrate carnivores provide options to examine how predation and food shape terrestrial communities and relate to the maintenance of biological diversity.

The work we present next summarizes findings on how grizzly bears and wolves may act as apex carnivores, and it is based on studies that we and our colleagues, Matthew Johnson and Lori Bellis, have published elsewhere (Berger et al. 2001). One reason for expecting that grizzly bears, either alone or in combination with wolves, may be apex carnivores is because of their well-established impacts on population growth in moose, which may in turn have subsequent impacts at the landscape level. Although debate still continues over whether moose are regulated by predation per se (Boutin 1992, Orians et al. 1997, Krebs 2000), a series of manipulative but imperfect field studies suggest lower moose population growth where wolves and grizzly bears are not at excessively low densities (Messier 1991; Gasaway et al. 1992; Boertje, Valkenburg, and McNay 1996).

Moose may have substantial localized effects on ecosystems (Pastor et al. 1993, Connor et al. 2000), partly because they consume large quantities of woody shrubs and young trees including aspen, willow, and cottonwood, and also because they achieve densities (Houston 1968) that, in riparian zones,

may exceed 20 individuals per km² for up to 5 to 6 months per year. In Alaska and the Yukon, moose density is affected by predation (Gasaway et al. 1992), although periodic severe winters may set an upper limit on population sizes (Messier 1991, Peterson 1999).

Some native herbivores, including cervids other than moose, have the capacity to attain extraordinarily high densities in the absence of carnivores (Alverson and Waller 1997, Schmitz and Sinclair 1997). And, although domestic species may severely impact sensitive habitats (Knopf and Cannon 1982, Kauffman and Krueger 1984, Saab et al. 1995), little is known about the effects of colonizing native browsers. In arid zones like the American West, this can be a critical issue because riparian habitats may constitute 1 to 2% of the landscape but harbor up to 80% of the local biodiversity (Ohmart 1994; Stacey 1995; Dobkin, Rich, and Pyle 1998). It is in these types of systems that intense herbivory may be expected to affect riparian biodiversity.

RATIONALE, RESEARCH DESIGN, AND STUDY AREAS

We studied interactions among moose populations, the structure of their major winter food supply in riparian zones, and avian species diversity in Grand Teton National Park and adjacent public lands managed by the U.S. Forest Service in the Jackson Hole region of the GYE (see Fig. 9.5). Until recently grizzly bears and wolves had been absent for about 60 to 75 years. Outside the national park, more than 10,800 moose were harvested by humans between 1971 and 1991 (Houston 1992). In the national park, the hunting of moose is not permitted, and coincident mean densities vary by a magnitude of almost five (5.2 vs. 1.1 individuals/km²), with densities being lower on lands adjacent to Teton Park.

During the 1800s moose were rare in much of western North America (Karns 1998). They were virtually absent from the Jackson Hole region about 150 years ago, and their rapid population growth appears to have reached a ceiling (see Fig. 9.2). Moose depend upon willow during winter (Peek 1998). Riparian vegetation may be altered more when moose occur at high densities than when they are controlled by predation or hunting. Alternatively, moose may have little if any impact on riparian vegetation.

We evaluated these possibilities by contrasting effects of moose herbivory on riparian willow communities using three areas within Teton Park (no hunting and no large carnivores) and three similar sites in adjacent forest lands (human hunting but no large carnivores). Thus the treatment was predation (absent or present), with each area containing three replicated riparian communities (Fig. 9.5).

TABLE 9.1. Summary of effects of how types of predation on moose influence subsequent browsing in willow communities in the southern Greater Yellowstone Ecosystem.

WILLOW STEMS	PREDATION ON MOOSE		<i>F</i>	<i>P</i>
	Human	None		
Alive—not browsed	0.53 (0.15)	0.10 (0.11)	18.56	0.0001
Alive—browsed	0.22 (0.15)	0.59 (0.10)	7.73	0.0025
Dead—not browsed	0.12 (0.07)	0.01 (0.01)	13.74	0.0002
Dead—browsed	0.13 (0.08)	0.29 (0.09)	5.04	0.0128

Mean (and standard deviation) reflect proportions of stems of dominant willows (Geyer's *Salix geyeriana*, Booth's *S. boothii*, and Wolf's *S. wolfi* ($N = 360$). Analyses are based on two-way, repeated measures analysis of variance (from Berger et al. 2001).

RIPARIAN WILLOWS AND AVIAN SPECIES DIVERSITY

Moose density affected both mean willow height and density. Where moose were reduced by humans, willows were taller and browsed less than in park areas that lacked predation. The proportion of willow stems longer than 100 mm that were browsed and either alive or dead was also associated with moose density (Table 9.1).

Five parameters were used to assess whether moose density was associated with the distribution or abundance of the riparian avian community. Moose density affected all, with each being greater where moose density was limited by predation: (1) species richness of breeding birds ($N = 23$ vs. 18; $p < 0.003$); (2) nesting density ($p < 0.002$); (3) Shannon's diversity index ($p < 0.004$); (4) Hill's Diversity Measure 1 ($p < 0.008$); and (5) Hill's Diversity Measure 2 ($p < 0.021$). Where moose densities were high, the density of nesting avifauna, including willow flycatchers (*Empidonax traillii*), calliope hummingbirds (*Stella calliope*), yellow warblers (*Dendroica petechia*), fox sparrows (*Passerella iliaca*), and blackheaded grosbeaks (*Pheucticus melanocephalus*) were substantially reduced (Table 9.2), and two other species—gray catbirds (*Dumetella carolinensis*) and MacGillivray's warblers (*Oporornis tolmiei*)—were absent. Overall, approximately 50% of the riparian willow bird species were reduced or absent from sites inside Teton Park where moose were protected from predation and thereby attained high local densities. The fact that typical riparian species were present at all sites (e.g., Yellow and Wilson's warblers; see Table 9.2 for others) substantiates that the samples were derived from the same ecological pool.

TABLE 9.2. Relationships between moose densities as influenced by predation (human versus none) and mean breeding densities/10,000 m² (and SD) of several bird species in Wyoming.¹

SPECIES	PREDATION BY		<i>F</i>	<i>P</i>
	HUMANS	NONE		
Calliope hummingbird	2.00 (0.87)	0.22 (0.44)	10.67	0.0004
Willow flycatcher	0.78 (0.44)	0.55 (0.53)	2.40	0.0994
Gray catbird	0.88 (0.92)	0.00 (0)	5.12	0.0096
Yellow warbler	3.78 (0.97)	2.33 (1.00)	3.12	0.0453
Wilson's warbler	0.11 (0.33)	0.67 (0.87)	1.86	0.1760
Yellowthroat	0.00 (0)	0.11 (0.33)	1.00	0.4582
MacGillvray's warbler	0.22 (0.44)	0.00 (0)	0.80	0.5705
Black-headed grosbeak	0.77 (0.44)	0.22 (0.44)	3.00	0.0552
Song sparrow	0.22 (0.44)	0.00 (0)	3.91	0.0245
Fox sparrow	0.44 (0.53)	0.11 (0.33)	0.85	0.5405
Lincoln's sparrow	0.22 (0.44)	0.66 (0.71)	0.91	0.5038
White-crowned sparrow	0.00 (0)	0.55 (1.13)	0.82	0.5612

¹Modified from Berger et al. 2001.

Although these data suggest that moose browsing shaped avian communities at a microgeographical scale, the link between the structural modification of riparian willows at our sites and avian diversity had been uncertain. Nevertheless, a direct relationship between willow volume (*X*; the product of density and cover using the proportion of live willow stems) and avian species diversity (*Y*) existed ($Y = 0.51X + 0.33$, $n = 18$, $r^2 = 0.24$; $p < 0.03$). Thus it appears that avian species diversity is partially affected through structural modifications of the willow canopy by moose whose densities, in turn, are controlled by humans, either by total protection (park) or hunting (adjacent forest lands).

LARGE HERBIVORES, CARNIVORES, AND TROPHIC CASCADES

Our analyses, though specific to the Jackson Hole area of the GYE, support the idea that a dynamic chain of interactions involving multiple tiers of biological organization were set in motion 60 to 100 years ago, principally by the removal of large predators. Among the key events were (1) human decisions to exterminate large carnivores, especially wolves (Murie 1940, Phillips and Smith 1996) but also grizzly bears (Craighead 1979) both in Yellowstone Park per se and in adjacent regions; (2) a resultant growth of an apparent

low-density moose population (see Fig. 9.2) that, although it began expanding from 1880 to 1910, interrupted partially due to a dampened effect on juvenile mortality; (3) increasing herbivory in riparian willow communities at sites lacking predation or hunting; (4) modification of these communities (see Table 9.1); and (5) decreased avian richness and diversity (see Table 9.2). Although the idea of top-down regulation of communities by carnivores, especially in terrestrial ecosystems, has been controversial (Polis and Strong 1996, Terborgh et al. 1999), our data offer support for its importance, at least in this system. To the north, in Yellowstone Park, where elk densities tend to be exceptionally high, evidence is now accumulating for an inverse relationship between elk abundance and wolf densities, with the effect being that aspen (*Populus tremuloides*) sucker heights may be increasing as elk densities drop (Ripple et al. 2001).

Conservation and the Relevance of Behavior in Predator–Prey Systems

Assuming an initial perspective from that of a pure “animal behaviorist” who desires to understand behavioral processes, it would seem desirable to place large carnivores back into their “natural” ecosystems. Obviously, questions of intrigue will always exist for scientists. Other than the financial cost of carnivore restoration, a purist’s argument might go something like this: the reestablishment of prey behavior once predators are reintroduced is important because predator–prey processes are likely to be more representative of balanced and naturally operating systems.

But this argument in favor of restoration is a personal judgment, not one steeped in science. Although behavioral studies have strong scientific components, the issue of relevance to conservation is not always obvious. If predator–prey interactions and the restoration of antipredator behavior can legitimately be considered as part of the complex of processes or phenomena involved in maintaining biological diversity (Wilson 1992, Berger 1999), then such processes should not be lost. Such issues aside, is there a more tangible role for behavior to play in conservation?

Some would argue no because many conservation biologists and wildlife managers are often less concerned about animal behavior in and of itself and more concerned that systems become (or are maintained as) functionally operating (Redford and Feinsinger 2001, Pyare and Berger 2003). Understanding a species’ behavior may at times help to detect when (or whether) that goal is achieved, but unless the benefit is substantial, the usefulness of behavioral knowledge for its own sake may be limited. Perhaps

the most relevant area where understanding prey behavior has been linked directly to conservation programs has been in situations in which population viability may be jeopardized. These situations tend to occur when prey are naive and unable to cope with predation, whether by native or alien species (McClean 1997; Blumstein et al. 2000; Berger, Swenson, and Lill-Persson 2001), and it is here that an understanding of mechanisms may be more germane to restoration, especially in areas with many alien species (Griffin, Blumstein, and Evans 2000; Short, Kinnear, and Robley 2002).

In shifting from behavioral-oriented approaches to on-the-ground approaches that confront the real management of protected areas, a curious irony is brought forth. In numerous ecological reserves, including (until recently) Grand Teton National Park, the intent has been to enhance biological diversity through “hands off” management, yet the opposite has occurred. Protection, after the localized extinction of large carnivores, has instead resulted in ecological processes such as the decline of taxa within a given park’s boundaries; in contrast, lands outside the park where the active management of wildlife has occurred resulted in greater levels of avian diversity (see Table 9.2). Studies of the behavioral implications of such ecological processes may not be relevant here, yet the conservation of biological diversity surely is, irrespective of whether it be birds, bats, or butterflies, ecological processes, or other levels of organization.

One thematic region where behavioral approaches may be combined with ecological ones to help the management of predator–prey systems involves functional redundancy. Can (indeed, should) human predation substitute for predation by carnivores if prey are so abundant that other tiers of biological diversity are lost? It is already obvious that major differences occur in gender- and age-specific predation and killing practices (Ginsberg and Milner-Gulland 1994, Berger and Gompper 1999), but the extent to which prey differ in their behavior in response to human and nonhuman predation is not totally clear. And, the extent to which ecological shifts occur under contrasting predation regimes and whether these have implications for conservation of ecosystems is still something for which data are only emerging (Ripple et al. 2001).

Conclusions and Recommendations

We argued that large carnivores have the capacity to play substantial roles in systems’ dynamics independent of whether the level is that of a single species or an entire landscape. The consequences of losing large carnivores can be long lasting. Cheetahs and other fleet carnivores have been gone from North

America since the Pleistocene, yet these “ghost carnivores” affect pronghorn (*Antilocapra americana*) who retain not only morphological adaptations for speed but behavior reflective of pressures derived from extinct predators (Byers 1997).

In today’s anthropogenically inflicted world, however, the alterations that we report stemming from loss of carnivores are not ones that have transpired over thousands of generations. Instead, they have occurred in as few as 10 generations, as in the abrupt decoupling of a prey–scavenger recognition system, or even in less than a year as in one-time experience-based learning by moose mothers who lost young to wolves. Although such behavioral changes are specific to the system we worked in, the implications are likely to be broader. The desensitization of prey to both scavengers and carnivores at sites lacking predation indicates that subtle, community-level interactions now no longer occur, at least in some landscapes. It is anyone’s guess as to how other interspecific interactions may have been shaped or reshaped by carnivore losses. Sublethal effects of predators can be significant (Sih and Wooster 1994, Lima 1998), and for ungulates may include habitat shifts, group size formation, sexual segregation, and changes in feeding, pregnancy, and many others still in need of testing (Berger 1998). The extent to which a system’s equilibria may shift as a result of behavioral alterations has only recently been receiving attention. So if one were set on providing insights on the consequences of predator–prey disequilibria, this may be one way in which behaviorists can contribute. Nevertheless, as the loss and replacement of carnivores is likely to continue, other processes will be unraveled, many of which have yet to be described (Wilson 1987, Crooks and Soulé 1999). How the study of animal behavior contributes to conservation at this level is not so clear.

Science, of course, is different from conservation, and progressive efforts concerning the latter are sources for both optimism and study. In localized regions of Europe, lynx (*Lynx lynx*), brown bears, and wolves may all be expanding, either naturally or through reintroductions, or both (Breitenmoser 1998; Swenson, Sandgren, and Soderberg 1998; Boitani 2000). Such conquests are relatively limited when viewed globally against remaining challenges. A larger issue is how best to discover and combat negative ecological responses of prey to replacement of native predators by aliens—the feral species and translocated native ones that we humans have disseminated across this planet and which now reduce our biological heritage through population reduction and extinction.

Restoration options steeped in biological principles will always be important and science will always play some needed role to further sort out ecological dynamics and pursue conservation gains. Yet, a more massive challenge

awaits us all—to spread our messages widely, to shape public opinion, and, in doing so, bring government to action. Though Shere Khan and el tigre may no longer exist in the environments where Rudyard Kipling and Aldo Leopold toiled, we need to focus our restoration efforts on the next generation while not ignoring the rich messages of the past.

Summary

The effects of losing large carnivores on the functioning of ecosystems and on individual prey have been uncertain. We offer empirical evidence about how the loss and restoration of wolves and brown bears is likely to affect temperate and boreal ecosystems, specifically on some of the interactions involving wolves, brown bears, ravens, avian Neotropical migrants, and one large herbivore—moose. We show through geographical contrasts of sites in Alaska and the Yellowstone region as well as experimental alterations of carnivore presence that (1) behavior of individual prey changes as a result of carnivore recolonization, and (2) demography is altered in ways in which maternal behavior is linked to changing predator regimes. We also infer that (3) released from predation, the irruption of moose led to a cascade of ecological interactions that diminished avian biodiversity.

Our findings underscore the importance of detailed single-species and community approaches as well as the adoption of experimental protocols set within an ecological framework to help facilitate biological restoration. The study of animal behavior per se has played only a limited role in functional conservation. Nevertheless, such study has increased knowledge about prey adjustments to predation and the extent to which demographic blitzkriegs may be avoided by beginning to understand rates at which effective antipredator behavior may be reinstalled in previously naive and exceptionally vulnerable prey. Research involving the application of animal behavior to conservation may be limited, but where the goal is to contribute to predator–prey systems one might profitably focus on population vulnerability in relation to predation pressure and habitat alterations, especially when predators are aliens.

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10.

Behavioral Aspects of Conservation and Management of European Mammals

Marco Apollonio, Bruno Bassano, and Andrea Mustoni

This chapter considers a few case studies where knowledge or ignorance of animal behavior led to the success or failure of wildlife management programs in Europe. We also comment on some of the commonest management problems on our continent, and argue that, despite recent strong calls to consider the links between wildlife conservation and ethology (Clemmons and Buchholz 1997, Caro 1998b, Gosling and Sutherland 1999), very often basic aspects of animal behavior are ignored. There are two main reasons why animal behavior is seldom accounted for in European wildlife management: many wildlife managers know little about behavioral ecology, and “traditional practices” persist despite evidence that they are inadequate. We examine case studies where ranging behavior, reproductive behavior, and social behavior have important implications for wildlife management.

Ranging Behavior

Spatial behavior is of great importance to management. Documentation of the ranging behavior of a mammal population, however, can be a demanding task because of the costs and the time necessary to obtain reliable data. This

is especially true in the case of wide-ranging species such as most large and medium-sized mammals (Harestad and Bunnell 1979), which unfortunately are also the most difficult to manage without information about their home range size and the frequency and potential speed of their movements. Information on ranging behavior is crucial to choosing the spatial scale of management plans and testing their validity over time. We illustrate this point with examples from two carnivores and one ungulate.

BROWN BEAR REINTRODUCTION AND CONSERVATION IN SOUTHERN EUROPE

The brown bear's (*Ursus arctos*) range in southern Europe was greatly reduced over the last few centuries. A few remain in the Alps and the Pyrenees, with small but viable populations in the Apennines (a few dozen bears) and in the Cantabrian Mountains (50–65 individuals). Larger populations persist in the Dinaric and Carpathian Mountains (Swenson et al. 2000).

Because the Alpine and Pyrenean populations were reduced to only three to four individuals (Swenson et al. 2000), reintroduction programs were planned for both. Information on the ranging behavior of bears played a key role in the planning of these operations. The political complexity of Europe, both between and within countries, required coordination among local and national governments for the reintroduction of a large carnivore that could potentially be in conflict with agriculture. “Old” data on home ranges of Alpine or Pyrenean brown bears were scarce and contradictory (Daldoss 1981). Couturier (1954) suggested that in the Pyrenees, home ranges were only 3 km². A pilot radiotelemetry study by Roth and Osti on the small remnant population in the Italian Alps monitored three individuals and found that home range size was about 300 km² for males and about 100 km² for females (Roth 1983, Osti 1999). Those results were possibly influenced by the old average age of surviving bears and by the small population size, confirmed by more recent studies (INFS 1998), of the remnant group of bears studied. The “recent era” in brown bear ranging behavior knowledge started with the first reintroduction in Austria in 1989. The first bear, a female, had a home range of about 335 km²; but the second, an adult female, ranged over 4730 km², moving up to 67 km from the release site (Rauer and Gutleb 1997; Zedrosser, Gerstl, and Rauer 1999). These results are similar to those obtained in recent reintroductions in the French Pyrenees and the Italian Alps (Table 10.1; P. Y. Quenette, 2000, pers. comm., Mustoni et al. unpublished). Meanwhile, data on ranging behavior of autochthonous brown bears in southern Europe were collected in Slovenia (see Table 10.1; Kaczensky 2000). Their home ranges appear smaller than those of reintroduced bears in

TABLE 10.1. Home range of reintroduced and native brown bears in southern Europe (calculated as minimum convex polygons)

AGE/SEX	ORIGIN	NUMBER	HOME RANGE (km ²)	HOME RANGE MEAN (km ²)	STANDARD DEVIATION (km ²)
Adult/males	Reintroduced	2	286–1230	758	667.5
Subadult/males	Reintroduced	2	1722–2376	2049	462.4
Subadult/males	Native	4	100–516	322	177.4
Adult/females*	Reintroduced	6	33–4730	1780.8	1637.1
Adult/females	Reintroduced	5	870–4730	2130.4	1560
Adult/females	Native	4	39–63	51.5	10.1
Subadult/females	Reintroduced	2	216–355	285.5	98.3
Subadult/females	Native	2	41–287	164	173.9

*Reintroduced bears data are from reintroduction projects in Austria, France, and Italy. Native bears were released near the capture site in Slovenia.

all possible comparisons (all males $U = 0$, all females $U = 3$, adult females $U = 1$, Mann Whitney U test, $p < 0.05$) if the second-year home range of a reintroduced female was excluded. If the small home range of the reintroduced female is included, the home ranges of native brown bears seem to be smaller only for all males ($U = 0$, Mann-Whitney U test, $I < 0.05$). It therefore seems likely that the reintroduced bears have an exploratory behavior compared with the native ones.

Reintroduced bears also made rapid and sudden movements. In the Italian Alps a male moved about 30 km in 4 days, and 16 km in just 1. In the same area a female traveled over 29 km in 36 hours. These results were also confirmed by the 23 km traveled in 24 hours by one of the “Austrian” reintroduced bears (Zedrosser, unpublished). Autochthonous bears can also make long-distance movements, as illustrated by a large male that traveled 110 km in less than 10 days in 1999 from the province of Belluno to the province of Trento (Wildlife Management Service, Trento Province, unpublished). Some of these movements occurred in December, contradicting the assumption of winter dormancy in brown bears, confirming recent findings on this species (G. Jonožovic, 2000, pers. comm., Swenson et al. 1997b, Kaczensky 2000).

The relevance of these data for brown bear conservation in southern Europe is easy to understand. A successful reintroduction requires three main components organized over a large geographical scale: public informa-

tion, damage prevention and compensation, and continuous monitoring of released bears. The sudden arrival of a bear in an area can lead to disaster if local people are not informed about the program, including the potential for damages (particularly to beehives). Lack of information may lead to hostility toward the bear reintroduction program. In Europe, administrative power is very fragmented. For instance, in Italy, regions and provinces are in charge of wildlife management. A province can vary in size from 2000 to 7500 km²; it is therefore obvious how important coordination can be. In the recent reintroduction program in the central Alps, conducted in Italy by the Adamello Brenta Natural Park, the success of the operation was due to careful planning of the three steps, previously mentioned, among five provinces. Currently, this is the largest brown bear reintroduction in Europe, with 10 bears successfully released and being monitored. After the first 3 years of the project, the bears have been documented in three provinces (Fig. 10.1), no illegal killings have occurred, and about €30,000 in damages has been paid out.

Another important aspect of bear conservation that can be influenced by the knowledge of their ranging behavior is population estimate. On many occasions wide movements can cause a gross overestimate of the population because a few bears with very large home ranges and very rapid movements are assumed to be many bears with small home ranges. The same bear can be seen tens of kilometers apart over a few days. An inexperienced wildlife manager may conclude that a flourishing population exists, instead of a small and threatened one. This problem may apply to the small Apennine populations where an overestimation of bear numbers is highly probable. In the long run, an erroneous overestimation of population size may delay restocking operations and possibly increase the risk of extinction.

WOLF RETURN TO THE WESTERN ALPS

Wolves (*Canis lupus*) once ranged throughout all of Italy and neighboring countries, but in the nineteenth century they gradually disappeared from the Alps. The last recorded killing was in 1923 in the Maritime Alps (Cagnolaro et al. 1974). The wolf in Italy decreased to its lowest numbers in the early 1970s, when it was reduced to a few areas of the Apennines and the Tyrrhenian coast. Beginning in the 1980s, however, the species expanded in distribution and probably in numbers. This reversal of fortune was due both to legal protection and to the rapid recovery of woodland that allowed the development of flourishing wild ungulate populations.

In 1985 a dead wolf was found less than 100 km from the Alps, on a northern Apennines range directly leading to them. Not surprisingly, wolves then appeared on the French side of the western Alps (Fig. 10.2). In 1988 one

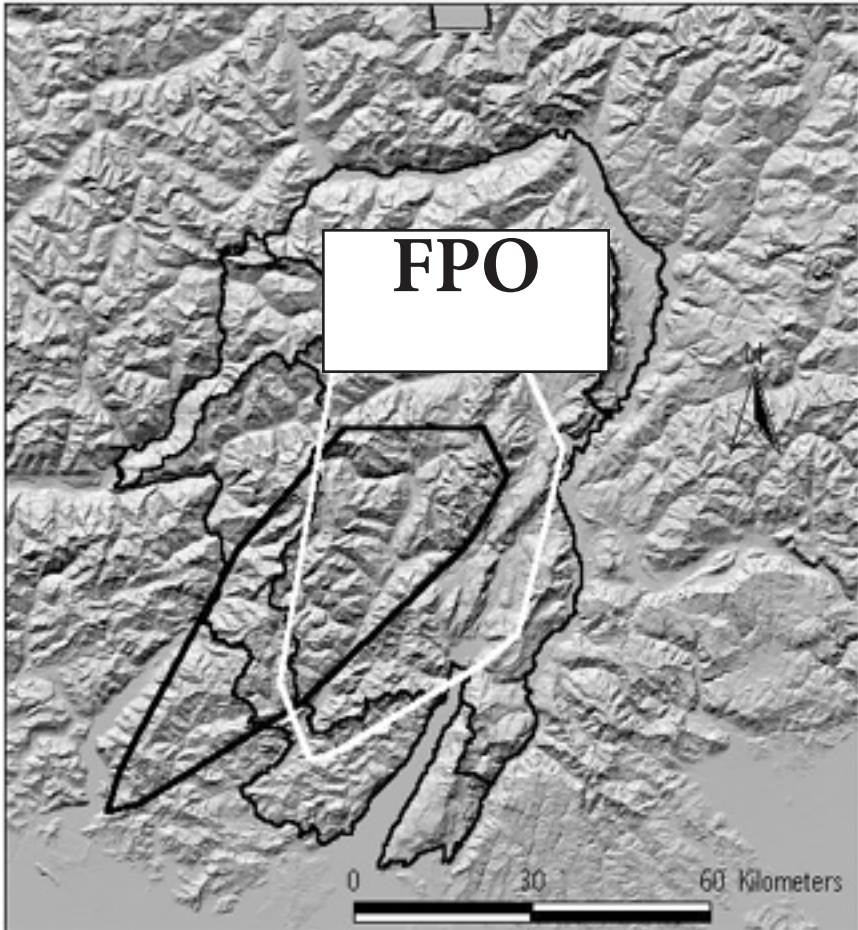


FIG. 10.1. Annual home ranges of reintroduced brown bears in the Italian Alps. In white, subadult male; in dark black, subadult female; in light black, province border.

wolf was found dead, then in 1992 a pack of wolves was observed in the Mercantour massif. Wolves were seen on the Italian side of the Alps in 1994 and in Switzerland in 1995. Genetic analyses showed that these wolves were of Italian origin (Scandura et al. 2001) despite claims of illegal reintroduction.

The recovery of wolves in the Alps was rapid (see Fig. 10.2) but not without consequences. The main conflict arose with sheep breeders, and its intensity varied among countries in relation to sheep numbers and breeding practices. In Italy and France reimbursements were established from the very beginning of wolf recolonization. In Italy the lower level of wolf damages (about €35,000 compared to about €342,000 in France in 2001) was due to a

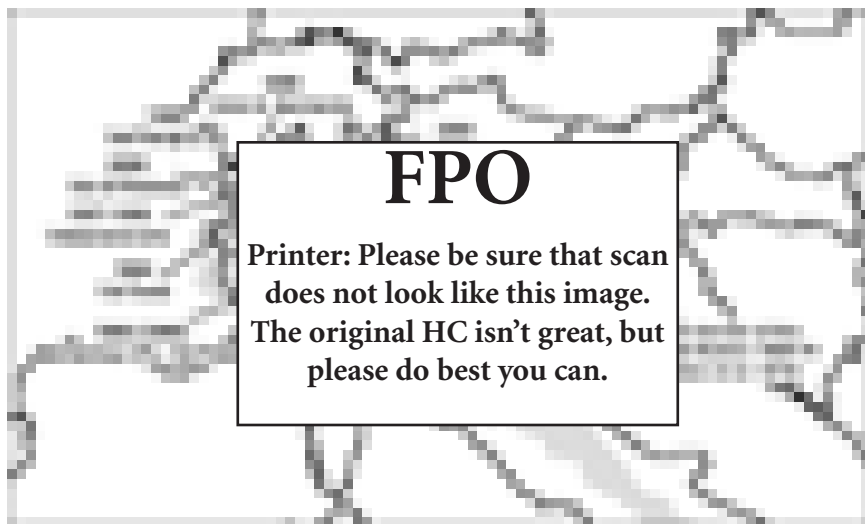


FIG. 10.2. Wolf recovery in the Alps. Each locality is labeled with the date of first occurrence. The year in brackets for the Mercantour is the date of the first recovery of a dead wolf in the Alps.

lower number of sheep and to the smaller size of sheep flocks. The decreasing human population of many alpine valleys in Italy is another cause of this difference. A further reason is likely a difference in sheep-raising practices. In France, flocks of up to 800 to 1000 are not uncommon, whereas flocks on the Italian side are roughly five to ten times smaller. In France, where the amount of damages increased from €8690 in 1993 to €227,234 in 1998 (Pouille et al. 2000), sheep breeders asked for controls on the wolf's distribution (French Ministry of Agriculture and Fisheries 2000) even though the number of wolves was estimated at only 14 to 19 in the period from 1996 to 2000 (French National Hunting Office, 2000, pers. comm). There were also six documented illegal wolf killings from 1995 to 2001. In Italy the low level of conflicts helped to maintain full protection of this species and to reduce illegal killings to only two between 1994 and 2001. In Switzerland, hostile public opinion led to the legal killing of any wolf believed to have killed 50 sheep. Given that it is impossible to properly establish which wolf kills which sheep, this measure opened the door to legal control of any wolf, leading to three legal, one illegal, and two suspected wolf killings. Not surprisingly, no evidence of wolf reproduction has been reported in Switzerland. The reported loss was 36 sheep in 1998, 266 in 1999, and 242 in 2000, out of about one million sheep in Switzerland (Kora unpublished data).

The pronounced tolerance of Italian authorities and citizens toward

wolves may also be due to a tradition of considering it a rare species that requires protection. Thirty years of legal protection and of public campaigns for wolf conservation, combined with an effective compensation scheme, likely contributed to acceptance of wolves in newly reoccupied areas. On the contrary, in France and Switzerland the species disappeared completely: there have been no resident wolves in Switzerland for more than a century and in France for more than 50 years. Consequently, the public had neither knowledge of nor tolerance toward these predators. Moreover, sheep-breeding practices in these countries increase the potential for conflicts. The most extreme position was taken in Switzerland, where wolves had been absent for a longer period and where the government heavily subsidizes sheep breeding in the Alps.

When the Italian wolf populations started to recover, much information was available in the scientific literature on the dispersal capacity of wolves (Fritts 1983, Van Vueren 1998) and on the social mechanisms leading to dispersal (Mech 1995). It was therefore easy to foresee the return of wolves to the Alps, but, at that time, nobody warned public administrations about the need to develop programs to increase public awareness about the return of the wolf, or about how to prevent damages. Lack of initiative taken by wildlife managers and scientists obviously worsened the conflicts arising from the recovery of wolves in the western Alps, creating a situation where three neighboring countries have three different attitudes toward the management of a wide-ranging species that ignores national borders. In western Europe wolves are considered a high-priority species by many national laws and by the Habitat Directive of the European Community: failure to prepare in advance for the return of the wolf led to several conflicts and possibly hampered recolonization of some areas.

RED DEER IN THE ALPS AND NEIGHBORING MOUNTAINS

The red deer (*Cervus elaphus*) is the largest herbivore in southern Europe. Its original wide distribution was reduced during the nineteenth century to mountain areas, especially in alpine countries such as France, Italy, Austria, Switzerland, Germany, and Slovenia. In the mountains deer must face difficult environmental conditions, including harsh and snowy winters. The strong seasonality of the Alps encourages traditional movements among seasonal ranges, determined by food availability and snow cover. Gossow and Stadlmann (1985) identified distinct summer and winter ranges on mountain slopes, showing how the availability of winter ranges was reduced by habitat modifications caused by human activities. Radiotelemetry studies, however, revealed a more complex situation: both on the north (Georgii

1980, Georgii and Schroeder 1983, Leoni 1995) and on the south side of the Alps (Luccarini and Mauri 2000) red deer populations include migratory and sedentary individuals. The former made long-range seasonal movements from a winter range at low elevation to a summer range at high elevation, whereas the latter remained in the same general area year-round. As a result, in winter the entire population was restricted to the same low-altitude areas that were used year-round by a substantial number of deer. Low-elevation areas in the Alps are intensively used by humans, reducing the availability of foraging and resting areas for red deer. In addition, artificial feeding stations can concentrate deer in small areas. The winter home ranges of artificially fed populations are smaller than those of unfed populations (Luccarini and Mauri, unpublished).

Supplemental feeding increases winter survival, and it is frequently used in the central and eastern Alps and neighboring mountains. Supplemental feeding is sometimes prescribed by national laws, for example in Austria, but it can result in major damage to trees. The combined effect of browsing and other problems such as acid rain can damage over 70% of the trees (Wotschikowsky 1978). A more extreme management practice consists of fencing all deer into corrals where they are fed over winter and then released. The enclosed area is completely devastated by browsing and the deer are vulnerable to contagious diseases (Wotschikowsky 1978).

Although red deer are now widely distributed over the Alps and neighboring mountains where they are an important game species, they are not taken into account when urban developments are planned. Even if some extreme forms of management such as massive winter feeding in otherwise unsuitable areas have kept some deer populations at high elevations in winter (Schmidt 1993), the forest damage caused by winter concentrations of deer at low altitudes is a widespread problem (Voelk 1998).

Reproductive Behavior

Reproductive behavior and mating systems affect wildlife conservation and management because they can have a profound impact on population structure (Clutton-Brock, Guinness, and Albon 1982), genetic variability (Apollonio and Hartl 1993), and, ultimately, species evolution. Because the rut is a key phase of the biology of a population, any perturbations to its regular course may have strong consequences for population dynamics. The interrelations of wildlife management practice with ungulate reproductive behavior are many. Here we consider the possible consequences of trophy hunting on ungulate males. The practice of hunting large males to obtain prestige is very old in Europe. According to Julius Caesar in his *De bello gallico* (first century

B.C.): “Aurochsen are smaller than elephants; they look like bulls. . . . Germans like to trap and kill them. This kind of activity is useful for young men to exercise themselves and become stronger, those that kill many aurochsen show the horns of their preys in public and receive great honors.” The human interest in displaying large horns or antlers can have major effects on the sex/age structure and population dynamics of ungulates. Horns and antlers are often secondary sexual characters, whose size is strongly correlated with age.

The outcome of the search for large trophies is an overkill of mature males. The structure of the male part of the populations can become highly skewed toward young age classes. Data on the age of chamois (*Rupicapra rupicapra*) shot over 7 years of hunting seasons in the free hunting districts of the Aosta Valley record that less than 5% of males were older than 9 years, and less than 10% were older than 7 years. Chamois age distribution can be quite different in areas with a less severe hunting effort. Those harvested over four seasons in private reserves in the Aosta Valley, where hunting pressure is lower than in free access areas, included 12% of males older than 9 years and 21% older than 7 years, more than twice the numbers in free hunting territories ($\chi^2 = 138.26$, $p < 0.001$) (Fig. 10.3A,B). If we consider that harvests were biased by the preference for older males, we obtain a discouraging picture of the management of the most common alpine ungulate, at least where shooting plans do not call for age-specific quotas. The same trend is evident comparing male census data of the un hunted alpine ibex (*Capra ibex*) population of Gran Paradiso National Park (Italy) and those of the Swiss hunted ibex population of the Graubunden Kanton: the differences in age class distribution in the male populations were very marked ($\chi^2 = 358.82$, $p < 0.001$ comparing years with lower presence of males older than 10 years in the populations; $\chi^2 = 457.52$, $p < 0.001$ comparing years with higher presence of males older than 10 years in the populations) (Fig. 10.3C,D). This last example could also indicate that moderate hunting pressure, such as that exerted on the Swiss alpine ibex population, may lead to significant differences in population structure from completely un hunted populations.

The consequences for the ungulate populations of intense removal of mature males in relation to reproductive strategies can be variable and complex. Male age is correlated with reproductive success, and there is often a clear age threshold below which males do not reproduce. In un hunted populations, this age is 5 years for red deer (Clutton-Brock, Guinness, and Albon 1982), 4 years for fallow deer (*Dama dama*) (Clutton-Brock, Albon, and Guinness 1988; Apollonio, Festa-Bianchet, and Mari 1989; McElligott and Hayden 2000), about 3 years for roe deer (*Capreolus capreolus*) (Liberg et al. 1998), 10 years for alpine ibex (Apollonio, Mauri, and Bassano 1997), and probably

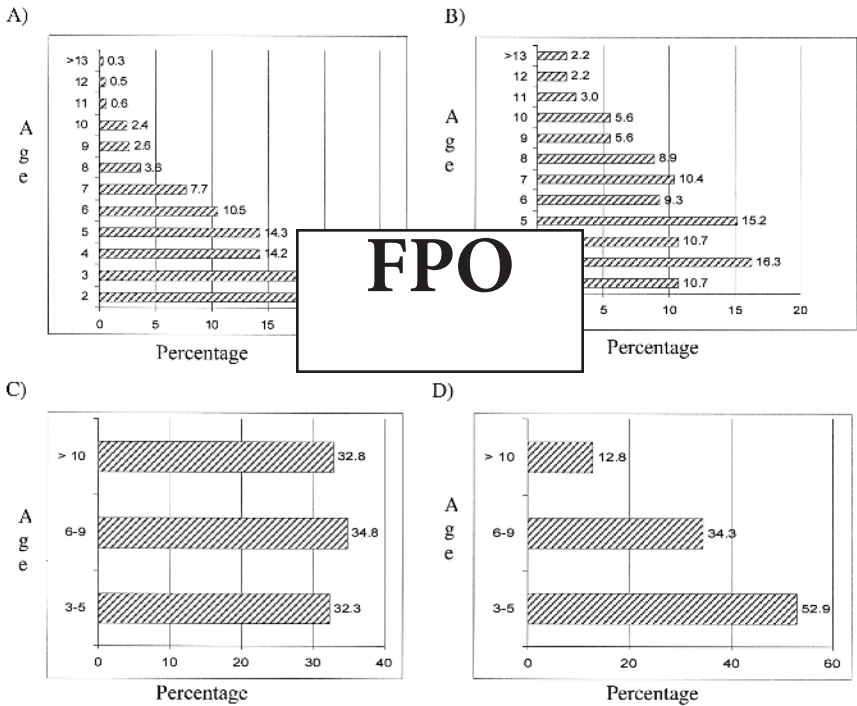


FIG. 10.3. (a) Age distribution of 2721 male chamois shot in free hunting area of the Aosta Valley from 1985 to 1991. (b) Age distribution of 270 male chamois shot in private hunting reservations in the Aosta Valley from 1989 to 1991. (c) Age distribution of 2682 male ibex in the unhunted population of Gran Paradiso National Park (1984 and 1992). (d) Age distribution of 3383 male ibex in the hunted population of Kanton Graubunden Hunting Districts (1996 and 2001).

7 to 9 years for chamois (the minimum age at which males defend territories) (von Hardenberg et al. 2000).

Given that older males potentially have high reproductive success and take an active part in reproductive behavior, their removal may have many serious consequences. One such consequence could be the possibility for younger males to take part in reproduction, including bearing the costs of this activity and therefore experiencing increased mortality (Geist 1971). This process can induce a steady decrease of the mean age of males to extremely low levels. There are also some indications that the removal of some old, highly successful males may decrease the mating rate of females, possibly because of the social instability and intense fighting among surviving males (Apollonio, Festa-Bianchet, and Mari 1989). Changes in male age structure can lead to a change in mating system (Byers and Kitchen 1994), possibly forcing females

to make suboptimal mate choices that could be associated with lower probabilities of conception.

Mature males are the most fit individuals, able to survive well past the age of first reproduction: the hunter's choice counters natural selection. This is especially true when individuals with high reproductive success are those that live longer, as recently reported in fallow deer (McElligott and Hayden 2000).

Criteria commonly used to assess the "value" of a trophy, such as size and shape, may have little to do with a male's reproductive success. Complex formulae used by the Conseil International de la Chasse to evaluate ungulate trophies are based on various measurements of length and width. On two occasions we obtained these antler measurements for lekking fallow deer bucks of known copulatory success ($n = 6$ and $n = 16$). In only one case (circumference of the right beam and copulatory success, $n = 16$, $r_s = 0.544$, $p = 0.029$), was there a correlation between reproductive success and individual measurements or the trophy score ($r_s \leq 0.676$, $n = 6$, ns; $r_s < 0.425$, $n = 16-14$, ns). It was obvious that differences among lekking bucks were so small that a clear trend relating antler size to reproductive performance was difficult to demonstrate. Although it is difficult to measure reproductive success of males, data from several other ungulate species suggest that antler morphology does not always predict male reproductive potential. For roe deer, age seems to be the major factor influencing mating success (Liberg et al. 1996).

Criteria used to decide which male to remove may not have any selective value. Consequently, any selective harvesting policy may resemble a random removal. In these conditions, the risk of a mistake is higher when shooting an old than a young male because the former has overcome more selective difficulties than the latter. Moreover, in species with polygynous mating systems, such as most European ungulates (Clutton-Brock 1989), male mating success is generally highly skewed (Clutton-Brock 1988; Apollonio, Festa-Bianchet, and Mari 1989; McElligott and Hayden 2000). Therefore, given the difficulties of recognizing high-quality males from morphology, the possibility of killing successful males is always present when mature males are removed.

Social Behavior, Social Structure, and Management Operations

Many mammals have well-defined social units and strong individual relationships. Sociality is often advantageous in cooperative predator detection, caring for the young, and searching for food. Attaining a critical population

size is often key to the survival of social species, which often show a metapopulation structure with dispersal among subpopulations. Here we discuss how ungulate reintroduction should be planned in relation to social and metapopulation structure (see chapter 7). Ungulate reintroductions are an important part of wildlife management in Europe: recovery of many species has been based on a series of reintroductions, often planned without a general framework.

ALPINE IBEX REINTRODUCTION IN THE SOUTHERN ALPS

ibex were almost extinct in the Alps, and their recovery was entirely due to protection of the last population and to reintroduction in six different countries. The only surviving population in the second half of the nineteenth century was on the southern slopes of the Aosta Valley, Italy, protected in a royal hunting preserve. The population estimate in 1879 was of 790 ibex (Passerin d'Entreves 2000). The first reintroductions took place at the beginning of the twentieth century, both in Italy and in neighboring countries. In 1940 there were just four populations in the southern Alps, one autochthonous, two expansions from reintroduced Swiss colonies, and one resulting from a reintroduction in the Maritime Alps in Italy. In 1999 there were about 70 populations in the Italian Alps, with more than 13,000 ibex. The average size of these populations was 192 individuals, but the standard deviation was very high, at 471 individuals, suggesting a very uneven reintroduction success, even if differences in time since reintroduction likely explain some of this variance.

Taking into consideration that the alpine ibex is a social species in which males and females segregate for most of the year (Nievergelt 1967, Toigo et al. 1998, Villaret and Bon 1998), and that individuals tend to move freely between valleys joining adjacent groups, we examined two possible effects of sociality and metapopulation structure on reintroduction success. We analyzed 14 reintroductions in Italy, for which data were available, to test whether the success of a reintroduction (measured as population size 5 years postrelease) was related to the number of ibex introduced in each release or to the number of males and females. Using stepwise multiple regression analysis we found that only the number of females introduced was a significant predictor of variation in population size 5 years after release ($R^2 = 0.83$, $p < 0.0001$), but the number of males and the total number of ibex introduced had no significant effects. A large number of females in the reintroduction nucleus was obviously important to obtain a large population as well as a rapid growth rate. We also examined the mean annual increase of isolated populations (with no other population within 30 km) and those

within less than 30 km from at least two other well-established populations. Preliminary results suggest that connected population may be growing faster 5 years after reintroduction than isolated ones (Mann Whitney U test, $U = 11$, $p = 0.02$). When we controlled for the number of ibex introduced, number of females introduced, and number of males introduced using analysis of covariance, however, the increase of the population after 5 years was not different between isolated and connected populations ($F_{1, 14} = 2.49$, $p = 0.14$).

Even if these results are not unequivocal in presenting evidence for the influence of size and composition of the founding nucleus or of the existence of a metapopulation frame, it is interesting to note that ibex reintroductions in Italy have often been planned with little consideration for the social characteristics of this species. In fact, the most common reason for ibex reintroduction is politically motivated, based on the desire of a given public administration to have ibex on “their” mountain. Consequently, there is no planning on a wider geographical scale to reestablish a viable ibex metapopulation. Moreover the composition and size of the reintroduction nucleus has often been dictated by casual context rather than planned with a scientific approach. A noteworthy exception is provided by some well-planned operations in the central Alps that used about 90 ibex as a starting group. But other difficulties included low financial support for these operations and the lack of postrelease monitoring, a critical aspect rarely planned after a reintroduction (the omission of which also complicated our analysis). Many opportunities remain to establish a wide-ranging plan for ibex reintroduction in the southern slopes of the Alps because more than 80% of all ibex in Italy are currently confined in the western half of the Alps.

Conclusions and Recommendations

Our chapter emphasizes the need for a new approach to management of large mammals in Europe. The economic and social importance of these species requires a consideration of their biology and conservation needs in the planning of many human activities. We should not limit our interest to hunting or recreation. For example, we suggest that it is necessary to include the conservation of large herbivores in the planning of urban areas in mountains or hilly districts. Much research is required to forecast the future demographic and geographical expansion of the large carnivore populations now existing in Europe. Behavioral ecologists are accustomed to formulating hypotheses and making predictions about their research subjects. They must also use their communication skills to advise politicians and land managers about policy options that take into account the current distribution of large mammals and also encourage their future recolonization of suitable habitats.

Summary

This chapter deals with some of the more recent and most relevant management problems for large mammals in western Europe. Brown bear reintroduction in the Italian Alps provides insights about how the ranging behavior of this species makes it necessary to formulate plans for public information, damage prevention, and compensation, and requires intensive monitoring of reintroduced individuals. The recent wolf recovery in the western Alps is a good example of contrasting approaches to the management of the same predator in neighboring countries. Lack of coordination across political boundaries hampers the conservation of large predators. Red deer management is a longstanding problem in western European mountains. Although some deer remain at low elevation all year, others migrate long distances over altitudinal gradients. The provisioning of artificial feeding stations has a negative effect on red deer population because it causes unnatural crowding, thereby reducing home range size. We examined the consequences for ungulate populations of heavy removal of mature males in relation to reproductive strategies. There are major differences in population structure between populations of the same species under different management regimes. Often, the criteria used to assess the “value” of a trophy male may not be related to reproductive success. We suggest that poor knowledge of male reproductive skew can lead to the use of nonselective harvest criteria and ultimately to unwanted genetic or demographic consequences. Finally, using the reintroduction of ibex in the Alps as an example, we examine how the planning of such operations at the metapopulation scale may influence the success of the individual reintroduced herds.

Acknowledgments

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11.

Implications of Sexually Selected Infanticide for the Hunting of Large Carnivores

Jon E. Swenson

When estimating sustainable harvest rates, wildlife managers are typically interested in population-level parameters, such as reproductive rates, survival rates, age distribution, sex ratios, density dependence, and the effect that hunting has on these parameters (Sutherland 2001). The potential effects of hunting on behavior, however, are usually not considered. As one might expect, hunting can affect wariness (Vosburgh and Irby 1998) and short-term habitat selection (Swenson 1982). In addition, effects of hunting on mating system and pair bonds have been documented. For example, pronghorn antelope (*Antilocapra americana*) may shift from resource-defense to harem-defense polygyny in response to a decline in the proportion of older males (Byers and Kitchen 1988). Also, killing male mallards (*Anas platyrhynchos*) after the pair bond has formed on the wintering area lowers subsequent reproduction by yearling females (Lercel et al. 1999). Greene et al. (1998) modeled the effects of hunting in relation to breeding behavior for some African mammals and concluded that the effect of harvest depends, in part, on the interaction between hunter selectivity and breeding system. They found that

for moderately polygynous ungulates, high-intensity hunting that focuses on either males or on adults of either sex has a greater effect on populations than hunting of all age and sex classes, and that monogamous and weakly polygynous species are particularly sensitive to hunting. In large carnivores, hunting dominant males can have a population effect through increased juvenile mortality due to sexually selected infanticide (SSI) following male turnover (Starfield, Furniss, and Smuts 1981; Swenson et al. 1997; Greene et al. 1998). In addition, decreased reproductive success has been reported when females choose less productive habitats to avoid potentially infanticidal males (Wielgus and Bunnell 1994, 2000).

In this chapter, I describe the SSI hypothesis and briefly summarize empirical evidence for SSI in many mammalian groups, including large carnivores, although SSI has been well described in many other groups of animals, including birds and invertebrates. I then focus on the evidence of SSI in large carnivores, particularly the lion (*Panthera leo*) in the Serengeti and the brown bear (*Ursus arctos*) in Scandinavia. I discuss the ramifications that SSI can potentially have for sport hunting of large carnivores and the controversy that this concept has generated.

Sexually Selected Infanticide

Infanticide is the killing of dependent offspring. A common formal definition is “any behavior that makes a direct and significant contribution to the immediate death of an embryo or newly hatched or born member of the perpetrator’s own species” (Hrdy and Hausfater 1984). Hrdy (1979) classified the potential reasons for infanticide and concluded that infanticide can benefit the perpetrator if it is linked to competition for limited resources. When that limited resource is mates, the competition is intrasexual and the infanticide is termed sexually selected. The requirements of the SSI hypothesis are (1) infanticidal males should not kill offspring they have sired, (2) infanticide should shorten the interbirth period of the victimized females, and (3) infanticidal males should mate with the mother of the dead infant and sire her subsequent offspring (Ebensperger 1998). If loss of part or all of a litter will increase the size or survival of the subsequent litter, however, the interbirth period does not have to be shortened for SSI to occur (van Schaik 2000a). I limit my discussion about infanticide to SSI because it has the most direct implications for sport hunting of large carnivores.

Because infanticide reduces the fitness of the victim’s parents, they are expected to evolve counterstrategies to prevent infanticide (Ebensperger 1998). For mothers, these may include (1) pregnancy termination to prevent additional investment on infants that would likely be killed (the Bruce effect), (2)

maternal aggression to protect the offspring, (3) female coalitions to repel infanticidal conspecifics, (4) avoidance of potentially infanticidal males, (5) promiscuity to confuse paternity and provide an incentive for males to tolerate the young, and (6) territoriality to keep potential intruders away from vulnerable infants (Ebensperger 1998). Behaviors consistent with these counterstrategies have been reported in various species of large carnivores (Craighead, Sumner, and Mitchell 1995; Craighead et al. 1995; Ebensperger 1998; Wielgus and Bunnell 1994, 1995, 2000; Logan and Sweanor 2001), although one would not necessarily expect to find all of these in every species showing SSI.

Patterns of Sexually Selected Infanticide in Mammals

A recent review revealed that various forms of infanticide have been observed in 91 species of wild or captive mammals (Ebensperger 1998). Van Schaik (2000a) investigated whether infanticide by males is concentrated in species with female life history patterns that are expected to promote SSI, especially long lactation (or any prolonged maternal care that delays conception) relative to gestation, because postpartum mating is unlikely given that it would produce two sets of young of different ages. Van Schaik (2000a) found that the gestation period is longer than lactation in most mammals. Species in which male infanticide has been documented, however, had significantly longer lactation:gestation ratios, as expected from the SSI hypothesis. The few species with short lactation and documented infanticide by males are rodents with large litters, where the loss of one litter either decreases the interbirth interval or increases the size of the next litter (Elwood and Ostermeyer 1984).

Van Schaik (2000a) found reports of infanticide in five taxonomic groups, all with lactation:gestation ratios greater than or equal to 1; primates, fissiped carnivores, odontocetid cetaceans, sciurognath rodents, and perissodactyls. In the other eight groups of nonvolant mammals examined, lactation:gestation ratios were significantly less than 1, and no deliberate infanticide by males had been recorded. The results of this analysis strongly support the SSI hypothesis and show that male infanticide is found primarily in three groups: primates, fissiped carnivores, and sciurognath rodents.

Another way to assess the importance of SSI is to determine whether females of species that are expected to show SSI also show counterstrategies against it. Van Noordwijk and van Schaik (2000) examined four predicted counterstrategies: (1) polyandrous preconception mating (leading to paternity confusion), (2) long mating periods (to promote polyandry), (3) post-conception mating (which also confuses paternity because a male mates

with a female that is already pregnant), and (4) embryo abandonment in response to the arrival of potentially infanticidal males. They classified species as vulnerable if lactation lasts longer than gestation, reproduction is not strictly annual and seasonal, or implantation is facultatively delayed or the birth interval shortened after a lost litter. Females in vulnerable primate species mate polyandrously more often (62% of 47 species) than females of nonvulnerable species (9% of 11). In carnivores, 87% of 40 vulnerable species mate polyandrously compared with 58% of 26 nonvulnerable species. They found no clear pattern for length of mating periods or post-conception mating, but the latter is common among the vulnerable species in two of the most vulnerable orders, primates and carnivores. Although the data on embryo resorption or abortion are limited, especially for wild mammals, it is observed in many species in circumstances where subsequent infanticide is likely.

Primates are the best-studied group of mammals exhibiting male infanticide. Van Schaik (2000b) examined 54 cases of infanticide to see if they correspond with the predictions of SSI. He found that 85% of the cases of infanticide occurred after a reproductively able male became dominant; 94 to 98% of the infants were not killed by their father; 67 to 100% of the infants, depending on species, were killed at an age that would have shortened the time to their mother's next estrus; and, in 78% of the cases, the male gained mating access to the mother. These results are consistent with SSI. Recent DNA analyses have shown that male langur monkeys (*Presbytis entellus*) killed or attacked only infants they had not sired, and were the likely fathers of subsequent infants (Borries et al. 1999).

Packer and Pusey (1984) predicted that carnivores were more likely to exhibit infanticide than any other mammalian order. These studies provide strong theoretical and empirical support for the occurrence of SSI in carnivore species with female reproductive patterns that make them vulnerable for SSI.

Lions in the Serengeti

Among large carnivores, SSI has been best documented in lions, especially in a 24-year study in the Serengeti (Pusey and Packer 1994a). The presence of resident males in a pride deters infanticide by alien males. Virtually all cubs less than 9 months of age died after groups of males took over a pride of females. There was a clear benefit for the males to kill the cubs after a takeover because the time from cub death to conception is about 5 months, compared with 20 months from birth to conception when the cubs survive. Because the average tenure of a male coalition is only 24 months, the advantage is

obvious. Another advantage to the overtaking males is that the mothers terminate their alliance with the former males after their young die, and begin to cooperate with the new males to keep out other males (Pusey and Packer 1994a).

As expected, female lions show counterstrategies to infanticide (Pusey and Packer 1994a). McComb et al. (1993) documented that mother lions can identify the roars of potentially infanticidal males. When mothers heard roars of alien males, they stood up, grimaced or snarled, and stared in the direction of the roars. Most mothers then ran or walked with their cubs in the opposite direction. When meeting alien males, females with cubs threaten or attack them, and may be wounded or killed in the fighting (Pusey and Packer 1994a). Grouping by females appears to be an important defensive strategy; cubs of solitary females were more likely to be killed than cubs of groups of two or more females (Packer, Scheel, and Pusey 1990), even though the typical number of females in a crèche exceeds the optimal group size for female foraging efficiency (Packer, Scheel, and Pusey 1990) and crèche formation leads to milk theft by nonoffspring (Pusey and Packer 1994b). Also, alien males are more reluctant to approach playbacks of three females roaring in a chorus than single females roaring (Grinnell and McComb 1996). Pusey and Packer (1994a) concluded that risk of infanticide by males was an important factor influencing pride size.

Another counterstrategy to infanticide is attracting large male coalitions (Pusey and Packer 1994a). Because the length of tenure increases with coalition size, females associated with a large male coalition suffer lower rates of infanticide. Following takeover, females show heightened sexual activity but reduced fecundity for about 100 days. The heightened sexual activity of many estrus females that have lost their cubs encourages competition among coalitions, and the largest coalition eventually becomes resident in the pride. The reduced fecundity is thought to be a strategy to attract a larger male coalition before conceiving (Pusey and Packer 1994a). Delayed conception would lead to a higher female lifetime reproductive success if it increased the chance of attracting a large coalition by 30% (Packer and Pusey 1983a). Packer and Pusey (1983b) found that females also produced a higher proportion of sons in the first 300 days after a takeover. This was expected because the young males in the pride will then produce potentially larger male coalitions when they mature, increasing their chances of invading new prides.

The research in the Serengeti clearly shows SSI in lions. The three requirements of SSI were met and females showed five of the six counterstrategies. When the effect of SSI after male takeover is incorporated into harvesting models, several authors have shown that killing harem-holding males

reduced population growth rates (Starfield, Furniss, and Smuts 1981; Venter and Hopkins 1988; Starfield and Bleloch 1991; Greene et al. 1998). It is important to note, however, that the occurrence of SSI seems to vary among lion populations. The smaller parks of East Africa contain small isolated populations, and dispersing males suffer high mortality outside the protected areas. In these parks male takeovers apparently occur at a much lower frequency than in the Serengeti and there is only anecdotal evidence of infanticide (Packer and Pusey 1984). Also, cub:female ratios were not affected by removal of adult males in a lion population in Zambia, where the mortality rate of adult males was especially high (Yamazaki 1996). This apparently influenced the social organization, allowing males to copulate with females from several prides. I suggest that SSI would be lower in this situation, with uncertain paternity.

Brown Bears in Scandinavia

Bears are a likely candidate for SSI (Packer and Pusey 1984). Female reproductive intervals are 2.0 to 3.0 years in American black bears (*Ursus americanus*) (Garshelis 1994), 2.6 to 4.6 years in North American brown bears (McLellan 1994), and an average of 3.7 years in polar bears (*U. maritimus*) (Derocher and Taylor 1994). During the breeding season, captive female American black bears breed 2 to 3 weeks after their cubs are removed (LeCount 1983), but there is some evidence that black and brown bears in the wild may come into estrus within 2 to 4 days after losing their cubs (LeCount 1983, Hessing and Aumiller 1994). Evidently, a male has much to gain by killing cubs he has not fathered if he can sire the subsequent litter. Observed female counterstrategies include aggressive defense of young, and mothers may be killed or wounded in the fighting (McLellan 1994; Craighead, Sumner, and Mitchell 1995; Swenson, Dahle, and Sandegren 2001b); polyandry (Craighead, Sumner, and Mitchell 1995; Craighead et al. 1995); and avoidance of habitats frequented by males (Pearson 1975; Murie 1981; Mattson, Knight, and Blanchard 1987; McLellan and Shackleton 1988; Wielgus and Bunnell 1994, 1995, 2000).

It is well known that bear cubs, as well as older bears, including females, are killed by adult conspecifics of both sexes (Garshelis 1994, McLellan 1994). Killing of nonkin offspring by females may reduce competition for resources (Hrdy 1979, Lindzey et al. 1986). Although much conspecific predation is clearly not SSI, I will concentrate on male infanticide because it is most relevant to sport hunting.

Unlike lions, male brown bears are not associated with a harem, and neither sex is territorial. Bear home ranges overlap those of other bears of

both sexes (Mace and Waller 1997, McLellan and Hovey 2001). During the breeding season (mainly May and June), males and females usually remain together for several days to 3 weeks, although consortships can be as short as a few hours (Craighead, Hornocker, and Craighead 1969; Murie 1981; Herrero and Hamer 1997). Both sexes are promiscuous, with females mating with up to eight males in one season (Craighead, Sumner, and Mitchell 1995). Cubs stay with their mothers until they are 1 to 2 years old in Scandinavia (Swenson et al. 2001), but in North America few cubs leave as yearlings, and they can stay with their mother for up to 4 years (McLellan 1994).

HARVEST OF ADULT MALES AND CUB SURVIVAL

The reported effects of hunting male bears on cub survival are equivocal. Some studies of brown and American black bears have reported a negative relationship between recruitment and density of adult males (McCullough 1981, Stringham 1983, Clark and Smith 1994), counter to the SSI hypothesis. The opposite effect has also been postulated, that increased hunting of adult males can increase cub mortality through SSI by immigrating males (Stringham 1980). Empirical evidence for SSI comes from one population of American black bears and a comparison of two populations of brown bears (LeCount 1987, Swenson et al. 1997). Miller (1990b) concluded that neither a positive nor a negative effect of killing adult males on cub survival has been adequately demonstrated.

My collaborators and I have been studying two populations of brown bear since 1984, one in northern Sweden (about 8000 km²) and one in central Sweden–southeastern Norway (about 13,000 km²); they are described in Bjärvall and Sandegren (1987). The study areas are about 600 km apart and are near the northern and southern edges of the species' range in Sweden. Both populations increased rapidly from 1984 to 1995, indicating they were below carrying capacity. The exponential rate of increase (r) was 0.13 in the north and 0.15 in the south (Sæther et al. 1998). Bear hunting was allowed during the autumn in both areas, but the northern area includes three national parks where hunting is forbidden. Hunting pressure has increased sevenfold since 1995 in the southern area. In the northern area, there is evidence of considerable poaching of bears, about 2.8 times greater than the legal harvest (Swenson and Sandegren 1999). Poaching is less important on the study area than in the surroundings, and it may restrict immigration to the study area (Swenson et al. 2001).

Swenson et al. (1997) examined data from 1985 to 1995 to test the following predictions of the SSI hypothesis: (1) premature loss of cubs would

shorten the interval to subsequent estrus, (2) cubs would disappear (presumably die) during the breeding season, (3) cub survival would be lower following the killing of adult (≥ 5 years) males in the south, where hunters killed males during the period from 1985 to 1995, and (4) cub survival would be high in the north, where no males had been killed by hunters. Unmarked cubs were monitored by following their radio-marked mothers. All the predictions were met (Swenson et al. 1997): (1) 8 of 10 females that lost all their cubs gave birth the next year, compared with none of 40 that kept their cubs; (2) 75% of the 20 cubs that disappeared did so during the breeding season; (3) survival of 74 cubs was significantly lower both 0.5 and 1.5 years after an adult male had been killed on the 11,200 km² study area in the south, but not 2.5 years after; and (4) cub survival was significantly lower in the south (0.72, $N = 74$) than in the north (0.98, $N = 50$). The time lags are not whole numbers because males were killed in the fall, and cub loss occurred the following spring.

We concluded that killing an adult male would disrupt the male social organization for 1.5 years and decreased the population growth rate (λ) by 3.4%. Killing an adult male in our southern study area led to a loss of recruitment equivalent to killing 0.5 to 1.0 adult females (Swenson et al. 1997). The time lag we recorded does not seem unreasonable for brown bears if the loss of cubs is primarily caused by infanticide by immigrating males that establish a home range on the study area after the death of a resident adult male. Bears are generally killed during the fall, when fattening for winter denning is important. The breeding season starts in the spring not long after den emergence and continues to midsummer. Thus there is a relatively short time for an immigrating male to become established in a vacancy from the dead adult male and to breed (Swenson et al. 2001). In addition, a young male will probably have difficulty killing defended young, but can become more effective with increasing age.

We have continued our research on SSI and reanalyzed our data using all adult male deaths, not just hunting kills, and extended the period to 1998. We changed the study area definition from a composite area containing all females with cubs for all years to an area containing the home ranges of females with cubs for each individual year. We made spatial and temporal comparisons to examine whether nutritional, social (SSI), or den disturbance factors best explained the observed variation in cub survival (Swenson et al. 2001). Cub survival was 0.96 in the north ($N = 78$) and 0.65 in the south ($N = 126$). The loss of cubs at both the spatial and the temporal levels of comparison was best explained by social factors.

Nutrition did not seem important because cub loss was greater in years when the mass of adult females and cubs was highest (Swenson et al. 1997,

2001). Disturbance was evaluated only in the south and explained some variation in cub survival. In the north, few adult males died and three adult males lost early in the study there were not replaced for many years, presumably due to little immigration of new males. In the south, five times as many males died annually. In years with recorded adult male mortality, an average of 20% died. The estimated number of adult males remained stable, presumably due to immigration. The number of adult males dying 1.5 years previously in the area containing all radio-marked females with cubs in a given year was correlated negatively with cub survival in the south. In the north, no factors correlated with temporal patterns of cub loss, but loss of adult males in these areas 0.5 to 1.5 years previously was the best explanatory variable among those tested. In the north, the few males present were young, and most first bred successfully as 3-year-olds, when they are possibly not large or experienced enough to kill cubs that are defended by their mothers. Swenson et al. (2001) concluded that immigrating males kill cubs, as predicted by the SSI hypothesis.

IDENTIFICATION OF INFANTICIDAL BEARS

It is extremely difficult to observe infanticide or to identify the perpetrator. We have assumed that the perpetrators were primarily immigrant males based on the findings in many other studies of SSI, described earlier, and other evidence. Cub survival was high in the north during a period with no known adult mortality and little or no immigration, and in the south following years when no adult males were known to have died. An increase in the local density of subadult males has been associated with removing adult males in American black bears (Sargeant and Ruff 2001), and the 1.5-year time lag in increased cub mortality suggested that immigrating males could be responsible, as did the stable adult male numbers in spite of adult male mortality in the south. In our earlier analysis, we also found that cub mortality was elevated 0.5 year after the killing of an adult male (Swenson et al. 1997). We did not find this in the second analysis, but it included all dead adult males, not just hunter-kills, and the definition of the study area had been changed. Therefore, these two results are not directly comparable.

We have continued our investigations about this phenomenon, followed females with cubs intensively in 1998–1999, and expanded our studies using DNA fingerprinting. Here I will report some preliminary results. We collected tissue samples from the mother, the infanticidal male, and the killed cub(s) on four occasions. In all cases, DNA analyses revealed that the infanticidal male was not the father of the cubs he killed (E. Bellemain et al.

unpublished). Two infanticidal bears were marked adult resident males, 9 and 11 years old. Also, we observed males with mothers within a few days after cub loss and determined the father of the subsequent litter on six occasions. Four of these males (aged 6, 9, 12, 27 years) were marked and all were the father of the next litter. Two (aged 6 and 9) were unmarked at the time the female was observed with an unmarked male. Our DNA records suggest that one 6-year-old male was probably a first-time breeder, and the other a nonresident. Although we have no proof that these males killed the cubs, it is likely that they did. This shows clearly that the first male with a female just after she lost her cubs has a high probability of siring her next litter. Both of these findings are critical for the SSI hypothesis; the perpetrator is usually not the father of the cubs he kills, and he has a substantial chance to father the next litter. The DNA results also gave some limited support for the hypothesis that immigrants can be infanticidal. In addition, the only year we documented a 3-year-old male mating successfully in the south was 1.5 years after four adult males had been killed there.

These new preliminary results show clearly that resident adult males are also infanticidal in a manner consistent with SSI. Others have also reported that primarily large adult males kill cubs (Troyer and Hensel 1962, Murie 1981, Mattson, Knight, and Blanchard 1992; Olsen 1993; Hessing and Aumiller 1994; McLellan 1994). This is a major difference from the SSI observed in lions. An explanation may be that brown bears are not territorial, and home ranges of adult males overlap. Of course, SSI increases the fitness of a resident male as much, or more, than that of an immigrating male, and nothing in the SSI hypothesis requires that the species be territorial or social. How can we reconcile the relationship between the death of adult males and cub mortality with the evidence that resident males also are infanticidal? We have still not examined the possibilities, but one is that resident males may shift their home ranges after an adult male dies, bringing them into contact with new adult females.

We also looked at the bear-caused deaths of 13 subadult bears (1–4 years old) in relation to the death of adult males from 1984 to 1999 (Swenson, Dahle, and Sandegren 2001b). Most yearlings separated from their mothers in May. We found area differences in the rates of intraspecific predation only for yearling females, which was higher in the south (0.162, $N = 38$) than in the north (0, $N = 28$). Bears killed no subadult females older than yearlings, but males were killed as 1-, 2-, and 3-year-olds. Neither population density nor food abundance influenced rates of intraspecific predation on yearlings, but intraspecific predation on yearling females increased with the number of adult males that had died 2.5 years previously and when any adult male had died 1.5 years previously. Because the pattern for intraspecific predation on

TABLE 11.1. Effects of loss of at least one adult (≥ 5 years) male Scandinavian brown bear, with a 1.5-year time lag, on cub survival, yearling female survival, and population growth rate in the southern study area in Sweden.

	ADULT MALE DIED	NONE KNOWN DIED	SOURCE
Cub survival	0.55	0.92	Swenson et al. (2001)
Yearling female survival	0.70	0.85	Swenson, Dahl, and Sandegren (2001b)
Population growth (λ)	1.078	1.128	

The reproductive rate was increased to account for the shortened interlitter interval due to higher litter loss for the years following adult male death.

yearling females was similar to that for cubs, we speculated that infanticidal males might be prone to kill subadult bears, although this is clearly not SSI (Swenson, Dahle, and Sandegren 2001b). Intraspecific predation on subadults was highest during the breeding season, as it was for cubs and as reported by Mattson, Knight, and Blanchard (1992).

When I combined the results of our studies (Swenson, Dahle, and Sandegren 2001b; Swenson et al. 2001) and calculated population growth using a standard deterministic model (Ferson and Akçakaya 1990), I found that the loss of adult male(s) was associated with a 4.5% reduction in the population growth (Table 11.1).

We also had the opportunity to test whether an increase in harvesting adult male bears would increase cub mortality through SSI. Because the southern population showed a 16% annual growth rate from 1985 to 1995 (Sæther et al. 1998), harvest quotas were increased markedly. In Dalarna and Gävleborg counties the annual number of harvested bears increased sixfold after 1995, the annual number of harvested adult (≥ 5 years old) males increased 35-fold ($U = 6$, $p = 0.001$), and the total annual mortality of radio-marked adult males doubled ($z = 1.12$, $p = 0.26$), as did mortality of cubs accompanying radio-marked females ($z = 2.82$, $p = 0.005$). Thus the results supported the SSI hypothesis (Table 11.2).

We also studied females with cubs to determine whether they showed counterstrategies to infanticide, as would be expected if SSI were an important factor affecting female reproductive success (Agrell et al. 1998, Ebensperger 1998). We followed adult males and females with and without cubs intensively to determine whether the females with cubs exhibited any of the following counterstrategies to avoid meeting males: (1) avoiding males by (a) different activity

TABLE 11.2. Annual legal harvest of all brown bears and adult (≥ 5 years) males in Dalarna and Gävleborg Counties, Sweden, the total annual mortality of radio-marked adult male bears, and the annual mortality of cubs accompanying radio-marked females in the southern study area (1985–1995 and 1996–2001).

	1985–1995	1996–2001
Total number harvested annually	2.8 ± 0.74 (SE)	17.7 ± 2.33
Number adult males harvested annually	0.1 ± 0.09	3.5 ± 0.85
Adult male mortality	0.07 ± 0.04	0.14 ± 0.05
Cub mortality	0.28 ± 0.05	0.47 ± 0.04

SE: Standard Error

rhythms than males, (b) less movement during the breeding season, (c) different use of habitat, and (2) by mating promiscuously.

We found support for the hypothesized counterstrategies: (1a) During the breeding season, females with cubs were less active than males and females without cubs, and most active when adult males were least active (Myre 2000). (1b) Females with cubs moved less than either males or females without cubs during the breeding season (Zakrisson 2000). One could argue that this is because cubs restrict female movement, but home range sizes of females with cubs were negatively correlated with population density (Dahle and Swenson in press). Thus it is not only the cubs causing females to move less. (1c) Females with cubs used different habitats during the breeding season than those without cubs. Bed sites for females with cubs were located in areas with better visibility and large Scots pine (*Pinus sylvestris*) trees (Katajisto 2001, Kristoffersson 2003). We observed several cubs that avoided infanticide by climbing large pine trees (Fig. 11.1). Males killed cubs more often than expected in areas without large pine trees (Kristoffersson 2003). (2) Females mated promiscuously and several litters had mixed paternity (Bellemain 2001), as observed in Alaska (Craighead et al. 1995). During the breeding season, females have one or two estrus cycles of 16 to 27 days each (Craighead, Hornocker, and Craighead 1969). We have shown that the first male with the female often fathers the litter; it is therefore possible that dual estrus cycles are an example of postconception mating.

In conclusion, our results show that the three requirements for SSI are met in brown bears. Females with cubs showed three or four of the proposed counterstrategies: aggressive physical defense (Craighead, Sumner, and Mitchell 1995), avoiding males, promiscuity, and perhaps postconception mating. As far as we know, however, females do not use pregnancy block, group defense, or territoriality as counterstrategies.

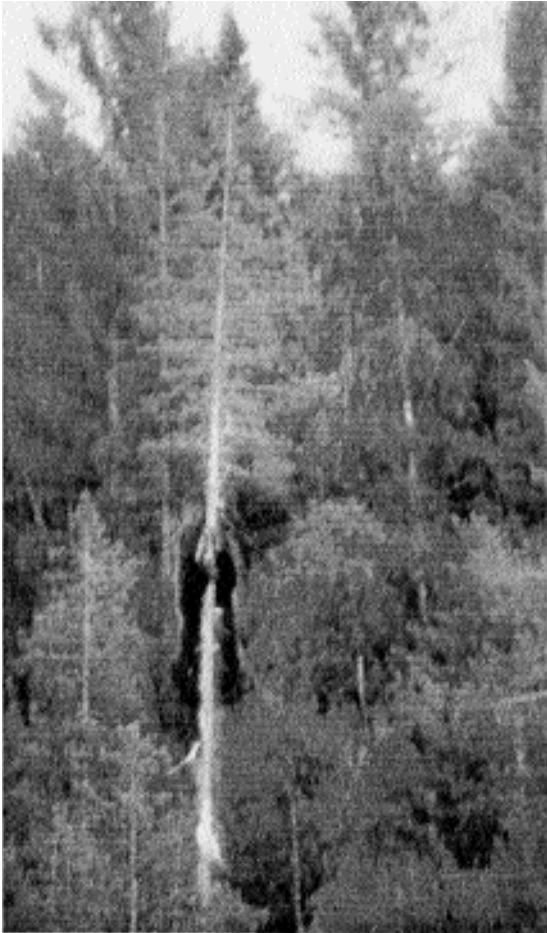


FIG. 11.1. Attempted infanticide by an unmarked brown bear male on a cub in Sweden, 1999. The cub saved himself by staying at the top of the Scots pine tree. The male had already killed the cub's two siblings when the picture was taken. DNA from hairs collected from the tree revealed that he was not the father of the cubs. The cub may himself have been a product of sexually selected infanticide (SSI) because his mother lost her litter in 1998, and his father was observed with her just after the litter disappeared. (Photograph by Jonna Katajisto).

EVALUATING THE EVIDENCE IN SCANDINAVIA AND NORTH AMERICA

Our recent research has strengthened our conclusion that SSI is an important factor in bear population dynamics. However, this does not mean that SSI is important in every population. Reviews of North American studies on black (Garshelis 1994), brown (McLellan 1994), and polar bears (Derocher and Taylor 1994) did not reveal conclusive evidence of SSI in any population. Infanticide was an important cause of cub mortality in one population of American black bears (LeCount 1987), but not in another (Elowe and Dodge 1989). In British Columbia, Hovey and McLellan (1996) found high cub survival in a hunted brown bear population adjacent to the unhunted Glacier National

Park, a potential source of immigrating males, and none of 44 cubs died during the breeding season (B. McLellan, 2002, pers. comm.). Miller (1990b) found no change in cub survival rates with increasing harvest rates of adult male brown bears in Alaska. However, there is not necessarily a linear relationship between the loss of adult males and cub mortality due to SSI (Swenson et al. 2001).

Is there a fundamental difference between Scandinavian and North American brown bear males? Perhaps we should remove some of the burden from the males because a high rate of infanticide also suggests that female counterstrategies are not functioning well (Janson and van Schaik 2000). What could inhibit these counterstrategies? North American and Scandinavian brown bears have very different histories. Humans tried to exterminate bears in Scandinavia with all available technology for hundreds of years, and almost succeeded (Swenson et al. 1995). This long history of persecution may have been an important selective force shaping life history strategies (Stearns 1992). After a long period with persistently high human-induced mortality rates and low density, it is not surprising that European brown bears are less aggressive toward humans (Swenson et al. 1999a), more nocturnal (Roth 1983), and more productive (Sæther et al. 1998) than North American brown bears. They are also poorer predators on adult moose (*Alces alces*) (Swenson, Dahle, and Sandegren 2001a). Lowered aggressiveness and increased productivity, perhaps as a trade-off against body growth, may make European brown bear females less able than North American females to defend their cubs from infanticidal males. This may not have been a problem in low-density, heavily hunted populations, but may be a problem in the present higher-density populations.

In contrast to Europe, brown bears in North America were exterminated rapidly after European immigrants arrived; they survived only in inaccessible areas, primarily in the north. In southwestern North America, for example, the brown bear was exterminated about 60 years after the first European settlement (Brown 1985). I am making essentially the same arguments regarding the effect of long-term heavy hunting pressure on the selection for life history traits that Festa-Bianchet discusses in chapter 12. An in-depth comparison of behavioral differences between European and North American brown bears may provide important insight into the mechanisms of SSI, the factors affecting the effectiveness of counterstrategies, and, ultimately, the implications for managing hunting of brown bears.

Evidence from Large Solitary Cats

There is also evidence of SSI in several species of large, territorial, nonsocial cats. Logan and Sweanor (2001) found that male cougars (*Puma concolor*) caused 44% of all kitten mortalities, but females killed no kittens; infanticidal

males were “apparently” not the fathers of the kittens they killed; and in 13 cases resident males, including 3 cases of known sires, associated safely with females with kittens. Two males that killed and ate entire litters subsequently sired litters with the mother of the killed kittens. The loss of newborns to 2-month-old kittens may accelerate breeding access to females by 8 to 10 months. Logan and Sweanor (2001) also found several counterstrategies among females with kittens: aggressive defense, avoidance of other cougars, and perhaps “pseudoeustrus.” Spreadbury et al. (1996) reported that two young kittens were killed by two different transient males. Ross and Jalkotzy (1992) recorded high kitten survival (97%) with a stable male population. Later, with a high turnover in adult males due to trophy hunting, the kitten survival rate declined (I. Ross, 2002, pers. comm.).

Leopard (*Panthera pardus*) males have also been documented siring the subsequent litter after killing kittens (Bailey 1993). A suggestion of SSI has also been reported in tigers (*P. tigris*). Smith and McDougal (1991) estimated 90% cub survival and no infanticide when resident males were stable, but 33% cub survival and much infanticide when new males were taking over the territories of former residents.

Although these results are not conclusive, they are consistent with SSI. They also strengthen the case for SSI in nonsocial carnivores.

The Controversy

Although there are few critics of SSI among behavioral ecologists, it is a very controversial hypothesis, especially among some anthropologists who view infanticide as maladaptive or aberrant (Sommer 2000). In a more extreme criticism of SSI in lions, Dagg (1999) stated that the SSI hypothesis “resonates with Western culture in which many people accept male dominance and aggression and condone in part the control of female sexuality by men.” For other reasons, the SSI hypothesis is also controversial among some North American wildlife biologists (Wielgus and Bunnell 2000), although some North American wildlife biologists have proposed its existence (Stringham 1980, LeCount 1987). SSI is also a controversial issue in hunting of cougars, where some managers apparently believe that harvesting males increases kitten survival (I. Ross, 2002, pers. comm.), just as some do for bears (Miller 1990b). Researchers have also speculated that harvesting males may increase juvenile mortality through SSI in cougars (Ross and Jalkotzy 1992; Murphy, Ross, and Hornocker 1999; Logan and Sweanor 2001) and wolverines (*Gulo gulo*) (Landa et al. 2000).

Some critics of SSI in bears believe that SSI should not be expected in nonsocial and nonterritorial species. The SSI hypothesis is not specific to any social organization, and the large number of species exhibiting SSI also

argues against it being restricted to any specific social organization. The evidence of SSI in solitary cats supports this. Our preliminary DNA-based results suggest that the pattern of SSI in nonterritorial species may differ from that in territorial species. In nonterritorial species, infanticide by resident males that are not the father to the young may be more common. Such behavior would be hindered in territorial species, where the male has a more exclusive access to the females in his territory. SSI is also easier to observe in social species. In an intensively studied red howler monkey (*Alouatta seniculus*) population, the infant mortality rate was 200 times greater within 1 month after a male status change than during nonchange periods of the same groups. However, less than 5% of the suspected infant killings by newly dominant males were observed (Crockett and Sekulic 1984). Also, infanticide was observed only seven times in the Serengeti and Ngorongoro Crater in Tanzania during intensive studies on lions between 1966 and 1982, but circumstantial evidence suggested that infanticide occurred almost every time a new coalition of males took over a pride (Packer and Pusey 1984).

Paradigm shifts always take time in science in general and in wildlife management in particular, and many wildlife managers remain skeptical. Conservatism was evident in a report that rejected SSI as a possible biological consequence of hunting brown bears, because only one study had suggested it, whereas others showed no clear trend, even though no study had clearly rejected it (British Columbia Ministry of Environment, Lands and Parks 1995). It is well known that many large carnivores can only sustain quite low levels of human-induced mortality, and that adult females are particularly sensitive (Knight and Eberhardt 1985, Miller 1990a). As a consequence, some agencies encourage large carnivore hunters to select males (e.g., Smith 1991).

Wildlife research is usually not optimal to document SSI because it involves marking many animals and monitoring them relatively infrequently to obtain rates of mortality and reproduction. Intensive, individual-based studies are the exception, rather than the rule. It is perhaps not surprising that behavioral ecologists, who work more intensively with their study animals, find evidence of SSI, rather than wildlife biologists. It is very difficult to observe infanticide in wild mammals and many conclusions are based on patterns in relation to hypotheses being examined, including our conclusions regarding SSI in brown bears.

Conclusions and Recommendations

How should managers react to the possibility of SSI in populations that they manage? The SSI hypothesis clearly predicts that many large carnivores should show SSI, but is that enough to accept it for management purposes? A

rodent that was expected to show infanticide did not (Ebensperger 2001). Should managers just ignore these hypotheses for now? I would argue that they should not. The review and tests of the SSI hypothesis in addition to the evidence of its existence in lions, brown bears, and some large solitary cats strongly suggest that SSI should be considered when managing harvest of large carnivores. Also, various estimates of the effects of SSI on population growth are large enough to have consequences for management. Given the controversy among researchers, however, it is not surprising that many managers are unsure about SSI.

Male infanticide has been observed in the wild in a context that is consistent with SSI in many species of large carnivores that are commonly exploited by humans: spotted hyena (*Crocuta crocuta*), cougar, Canada lynx (*Lynx canadensis*), bobcat (*L. rufus*), lion, leopard, tiger, American black bear, brown bear, and polar bear (van Schaik 2000). I would add the wolverine. Although it is a seasonal breeder and most adult females mate every year (Magoun 1985), only 40 to 60% of the females raise cubs each year (Landa et al. 1998), and infanticide is a common cause of cub death in some years (Persson et al. in press). If the killing of cubs in 1 year increases the probability of successfully rearing cubs the following year, SSI would be adaptive, as has been suggested in a captive population of another seasonal breeder, the red deer (*Cervus elaphus*) (Bartos and Madlafousek 1994).

The ramifications for hunting are more difficult to predict. Because SSI is associated with the turnover of adult resident males, hunting should have a greater impact on the level of SSI in species in which hunters can distinguish the sexes in the field, such as lions and cougars (and somewhat for bears, Smith 1991). However, hunting should have an effect on SSI whenever it reduces the survival rate of adult males, as it does for brown bears (McLellan et al. 1999). The death of 20% of the adult male brown bears reduced population growth rate by 4.5% (from 1.13 to 1.08) in the local area, and the hunting death of a male reduced population growth by 3.4% (Swenson et al. 1997). Using a very different approach, Wielgus et al. (2001) estimated that a grizzly bear population could experience a 5.7% reduction in growth if females avoided productive habitats frequented by potentially infanticidal males that immigrated after resident adult males were killed. Actual infanticide was not included in their model. Models of lion population dynamics have also showed reduced population growth when adult males are killed (Starfield, Furniss, and Smuts 1981; Venter and Hopkins 1988; Starfield and Bleloch 1991; Greene et al. 1998).

It appears that some populations of lions, brown bears, American black bears, and probably other large carnivores are more susceptible to losses of young than others. Also, in some species both resident adults and immigrants

can be expected to exhibit SSI. If many ecological and environmental factors affect the expression of SSI, it will be difficult for a manager to predict the effects of killing adult males in a given population. Obviously, we need more research on SSI in hunted large carnivores, particularly to allow us to predict when SSI should be expected.

Generally, too little is known about the effects of hunting on the behavior of hunted species. Festa-Bianchet (chapter 12) discusses the effects of hunting in terms of selection pressure on life history traits, and notes that there is little research in this important area. This applies equally well to effects on social organization and mating systems. I searched the last 5 years of the *Journal of Wildlife Management* and *Behavioral Ecology* for articles on this subject. I found that no papers in *Behavioral Ecology* and only 0.7% of the species-oriented papers in the *Journal of Wildlife Management* were on the behavioral effects of hunting (Table 11.3). Who will study the effects of hunting on animal behavior, if not behavioral ecologists or wildlife biologists? I reiterate Festa-Bianchet's (chapter 12) ethical concerns about manipulating the morphology and behavior of hunted species by hunting. Is it ethically right to allow hunting when we do not understand its consequences? One could counter that it is usually necessary to hunt large carnivores where the landscape is human-dominated and tolerance to depredations caused by large carnivores is low, but that does not release us from our ethical obligation to understand what we are doing to these species when we hunt them.

Now, back to the manager. A biologist responsible for managing the hunting of large carnivores can either ignore SSI until it has been conclusively demonstrated, or assume a population consequence of harvesting adult males unless SSI has been documented not to occur in a species and area. I recommend the latter, which follows the precautionary principle, and which I believe is only good management procedure. Just as harvesting should be more conservative when population estimates are uncertain (Tufto et al. 1999), it should also be more conservative when the effects of hunting are

TABLE 11.3. Articles published in the *Journal of Wildlife Management* and in *Behavioral Ecology* (1996–2000) that examined the effects of hunting on behavior.

	JWM	BE
Number of articles	698	439
Species-oriented articles:	651	386
about commonly exploited species	65%	10%
effects of hunting reported	3.6%	0.7%
behavioral effects of hunting reported	0.7%	0

uncertain because of factors such as SSI (Boyce, Sinclair, and White 1999; Anthony and Blumstein 2000).

Summary

Sexually selected infanticide (SSI) can occur when a male, who is not the father of a dependent young, may gain increased mating success by killing the young. It is promoted by disruption of the male social organization by killing resident adult males, thus allowing new males into an area or perhaps allowing other resident males to realign their home ranges. It has a solid and well-documented theoretical basis and should be expected in many species of large carnivores. SSI has been well documented in one population of lions, strongly indicated in brown bears in Sweden, and suggested for cougars, leopards, tigers, American black bears, and wolverines. Estimates of the effects of SSI following killing adult males on population growth (3.4–5.7% reductions in r) are large enough to have consequences for management. In species exhibiting SSI, hunting adult males can promote it. According to the precautionary principle, we should consider SSI when managing the hunting of large carnivores. Because there may be geographical or population differences in the occurrence of SSI, however, much more research is required before we can reliably apply knowledge of SSI to carnivore hunting management. The effects of hunting on the behavior of the hunted animals should receive increased attention from behavioral ecologists and wildlife biologists.

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12.

Exploitative Wildlife Management as a Selective Pressure for Life-History Evolution of Large Mammals

Marco Festa-Bianchet

This chapter explores the usefulness of behavioral ecology when sport hunting is either a component or the major objective of a wildlife management strategy. I examine the potential selective effects of different management practices, and argue that wildlife managers' ignorance of those effects could have long-term negative ecological and economic consequences. Knowledge of the selective pressures caused by sport harvest could help define harvesting programs that avoid or reduce artificial changes in the genetic makeup of harvested populations. I will assume that the main goal of sport hunting is to provide recreational opportunities, not to maximize meat production or the number of animals killed. Within that framework, I suggest that minimizing the impact of sport hunting on the evolution of the hunted species should be a major preoccupation of wildlife managers.

Until recently, most wildlife management was concerned with numbers of animals within a hunted population, and their relationships with their habitat. Hunting regulations and harvest quotas are typically based on population goals. Managers seek either to harvest enough animals to prevent some

type of habitat or health degradation (such as allowing forest regeneration or decreasing the risk of epizootics), or to avoid overharvesting and thereby maintain the ability to harvest the population in the future or to increase long-term yield (Caughley and Sinclair 1994). Consequently, much management-oriented research has focused on population dynamics, particularly questions of density dependence and of time lags in population and habitat responses, or on the relationships between herbivores and predators (Fryxell et al. 1991, Clutton-Brock and Loneragan 1994, Messier 1994, Solberg et al. 1999). Hunting regulations often direct the harvest to particular sex/age categories, depending on the harvest or population goals (Kokko, Lindström, and Ranta 2001). For example, male-only harvest is used in cases where female harvests are expected to decrease the population below the management goal. Adult male and young-of-the-year harvests are often used when populations are at the desired density, and finally all sex/age classes, including adult females, are taken where either the population would grow rapidly in the absence of harvests, or a reduction in density is desired.

In North America, little attention has been paid to the potential selective effects of sport hunting (Harris, Wall, and Allendorf 2002). In parts of Europe, on the contrary, there is a rich tradition of “selective” hunting, sometimes with painstakingly detailed hunting regulations that direct the harvest to particular sex/age classes or even to particular phenotypes. Some of these practices include the selective removal of individuals that appear weak, or with “undesirable” antler or horn shape and size. In some cases, the apparent intent of selective harvests is to decrease intraspecific competition and maintain future recruitment by removing those individuals that are least likely to survive. In other cases, however, the goal of selective harvest is indeed to select, by favoring certain phenotypes over others. There is evidence that European harvest practices can affect the genetic variability of hunted populations, at least for red deer (*Cervus elaphus*) (Hartl et al. 1995, 1991) and foxes (*Vulpes vulpes*) (Fрати, Lovari, and Hartl 2000).

In North America, hunting rules are not as detailed as some European regulations, but often go beyond specifying the sex of the animals that can be harvested. For example, a minimum horn size is often set for male pronghorn (*Antilocapra americana*), mountain goat (*Oreamnos americanus*), and mountain sheep (*Ovis* spp.), and a minimum number of antler points for cervids.

In addition to legal requirements, hunters’ preferences affect the type of animals they are more likely to harvest. Hunters may avoid shooting females accompanied by young (Solberg et al. 2000). Given a choice, most hunters will take the largest individual, or the one with the largest horns or antlers. Because in many populations of ungulates sport hunting is the principal

cause of death for adult animals (Langvatn and Loison 1999), it is reasonable to suppose that nonrandom hunting mortality may have a selective effect. Recent studies of wild ungulates have shown strong heritabilities for morphological traits such as body size, and varying levels of heritability for life history traits, particularly those affecting female fertility (Hewison 1997; Réale, Festa-Bianchet, and Jorgenson 1999; Kruuk et al. 2000). Hunting-induced mortality of nonlactating females may select for increased investment in reproduction by generating an artificial positive correlation between reproductive effort and survival, whereas hunter selection for large-horned males could lead to either a selective advantage for small-horned males or selection for an earlier investment in rutting activities (Heimer, Watson, and Smith 1984).

Trophy hunting is well developed in many parts of the world and is a major economic activity. There is considerable interest in the use of sport hunting as part of a conservation strategy. Trophy hunting of ungulates is particularly appealing from a conservation viewpoint because a very large income can be generated from the harvest of a small number of animals (Lewis and Alpert 1997). Consider for example the markhor (*Capra falconeri*), an endangered species. Like many other ungulates in Asia, it is threatened by poaching and habitat destruction (Shackleton 1997). Trophy hunters will pay several tens of thousands of dollars to kill a mature male. That money could be used for conservation and could show the value of habitat protection to the local population. At the same time, the demographic impact of removing a few mature males is minor. Indeed, although the markhor is listed in Appendix I of the Convention on International Trade of Endangered Species (CITES), a program in Pakistan for limited trophy hunting of this species is supported by the World Conservation Union (IUCN) Caprinae Specialist Group.

There are two questions related to the potential selective effects of trophy hunting. First, what is the effect of increasing the mortality of males with a trait (large horns or antlers) that is favored by sexual selection and is likely correlated with individual reproductive success? Second, if trophy hunting selects for smaller horns or antlers, then it will decrease the availability of large-horned or large-antlered males over the long term. Therefore, what management strategies may ensure that trophy hunting can be sustained, particularly given the direct relationship between the expected trophy size and the amount of money hunters are willing to pay?

There are many possible selective effects of sport hunting upon the hunted species. For example, about half of the adult mortality of snow geese (*Anser caerulescens*) in North America is due to hunting (Gauthier et al. 2001), and there are untested speculations that wild geese have evolved (or

learned and then culturally transmitted) behaviors to avoid sport hunters. Sport fishing has been suggested to select for “smarter” fish (Miller 1957), more adept at avoiding anglers’ lures. I will consider two specific cases where sport hunting may have a selective effect on large mammals: changes in reproductive strategy caused by high hunting-induced adult mortality, and changes of horn and antler morphology caused by trophy hunting. The evidence for or against a selective effect of sport hunting is limited because this problem has apparently attracted little attention from either wildlife managers or behavioral ecologists (Law 2001). Rather than review all the available evidence, therefore, my goal is to point out that artificial selection through sport hunting can be a serious ecological, economic, and ethical problem, and therefore research is urgently required to determine the extent to which it may occur.

Sport Harvest and Life-History Evolution

For many species of ungulates, hunting, legal or otherwise, is the most common cause of adult mortality. In areas where large predators have been eliminated, hunting and road accidents account for almost all adult mortality (McCorquodale 1999, Ballard et al. 2000). In Europe, outside protected areas, hunting probably accounts for most mortality of adult chamois (*Rupicapra rupicapra* and *R. pyrenaica*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), moose (*Alces alces*), and red deer. In North America, the same could be said for white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), pronghorn antelope, male bighorn (*Ovis canadensis*) and Dall sheep (*O. dalli*), and some populations of moose, wapiti, and black bear (*Ursus americanus*). Modern wildlife management can claim a numerical success: many hunted species are much more abundant now than they have been for several centuries. In these populations, high density coexists with high levels of hunter harvest, a situation made possible by past restraint in harvests, controls over poaching, good habitat, and absence or near-absence of predation on adults. Artificial feeding is also partly responsible for high ungulate densities, particularly in central Europe.

DEMOGRAPHIC EFFECTS OF HUNTING

What are the demographic characteristics of a hunted population, and how do they differ from those of ungulate populations limited by food availability or by predators? There are two major effects of hunting: an age distribution heavily skewed toward younger animals, and a sex ratio biased in favor of females (Squibb 1985, Ginsberg and Milner-Gulland 1994, Laurian et al. 2000).

These effects can be extreme: posthunt sex ratios of less than 5 males per 100 females have been reported for elk (Noyes et al. 1996).

Few studies have measured the survival of marked individuals in sport-hunted populations of ungulates. In a population of red deer in Norway, natural survival of stags from weaning to 5.5 years of age was 56%, but was reduced to 5% by hunting; in the same population and over the same age interval, survival of females was reduced from 59% to 32% (Langvatn and Loison 1999). In a trophy-hunted population of bighorn sheep in Alberta, natural survival of rams from 4 to 8 years was 58%, but actual survival was reduced to 27% by sport hunting. Because that population was partially protected by a wildlife sanctuary where most rams spent most of the hunting season (Festa-Bianchet 1989), it is likely that in other hunted populations survival to 8 years would be even lower. In one population in Alaska, 10 of 23 mature Dall rams were shot within 2 years of marking, an average harvest-induced yearly mortality of about 25% (Heimer, Watson, and Smith 1984). In a population of Norwegian moose, about 15% of adult females were shot each year, in addition to the 2.5% yearly natural mortality (Stubsjøen et al. 2000). Therefore, fewer than 50% of yearling female moose would survive to 5 years in hunted populations, compared to about 90% in unhunted populations. Data on survival of marked individuals from other hunted populations are scarce, but it is reasonable to suspect that in many heavily hunted species, fewer than 5 to 10% of yearling males and perhaps fewer than 15 to 20% of yearling females survive to 5 years. In unhunted populations the corresponding figures would be about 50 to 60% for males and 60 to 70% for females (Loison et al. 1999a, Gaillard et al. 2000). Because almost all studies of marked individuals report that adult survival of ungulates is not density-dependent, natural survival should not be lower in unhunted than in hunted populations (Gaillard et al. 2000).

SPORT HUNTING AS A SELECTIVE PRESSURE FOR REPRODUCTIVE STRATEGY

Sport hunting causes high mortality of prime-aged adults, whereas most natural mortality affects young of the year and senescent individuals (Gaillard, Festa-Bianchet, and Yoccoz 1998; Gaillard et al. 2000). Life-history strategy and demography are linked: early comparative approaches to life-history evolution suggested trade-offs between, for example, age of first reproduction and longevity (Harvey and Zammuto 1985), or litter size and juvenile survival (Promislow and Harvey 1990). Over the long term, however, those trade-offs are inevitable: a species where first reproduction occurs late in life and average life span is short will go extinct and therefore will not be around for biologists

to study. If adult mortality is high, either fecundity or juvenile survival must be high, or extinction will follow. Conversely, if adult mortality is low, either fecundity or juvenile survival will decrease because populations cannot increase indefinitely.

If ungulates evolved with low adult mortality, what are the possible consequences of high adult mortality through hunting? The most likely consequence is an increase in reproductive investment by young adults. In ungulates, strong iteroparity and small litter size select for low maternal investment to avoid compromising the female's survival and future chances to reproduce, particularly when combined with high and temporally variable juvenile mortality, much of which is independent of the amount of maternal care (Festa-Bianchet and Jorgenson 1998). Indeed, interspecific comparisons show that the survival of prime-aged females (before senescence) in unhunted populations is high and varies little, regardless of the causes of mortality (disease, predation, starvation, weather) (Gaillard, Festa-Bianchet, and Yoccoz 1998; Gaillard et al. 2000). A female with a 92 to 96% yearly survival probability should not increase her current maternal investment to a point where it may affect her viability, given that her offspring faces a much lower and widely varying probability of surviving to 1 year, and then a yearling survival that is typically lower than adult survival (Gaillard et al. 2000).

In heavily hunted populations, however, female survival is greatly diminished, independently of current reproductive effort. In addition, a dependent offspring may increase survival, as hunters are often reluctant to kill lactating females (Solberg et al. 2000). Hunting regulations for alpine chamois in many jurisdictions prohibit the killing of lactating females. Similar regulations protect members of grizzly (*Ursus arctos*) and black bear family groups in much of North America. In Alberta, there is a high proportion of 2-year-old ewes among the harvest of "nontrophy" bighorn sheep. Two-year-old ewes often do not produce lambs, and hunters may select ewes without lambs (W. D. Wishart, 1982, pers. comm.). In hunted populations, therefore, there could be selection for increased maternal expenditure. In species like chamois and bighorn sheep that are usually hunted in open areas, selection against females without dependent offspring is likely stronger than for forest-dwelling species such as white-tailed or roe deer, where hunters have fewer opportunities to evaluate female reproductive status before they shoot.

When populations are kept below carrying capacity through hunting, female reproductive performance is enhanced: age of primiparity decreases, whereas fecundity, juvenile survival, and litter size usually increase (Swenson 1985; Jorgenson, Festa-Bianchet, and Wishart 1993; Jorgenson et al. 1993; Swihart et al. 1998). Over the short to medium term, these effects can largely be explained by density-dependent mechanisms: observational and experimental

studies of ungulates show that female reproduction, particularly age of primiparity, is very sensitive to resource availability (Langvatn et al. 1996). An additional, potentially confusing variable is the modified age distribution, which in hunted populations is typically heavily skewed toward younger and more productive age classes. This latter effect, however, should be weak: reproductive senescence in female ungulates occurs at an age reached by a very small proportion of females even in unhunted populations (Benton, Grant, and Clutton-Brock 1995; Bérubé, Festa-Bianchet, and Jorgenson 1999). Age differences between hunted and unhunted populations, however, are very likely to cause differences in mortality because survival senescence typically sets in several years before reproductive senescence (Benton, Grant, and Clutton-Brock 1995; Loison et al. 1999a). Therefore one may expect greater natural (i.e., unhunted) female survival in hunted than in unhunted populations, simply because in hunted populations there are few if any females older than 8 to 10 years.

In addition to the ecological effects due to lowered intraspecific competition, I suggest that heavy harvest may select for a life-history strategy that is normally disadvantaged in natural populations. Consider a set of genes whose phenotypic expression led to females that invested heavily in early reproduction, leading to early primiparity and an increase in offspring survival at the expense of maternal survival. In a naturally regulated population of ungulates, that genotype would be selected against because longevity is the greatest determinant of lifetime reproductive success for females (Clutton-Brock 1988; Bérubé, Festa-Bianchet, and Jorgenson 1999). If very few females survive more than two to four hunting seasons, however, a reproductive strategy leading to greater reproductive success early in life would be favored even if it had a negative effect on life span. If the average life span including natural and hunting mortality is 5 years, a gene that increased mortality of 6 to 10 years of age would not be selected against. Selection for high maternal investment would be strengthened by hunter preference for females without dependent offspring. This scenario is not dissimilar to what may be expected in other ungulate populations under artificial selection, such as domestic sheep, cows, or goats. Domestic ungulates have a shortened life expectancy compared to their wild counterparts, possibly because of artificial selection for increased reproduction (or milk production) early in life.

We readily accept that many traits of domestic animals are the result of artificial selection, and some life-history traits of wild animals could also be affected by artificial selection. With sport hunting, most adult mortality is human-caused and human predation is not random with respect to reproductive status or morphology. Obviously, a major methodological challenge in studying the selective effects of hunting is to separate the environmental

effects due to lowered intraspecific competition and the genetic effects due to selection for a less iteroparous reproductive strategy. A modeling exercise (Benton, Grant, and Clutton-Brock 1995) suggested that the reproductive strategy of red deer hinds that were hunted until a few generations before the study may be suboptimal, possibly because it was shaped by culling that for many generations resulted in a high level of adult mortality. Researchers have recently expressed concern that the life-history strategies of moose in heavily harvested populations in Sweden may be affected by hunting-induced mortality, which may select for high reproductive effort in early life and lead to premature senescence (Ericsson and Wallin 2001, Ericsson et al. 2001).

My review concerns large herbivores (and possibly some bear populations) that are subject to intense sport hunting, but a similar line of reasoning could apply to large carnivores that are the target of both sport hunting and trapping (or even predator control programs): for example studies of wolves (*Canis lupus*) outside protected areas report very high levels of human-caused mortality (Potvin et al. 1992).

The potential selective effects of harvesting have preoccupied some fisheries scientists for a long time (Miller 1957). Heavy fishing pressure may have not only a demographic effect on fish populations but also a selective effect (Kirkpatrick 1993, Policansky 1993, Reznick 1993, Rochet et al. 2000). Fishing disproportionately increases mortality of adult fish, and nets with mesh sizes allowing the escape of some of the smaller individuals further select against large fish (Law 2001). A logical outcome of these selective pressures is an earlier age of maturity, as reported by a number of studies (Rijnsdorp 1993, Rowell 1993, Rochet 1998). It is often problematic to partition environmental and genetic effects: early reproduction could occur in the absence of selection simply because resources may be more abundant in heavily harvested populations (Rochet et al. 2000).

High predation on adult guppies (*Poecilia reticulata*) is associated with earlier maturation, higher reproductive effort, and more and smaller offspring compared to populations where predation is mainly on juveniles. Differences in life-history strategies are heritable. Translocation experiments to areas where predation was mostly on juveniles led to life-history changes in 11 years (30–60 generations) (Reznick, Bryga, and Endler 1990), providing experimental evidence that life-history traits respond quickly to strong selective pressures. Fisheries scientists are interested in the possible evolutionary impacts of fishing upon fish populations that are exploited either commercially or for sport fishing. Because most of these populations are very difficult to study, however, the evidence for genetic changes consists mostly of phenotypic measurements on exploited stocks and controlled experiments in short-lived species that are not exploited (Reznick, Bryga, and Endler 1990;

Reznick 1993). A more direct approach is possible with exploited ungulates, where individual-level information on morphology, life-history, and genotype can be obtained. Different ungulate hunting regimes in adjacent areas offer great potential to compare life-history differences associated with differences in age-specific mortality.

Trophy Hunting and Selective Pressures on Horns and Antlers

Trophy hunting has a competitive component. Complex scoring formulae measure various aspects of an animal's horns, antlers, or skull, and records are kept by a number of organizations. Trophy scores are strongly correlated with size, therefore most trophy hunters seek adult males with large horns or antlers. Trophy hunting is big business: hunters are willing to pay very large sums in the hope of harvesting a "record book" trophy. Guides and outfitters typically advertise the trophy scores of animals shot by their clients, and areas reputed for producing large trophies attract much greater revenues than areas where males have smaller horns or antlers. For example, consider the bids received by the Foundation for North American Wild Sheep during its auctions of special permits for bighorn sheep (Erickson 1988). These permits are offered by some American states and Canadian provinces to the highest bidder, and typically sell for tens to hundreds of thousands of dollars that should then be used for conservation, research, or wildlife management activities. Recent auction results reveal that, although most jurisdictions obtain bids for special permits of between \$20,000 and \$60,000, those with a reputation for producing large rams (Alberta, Montana, Arizona) regularly receive up to 10 times as much, with bids topping \$400,000 (<http://www.fnaws.org/page1.html>). Some hunters are willing to pay great sums of money to obtain a few extra centimeters of horn, and the availability of large trophy males can play a strong role in the economics of a wildlife management program.

By definition, the trophy hunter selects according to morphological criteria. For most bovids, the criterion is simply horn size; for cervids, the number of tines, antler symmetry and branching pattern can affect a trophy's score. Given that a proportion of the variability in horn and antler size is genetically determined (Fitzsimmon, Buskirk, and Smith 1995; Hartl et al. 1995; Lukefahr and Jacobson 1998; Moorcroft et al. 1996), trophy hunting may create the somewhat paradoxical situation of selecting against the preferred phenotype. It is therefore surprising that wildlife managers, especially in North America, have paid so little attention to the genetic effects of trophy hunting (Harris, Wall, and Allendorf 2002).

ECOLOGICAL VARIABLES AND ARTIFICIAL SELECTION

The strength of artificial selection caused by trophy hunting will depend upon ecological variables and harvest regulations. Obviously, a high level of harvest of trophy-class males should have a stronger selective effect than a low level of harvest. Harvest regulations based on a simple morphological criterion, without a limit on the number of permits issued, are likely to have a stronger selective effect than management regimes that limit the number of males harvested within each age class or morphological grouping. The timing of the hunt in relation to the reproductive cycle will also affect the selective pressure caused by trophy hunting: a pre-rut hunt will have a stronger effect than a post-rut hunt. The pattern of age-specific horn growth may also play a strong role. For example, species like chamois, mountain goat, and roe deer have a relatively rapid horn or antler growth: mountain goats and chamois achieve over 90% of their horn growth by 3 years of age (Côté, Festa-Bianchet, and Smith 1998). In these species, males become desirable trophies at a relatively young age, and therefore large-horned individuals risk being killed before contributing to future generations. The horns of ibex (*Capra ibex*), on the other hand, grow substantially up to about 10 to 12 years, and ibex may reproduce actively for several years before being selected by trophy hunters (Toïgo, Gaillard, and Michallet 1999). Bighorn sheep are somewhat intermediate; the horns of 6-year-old rams are about 90% of the length they will attain by 9 or 10 years (Jorgenson, Festa-Bianchet, and Wishart 1998). The mating system will also affect the strength of artificial selection for small horns or antlers caused by trophy hunters: where alternative mating tactics account for a substantial proportion of paternities (Hogg and Forbes 1997), selection is likely weaker than where paternities are monopolized by a few highly successful males (Apollonio, Festa-Bianchet, and Mari 1989).

If mating success is affected by both weapon size and male age, an intense level of trophy hunting of young males will have a stronger selective effect than in species where only older males are removed by hunting. For example, although precise information on male reproductive success is not available, studies of both chamois and ibex suggest that in unhunted populations most matings are achieved by males 10 years of age and older (Lovari and Cosentino 1986; Toïgo, Gaillard, and Michallet 1999). An ibex male may not achieve “trophy” status until about 10 to 12 years of age, but the horns of a 5-year-old chamois are not much smaller than those of a 10-year-old. If in a trophy-hunted population of ibex most matings are done by 10-year-olds rather than 12-year-olds, there will still be 10 years of time for natural selection to potentially affect pre-mating male survival. In trophy-hunted popula-

tions of chamois, on the other hand, most matings may be by males aged 4 to 5 years because few males may survive to older ages, possibly allowing some reproduction by males that normally would not survive to mating age.

The potential selective strength of trophy hunting is illustrated by fallow deer (*Dama dama*), where a single male can mate with 25% of the females during one rut (Apollonio, Festa-Bianchet, and Mari 1989). If the traits that favor male reproductive success were the same as those selected by trophy hunters, a single male shot before the rut could lead to a large difference in the genetic makeup of fawns born the following year.

Male reproductive success in most ungulates appears to be determined mainly by an individual's ability to beat other males. Antler or horn size is, presumably, only one component of fighting ability: body size and condition can also play a role, especially if very large weapons suffer a risk of breakage (Alvarez 1994). Both size and shape of antlers and horns could be modified by selection to preserve their effectiveness as intraspecific weapons but make them less attractive as trophies. For example, in most of the Canadian province of Alberta, hunting regulations specify that only bighorn rams whose horns describe at least four-fifths of a curl can be shot.

A ram with a large body mass and whose horns were massive but did not reach the minimum legal size until 6 or 7 years of age would enjoy greater survival than a ram with fast-growing horns that became "legal" at 4 or 5 years of age (Jorgenson, Festa-Bianchet, and Wishart 1998). In areas with good hunter access, few rams survive more than one hunting season after becoming legal, and in areas with moderate access, about 30 to 40% of legal rams are shot each year (Festa-Bianchet 1986). A ram that survives the hunting season will face little competition during the following rut because many potential competitors will have been shot. It is therefore reasonable to predict that any genetic trait that retards the age at which a ram's horn becomes legal will be strongly selected for. There is considerable interindividual variability in the age at which rams reach legal status, from as early as 3 years in exceptional cases, to never (Jorgenson, Festa-Bianchet, and Wishart 1998). Rams that reach legal status later in life may have greater lifetime reproductive success than those whose horns are legal by 4 or 5 years of age. In addition, recent evidence suggests that horn size plays an important role in male mating success only after about 7 years of age (Coltman et al. 2002). Rams with fast-growing horns therefore risk being shot before their large horns give them a reproductive advantage, compounding the potential selection for small horns.

Similarly, imagine a wapiti or red deer male with large antlers but with only a few tines: such an individual would do well in an area where hunting regulations state a minimum number of tines for harvestable males, or could

enjoy greater survival under a trophy hunting regime simply because hunters would “pass him up” in favor of what they may see as a more attractive set of antlers. Trophy hunting favors a “nontrophy” phenotype by increasing its survival relative to the population mean, and by removing potential competitors. The harvesting scheme prevalent in parts of Europe, where “undesirable” horn or antler phenotypes are selectively harvested in addition to trophy-class males, would obviously complicate the situation.

Of course, the preceding scenario does not take into account potential gene flow among populations subject to different hunting regimes, changes in hunting regulation or harvest levels, and the strengths of several competing selective pressures, many of which are likely temporally variable. For example, there could be a net outflow of genes from protected into hunted areas because males who survived the hunting season by staying within protected areas would be in a very good position to compete for estrous females in neighboring populations where most resident males were shot by hunters (Hogg 2000).

In addition to selection for horn or antler morphology, a high level of trophy hunting may select for greater reproductive effort by young males. Over the short term, there may be a demographic effect without evolution of novel mating strategies: if most mature males are removed by hunters, younger males may take over the role of breeders and possibly suffer higher mortality as a result, as suggested by Geist (1971) and Heimer, Watson, and Smith (1984).

Over the long term, selection could favor males with high reproductive effort over their first few years of life, possibly including faster growth, lower fat reserves, and riskier behavior during the rut. A shortened life expectancy would weaken selective pressures for less risky behavior that may increase the chance to survive to breed again. The consequence could be higher nonhunting mortality for young males. Consider the many white-tailed deer, roe deer, chamois, or moose populations that are subject to very high harvest levels: in these populations very few males survive past 2 or 3 years of age. In three management areas in Oregon, over 90% of wapiti males were killed before 4 years of age (Biederbeck, Boulay, and Jackson 2001). High hunting mortality of males could lead to a high selective advantage for those few that survive beyond 4 years (possibly because they have small horns or antlers, or because their behavior decreases their chance of being shot), or strong selection for early reproduction. In either case, sport hunting could lead to evolutionary change.

The Implications for Consumptive Management

Harvest of large mammals through sport hunting can lead to economic and social benefits that can stimulate conservation. It is therefore important that management decisions be based upon the best available information.

It is reasonable to suspect that any selective harvest may have evolutionary consequences by altering selective pressures and gene frequencies compared to naturally regulated populations. There is clearly a need for more information, particularly about the levels and types of hunting that may lead to evolutionary change. Sexual selection and possibly female choice may favor males with large horns or antlers, and partly compensate for the effects of selective hunting. If the hunting mortality is not very high, it may be insufficient to change the genetic makeup of future generations. Immigration from protected areas may reduce the potential for selection for a “short and fast” reproductive strategy among both sexes. Finally, harvest schemes that simply stipulate a minimum size or minimum number of tines required for legal harvest will likely have stronger selective effects than the more complex harvest strategies prevalent in central Europe.

Three potential problems should be considered. First, some current harvest policies may select for unwanted morphological or life-history attributes that may lead to loss of economic and recreational opportunities. This would be the case for selection for small horns or antlers by high levels of trophy hunting, but also for selection of a reproductive strategy favoring high early investment in reproduction, if it increased nonhunting mortality of young adults. Selective hunting may lead to a loss of genetic variability (Hartl et al. 1995), which may negatively affect a population’s ability to survive environmental changes over the long term.

Poaching of African elephants (*Loxodonta africana*) for the illegal ivory trade may select for tusklessness (Jachmann, Berry, and Imae 1995). Second, artificial “adaptive” changes in hunted populations may compromise their long-term ability to persist. A cessation of hunting may have unpredictable consequences for a population that has undergone adaptations to a high level of hunting mortality: both evolutionary and demographic effects should be considered when hunting is stopped because of changes in land designation. Artificial selection is not necessarily reversible (Law 2001). Third, there are ethical concerns: should hunting shape evolution? Much of the nonhunting public and many hunters dislike the competitive nature of scoring trophies. The competitive aspect of trophy hunting spurs a negative reaction by many people that accept or even support other forms of sport hunting. As public attitudes change, the conservation of ungulates will increasingly require the support of people with little interest in hunting. I suggest that the best outcome for both hunting and conservation would be a decreased emphasis on trophy scores, and more emphasis on the enjoyment of hunting, independent of the particular attributes (sex, age, horn size) of the animals that are harvested.

Conclusions and Recommendations

The ideas I have put forth in this chapter, if correct, justify changes in several sport hunting practices. If these ideas are incorrect, however, changes in wildlife management would not be required and could have a negative effect. It is therefore important to test these ideas, ideally through long-term studies conducted in cooperation with researchers, wildlife management agencies, and sport hunting groups. Wildlife management agencies can do the required experiments by manipulating hunting regulations. For example, an experimental change in the definition of legal ram was approved in Alberta partly to test the effects of different management schemes on bighorn ram survival and harvest. Changes in regulations, however, require the support of the hunting public. Future research should combine the analysis of genotype frequencies, morphology, and life-history attributes in populations subject to different levels of hunting or to different harvest regimes.

An alternative to experimental manipulation of hunting regulations would be to better exploit available information. There are vast repositories of data on morphology, sex, and age of harvested animals, in computers and file drawers of wildlife management agencies all over Europe and North America. Additional information on morphological measurements (or trophy scores) is available from private organizations and individuals, including records and actual specimens (stuffed heads) from several decades ago. This information could be used to investigate hypotheses about the selective effects of sport hunting, or to form the basis of future research programs. There are several recent examples of how long-term information gleaned from wildlife management agencies can provide very valuable scientific contributions (Loison, Gaillard, and Jullien 1996; Post et al. 1999; Schneider and Wasel 2000).

The diversity of wildlife management schemes in different areas, including different sex/age restrictions, could also be used to test specific hypotheses. The main difficulty will be teasing apart environmental and genetic effects: a high level of harvest that reduces population density will almost certainly lead to a phenotypic response, but it may or may not also select particular genotypes. The most powerful test of these hypotheses will be a long-term study of the survival and reproduction of a large sample of marked individuals. Long-term studies of marked large mammals are rare, and very few have been done in hunted populations (Festa-Bianchet 1989; Jorgenson, Festa-Bianchet, and Wishart 1993; Langvatn and Loison 1999), partly because researchers are reluctant to invest time and money for marking animals that may be shot within a few months or years. As a result, much of the information on the evolutionary ecology of wild ungulates comes from populations

that are either un hunted or very lightly hunted (Byers 1997; Clutton-Brock, Rose, and Guinness 1997; Festa-Bianchet, Gaillard, and Jorgenson 1998; Gaillard et al. 1998a), and little is known about the evolutionary effects of sport hunting. Because of the high cost of marking and monitoring programs, and because a long-term study in a hunted population would be unable to consider many questions of theoretical interest, there is a need for government agencies to become involved. The long-term monitoring program of polar bears (*Ursus maritimus*) in Canada (Messier, Taylor, and Ramsay 1992; Derocher and Stirling 1998) is an excellent example of a successful study supported by government agencies.

The effects of gene flow in and out of protected areas is a research subject that holds particular promise and particular urgency, for both its practical and its theoretical interest. The amount of gene flow among areas subject to different harvest regimes will likely decrease the selective pressures brought about by selective hunting. On the other hand, selective hunting may itself affect the rate and direction of gene flow (Hogg 2000). There are complex patchworks of protected and exploited ungulate populations that would lend themselves to a very productive study.

The possibility that life-history strategies of large mammals have been shaped by hunting also has potential applications for our understanding of interspecific differences in behavior and reproductive strategies (Benton, Grant, and Clutton-Brock 1995). Consider two mountain ungulates, the alpine ibex and the bighorn sheep. The former has been protected from hunting in most of its range since early in the twentieth century, and is still protected from legal harvests in both Italy and France. Bighorn sheep, on the other hand, have been and are heavily hunted for trophies in most of their range in North America. Ibex males have a very high survival rate until about 11 to 12 years of age (Girard et al. 1999; Toïgo, Gaillard, and Michallet 1997) and a very gradual pattern of age-specific horn development (Toïgo, Gaillard, and Michallet 1999), whereas bighorn rams have low survival at 3 to 8 years of age (Jorgenson et al. 1997, Loison et al. 1999a), rapid horn growth (Jorgenson, Festa-Bianchet, and Wishart 1998), and subadult adoption of risky but successful alternative mating strategies (Hogg and Forbes 1997). These interspecific differences could be due to a wide range of plausible ecological explanations but may also result from selection for greater reproductive effort at a younger age in bighorn sheep, brought about by high hunting mortality over the last century. If this is the case, then one may predict higher natural mortality rates and faster horn growth of ibex in areas where they are hunted, such as in Switzerland (Giacometti et al. 1997), and higher survival and slower horn growth (but not smaller asymptotic horn size) of bighorn rams in protected areas, such as large national parks. Information on genetic

differences, however, would also be required to test this prediction because differences in survival could be due to changes in age ratios and therefore in age-specific rutting behavior (Heimer, Watson, and Smith 1984), and changes in horn growth would be expected simply from differences in population density (Jorgenson, Festa-Bianchet, and Wishart 1998).

A Final Thought: Is Human-Induced Selection a Modern Phenomenon?

The current extinction crisis caused by human activities is unprecedented, but there is evidence that humans have had a strong impact on the species composition of several ecosystems for thousands of years (Kay 1994a, Balmford 1996, Caughley and Gunn 1996), although the exact nature and strength of historic human impacts are unclear and often controversial (Beck 1996, Choquenot and Bowman 1998). Nevertheless, it is reasonable to suspect that changes in density, distribution, and behavior of many species of large mammals have been affected by human hunters for a long time.

Consider the differences in behavior toward humans of brown bears in Europe and North America. European bears are less aggressive, possibly as a result of coevolution with humans, who may have selectively killed aggressive individuals. Similarly, although North American wolves appear unable to survive outside wilderness areas (Mladenoff, Sickley, and Wydeven 1999), in parts of Europe wolves coexist with very high human population densities (Okarma 1993, Meriggi and Lovari 1996). Differences in response to habitat fragmentation and other human activities also appear to vary according to the potential for coevolution of humans and other species, measured by the length of time since recorded human occupancy (Balmford 1996, Martin and Clobert 1996). Hunting by humans has likely affected adult mortality of many large mammal species in much of the world for several centuries, possibly for millennia. If this is the case, then the reverse argument of the one I have presented may have some merit: the “new” selective pressures may be those experienced by ungulates in several European and North American national parks, particularly southern parks without large predators.

We should be concerned about the potential selective effects of sport hunting because they may limit the future ability of populations to adapt to a changing environment, or future opportunities for trophy hunting. There is also an ethical concern that sport hunting may lead to “artificial” selection. If we wish to avoid the evolution of “artificial” phenotypes, however, we must know what is “natural.” Establishing what is “natural” for species whose evolution has been shaped by human predation may be very difficult.

Summary

Game management is mostly concerned with what determines the size and sex/age composition of populations of hunted animals. Consequently, principles of population dynamics are most often applied to wildlife management, including considerations of sex- and age-specific survival and reproductive rates. It is often assumed that sport hunting affects population dynamics but is not a selective force. For many game species, however, avoiding getting shot is a major selective force because most mortality is due to human hunters.

The age-specific mortality caused by sport hunting of large mammals is usually very different from natural mortality. Hunters often kill prime-aged individuals, which normally have a very high survival rate. Regulations often specify the sex and the age class of animals to be killed. Hunters may select prey according to sex, age, reproductive status, or morphology. In much of Europe, morphology-based harvests favor certain phenotypes, particularly with regard to antler or horn size. The term *selective hunting* is somewhat foreign to North American managers, but it is often used in Europe. In North America, harvest is directed to certain age classes through morphology-based definitions of what can be killed, particularly with regard to horn size and antler points. Principles of evolutionary theory suggest that “selective” harvesting may indeed “select,” but not necessarily with the results that managers or society may seek. Intensive hunting may select for precocious maturity and increased reproductive effort, and trophy hunting may select for small horns or antlers. Long-term management plans must take into account the potential selective pressures of alternative harvest schemes, as is recognized by some fisheries scientists. Because sport hunting is as much a social issue as a biological one, changes in wildlife management require changes in attitudes, particularly in the case of trophy hunting. Relegating the competitive attitude to the past will benefit both hunters and biodiversity.

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Part IV

Genetic Diversity and Individual Differences

All chapters in part IV underline the importance of looking at variability among individuals, either in genotype or in phenotype. The maintenance of genetic diversity within a population is a major preoccupation of conservation biology. Populations with low genetic diversity may be at greater risk of extinction in the face of environmental change, and genetic variability is essential to preserve the potential to evolve. Just how much genetic diversity is required to reduce the risks of extinction, however, is often unclear, and it is only very recently that some studies have provided clear evidence of the deleterious effects of inbreeding and loss of genetic variability in wild populations. From a practical viewpoint, the preservation of genetic diversity must be balanced against other conservation priorities, such as habitat protection or disease prevention.

The next two chapters explore how genetic diversity within a population can be affected by differences in social structure and by variance in individual mating success. First, Dobson and Zinner show the sometimes surprising effects of mating system on effective population size, which is of interest to geneticists because it affects how genetic diversity may be lost over time. Some captive breeding techniques that are commonly used for restocking fish for either commercial or sportfishing lead to variance in reproductive success that is very different from that produced by matings in the wild. Although at first sight any kind of artificial interference with what appears to be “natural” is generally frowned upon, Claus Wedekind points out that in some cases the “natural” system is not the best one for conservation. Animals are not selected to do what’s best for their population; they are selected to increase their individual fitness, even if that occurs to the detriment of their population. In some cases, the interests of managers and the interests of the

fish can diverge! In other cases, however, artificial insemination techniques can lead to unwanted selection for fish that are adapted to artificial insemination rather than to survival in their natural environment.

One result of genetic variability is phenotypic variability, although individual differences in phenotype can be caused by many environmental and epigenetic effects. As more researchers accumulate long-term databases on individually marked animals, they face the opportunity to look at how persistent individual characteristics affect behavior and reproduction, as well as the problem of how to analyze repeated observations from the same individuals without violating the assumption of nonindependence that is key to statistical analyses. While presenting a primer of recently developed statistical techniques, Brian Steele and John Hogg also show how individual differences can indeed affect our interpretation of results from wildlife studies.

Finally, Peter Arcese examines a series of potential measures of “individual quality” for consistency among years. After analyzing an unusually detailed long-term data set on song sparrows, he concludes that none of the apparent measures of individual quality are very useful to predict population growth. He consequently cautions against the uncritical use of traits that appear correlated with individual fitness in setting priorities for conservation program. His chapter raises a number of important theoretical and practical questions about the differences between individual performance and population growth.

13.

Social Groups, Genetic Structure, and Conservation

F. Stephen Dobson and Bertram Zinner

Many vertebrate species, especially mammals, exhibit social groupings that depend at least to some degree on kinship (Wilson 1975, Trivers 1985). Social groups provide opportunities for a variety of mating patterns, and thus for varying levels of reproductive competition. Mating patterns influence the genetic properties (or “gene dynamics”) of populations (Wright 1969). The influences of different mating patterns on gene dynamics have been studied mainly by theoreticians and are controversial (Nunney 1999). These influences are important for two reasons. First, the genetic properties of populations constrain and influence the evolutionary potential of species (Nunney 1999). For example, social behaviors within a population may constrain or promote both cooperation and competition among individuals (Chesser 1998a). At the same time, existing cooperative and competitive social behaviors may influence gene dynamics of a population through their influence on mating patterns (Dobson 1998). Thus gene dynamics and social behaviors probably coevolve, each influencing the properties of the other and their potential for change.

Second, gene dynamics are important in devising effective management

plans for species of conservation concern. The genetic properties of populations may influence the flexibility with which species react to environmental changes (Chesser, Rhodes, and Smith 1996; Nunney 1999). In general, it is assumed that populations with greater genetic variation are more viable in the face of dramatic environmental changes. To provide an example of how gene dynamics might inform conservation, Sugg et al. (1996) considered the case of possible translocations of black-tailed prairie dogs (*Cynomys ludovicianus*), given knowledge of the gene dynamics of this species. Although black-tailed prairie dogs are not currently of global conservation concern, a closely related species with very similar biology, the Mexican prairie dog (*Cynomys mexicanus*), is rare and endangered. Sugg et al. (1996) found that translocations of female prairie dogs would break up genetic substructuring of colonies that is caused by social groups of closely related kin, and that this in turn would cause more rapid loss of genetic variation from prairie dog colonies. Low genetic variability could render such colonies more vulnerable to extinction after changes in the environment.

Empirical studies have lagged behind theoretical work on mating patterns and gene dynamics. In some cases, however, it is clear that some social mammalian species have genetic properties that are influenced by their polygynous mating systems and social groups (Schwartz and Armitage 1980, Patton and Feder 1981, Chesser 1983, Pope 1992, Dobson et al. 1998, but see Storz 1999). These studies used Wright's (1965, 1969) *F*-statistics to describe gene dynamics. *F*-statistics describe deviations of a population from random mating: (1) within subpopulations, (2) among subpopulations, and (3) within the population.

The above studies differed from studies of regional gene dynamics under the classical island model of population genetics (reviewed by Slatkin 1987) because they used social groups (or "breeding groups," the lowest level of population structure within which mating is random) as subpopulations, and a colony or an aggregation of families as the population (Fig. 13.1). In general, these studies found that mating among the offspring of a social or family group occurred less frequently than expected if mating was random, and that significant genetic differences occurred among social groups.

Wright (1969, 1978) also devised the concept of effective population size to describe the rate of loss of genetic variation from a population. Effective size is the number of individuals in an ideal population that lose genetic variation at the same rate as the census population. An ideal population is one with equal numbers of randomly mating males and females, and no migration, mutation, or selection. Because effective size is estimated in relation to the actual census population size, it is helpful to compare the two (Nunney 1993, Nunney and Elam 1994). Effective size has been typically estimated at

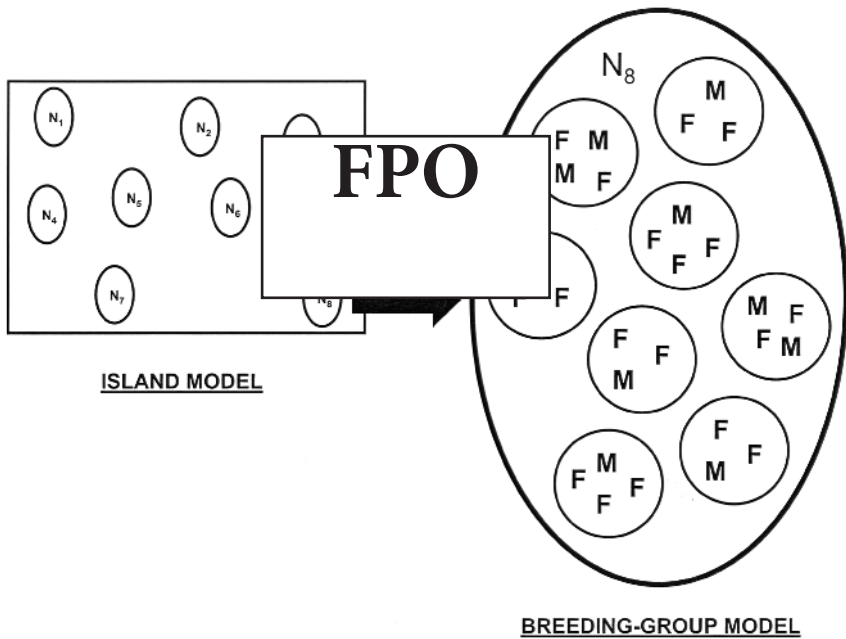


FIG. 13.1. An illustration of the difference between Wright's classical island model of gene dynamics (left) and population structure at the breeding-group level (right). Because F -statistics are hierarchical, these two views of population subdivision are compatible and overlapping. Thus genetic variation can be partitioned within individuals, within breeding groups in subpopulations as on the right, among breeding groups on the right, within subpopulations such as N_8 , among the 8 "N" subpopulations on the left, and within the regional population of "islands" on the left. In the original island model, individuals within the subpopulations mated randomly, rather than in breeding groups. M = male, F = female.

between half and the full census population size, indicating that real populations lose genetic variation more rapidly than expected from ideal populations. Over several generations, effective sizes may be lowered even further by historical population declines (Frankham 1996). Recent empirical studies of mammals with social groups, however, indicate that effective size may be nearly as high or even higher than census population size (Long et al. 1998; Pope 1998; Dobson, Smith, and Wang 2000).

In an attempt to model the influence of social groups on gene dynamics, Chesser (1991a,b, Chesser et al. 1993) incorporated the influence of female philopatry and male polygyny on changes in gene dynamics. Matings were assumed to occur only within social or family breeding groups, and models that described gene dynamics of colonies or subpopulations within such

groups were called breeding-group models (Sugg et al. 1996, Dobson 1998). Cockerham (1967, 1969, 1973) had shown how Wright's F -statistics could be derived from changes in genetic correlations among individuals in populations, and Chesser (1991a,b) showed how gene correlations, and thus F -statistics, should change over the generations, under conditions of female philopatry and a polygynous mating system. Gene correlations measure such things as the average coefficient of inbreeding and average relatedness within and among breeding groups. With further assumptions, Chesser et al. (1993) showed how effective population size could also be estimated using gene correlations and the F -statistics derived from them. To provide more realistic estimates of F -statistics and effective sizes, Sugg and Chesser (1994) incorporated the influence of multiple paternity, which could result from a female mating with different males during the same or different breeding events.

Not all social birds and mammals are polygynous, and breeding groups in some species contain only two breeders at a time. Apparently monogamous species are quite common in birds (Greenwood 1980, Greenwood and Harvey 1982) and occur less commonly in mammals (Dobson 1982). Of course, many species thought to be monogamous may in fact exhibit extra-pair paternity, or females may change mates from one breeding season to the next (Westneat and Sherman 1997, Goossens et al. 1998). These species may be described as exhibiting social monogamy, but the actual mating system may be somewhat promiscuous or even polygynous (Bouteiller and Perrin 2000). The gene dynamics of socially monogamous species may depend on rates of dispersal away from the natal area (Balloux, Goudet, and Perrin 1998), as well as on the degree of multiple paternity (Parker and Waite 1997).

The breeding-group model makes some important predictions for both conservation and evolutionary biology. The essential insight of the model is that genetic structure may occur within colonies; that is, within what Wright called subpopulations (Sugg et al. 1996). If this finer scale of genetic structure is ignored, aspects of a population's gene dynamics that occur at the level of social breeding groups are also ignored. The first prediction that can be made from the model is that when social groups are based on kinship, there should be genetic differences among the social groups (Dobson 1998). Relatives within a group should be more closely correlated to each other through common descent, than they are to individuals in other groups. A second prediction is that if dispersal evolved to reduce inbreeding (reviewed in Greenwood 1980, Dobson 1982, Thornhill 1993), then the F -statistics that compare the rate of inbreeding to random mating within the breeding groups should be strongly negative (Dobson et al. 1997). Finally, under a

pattern of strong female philopatry and harem polygyny by a single male, the rate of loss of genetic diversity should be considerably slowed (Chesser et al. 1993; Chesser, Rhodes, and Smith 1996).

The breeding-group model and its empirical tests indicate that social groups can be extremely different genetically (reviewed by Dobson 1998, but see Storz 1999). The loss of genetic variation from socially structured populations may be much slower than predicted by classical approaches to population genetics (Sugg et al. 1996), although this conclusion has been questioned by Nunney (1999). Thus estimates of gene dynamics and our understanding of the genetic properties of populations could be very different if the breeding-group approach were supported. In fact, the breeding-group model has been supported when tested against two other means of calculating gene dynamics: biochemical data and estimates from pedigrees (Dobson et al. 1997, 1998).

Our purpose in this chapter is threefold. First, we will review the predictions of the breeding-group model. Second, we will examine the empirical evidence that supports the model's usefulness for polygynous species, including an example that assumed both multiple paternity and its absence. And third, we will examine theoretical and empirical tests of the model's usefulness for monogamous species, and briefly consider the possible influence of multiple paternity on the gene dynamics of socially monogamous species.

Model Description

Mathematical details of the breeding-group model appear in Chesser (1991a,b), Chesser et al. (1993), Chesser, Willis, and Mathews (1994), and Sugg and Chesser (1994). Rather than repeat the mathematical details, we will explain the reasoning that forms the basis for operation of the model. Our purpose is to provide a guide to application of the breeding-group model to real situations in nature. Consequently, we will restrict our description to the most familiar gene dynamics, F -statistics and effective population sizes, that are commonly reported in the literature. The model has been extended to autosomal inheritance (Chesser 1998b), as well as to various forms of paternal and maternal inheritance (Chesser and Baker 1996), but we will not discuss these further advances.

Cockerham (1967, 1969, 1973) defined three gene correlations: F , the inbreeding coefficient; θ , the average genetic correlation between individuals in a group (in the absence of inbreeding, this is half the average coefficient of relatedness = r); and α , the average genetic correlation between individuals that are not in a group together. These gene correlations can be used to calculate Wright's (1965, 1969) F -statistics (after Chesser 1991a,b):

$$F_{LS} = \frac{\theta - \alpha}{1 - \alpha}, \quad F_{IL} = \frac{F - \theta}{1 - \theta}, \quad F_{IS} = \frac{F - \alpha}{1 - \alpha}. \quad (\text{Equation 1})$$

The first F -statistic, F_{LS} , indicates the degree of genetic differentiation among social or family breeding groups (L stands for the “lineage” in a social group and S for “subpopulation”), so if its value is 0.15, the breeding groups are on average 15% different genetically. The second F -statistic, F_{IL} , shows how the rate of inbreeding compares with that expected from random mating among the offspring of a breeding group (where I stands for “inbreeding”). If F_{IL} is positive, then offspring mate with closer kin than expected at random. If negative, mating is with more distant kin, as expected with dispersal out of the breeding group. A value of zero indicates that mating among offspring within the breeding group is about as expected at random. These same interpretations apply to the last F -statistic, F_{IS} , but here the random mating expectation is for the whole colony or subpopulation, rather than the breeding group.

F -statistics are hierarchical, so that the genetic properties at greater levels of spatial scale are easily examined. Thus an F -statistic, F_{ST} , indicates the degree of differentiation among colonies or subpopulations in a larger regional population. At this level, F_{IS} , the deviation of the rate of inbreeding from that expected under random mating of the subpopulation, also occurs and is the same value as the F_{IS} calculated above, assuming that all subpopulations have this same value. Finally, F_{IT} is the deviation of the inbreeding coefficient from that expected if matings within the entire population were random. The notation of F_{ST} , F_{IS} , and F_{IT} , were what Wright (1965, 1969) originally used when he defined F -statistics because he envisioned genetic differentiation and inbreeding in populations that were isolated or semi-isolated by geography, rather than by social grouping (Fig. 13.1).

In addition to the F -statistics, effective population sizes can be estimated from gene correlations, according to a simple formula developed by Wright (1969):

$$N_{eI} = \frac{1}{2\Delta F}, \quad N_{eV} = \frac{1}{2\Delta\alpha}. \quad (\text{Equation 2})$$

N_{eI} is termed the inbreeding effective population size, and N_{eV} is called the variance effective size. At genetic equilibrium, these estimates give the same value. Thus, for practical purposes, it doesn't matter which formula is used to estimate effective size. It may sometimes be easier to use formulas for effective size that are based on the F -statistics (Balloux, Goudet, and Perrin 1998), however, and a formula for doing so was presented in Chesser et al. (1993) and Sugg and Chesser (1994):

$$N_e \equiv \frac{4s - 3F_{IS} - 1}{6(F_{LS} - F_{IS})} \quad (\text{Equation 3})$$

where s is the number of breeding groups in the population, and the F -statistics can be determined from Equation (1).

Chesser's (1991a,b) basic method was to track the change in gene correlations over time. Gene correlations of offspring can be calculated from the gene correlations of their parents (Cockerham 1967, 1969, 1973):

$$\theta_{i,j} = \frac{1}{4} (\theta_{S_i S_j} + \theta_{S_i D_j} + \theta_{S_j D_i} + \theta_{D_i D_j}) \quad (\text{Equation 4})$$

Here, i and j refer to two different individuals, and S and D refer to their sires and dams, respectively. By averaging across pairs of individuals, this formula can estimate the average genetic correlation between individuals of the offspring generation that are in the same breeding group (viz., θ), and the average gene correlation between individuals that are in different breeding groups (viz., α). Also needed is the average inbreeding coefficient ($F = \theta_{S_i D_i}$), the correlation due to common ancestry between the gametes that form an offspring individual. Given a pedigree, estimates of gene correlations are fairly easy to make, even after only a few generations (Dobson et al. 1997, 1998). Unfortunately, such pedigrees are seldom available for wild populations.

Chesser (1991a) recognized that the change in gene correlations from one generation to the next depends on patterns of mating and thus could be calculated using a transition matrix that represented the way that the mating system influenced gene correlations from the parental to offspring generations. First, he began with the notion of an ideal population that was subdivided into several social or family breeding groups. He assumed that generations do not overlap, to make the accounting of gene correlations simpler. He defined terms for the average number of adult males and females in breeding groups, the number of breeding groups, and dispersal among breeding groups. The dispersal term was based on the rate of both male and female movements, and thus could indicate the importance of female philopatry on changes in gene correlations. Because several females may occur in a breeding group, and their reproductive success may vary, he also incorporated a term ϕ_f , the mean probability that two randomly chosen surviving offspring in a breeding group share the same mother (this must be calculated or estimated over the lifetimes of mothers, due to the assumption that generations do not overlap). In the transition between generations, only individuals that potentially breed should be counted, so "surviving offspring" refers to young that both survive to adulthood and

mate successfully. ϕ_f varies from 1 for monogamy to lower values as the number of mothers in a breeding group increases.

Next, Chesser (1991b) incorporated the influence of male polygyny. If one male does all the breeding in a group, the offspring of different females are more closely correlated genetically than if mothers mated with different males. For this, he introduced the term ϕ_m , the mean probability that two randomly chosen surviving offspring of different mothers in a breeding group have the same father. Again, this must be calculated or estimated over the lifetimes of mothers. This term is zero when there is only one mother (Sugg and Chesser 1994, Balloux, Goudet, and Perrin 1998), but for multiple mothers in a breeding group, it primarily depends on the number of fathers and their contributions to offspring. If only one male breeds in each generation, the value of ϕ_m is 1, and declines as more males father surviving offspring. The last innovation was to incorporate the influence of multiple paternity, which was not taken into account in earlier modeling. For this, the term ϕ_w was defined as the mean probability that two randomly chosen surviving offspring, produced over the lifetime of a female, have the same father (Sugg and Chesser 1994). The value of ϕ_w is 1 for single paternity, and zero for complete multiple paternity. Notice that multiple paternity can occur in two different ways: from a mother mating with different males in different years, and from multiple paternity within a clutch or litter.

Nunney (1999) questioned the efficacy of the breeding-group model and the realism of its assumptions (nonoverlapping generations and the “local” population regulation that philopatry of females indicates). As an alternative, he offered models for estimating effective population sizes, based on *F*-statistics, that have arbitrary groupings that might be treated as social groups, as well as a variable that represents the degree of local population regulation. In a locally regulated population, group size and group number are relatively constant over time. This alternative breeding-group model requires estimation of variation in reproductive success for males, females, and the designated groups. Dispersal patterns of males and females among groups do not explicitly appear in Nunney’s models and thus do not need to be estimated. Because multiple mating precludes knowledge of paternity patterns for many species, however, this method may be difficult to apply broadly. Also, means of estimating the degree of local population regulation are unknown. Applications of empirical data to this model have not yet been made. However, if the above difficulties could be overcome, more accurate estimate of effective population sizes might be produced than with Chesser’s models, at least under some conditions of mating and dispersal (Basset, Balloux, and Perrin 2001).

From the preceding description, it is clear that some sort of “group” model

could be used to predict the gene dynamics of a monogamous population. Assuming single paternity, Chesser, Willis, and Mathews (1994) did this and found that the breeding-group model reduced to the classical gene dynamics predicted by Wright's (1969) methods, with the important difference that F -statistics are calculated at the breeding-group level, no matter how small the breeding group is. Basset, Balloux, and Perrin (2001) showed, however, that Nunney's (1999) group model was much more accurate for monogamous species than Chesser et al.'s (1993) breeding-group model. For those bird species that are genetically monogamous, a family group (equivalent to a breeding group) consists only of the paired male and female and their current offspring. A similar mating and family situation might occur in a few mammalian species as well (but see Balloux, Goudet, and Perrin 1998; Goossens et al. 1998).

Tests of the Model

Two questions need to be answered concerning the breeding-group model. First, is the concept of breeding groups important? That is, do social breeding groups have distinct genetic properties? This question can be answered in the affirmative (Dobson 1998). Three studies of rodent species have found that polygynous breeding groups are significantly genetically differentiated from one another (Schwartz and Armitage 1980, Patton and Feder 1981, Dobson et al. 1997, 1998). Three studies of primates, one of red howler monkeys (*Alouatta seniculus*) and two of humans (*Homo sapiens*), yield similar results (Long 1986, Long et al. 1998, Pope 1992, 1998). The primate studies also found that estimates of effective population sizes were elevated when polygynous social breeding groups were analyzed. Second, does the breeding-group model reflect the same patterns of gene dynamics that can be found empirically from studies of pedigrees or biochemical alleles? This question can be answered by comparing predictions of the model with other empirical results.

The efficacy of the breeding-group model was examined in a case study, and indicated empirical verification of the model under a polygynous mating system, male dispersal, and a high degree of female philopatry. From a long-term study of social breeding groups (called coteries) in a colony of black-tailed prairie dogs, Dobson et al. (1997, 1998) estimated F -statistics from three different sources of data: the breeding-group model, pedigrees, and allozyme alleles (Table 13.1). They found that the first prediction, genetic differences among breeding groups, was strongly supported: all three methods indicated about 17% (viz., $F_{LS} \approx 0.17$) genetic differentiation among the coteries of prairie dogs. Previously, Hoogland (1992) had shown that mating

TABLE 13.1. *F*-statistics from studies of the gene dynamics of mammals

SPECIES	F_{LS}	F_{IL}	F_{IS}	N_e	N_C	RATIO
Black-tailed prairie dog ¹	0.16	-0.18	0.01	95	85	1.12
Black-tailed prairie dog ²						
breeding-group model ³	0.16	-0.18	0.00	89	74	1.21
pedigrees	0.19	-0.23	0.00	79	74	1.07
allozyme alleles	0.17	-0.21	-0.01	89	74	1.21
Plateau pika ⁴						
single paternity	0.30	-0.37	0.04	61	67	0.91
multiple paternity	0.28	-0.34	0.04	66	67	0.99
White-toothed shrew ⁵	0.09	-0.02	0.08	26	44	0.59

¹Sugg et al. 1996, based on Hoogland 1995. N_e calculated from Equation (3).

²Dobson et al. 1997, 1998, unpublished data. N_e calculated from Equation (21) in Sugg and Chesser (1994), of which Equation (3) is an estimate.

³The model estimate of N_e based on Equation (2) was 93, yielding a ratio of 1.25.

⁴Dobson, Smith, and Wang 2000. N_e calculated from Equation (2).

⁵Balloux, Goudet, and Perrin 1998; Bouteiller and Perrin 2000. N_e calculated after Nunney (1999).

Definitions of *F*-statistics are given in the text, except for N_C , the census number of breeding adults in the study population.

with respect to kinship was close to random within the colony, with the exception that parents and offspring, and full siblings, seldom bred together. This exception, along with a strong pattern of male-biased dispersal away from the natal area and equally strong female philopatry, was sufficient to fulfill the second prediction: within breeding groups, inbreeding was much less frequent than expected if offspring were mating randomly in their natal coterie ($F_{IL} \approx -0.20$). Again, all three methods of estimating gene dynamics produced very similar results and the same conclusion. These results confirmed similar conclusions by Sugg et al. (1996), who used results from Hoogland's (1995) book on the prairie dogs to estimate *F*-statistics using the breeding-group model to produce similar estimates of fixation indices (see Table 13.1).

Sugg et al. (1996) also used the breeding-group model to estimate effective population size and found that effective size was about 12% greater than the size of the census population (see Table 13.1). Estimates of effective population sizes over a 10-year period during the prairie dog study, using estimates

from the breeding-group model, pedigrees, and allozyme data and comparing them to the actual mean census population size, confirmed the above results using the complete data set on the prairie dogs (harmonic means used in all calculations; see Table 13.1). Estimates of effective population sizes averaged about 10 to 20% larger than the census population size. It may seem anomalous that effective size can be greater than the number of individuals in the census population. Effective population size, however, does not reflect an actual number of individuals. Rather, effective size is a measure of the rate at which genetic variation is being lost from the population (equation [2]). If the census population loses genetic variation more slowly than would be expected under an equal number of randomly mating males and females, then effective size can be larger than census size (Chesser et al. 1993). Because the great majority of surviving females settle in the breeding group where they were born, social structure causes slower loss of genetic variation due to the genetic isolation of unrelated females from each other. Different breeding groups may lose genetic alleles, but they will often lose different alleles, thus slowing the loss of genetic variants from the overall colony (Chesser, Rhodes, and Smith 1996).

One reason why Nunney (1999) criticized the results presented by Sugg et al. (1996) was because prairie dogs have overlapping generations, and the breeding-group model assumes nonoverlapping generations. Dobson et al. (2000) applied the breeding-group model to highly social Tibetan plateau pikas (*Ochotona curzoniae*). Plateau pikas have tightly knit family groups, variable mating patterns that average out to a low degree of polygyny, and philopatry and dispersal by both sexes (Dobson, Smith, and Wang 1998). When dispersal among pika families does occur, it is male-biased but restricted to very short distances, so that some close inbreeding is possible. Most individuals live for only about 1 year, and they do not breed until about a year old. Thus they are nearly an “annual” species, and they come close to having nonoverlapping generations. Unfortunately, patterns of paternity were unknown, but some females mate multiply when there are more than two males in a family (Smith and Wang 1991). Thus analyses were run twice: first under the assumption of single paternity, and then assuming complete multiple paternity wherever it was possible.

Results of the breeding-group model indicated that pika families were even more genetically differentiated than coterries of prairie dogs, at about 29% genetic differentiation among families (see Table 13.1; Dobson, Smith, and Wang 2000). Again, inbreeding was much less frequent than expected from random mating of offspring within families (reflected by strongly negative F_{IL} values), despite the limited dispersal pattern. Inbreeding within the pika colony could barely be distinguished from random, as indicated by

F_{IS} values that were close to zero. Effective population size was slightly lower than the number of breeding adults in the population; but classical estimates of effective size that do not take breeding groups into account produced much lower values (at about 42 adults), probably due to the fact that some females were more successful at leaving surviving offspring than others (variance in female reproductive success ≈ 4.20 , expected Poisson variance = 2.00). Analyses that assumed single and multiple paternity yielded very similar results and the same conclusions.

One socially monogamous species, the greater white-toothed shrew (*Crocidura russula*), has been studied using the breeding-group model. Balloux et al. (1998) used biochemical estimates of gene dynamics and knowledge of the mating system to “back-calculate” the influence of dispersal patterns. F -statistics indicated that “family” groups of shrews were based on male philopatry, producing significant genetic differentiation among families (see Table 13.1). Female dispersal from the natal family was only about 40%, and thus considerable inbreeding occurred within subpopulations of shrews. This study showed the utility of the breeding-group model, even under the case of monogamy, as an exploratory tool. Balloux et al. (1998) concluded that the female-biased pattern of dispersal probably accounted for an extremely high effective population size. The analysis assumed single paternity, and that was likely common (Bouteiller and Perrin 2000). This last study, however, showed that, although they are socially monogamous, the mating system of the shrews is slightly polygynous due to some males mating with the females that live with other males. Multiple paternity of litters was not found, however, so the breeding-group model was probably appropriate for modeling the shrew population. Bouteiller and Perrin (2000) recalculated effective population size for the shrews (using the approach of Nunney 1999), and found that it was about 60% of the census population size.

Basset, Balloux, and Perrin (2001) compared estimates of effective population sizes from Chesser et al.’s (1993) version of the breeding-group model to an alternative model designed by Nunney (1999). A major difference between the models is the timing of estimates of gene dynamics, which occurs before dispersal in Chesser’s model and after dispersal in Nunney’s model. Effective population sizes were overestimated by the Chesser model under the conditions of monogamous mating and equal dispersal of the sexes. Otherwise the models yielded similar results. This indicates that Nunney’s (1999) model, which is more difficult to apply because it requires more parameters (especially variation in male reproductive success and the degree of local population regulation), should be used for monogamous species that exhibit little sex bias in natal dispersal.

In summary, the studies of black-tailed prairie dogs verified the breeding-group model by showing that the model results (estimated from demography, dispersal, and mating patterns) were closely consistent with empirical results from pedigrees (where genetic correlations due to descent can be calculated directly) and allozyme alleles (where F -statistics are estimated indirectly from heterozygosity, and effective sizes are estimated from F -statistics). Although the three sources of data came from the same prairie dogs and were thus biologically interdependent, there was little overlap in the application of variables used to estimate gene dynamics under the three methods. So the different methods were as independent as one might expect. The results of the breeding-group model were strongly supported by the empirical results. The study of somewhat polygynous plateau pikas applied the breeding-group model to a species with little overlap of generations and indicated the importance of family social structure on gene dynamics. The pikas also indicated little influence of multiple paternity on gene dynamics in a slightly polygynous (though with variable mating systems among families) species. Finally, the study of white-toothed shrews indicates the usefulness of the breeding-group approach for estimating gene dynamics of monogamous species. The group model of Nunney (1999) should be applied, however, to obtain more accurate estimates of effective sizes under monogamy or equal dispersal of males and females (Basset, Balloux, and Perrin 2001), and when accurate information about F -statistics; variation in male, female, and group reproductive success; and mode of population regulation are all available.

Multiple Paternity

With the exception of Sugg and Chesser's (1994) breeding-group model, the influence of multiple paternity on gene dynamics is seldom taken into account. Social species may not always exhibit single paternity and thus may not always exhibit the mating system that is apparent from the composition of social groups. For example, multiple male matings with individual females were found in polygynous social groups of prairie dogs and plateau pikas (Smith and Wang 1991, Hoogland 1995). In an apparently different mating system, litters of the socially monogamous alpine marmot (*Marmota marmota*) were found to average only about 70% of offspring sired by the family male (Goossens et al. 1998). To apply genetic models that incorporate social groups to these situations, it is necessary to take multiple paternity into account. Naturally, if a pedigree were available for a population, accurate estimates of gene dynamics could be made. However, species like alpine marmots are long-lived. This has several consequences. First, the estimate of

multiple paternity for this species is an underestimate because females may mate with several males over their lifetimes. Second, some degree of multiple mating by males (polygyny) may occur, both within a single breeding season and over the lifetimes of males. Third, the generations overlap (Nunney 1999), though this problem might have more influence on the number of generations that it takes to reach genetic equilibrium, rather than the equilibrium values of gene dynamics (Hill 1979; but see Nunney 1993). In short, the influence of multiple paternity on socially monogamous species needs to be investigated.

There are two ways that multiple paternity might influence the gene dynamics of polygynous species. One is when males that otherwise would not mate gain access through extra-pair fertilizations to females that are otherwise mated to dominant or territorial males. In this case, effective population size likely increases because more individuals participate in breeding, and the variance in male reproductive success of males becomes lower. The other is when all males are mated, but some males gain extra copulations with neighbors. In this case, variance in male reproductive success could become lower or higher (or even remain unchanged), and effective population size would accordingly become higher or lower, respectively. The influence of multiple paternity on F -statistics is unclear. But in general, when more males breed in local social groups, genetic correlations within the breeding groups will be diluted as the number of fathers increases. With the value of θ lower, Equation (1) suggests that genetic differentiation among breeding groups (viz., F_{LS}) should become lower as well.

Socially monogamous species should also have higher effective population sizes if more males father offspring and the variance in male reproductive success decreases. The number of fathers in such populations may exceed the number of breeding females. If the number of fathers decreases, producing *de facto* polygyny, then effective population size should decrease (Parker and Waite 1997). It is not so clear, however, how multiple paternity would influence effective population size if all breeding males in a population were otherwise mated. With single paternity, the variance in male and female reproductive success would be equal. As multiple mating occurs, differences among males, but not females, in reproductive success might be diluted. If the variance in male reproductive success was lowered via multiple paternity, the effective size of the population should be increased (Nunney 1999). We examined this possibility in a simple model.

Consider a population of n couples (male and female). Denote by X the number of total offspring of a given female during a certain time interval. Assume that a certain proportion of her offspring are not fathered by her partner. Suppose that this proportion is p , on average. Denote by Y the number

of total offspring fathered by her partner, a given male, during the same time interval. Note that these may or may not be born to the given female. We are then interested in how the variance of Y is related to p .

We made the following assumptions. Each of the X offspring is fathered by the given male with probability $1 - p$. Each male also has a chance q of being the father of any of the offspring of a number k of other females.

Denote the total number of offspring of these k females by Z . Denote by Y_1 the number of offspring fathered by the given male and born to his partner, the given female, and denote by Y_2 the number of offspring fathered by this male but born to other females. Then the distribution of Y_1 given $X = x$ is binomial with parameters x and $1 - p$ and the distribution of Y_2 given the number of offspring from the other k females, say $Z = z$, is also binomial with parameters z and q .

Since the mean of Y must be the same as the mean of X , one can express q in terms of p using the Law of Total Expectations:

$$\begin{aligned} E[X] &= E[Y] = E[Y_1 + Y_2] = E[Y_1] + E[Y_2] = E[E[Y_1|X]] + E[E[Y_2|Z]] \\ &= E[(1 - p)X] + E[qZ] = (1 - p)E[X] + kqE[X], \end{aligned}$$

which implies

$$q = \frac{p}{k},$$

Then

$$\begin{aligned} \text{Var}(Y_1) &= E[\text{Var}(Y_1|X)] + \text{Var}(E[Y_1|X]) \\ &= E[p(1 - p)X] + \text{Var}((1 - p)X) \\ &= p(1 - p)E[X] + (1 - p)^2 \text{Var}(X) \end{aligned}$$

and

$$\begin{aligned} \text{Var}(Y_2) &= E[\text{Var}(Y_2|Z)] + \text{Var}(E[Y_2|Z]) \\ &= E[q(1 - q)Z] + \text{Var}(qZ) \\ &= kq(1 - q)E[X] + kq^2 \text{Var}(X) \\ &= p \left(1 - \frac{p}{k} \right) E[X] + \frac{p^2}{k} \text{Var}(X). \end{aligned}$$

Since Y_1 and Y_2 are independent, $\text{Var}(Y) = \text{Var}(Y_1 + Y_2) = \text{Var}(Y_1) + \text{Var}(Y_2)$ and therefore the previous two results yield

$$\text{Var}(Y) = E[X] + (\text{Var}(X) - E[X]) \left(\frac{p^2}{k} + (1-p)^2 \right).$$

Since $0 \leq \frac{p^2}{k} + (1-p)^2 \leq 1$, it follows from this equation that $\text{Var}(Y)$ must always be contained in the interval determined by the values of $E(X)$ and $\text{Var}(X)$, regardless of the values of p and k . In particular,

$$|\text{Var}(Y) - \text{Var}(X)| \leq |\text{Var}(X) - E[X]|.$$

So far we did not specify the distribution of X . Usually X is assumed to be Poisson distributed. In this case $\text{Var}(X) = E[X]$ and the equation above implies that $\text{Var}(Y) = \text{Var}(X)$ regardless of the values of p and k . When the expected value of X is approximately equal to the variance of X , then the equation above implies that the $\text{Var}(Y)$ must also be approximately equal to the $\text{Var}(X)$. For example, suppose the distribution of X would be a truncated Poisson distribution with parameters m and λ , where m is the maximum number of surviving offspring over a female's lifetime (thus truncating the Poisson distribution) and λ is the mean of the untruncated Poisson distribution:

$$P(X = x) = \begin{cases} \frac{\lambda^x}{x!} e^{-\lambda}, & x = 0, \dots, m-1 \\ 1 - \sum_{j=0}^{m-1} \frac{\lambda^j}{j!} e^{-\lambda}, & x = m \end{cases}$$

Then $\text{Var}(Y) \approx \text{Var}(X)$ regardless of the values of p and k , provided that m is not too small. For instance, if $m = 6$ and $\lambda = 2$ one calculates that $\text{Var}(X) = 1.943$ and $E[X] = 1.994$, accurate to three digits. Therefore $1.943 \leq \text{Var}(Y) \leq 1.994$ for any p and k . As m becomes smaller, $\text{Var}(X)$ declines relative to $E[X]$.

This simple model suggests that the variance in male reproductive success, and therefore effective population size, may change only slightly for multiple paternity when the mating system is socially monogamous. The effect of this slight change, under the model conditions, is a slight decrease in the rate of loss of genetic variation from the population, and thus a slightly larger effective size. Although preference by females for particular males for extra-pair matings might be expected to cause a shift from strict monogamy to some degree of promiscuity or even polygyny (Parker and Waite 1997), multiple paternity in the absence of such preferences likely causes little change in effective size of populations unless otherwise unmated males gain matings.

Conclusions and Recommendations

Chesser's breeding-group model (Chesser 1991a,b, Chesser et al. 1993, Sugg and Chesser 1994) uses behavioral ecology data to calculate the gene dynamics of kin-based social groups. Because of this, the model could be applied to studies of polygynous and promiscuous species, where information about demography, dispersal, and mating patterns has been studied. Breeding groups appear to have important implications for gene dynamics and thus for genetic management of endangered species. Family breeding groups can be extremely different from one another genetically. Dispersal generally reduces the rate of inbreeding, and rates of loss of genetic variation may be slowed in populations that have polygynous social breeding groups. Under any mating system, an increased number of fathers should lead to decreases in genetic correlations within breeding groups, decreased genetic differentiation among breeding groups, and increased effective size. In socially monogamous species where all males are mated, however, and other things being equal, effective size should remain little changed when multiple paternity occurs.

Study of the sensitivity of model estimates to the different model parameters is needed for both the Chesser and the Nunney approaches. Also, population genetic models generally assume equilibrium populations, but real populations rarely exhibit demographic or genetic equilibrium. In particular, populations of conservation concern may be out of genetic equilibrium due to population decline (with attendant genetic sampling effects associated with small population size), or due to population increases because of management. The influences of deviation from genetic equilibria on both genetic models and the gene dynamics of wild populations are largely unknown and need to be investigated. Applications of Nunney's (1999) models to organisms in the wild should prove useful, both for verifying the models and for finding ways to estimate the models' parameters. Such models are needed for estimating the gene dynamics of monogamous species and those with equal male and female dispersal patterns (Basset, Balloux, and Perrin 2001). The strength of Chesser's breeding-group model is that gene dynamics can be estimated from the sorts of behavioral and demographic data that are often collected in field studies of behavioral ecology. The utility of this breeding-group model, however, appears limited to polygynous mating systems with sex-biased dispersal.

Summary

Maintenance of genetic diversity is a concern for conservation biologists. Genetic diversity may be lost through inbreeding and genetic drift, but the rate of loss depends on mating patterns. In social species, such as some birds

and many mammals, matings often occur within kin-based groups. Breeding-group models of gene dynamics describe the partitioning and loss of genetic variation in such social groups, primarily through estimates of F -statistics and effective population sizes. Our purpose was to review evidence on the utility of breeding-group genetic models. When male polygyny and female philopatry are coupled with tight social structuring of populations, considerable genetic differences among breeding groups occur. In addition, the loss of genetic variation may be considerably slowed by the presence of sociogenetic structuring within breeding groups. Under monogamous mating systems, breeding-group models must be chosen with caution because some produce biased estimates of gene dynamics. Under polygynous mating systems, multiple paternity may slow the rate of loss of genetic variation, especially if cuckolding males have no other mating options. The same is likely under “socially” monogamous mating systems (apparent monogamy, but actual promiscuity). We show, however, that when all socially monogamous males are paired, multiple paternity should not greatly influence effective population size. The most practical aspect of breeding-group models (termed demographic models by Nunney and Campbell 1993) is that they can be used to estimate gene dynamics from the sorts of data that behavioral ecologists frequently collect in their research: mating and dispersal patterns and population demography.

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14.

Pathogen-Driven Sexual Selection for “Good Genes” versus Genetic Variability in Small Populations

Claus Wedekind

Even in cases where we know little about a particular species or population, it is safe to assume that mating is not normally at random (Andersson 1994), and that nonrandom mating and sexual selection influence the genetics of the next generation. Therefore, mate choice and breeding systems are important topics for the management of free or captive populations—especially in small or declining populations. An important management concern is whether free mate choice should be encouraged or prevented. The best management practice will depend on population size, mating system, and the mate preferences that would be expressed if individuals were given the opportunity to choose.

In this chapter I briefly outline some principles about supportive breeding and breeding in captivity, and explain some terminology (see also Lacy 1995). I summarize, from an evolutionary point of view, why we should expect nonrandom mating in nature, and what factors are most likely to influence mate choice. I concentrate on the genetic aspects of mate choice, rather than on choice based on body condition, territory quality, mating

gifts, and other mate preferences that may be roughly classified as “preferences for good fathers.” Many supportive measures, especially in captive populations, reduce the effect of different paternal investments, whereas genetic aspects become increasingly important with decreasing population size.

There are a number of so-called good genes hypotheses for sexual selection. A common prediction of these hypotheses is that mate choice increases the survival prospects of the average offspring. However, it would be too simplistic to conclude from this that managers should generally support free mate choice. Mate choice often leads to variance in reproductive success: some males are more successful than others. Anything that increases the variance in reproductive success also increases inbreeding and thereby the rate by which a small population loses genetic variation and rare alleles, the rate of decrease in average heterozygosity, and the loss of any heterozygote advantage. Minimizing inbreeding on the one hand and allowing for potential “good genes” effects of mate choice on the other hand is an optimization problem. This optimization problem cannot easily be solved, especially when we do not know how important genetic aspects of mate choice are in a particular population, and to which extent good genes effects from free mating can potentially outweigh the loss of genetic variability due to increased inbreeding. I discuss this in the context of management recommendations.

Free or suppressed mate choice is relevant not only to the genetics future generations but also to life-history decisions of the parents. Life-history decisions, such as the amount of resources a mother is willing to invest in a particular offspring, often evolved under conditions different from those faced by small or declining populations, especially captive ones. In some cases, maternal investment could be manipulated to optimize breeding success, and here I suggest some preliminary ideas about the methods for such manipulation.

N_e , Supportive Breeding, and Reproduction in Captivity

The more a population decreases in number, the more likely it is that the mean fitness of its members, and thereby the population’s probability of long-term persistence, will decrease due to genetic problems (Lande 1998b). These problems include (1) an increase in inbreeding and hence an increase in inbreeding depression (Hedrick and Kalinowski 2000), (2) a general loss of genetic variability and therefore a reduced potential for adaptation to changing environments, and (3) the risk of fixation of deleterious mutations due to random drift. Therefore, an obvious aim in conservation is to stop the decrease in number of individuals and even to achieve population growth.

The genetic problems just outlined are only indirectly dependent on

population size (i.e., the census size), but are directly related to the genetically effective population size, N_e (e.g. Hartl 1988). N_e is therefore an important parameter in population genetics and conservation biology (Caughley and Gunn 1996). N_e is the size of an ideal population that would lose genetic variability at the same rate as the real population. Hence, N_e corrects for a number of factors, such as age-related differences in reproductive rates, unequal family size, or unequal numbers of males and females. These corrections are necessary because any skew in sex ratio increases the variance in individual reproductive success and leads to increased inbreeding and further loss of genetic variability.

Supportive breeding, the practice of supporting weak, wild populations by releasing captive-bred individuals, is a technique used in the conservation of many species. Its first aim is obviously to maintain or increase population size, or to provide more harvest opportunities for species that are sport harvested. Supportive breeding, however, could have harmful long-term effects, and its potential impact on the genetics of a population must be given serious consideration (Hedrick and Miller 1994, Lande 1998b).

A first important rule is to avoid mixing individuals from different populations to reduce the risk of maladaptive hybridization and outbreeding depression (Hindar and Balstad 1994). Interpopulation mixing may only be desirable in very exceptional cases, such as for populations suffering from severe inbreeding depression (Madsen et al. 1999).

A second potential genetic problem of supportive breeding (especially of captive populations, as will be explained here) is the potential effect of artificial selection on the offspring that leads to a certain genetic adaptation to captivity. Adaptation to captivity is likely to reduce reproductive fitness of individuals reintroduced to the wild (Bryant and Reed 1999, Frankham 1999). Fleming and Gross (1993) compared hatchery-born and wild Coho salmon (*Oncorhynchus kisutch*) in direct competition and found that males and females from hatcheries had significantly reduced breeding success.

A third important genetic risk or disadvantage of supportive breeding is the fact that dividing a given population into a wild breeding and a captive breeding segment could have a negative impact on N_e . According to Ryman and Laikre (1991), splitting a population into wild and captive breeders can increase inbreeding in the total population because supportive breeding increases the variance in reproductive success by giving a reproductive advantage to a few randomly chosen individuals (Ryman, Jorde, and Laikre 1995; Nomura 1999; Ryman, Jorde, and Laikre 1999; Wang and Caballero 1999). Recent empirical studies provide support for this “Ryman–Laikre effect” (Tessier, Bernatchez, and Wright 1997). An increase in the inbreeding coefficient can eventually lead to population extinction (Saccheri et al. 1998).

The fourth potential genetic problem of supportive breeding is the elimination of mate choice. In nature, mating is not normally random with respect to genetic characters (Andersson 1994, Møller and Alatalo 1999, Wedekind 2002a). Circumventing mate choice may be significant with respect to offspring genetics and viability and may also decrease the amount of parental investment an offspring will obtain.

Some species have been or still are maintained under semi-natural conditions in captivity for several generations because their natural habitat is largely destroyed or the wild population is severely endangered. Hunter (1996) lists a number of species that would probably be extinct today without ex situ conservation. The list includes such charismatic species as the California condor (*Gymnogyps californianus*), the wisent (*Bison bonasus*), the Przewalski's horse (*Equus caballus przewalski*), the black-footed ferret (*Mustela nigripes*), and the Arabian oryx (*Oryx leucoryx*), but also contains less known species such as several cichlids of Lake Victoria (Kaufman 1992) or several viviparous tree snails (see also the list at www.earthwithness.com). In such cases, the mating system and natural mate choice may remain intact. However, some mating systems may be very damaging to the genetics and demographics of a population over the long term, even leading to extinction of captive populations. It may therefore be of interest to manipulate mate choice and breeding behavior to prevent the captive population from generating high inbreeding coefficients.

A recent study on the effective population size of a captive-bred fish (Fiumera, Parker, and Fuerst 2000) provides an alarming example. The piscivore *Prognathochromis perrieri* is a highly endangered Lake Victoria cichlid (Kaufman 1992). As part of a species survival plan, this fish is bred in captive populations spread over several institutions. Fiumera, Parker, and Fuerst (2000) collected data from subpopulations spanning five captive generations. Using microsatellite DNA markers, they found that N_e ranged from 2.5 to 7.7 individuals per subpopulation, which was far smaller than the census sizes of 32 to 243 individuals and suggested that very few individuals contributed to reproduction. Through inbreeding, approximately 19% of the initial alleles were lost within the first four generations of captive breeding. The loss of heterozygosity at each generation was 6 to 12%. A first (but late) measure against this loss of genetic variability was the removal of dominant breeders after they had reproduced to encourage reproduction by other individuals.

Why sex at all? And why are pathogens important for the maintainance of sex? Before I discuss different forms of mate choice, I will briefly summarize the prevailing theory as to why sexual mixing of genes is such a successful evolutionary program. The evolution of sex is somewhat difficult to understand because sex involves a number of significant evolutionary disadvantages

(Michod and Levin 1987, Stearns 1987). The major disadvantage has been termed the cost of meiosis: a female that reproduces sexually is only 50% related to her offspring, whereas an asexual female transmits 100% of her genes to each of her daughters. Hence, gene transmission (and population growth in terms of absolute numbers) is about twice as efficient in asexuals as it is in sexuals. If asexuals had the same survival probability as sexuals, a mutation causing a female to produce only asexual daughters would, when introduced into a sexually reproducing population, rapidly increase in frequency and outcompete sexuals in numbers within just a few generations (Williams 1975, Maynard Smith 1978). Why doesn't this happen? What are the evolutionary advantages of sex? or what are the disadvantages of asexual reproduction?

"Muller's ratchet" (Muller 1932) is one major disadvantage of asexuality: it predicts that slightly deleterious mutations accumulate in asexuals from generation to generation until the genome no longer codes for a viable organism, and the population goes extinct (Andersson and Hughes 1996). Thus, at first glance one may think that sex must be so successful because recombination and natural selection can efficiently remove deleterious mutations. Asexual reproduction is so much more efficient than sexual reproduction that, all else being equal, asexuals would need only a few generations to outcompete sexual conspecifics, probably long before the effects of Muller's ratchet become significant (Kondrashov 1993).

A second set of hypotheses suggests that sex enables the spread, or even the creation of, advantageous traits. These hypotheses require that the direction of selection be continuously changing, therefore the main source of fitness reduction must be short-term environmental changes. This condition is especially likely in the coevolution of hosts and pathogens because host–pathogen systems are more deeply interdependent than predator–prey or competitor systems. Host resistance genes that are advantageous today will become disadvantageous in the near future if pathogens evolve to overcome them. Therefore, hosts must continuously change gene combinations, and sex is an efficient means to do so (Hamilton, Axelrod, and Tanese 1990). Genetic heterogeneity within a sexually produced clutch may increase the chances that the clutch contains an optimal genotype ("lottery model"; Williams 1975, Kondrashov 1993), and it may decrease the risk of competition between relatives (the "elbow-room model"; Maynard Smith 1978, Kondrashov 1993). The possibility that sex reduces the risk of transmission of pathogens between relatives because of their reduced genetic similarity (Baer and Schmid-Hempel 1999) can be seen as a variant of Williams's lottery model.

To summarize (see also Howard and Lively 1994), the coevolutionary

conflict between pathogens and hosts selects for sexual mixing of genes as a diversity-generating mechanism, which allows both parties, hosts and pathogens, to survive Muller's ratchet.

Inbreeding Avoidance

If sex evolved as a diversity-generating mechanism, it is not surprising that there is mate choice and that mate choice often takes the degree of kinship between two individuals into account. Many population models, however, assume random mating, even with respect to kinship. Many breeding programs, such as those in fish hatcheries, do not account for potential inbreeding avoidance in the wild. Examples where there is no evidence for kin recognition and inbreeding avoidance span a broad taxonomic range, from invertebrates (Baur and Baur 1997, Peters and Michiels 1996) to vertebrates (Keane, Creel, and Waser 1996; Keller and Arcese 1998). However, there are probably more examples of species where inbreeding avoidance is known to occur, often through sex-biased dispersal (Pusey and Wolf 1996). Active avoidance of kin as mates has been demonstrated in a number of species, often relying on recognition of familiarity (Penn and Potts 1998, Clarke and Faulkes 1999). In some species, odors that reveal information about highly polymorphic loci like the major histocompatibility complex (MHC) seem to play a crucial role in kin recognition and inbreeding avoidance (review in Brown and Eklund 1994, Penn and Potts 1999).

“Good Genes” Models of Sexual Selection

Apart from inbreeding avoidance, there are a number of more sophisticated forms of sexual selection based on general phenotypic appearance or on sexual signals such as odors or secondary sexual ornaments. The literature usually groups criteria for mate choice into three classes (Andersson 1994): (1) direct benefits, such as parental care or nuptial gifts; (2) “Fisherian-traits,” which are attractive to members of the other sex but do not reveal anything else (Fisher 1930); and (3) good genes (Zahavi 1975, Hamilton and Zuk 1982, Grafen 1990, Wedekind 1994a, Johnstone 1995). The third class of criteria is of special interest here, because good genes are expected to increase offspring survival. Good genes in the context of sexual selection are mainly alleles at loci that are important in the coevolution between hosts and their pathogens because continuously changing selection pressures in this coevolutionary process maintain enough additive genetic variability for sexual selection to act on. Mate choice for good genes may therefore be important in determining

virulence in natural host–pathogen systems. Hence, not only sex itself but also some forms of sexual selection could be strongly influenced by the coevolutionary dynamics of host–pathogen systems.

Møller and Alatalo (1999) concluded that sexual selection for good genes is widespread across taxa, but its effect on offspring survival varies. Their meta-analysis found that male sexual characters chosen by females on average accounted for 1.5% of the variance in offspring viability, but they stressed that many of the studies included in their analysis may only partly estimate the full fitness consequences of mate choice for offspring survival. The effects were generally stronger for studies where the target of selection had been identified than for those with an unknown target of selection. Indeed, a recent experimental study demonstrated that the good genes effect of mate choice can be very strong: optimal mate choice in a whitefish would reduce pathogen-correlated egg mortality by 67% as compared to random mating (Wedekind, Müller, and Spicher 2001). Differences in male breeding ornamentation accounted for 32% of the variance in offspring mortality.

Levels of Selection

Mate choice for criteria that reveal good genes is only one possible level of pathogen-driven sexual selection. Other possible levels may include selection of sperm within the female reproductive tract, selective fertilization, or selective support of the embryo or the offspring (Wedekind 1994a). All these levels could potentially be connected to host–pathogen coevolution, or at least help to prevent inbreeding.

Preferences for sperm of genetically dissimilar types have been observed in vertebrates and invertebrates (reviewed in Eberhard 1996, Birkhead 2000). In many plants, growth of the pollen tube is often affected by the stigma and depends on the combination of male and female alleles on the self-incompatibility locus (Jordan et al. 2000). In all these examples, the connection between cryptic female choice and the offspring's immunocompetence is unclear. In mice, however, a series of experiments revealed that gamete fusion is not random with respect to the sperm's and the egg's MHC-type, and with respect to current epidemics of hepatitis virus (Wedekind et al. 1996, Rüllicke et al. 1998). In these studies, mice of two inbred strains that were bred to differ only in MHC but otherwise had an identical genetic background, and F1's of both strains, were paired or used for in vitro fertilization experiments, and the MHC of the resulting blastocysts was analyzed by polymerase chain reaction. Infected mice produced more heterozygous blastocysts than sham-infected mice. The difference was not a result of selection by the

pathogen but was due to nonrandom fertilization of the oocytes. The physiology behind such nonrandom fertilization is, however, unknown.

Different Types of Mate Preference versus N_e

An important aspect of mate preferences is whether they are uniform, and all members of one sex have the same preference, or variable, and mate preferences vary among individuals. As I will outline in the following, whether preferences are uniform or variable influences the variance in reproductive success among individuals. Variance in reproductive success in turn influences effective population size N_e (Hartl 1998), and with it the long-term viability of small and endangered populations.

Hamilton and Zuk (1982) suggested that individuals in good health and vigor are preferred as mates because they are likely to possess heritable resistance to predominant pathogens. By preferring healthy partners one may thereby produce robust, vigorous, and resistant progeny, better adapted and therefore less susceptible to local pathogens (review in Grahn, Langesfors, and vonSchantz 1998; Westneat and Birkhead 1998; Møller, Christe, and Lux 1999). There is much empirical support for this hypothesis (Møller, Christe, and Lux 1999). The mechanisms Hamilton and Zuk (1982) and later von Schantz et al. (1999) suggested, however, lead to populations where all individuals of one sex have the same mate preference, so that members of the opposite sex can be ranked in a universally valid order of attractiveness, and less attractive individuals will only mate if the more attractive ones are not available. A universal ranking would increase variance in reproductive success (Petrie and Lipsitch 1994) and decrease N_e . The effect often exists even in species thought to be monogamous because females sometimes solicit extra-pair copulations with more attractive or more viable males than their social partner (Kempenaers et al. 1992; Hasselquist, Bensch, and von Schantz 1996; Petrie, Doums, and Møller 1998).

Inbreeding avoidance can be seen as a simple form of variable preferences because members of the opposite sex cannot be ranked in a universally valid order of attractiveness according only to inbreeding. Consequently, in populations where inbreeding avoidance is the only criterion for mate choice, the variance in reproductive success is expected to be lower than where mate choice is based upon universal criteria. The difference between N_e and the actual population size, N_a , would also be lower.

Inbreeding avoidance often leads to offspring with increased degrees of heterozygosity, especially on important loci such as the MHC. Those loci often affect body or urine odors used in kin recognition (Brown and Eklund 1994, Penn and Potts 1999). In some systems, however, mate preferences may

specifically aim at reaching heterozygosity on the MHC and other important loci (Brown 1997, Wedekind and Füre 1997). Although there is a conceptual difference between such a mating system and inbreeding avoidance, in practice it is difficult to discriminate between these two types of mating preferences. The mechanisms that lead to heterozygosity on specific loci could have evolved to avoid inbreeding, and their effect on N_e may be about the same as the effect of inbreeding avoidance: in both cases the deviation from N_a would be small.

Some good genes models predict variable mate preferences and therefore differ from the original Hamilton and Zuk (1982) model, because an offspring's level of resistance would depend on the genetic contribution of both parents. At loci important for the host–pathogen interaction (e.g., immunogenes), certain combinations of alleles may be more beneficial than others. If individuals choose their mates to obtain such beneficial allele combinations, their preferred mate should vary according to their own genotype. Individuals with different resistance genes should then show different preferences, and there would be no universally valid order of sexual attractiveness with respect to signals that reveal heritable disease resistance or immunogenes (Wedekind 1994b). Wedekind and Füre (1997) specifically searched for evidence for such preferences but did not find any. Experimental evidence for such a mating preference was, however, provided by Rüllicke et al. (1998), who showed that gamete fusion depends on the MHC and on the presence or absence of mouse hepatitis virus. In the absence of further examples for such mate preferences, their relevance for conservation programs remains unclear. Nevertheless, this form of good genes sexual selection would lead to variable mate preferences. Hence, the variance in reproductive success would be low, and inbreeding would not increase much if one would allow free mate choice in small or captive populations.

Fisherian models of sexual selection, in which preferences exist for traits that are sexually attractive but do not reveal anything else, typically assume that females in a population have similar levels of preferences for male ornamental traits. These models therefore predict an increased variance in individual reproductive success and thereby a decrease in N_e .

Many of the preceding models of sexual selection predict rather uniform mate preferences, whereas a number of empirical studies provide evidence for genetic variability in female mate preference (review in Bakker and Pomiankowski 1995, Jennions and Petrie 1997). In real systems, different forms of sexual selection may act at the same time and interfere with each other. It is therefore difficult to make clear predictions in a given population about the effects of natural mate preferences on the variance in reproductive success

and on N_e . Moreover, the competition of members of the same sex for access to mating partners often interferes strongly with free mate choice. The combination of inter- and intrasexual selection leads to the mating system of a population and should have a strong impact on the life-history decisions of parents.

Parental Investment

Mate choice has often been shown to influence not only the genetics of offspring but also different kinds of parental life-history decisions, including offspring sex ratio, the timing of reproduction, and the amount of parental investment. Each one of these parental life-history decisions could potentially be manipulated.

Evolutionary theory predicts that parents should invest in each offspring according to the potential fitness return of that offspring (Fisher 1930). If, for example, the relative reproductive value of sons and daughters differs for different females or different males, sex allocation theory predicts that females should adjust the sex ratio of their offspring according to their own condition or according to their mate's attractiveness (Trivers and Willard 1973). If sex ratio adjustments led to an uneven population sex ratio, they would become important for conservation. Inbreeding and loss of genetic variation increase with any deviation from an even sex ratio because $N_e = 4N_mN_f / (N_m + N_f)$ (Hartl 1988). If the number of available eggs limits population growth, however, there are female-biased sex ratios that lead, in the longer term, to increased N_e and to population sizes that are safe against the Allee effect. Because there are a number of potential invasive and noninvasive methods to influence sex ratio, sex ratios could be optimized with respect to N_e and the long-term survival of a population (Wedekind 2002b).

Many birds and mammals with attractive mates increase their investment into their current offspring, probably decreasing their future reproductive potential. Parental investment conditional on mate quality is predicted from life-history theory (Williams 1966) and was first demonstrated in experiments and field studies that showed that females increase their investment into the current brood when mated with a preferred male (Burley 1982, Delope and Møller 1993, Petrie and Williams 1993). Increased parental effort may lower one's own survival and future reproductive potential (Saino et al. 1999).

Recent studies on birds have identified the mechanisms of these life-history decisions. Some female birds lay more eggs (Petrie and Williams 1993) or larger eggs (Cunningham and Russell 2000) after copulating with preferred males. In the latter case the females produced offspring of

better body condition when paired with preferred males. Gil et al. (1999) found that females deposit higher amounts of testosterone and 5 alpha-dihydrotestosterone in their eggs when mated to attractive males. In kestrel, maternal hormones influence offspring survival (Sackman and Schwabl 1999), and in canaries, chick social rank is positively correlated with concentration of yolk testosterone in the eggs from which they hatched, suggesting that the development of aggressive behavior of offspring may be modified by maternal testosterone (Schwabl 1993; Schwabl, Mock, and Gieg 1997).

The preceding examples are mostly from birds, but there is evidence that the effect exists also in other taxa. The tapeworm *Schistocephalus solidus*, for example, produced large eggs if given the opportunity to outbreed, but relatively small ones if forced to reproduce by selfing (Wedekind, Strahm, and Schärer 1998). There is even evidence that a somewhat comparable effect exists in humans: in some populations, the degree of MHC-similarity influences mate preferences (Ober et al. 1997, Wedekind and Furi 1997), and in one study, baby birth weight and weight of the placenta were negatively correlated to the degree of similarity of MHC-alleles between the parents (Reznikoff Etievant et al. 1991).

In species where male characteristics influence decisions about maternal investment, it may be possible to exploit the rules used by the females to determine the attractiveness of a given male. It is rather unlikely that the decision rule about whether a given male is perceived as attractive or not is entirely genetically fixed (Real 1991). In most species such a decision rule may be adaptable to a certain degree to a sampling template given by the population (Milinski and Bakker 1992). If, for example, females have a general preference for males with a red belly, then a male with a medium red belly might be perceived as very attractive in a population of (real or dummy) dull males, but as unattractive in a population of bright red males. To make the female invest much into the offspring of a medium red male in response to his attractiveness, it may be useful to avoid exposing her to bright red males before mating. Moreover, instead of changing the template a female uses to judge the relative attractiveness of a male, it may sometimes be possible to alter the attractiveness of the male directly, for example by cutting or attaching feather ornaments. However, it will often be necessary to test whether such an option for noninvasive manipulation exists in a given species.

Conclusions and Recommendations

Traditional methods in breeding programs normally attempt to avoid inbreeding (Montgomery et al. 1997, Bryant et al. 1999, Frankham 1999, Frankham et al. 2000), but breeding programs could potentially be further

optimized with respect to genetics. Apart from the general potential problems of supportive breeding programs that have been outlined here, details about the methods used in supportive breeding can also be crucial with respect to N_e . Imagine, for example, the situation in a fish hatchery where only the sperm of a few males was available to fertilize the eggs of many females. The skewed effective sex ratio would decrease N_e , which would decrease further if variance in male reproductive success was artificially increased by using different amounts of sperm from the few males available, or by using their milt sequentially, stripping the males' milt directly one after the other into the container that already holds all the eggs, and thereby giving the first males a reproductive advantage.

If we assume that all males are of equal genetic quality to all females, and if our only concern was a high genetic variation in the offspring, probably the best method for supportive breeding in fish hatcheries would be the following (analogous methods could be used in other breeding programs): (1) Catch a number of adults that result in a N_e of at least 50 (a rule of thumb, suggested by Ryman, Jorde, and Laikre 1999). (2) Catch an equal amount of males and females, or at least avoid using far fewer males than females because $N_e = 4N_mN_f/(N_m + N_f)$; that is, using only six males to fertilize the eggs of 20 females leads to an effective population size of less than 20! If, however, more males than females are available, they should all be used, regardless of the skewed sex ratio, because N_e in the captive population increases with every male used. (3) Pool and carefully mix equal amounts of sperm of all the males (using appropriate methods sperm can normally be stored for some hours), and use this mix to fertilize the eggs, either together (Billard 1985) or each female's batch separately. When fertilizing each batch separately, potential negative effects of swollen or broken eggs on the fertilization of healthy eggs would be avoided. Alternatively, combining the gametes of one male and one female could minimize potential negative effects of sperm interactions and restrict transmission of pathogens (Crim and Glebe 1990).

There are several possible methods to incorporate the fact that males normally vary in genetic quality and that female mate choice may take this variability into account.

1. Allowing free mate choice in monogamous or nearly monogamous species. Variance in reproductive success is lower in monogamous than in polygamous breeding systems. Therefore, N_e is not much affected by mate choice. Free mate choice may be beneficial for a number of reasons: inbreeding avoidance and hence reduced inbreeding depression, good genes

effects of sexual selection, and, possibly, increased parental investment of females (or males) with attractive mates.

2. Allowing for some degree of mate choice but keeping N_e as close as possible to the census population size, by avoiding high reproductive variance among the males and females of a population. Females should be presented to different males so that mate choice can happen, but if a few individuals become highly successful at the cost of the reproduction of others, the manager should remove them for part of the breeding season. In cases where presenting different males is not possible, mate preference tests of the type that have been used in behavioral research (Andersson 1994) may be considered. If, for example, odors are important in sexual communication, it may be possible to provide odor samples of different males and assess female reaction before bringing male and female together. Such behavioral tests could also be performed in advance of artificial insemination and other reproductive technologies often used in captive breeding programs (Gibbons, Durrant, and Demarest 1995; Dobson and Lyles 2000). Mate preference tests may increase the success of assisted reproductive technologies by reducing the risk of miscarriage (Wedekind 1994a).
3. Allowing free mate choice in nonmonogamous populations, disregarding the possibility that it may lead to high reproductive variance and hence lower N_e . The negative effect of increased inbreeding would then need to be compensated by the good genes effects of sexual selection. Comparing good genes effects in sexual selection with the effects of increased inbreeding coefficients is a challenge that requires good data and realistic models for different types of populations (see also, for example, Lacy 2000). It may therefore be too early to suggest a rule of thumb for conservation managers. Probably, the larger the population, the more likely that good genes effects will outweigh increased inbreeding coefficients caused by high reproductive variance. Although our knowledge of good genes effects on sexual selection is limited, it is probably reasonable to suggest that for small and medium-sized populations, free mate choice without any efforts to keep N_e close to the census size may be detrimental (Fiumera, Parker, and Fuerst 2000).

Summary

Sexual mixing of genes has two main evolutionary advantages; namely, that recombination followed by selection results in the efficient removal of deleterious mutations, and that it creates genetic diversity, which is important in evolutionary arms races, especially in host–pathogen coevolution. It may

therefore not be surprising that mating in nature is often not random with respect to genetics, and that it may often be linked to host–pathogen coevolution. Although nonrandom mate choice may affect the persistence of small populations, many population models and conservation breeding programs seem to ignore mate choice. Different kinds of sexual selection can have different consequences on the effective population size, N_e , and thereby affect the loss of genetic variability and heterozygosity over time. In some cases, supportive breeding programs may benefit from providing mate choice opportunities, which may sometimes promote offspring health and enable host populations to react to coevolving pathogens. In other cases, however, especially in small populations with high variance in reproductive success, natural breeding systems and free mate choice could have severe negative effects on the long-term survival chances of a population. In such cases, free mating should not be fully allowed, and natural breeding systems need to be manipulated to avoid an extensive reduction of N_e .

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15.

Measuring Individual Quality in Conservation and Behavior

Brian M. Steele and John T. Hogg

Individual variation in phenotype is ubiquitous across species and traits. When associated with traits related to individual fitness, such variation can, in principle, lead to population-level dynamics different from those predicted on the assumption that individuals do not vary, or in the absence of information on the full extent and nature of individual differences (Huston, DeAngelis, and Post 1988; Lomnicki 1988). Nonetheless, the practical value of considering individual variation in conservation programs has not been fully determined. This is partly because individual-based population models are a relatively recent addition to conservation's toolbox (Judson 1994). Another reason is that appropriate methods for the analysis of individual variation in natural populations have not been generally available. An appropriate method is one that partitions individual variation into its sources. This, in turn, requires statistical models that, although developed, have not been widely adopted in conservation and behavior. In this chapter, we present an introduction to the application of these models (referred to herein as generalized linear mixed models) for the analysis of individual variation in phenotype.

Individual variation has two fundamental components. To see this, consider that individuals vary in phenotype for many reasons. These include developmental stage, genetic architecture, environment, and the effects of purely stochastic processes (Williams 1992). These sources of variation differ, among other things, in the persistence of their phenotypic effects. Now consider a behavior or life-history event that is repeated at intervals over an individual's lifetime. At one extreme, genotype can affect every repetition of the trait in a consistent direction. At the opposite extreme, certain environmental influences might affect single repetitions in directions that are independent of the individual's performance in any past or future repetition. Other causes of individual variation (e.g., repairable injury) could influence more than one but not all repetitions in a consistent manner. "Individual quality" can be thought of as a measure of the extent to which individual differences in a specific phenotypic trait are due to genetic and environmental causes that have persistent versus transient phenotypic effects.

Under this definition, individual quality is similar to Kokko et al.'s (1999) notion of "propensity," and variation in individual quality is similar to Nunney's (1996) concept of fixed variation. Fixed variation, in Nunney's lexicon, originates from differences among individuals that are maintained throughout their lifetime, whereas random variation originates from non-age-related events that generate transient effects on the expression of a trait. To avoid confusion with the statistical meanings of fixed and random effects, we use *persistent* and *transient* rather than *fixed* and *random*, respectively, when referring to these two components of individual differences. We emphasize that these terms refer to the duration of the phenotypic effect rather than the duration of the condition or event giving rise to the effect. These durations can be very different. For example, an environmental cause of individual variation may operate only briefly yet have lifelong consequences for the affected individuals (e.g., food deprivation in early development).

The distinction between persistent and transient individual differences is relevant to both behavioral ecology and conservation science. For example, the extent to which males differ consistently and heritably in some aspect of performance is important to the "good genes" class of theories for the evolution of female mate choice (Andersson 1994). In conservation settings, persistent individual differences are under scrutiny for their effects on the likelihood of population extinction. Goss-Custard and Sutherland (1997) suggested that individual differences in resource acquisition provide a demographic buffer to extinction by directing mortality onto lower-quality individuals when resources decline. Similarly, Conner and White (1999) found that populations experienced lower rates of extinction when persistent individual heterogeneity in mean fecundity and survival was added to a demographic

model. The population genetic effects of persistent individual differences may have opposite consequences for population viability. By increasing individual variation in lifetime reproductive success, persistent differences may lower effective population sizes and accelerate the rate at which deleterious mutations are fixed by genetic drift (Nunney 1996). Transient effects on individual reproductive success, in contrast, contribute relatively little to variation in lifetime reproductive success because they tend to average out across individuals over lifetimes (Nunney 1996).

In both disciplines, the concept of individual quality is typically used as a theoretical or heuristic construct. The question of how to measure individual quality in field settings has received much less attention. This problem is similar to one faced by animal breeders wishing to identify, for example, the best sires for a particular breeding program and for which formal statistical methods have been developed. Of particular interest here are regression methods based on the generalized linear mixed model. Although mixed model analysis was first introduced over 40 years ago, conceptual subtleties and computational difficulties have until recently largely limited its application to clinical trials and applied quantitative genetics.

Our objective in this chapter is to develop a generalized linear mixed model approach to the measurement of individual quality in conservation and behavior. We begin with a description of statistical concepts and procedures. This section is fairly technical and may prove challenging for some readers. Therefore, we follow with three mixed-model analyses of longitudinal field data from two natural populations of Rocky Mountain bighorn sheep (*Ovis canadensis*). These examples are intended to illustrate the main statistical points in a less abstract way. Finally, we consider the practical interpretation of the “individual effects” predicted by these models and comment on the potential scope of application of generalized linear mixed models in conservation and behavioral ecology.

Statistical Models

We will use *generalized linear mixed model* to refer to regression models that allow for both fixed and random explanatory factors and are appropriate for the analysis of response variables having a variety of distributions including normal, Bernoulli, and Poisson. We use *linear mixed model* to indicate the special case of the generalized linear mixed model in which the response variable is normal in distribution. Because the linear mixed model has been more thoroughly developed than the generalized linear mixed model, we start with it.

Although the following presentation is for the most part general, we have framed it in terms of the measurement of individual quality. Thus we assume

that repeated measurements on some fitness-related trait are available for a set of recognizable individuals sampled at random from a population and that individual identity is included in the analysis as an explanatory (random) factor.

The Linear Mixed Model

We begin our discussion of the linear mixed model with a review of the ordinary linear model. The ordinary linear model specifies that the mean, or expected value of the response variable, is a function of one or more of the measured explanatory variables. It is often forgotten that one of the assumptions of the linear model is that the levels, or values, of each explanatory variable are fixed (i.e., chosen) by the researcher. When explanatory variables have fixed levels, such as in a designed experiment, they are referred to as fixed factors. Explanatory variables with levels that are not fixed in this sense are referred to as random factors because the observed levels are the result of a random process such as sampling.

To see the importance of the distinction between fixed and random factors, it is useful to concentrate on the origins of their levels. The levels of a fixed factor are finite in number, and in the control of the researcher, whereas the levels of a random factor are not under the control of the researcher and usually determined by a random mechanism such as sampling. For example, gender is a fixed factor with two levels, male and female. In a designed experiment, the researcher can ensure that equal numbers of male and female animals belong to each treatment group. In contrast, we generally cannot select individuals that are, say, better than the average individual by a particular amount. Instead, the quality of individuals is out of our control. If we think of each individual as a source of variation in the response variable, then individuals correspond to levels of a random factor, which we call identity. The identity factor accounts for persistent differences among individuals, and each level of identity is the difference between one particular individual and the average level of all sampled individuals. If a data set of this type is analyzed using the ordinary linear model by treating identity as a fixed factor, then any conclusions of a statistical nature (e.g., hypothesis tests) apply only to sampled individuals (observed levels). Hence, there is no opportunity for conducting formal statistical inference about the larger population, and the study must be considered anecdotal in nature. This limitation on the scope of inference can be remedied by using linear mixed model methods. Inferences drawn from a linear mixed model analysis using identity as a random factor apply to the sampled population of individuals.

The levels of a random factor are not repeatable. If a study is observa-

tional in nature and a factor is random, then we cannot exactly replicate the levels appearing in the sample by sampling again from the population. Often it is said that there are infinitely many levels of a random factor, and that the observed levels are a random sample from this population of levels. It is more practical, though, to say that a factor is random if there exists a population of levels from which the levels have been sampled, and the desired scope of inference is the sampled population.

With these concepts in mind, suppose that a demographic variable such as fecundity has been measured on each of q_1 animals over the course of q_2 years. A useful linear mixed model that identifies animal identity and years as random factors and age as a fixed factor is

$$Y_{ij} = \alpha_0 + \alpha_1 x_{ij} + b_{1,i} + b_{2,j} + \varepsilon_{ij}, \quad (\text{Equation 1})$$

where Y_{ij} is an observation on the demographic variable obtained from the i th animal for the j th year of the study, $i = 1, \dots, q_1$, $j = 1, \dots, q_2$, and x_{ij} is the age of the i th individual in year j . The parameters α_0 and α_1 are constant and age effect coefficients. Persistent differences between individuals are accounted for through the individual random effects $b_{1,i}$, $i = 1, \dots, q_1$. We assume the individual effects to be independent and normally distributed with mean 0 and variance γ_1 . Similarly, systematic differences between years are accounted for through the year random effects $b_{2,j}$, which are assumed independent and normally distributed with mean 0 and variance γ_2 . Residual variation is accounted for by the random errors ε_{ij} , also independent and normal with mean 0, but with variance σ^2 . The parameters γ_1 , γ_2 , and σ^2 are referred to as variance components. Because our interest lies in the population, it is critical to treat identity as a random factor. Years are also treated as random so that statistical inference is not limited to the observed years but to a longer span of time. The relative importance of individuals and years in explaining variation in the demographic rate variable can be assessed by comparing estimates of the variance parameters γ_1 and γ_2 . Equation (1) may be extended to allow $p - 1$ fixed factors by writing

$$Y_{ij} = \alpha_0 + \alpha_1 x_{ij,1} + \dots + \alpha_{p-1} x_{ij,p-1} + b_{1,i} + b_{2,j} + \varepsilon_{ij}.$$

The assumptions of independence and normality of the random effects and errors for this model are the same as for Equation (1). The extension to more than two random factors is straightforward, though the notation is troublesome. See Searle, Casella, and McCulloch (1992) for details.

When a linear mixed model is adopted, there is an implicit assumption that some observations are *not* independent. Specifically, two observations

are dependent if they are modeled as a function of the same random effect. Equation (1), for example, implies that observations made on the same individual in different years (Y_{ij} and $Y_{i,j+1}$) are correlated because both observations are modeled as a function of the same random effect $b_{1,i}$. Similarly, observations made on different individuals in the same year are correlated because year is a random factor. This correlation structure may be overly simplistic because the correlation between any pair of observations on an individual is assumed to be the same, regardless of how far apart in time the observations were made. However, the model is tractable computationally and conceptually, and a substantial improvement on the usual linear model. Diggle, Liang, and Zeger (1994) discuss a variety of models with more sophisticated correlation structures.

Parameter Estimation

The parameters of the linear mixed model are the fixed effects parameters $\alpha_0, \dots, \alpha_{p-1}$, and the variance components $\sigma^2, \gamma_1, \dots, \gamma_r$ where r is the number of random factors. For convenience, these parameters are collected in the parameter vector θ . The linear mixed model poses some computational difficulties for estimating θ , primarily because observations are not assumed to be independent. There are a variety of methods for parameter estimation, though the most commonly used method is maximum likelihood. Maximum likelihood estimators are popular because they are approximately normal in distribution, nearly unbiased, and have small standard errors (compared to other estimators) when the sample size is large. Moreover, methods of computing maximum likelihood parameter estimates and standard error estimates are tractable (though not necessarily simple). In brief, the maximum likelihood estimate $\hat{\theta}$ is the value of θ that is most consistent with the observed data in the sense that the likelihood of observing the actual data values is at its maximum *for a given probability model* (here normal but possibly Bernoulli, Poisson, etc. in the generalized linear mixed model). In contrast, ordinary least squares estimates are those estimates that minimize the sum of the squared differences between the observed data and the fitted data. Searle, Casella, and McCulloch (1992) and Longford (1993) discuss estimation methods for the linear mixed model.

Prediction of the Random Effects

In the statistical literature, the random effect b_i is said to be predicted rather than estimated. The term *estimation* is usually reserved for parameters, whereas b_i is a random variable. The term *prediction* is used because this task

is essentially the same as predicting a future observation, say, the future price of a commodity based on past pricing. The usual prediction method is best linear unbiased prediction (Searle, Casella, and McCulloch 1992). When the b_i 's represent individual effects, then the best linear unbiased predictor of the individual effect b_i is a weighted average of the linear mixed model residuals associated with the i th individual. The weights are determined in such a way that, if the model parameters were known, then the sum of the mean squared prediction errors for the b_i 's is minimized.

Hypothesis Testing and Confidence Intervals

The problem of inference for the linear mixed model is relatively straightforward for the fixed effects parameters $\alpha_0, \dots, \alpha_{p-1}$. Arguably, the most important inferential procedure is determining the significance of an individual explanatory variable, say, x_k . This is accomplished by testing whether α_k is 0 or not. Specifically, we test $H_0 : \alpha_k = 0$ versus $H_1 : \alpha_k \neq 0$ using the test statistic $Z = \hat{\alpha}_k / \hat{\sigma}(\hat{\alpha}_k)$ where $\hat{\sigma}(\hat{\alpha}_k)$ is an estimate of the standard error $\sigma(\hat{\alpha}_k)$. When the sample size is large, Z is approximately standard normal in distribution. Consequently, p -values and confidence intervals (Verbeke and Molenberghs 1997) for fixed effect parameters are readily obtained with statistical packages such as S-PLUS or SAS.

The significance of a random factor is assessed by testing whether the associated variance component is zero. Suppose that γ is the variance component of interest. A test of the hypothesis $H_0 : \gamma = 0$ against the alternative $H_1 : \gamma > 0$ is used to determine if the random factor is a significant source of variation in the response variable. If H_0 is rejected in favor of H_1 , then it is concluded that the random factor associated with γ accounts for some of the variation of the response variable. In the ordinary linear model analysis, an analysis of variance would compare the regression sums of squares with and without the factor in the model via an F -statistic. In a linear mixed model analysis, the likelihood ratio statistic $l = 2\log[L(\hat{\theta}_2; y) / L(\hat{\theta}_1; y)]$ compares the likelihood $L(\hat{\theta}_1; y)$ of the model without γ and with parameter estimate $\hat{\theta}_1$ to the likelihood $L(\hat{\theta}_2; y)$ of the model that includes γ and with parameter estimate $\hat{\theta}_2$. The distribution of the likelihood ratio statistic is somewhat unusual (see Verbeke and Molenberghs 1997). For example, if the linear mixed model contains a single random factor with variance component γ , then the distribution of l is approximated by a mixture of two chi-square distributions having degrees of freedom 0 and 1, respectively. An approximate p -value for this test is $p\text{-value} \approx \frac{1}{2}P(\chi_1^2 > l)$, if $l > 0$, and $p\text{-value} \approx 1$, if $l = 0$, where χ_1^2 denotes a chi-square random variable with 1 degree of freedom. Alternatively, Pinheiro and Bates (2000) suggest a conservative approximation

given by $p\text{-value} \approx P(\chi_1^2 > l)$. Khuri, Mathew, and Sinha (1998) discuss exact tests for specific linear mixed models.

The Generalized Linear Mixed Model

A limitation of the linear mixed model is that the random errors, or residuals, are assumed to be independent and normally distributed with a common variance σ^2 . Often, the residuals fail to meet these assumptions, and consequently, some or all of the parameter estimates and test statistics may be biased. A plot of the residuals against the fitted values is usually sufficient to detect failures of model assumptions. Draper and Smith (1998), Bryk and Raudenbush (1992), and Ramsey and Schafer (1997) discuss model checking and transformations. Certain types of data are not amenable to transformation. Two important cases are presence/absence data and counts that are dominated by small values (e.g., 50% or more of the counts are < 5). In the case of small counts, the distribution of the residuals from the fitted model is likely to be right-skewed, and not even approximately normal. A transformation yielding approximately normal residuals usually cannot be found when the plurality of observations is zero, and consequently, inferences derived from a linear mixed model analysis will be suspect. An example of such a response variable might be the number of offspring sired in a given year by individual males in a highly polygynous mating system.

Here we provide a brief discussion of models appropriate for response variables that are not normal. These models extend both the generalized linear and the linear mixed models, and hence, are named generalized linear mixed models. The generalized linear model (Dobson 1989, McCullagh and Nelder 1992, Fahrmeir and Tutz 1994) is used for a variety of response variables, but most importantly, for those that are binomial, multinomial, or Poisson in distribution. The generalized linear model specifies that some transformation of the mean, or expected value, of the response variable, say $\mu = E(Y)$, is a linear function of fixed explanatory variables x_1, \dots, x_{p-1} . We write the model as $k(\mu) = \alpha_0 + \alpha_1 x_1 + \dots + \alpha_{p-1} x_{p-1}$. The function k is called the link function, and the right-hand side of the model is called the linear predictor η , i.e., $\eta = \alpha_0 + \alpha_1 x_1 + \dots + \alpha_{p-1} x_{p-1}$. In the case of logistic regression, Y is assumed to be a Bernoulli random variable taking on the value of 1 with probability π , and 0 with probability $1 - \pi$. The expected value of Y is $\mu = \pi$, and k is known as the logistic function; thus $k(\mu) = \log[\mu/(1-\mu)] = \log[\pi/(1-\pi)]$. The probability of success can be recovered by computing $\pi = e^\eta/[1+e^\eta]$. Parameter estimation and hypothesis testing are accomplished by maximum likelihood methods, and there is a large literature

on practical aspects of generalized linear models. Most statistical analysis packages produce parameter estimates for the more common generalized linear models such as logistic and log-linear models.

The extension of the generalized linear model to the generalized linear mixed model is simple in principle: introduce random effects into the linear predictor. For example, we may model reproductive success of the i th female in year j by defining Y_{ij} to be 1 if at least one offspring survives 1 year, and 0 if not. The probability that $Y_{ij} = 1$ is π_{ij} , and we assume that Y_{ij} is a Bernoulli random variable with expected value $E(Y_{ij}) = \mu_{ij} = \pi_{ij}$. Moreover, we assume that there are persistent differences among individual females with respect to the likelihood of offspring survival. In this case, we assume that differences may be accounted for by independent random effects $b_i \sim N(0, \gamma)$, $i = 1, \dots, q$. A generalized linear mixed model of the response variable states that if b_i were known and included in the linear predictor, then Y_{ij} has a Bernoulli distribution, and the parameter π_{ij} is related to η_{ij} through the logistic link function. Mathematically, we write $Y_{ij} \mid b_i \sim \text{Bernoulli}(\pi_{ij})$ where $\log[\pi_{ij}/(1 - \pi_{ij})] = \eta_{ij}$ and $\eta_{ij} = \alpha_0 + \alpha_1 x_{1,ij} + \dots + \alpha_{p-1} x_{p-1,ij} + b_i$. The notation $Y_{ij} \mid b_i \sim \text{Bernoulli}(\pi_{ij})$ is shorthand for stating that Y_{ij} is conditionally Bernoulli in distribution given the b_i 's.

The application of the generalized linear mixed model is, however, complicated by the fact that, in the case of nonnormal response variables, there are no general and exact methods of computing maximum likelihood estimates of model parameters. Breslow and Clayton (1993), McCulloch (1997), and Steele (1996) provide approximate estimation methods. We use the approach proposed by Steele (1996) in our examples of the generalized linear mixed model (below). Although these methods often produce relatively unbiased estimates of parameters, standard errors, and confidence intervals for the fixed model coefficients $\alpha_0, \dots, \alpha_{p-1}$, tests of the variance components are not well understood and hence not currently available. The mixed model analysis of binary data presents some additional difficulties. The method of McCulloch (1997) produces unbiased maximum likelihood parameter estimates, yet the algorithm is both difficult to program and not widely available. Earlier methods, such as those proposed by Breslow and Clayton (1993) and Steele (1996) are somewhat simpler but also not widely available. Both algorithms are known to yield biased parameter estimates when applied to binary response variables (Shun 1997). Consequently, the binary response, generalized linear mixed model is at this time largely a theoretical model, though one holding substantial promise for future empirical application.

In the generalized linear model setting, a test of the hypothesis $H_0 : \alpha_i = 0$ against the alternative $H_1 : \alpha_i \neq 0$, where α_i is a fixed effect parameter, is best carried out using a likelihood ratio statistic (see McCullagh and Nelder

[1992] for details). As discussed previously, the likelihood ratio statistic l compares the likelihood of the model without α_i to the likelihood of the model that includes α_i . The likelihood ratio test statistic is well approximated by a χ^2_1 random variable when the sample size is large. The test may be extended to simultaneously test the significance of more than one parameter; if so, then the asymptotic distribution of l is chi-square where the degrees of freedom are the difference in numbers of parameters between the full and reduced models. In the generalized linear mixed model setting, we informally use this test statistic to assess the importance of a fixed effect. We use an informal treatment because the generalized linear mixed model parameter estimates are usually not exactly equal to the true maximum likelihood estimates, and, consequently, the large-sample approximation of the distribution of l by the chi-square distribution may not be very accurate.

Computation Aids

There are good procedures for linear mixed model analysis in several widely available statistical packages. We mention two because there are also detailed books dedicated to linear mixed model analysis using these packages. Specifically, the book by Verbeke and Molenberghs (1997) discusses linear mixed model analysis in SAS, and the book by Pinheiro and Bates (2000) discusses the use of S and S-PLUS for linear mixed model analysis. Computational support for mixed model analysis of nonnormal response variables is not well developed at this time. Because S-PLUS is widely used for research in the statistical community, some authors have made programs for computing generalized linear mixed model estimates available to other S-PLUS users. The SAS GLIMMIX macro for fitting generalized linear mixed models is also widely available. Finally, a set of GAUSS programs for linear and generalized linear mixed model estimation can be obtained from the GAUSS archives at www.american.edu/academic.depts/cas/econ/gaussres/regress/GLMM/GLMM.HTM.

The Generalized Linear Mixed Model and Individual Quality

Field studies in conservation and behavior frequently focus of necessity on small populations. Even when the population of interest is quite large, practical constraints may limit the number of individuals that can be recognized and studied in detail. Repeated measurements on individuals in such situations are possible and may be unavoidable. These considerations alone suggest wide applicability of the generalized linear mixed model in both conservation and

behavior. In many applications, the generalized linear mixed model may be helpful as a way of removing the effects of statistical dependence among repeated measurements and allowing evaluation of the effect of an ecological or other factor of interest. In contrast, when applying the generalized linear mixed model to estimate individual quality, one is primarily interested in statistics associated with the variables representing individual identity. For this application, repeated measurements are necessary assets rather than a potential complication.

We have chosen life-history traits relevant to individual-based, demographic models as a context for illustrating generalized linear mixed model analyses of individual quality. In this setting, it is not so much the variance component associated with individual identity that is of interest, but the distribution of individual random effects. This is because these demographic models introduce variation in demographic rates by incrementing some base rate by an amount appropriate to each individual's circumstance (e.g., see Harris and Allendorf 1989). In the case of differences due to identity, this increment is assigned at birth and drawn from some specified distribution of increments (Conner and White 1999). The generalized linear mixed model is well suited for providing a data-based estimate of this distribution; the (persistent) effects of identity are predicted as individual-specific deviations from a population mean once the independent effects of other variables are accounted for. Although the conceptual relevance of the individual effects is particularly clear in this context, the generalized linear mixed model has not, to our knowledge, been previously applied to problems of this kind.

Equation (1) is a suitable framework for assessing most, if not all, of the four sources of process variation affecting demographic performance (individuality, environmental change in time and space, and stochasticity) (Akçakaya, Burgman, and Ginzburg 1999). This model explicitly addresses (1) individual variation due to developmental stage (age) and persistent phenotypic differences (identity), (2) temporal variation in the environment (year), and (3) variation due to demographic stochasticity. The latter is part of the unexplained variation represented by the error term. Spatial variation in the environment is not explicitly addressed. However, to the extent that there is population-wide competition for better sites, and individuals vary consistently in competitive ability, spatial variation in demographic performance may be reflected in the individual effects.

A model such as Equation (1) does not provide insight into the causes of persistent individual differences. It merely provides a basis for allocating variation in the response variable to persistent differences versus all other terms in the model, including residual, or unexplained, variation. When identifying specific causes of persistent variation is of interest and the

relevant field measurements are available, it might seem straightforward to test a plausible explanatory factor (inbreeding coefficient, territory quality, social dominance, etc.) by adding it to the regression and testing for significance. However, if an added variable can change value during an individual's lifetime (e.g., territory quality), it may test significant because it is a source of persistent individual differences or because it is a source of transient individual differences. These cases might be distinguished by examining changes in variance components. The variance component for identity should decline relative to the basic model in the first case, whereas the variance component for the error term should decline in the second. The important point in the present context is that, when an added variable is a source of differences in individual quality, individual effects predicted by the more elaborate model are no longer measures of individual quality. Rather, they are measures of residual individual quality. Similar comments apply in the case of attempts to identify the specific causes of random year effects.

Response Variables

In a demographic context, the ideal response variables for which to obtain estimates of individual quality are fertility, fecundity, and survivorship. Because many species of conservation concern have extended periods of parental care, it may often be appropriate to also consider the survivorship of dependent young as a function of the individual quality of one or both parents rather than that of the offspring. In sufficiently long-lived species, fertility, fecundity, and offspring survival are subject in principle to repeated measurement as required for the estimation of individual effects in a generalized linear mixed model framework.

Modeling individual heterogeneity in survival probabilities poses fundamental difficulties associated with the fact that individuals may meet (survive) many environmental challenges but can die only once. Consequently, there is no opportunity to collect more than one observation of failure on any individual, and no possibility of using generalized linear mixed model analysis to estimate the proportion of variation in survival attributable to individual quality. Conner and White (1999) suggested that one might circumvent this problem by identifying traits that correlate with survival and then sampling individual adjustments of survival probabilities from a distribution modeled on that of the surrogate trait. They further suggested that age-specific size may often be an appropriate surrogate trait and developed an example based on the result from Bartmann, White, and Carpenter (1992) that over-winter survival of mule deer (*Odocoileus hemionus*) fawns was correlated with fawn weight at the beginning of winter.

The problem with this method is that it does not utilize repeated measures and hence cannot establish the extent to which individual variation in the surrogate trait reflects persistent versus transient individual differences. In the mule deer example, individuals were weighed once as fawns. Variation in fall fawn weight was then some unknown mix of persistent and transient sources of individual variation. It follows that this method also cannot establish or estimate persistent individual heterogeneity in survival probability. A generalized linear mixed model version of Conner and White's suggestion is to estimate individual effects for the surrogate trait and then sample individual-specific adjustments of survival probability from a distribution modeled on that of the *individual effects* estimated for the surrogate trait.

Examples

We will illustrate the application and interpretation of the generalized linear mixed model in a demographic context with three data sets from a field study of bighorn sheep. In each example, we develop a model based upon Equation (1) and tailored to the response variable of interest. Estimates of the parameter vector, random effects, and likelihoods were, in all cases, obtained using GAUSS programs written by B. Steele.

Normal Response Variable: Breeding Date

We begin with the relatively straightforward case of traits with the normal distribution. Traits reflecting overall physiological condition (quality) should often approximately follow a normal distribution because they summarize success across many independent, fitness-related activities. For our example, we have chosen annual date of first breeding by bighorn females. Females of many mammalian species are known to breed earlier when in better nutritional condition (Mitchell and Lincoln 1973, Frisch 1984, Byers and Hogg 1995).

A linear mixed model analysis of individual breeding date predicts timing of breeding for the i th animal in year j , given random effects $b_{1,i}$ and $b_{2,j}$ accounting for differences among individuals and among years. The conditional mean is denoted by $\mu_{ij} = E(Y_{ij} \mid b_{1,i}, b_{2,j})$. Our model of μ_{ij} involves parameters $\alpha_0, \alpha_1, \alpha_2$ and variables $x_{1,ij}, x_{2,ij}$ observed on the i th animal in year j . Specifically, the model is

$$\mu_{ij} = \alpha_0 + \alpha_1 x_{1,ij} + \alpha_2 x_{2,ij} + b_{1,i} + b_{2,j}, \quad (\text{Model 1})$$

where $x_{1,ij}$ is a dummy variable identifying whether the i th animal in year j is a member of the 1-year-old age class, and, similarly, $x_{2,ij}$ is a dummy variable identifying membership in the 3-year or older age class. Females in our study population typically had a first estrus at 1 year of age. Thus, these age classes, and the reference 2-year-old age class, generally indicate first-time breeders (age 1 year), second-time breeders (age 2 years), and veteran breeders (age ≥ 3 years). The random effects are assumed to be realizations from independent normal distributions with means 0 and standard deviations σ_1 and σ_2 .

Copulation may occur over a period of 2 or more days in bighorn. Therefore, we used the day of ovulation to represent breeding date, assumed that ovulation occurred on the last day of behavioral estrus (Hogg, Hass, and Jenni 1992), and measured ovulation date categorically as the number of days from November 1 to the ewe's final day of estrus. We obtained a total of 464 measurements on 118 ewes from the Sheep River (Alberta) population in the period from 1989 to 2000. The average individual was measured for ovulation date 3.9 times. However, one and two observations were most frequent (Fig. 15.1).

A summary of regression results is given in Table 15.1. The interpretation of the fixed effect coefficients is straightforward. They are the advance (if negative) or delay (if positive) in ovulation date, measured in days, relative to the reference age category (here 2 years). There is no comparable coefficient summarizing the effect of the two random factors because the effect of each individual and year on ovulation date is assumed to be different; that is, the random effects have a distribution rather than a value. The distribution of the individual-specific coefficients (effects) for the 118 ewes

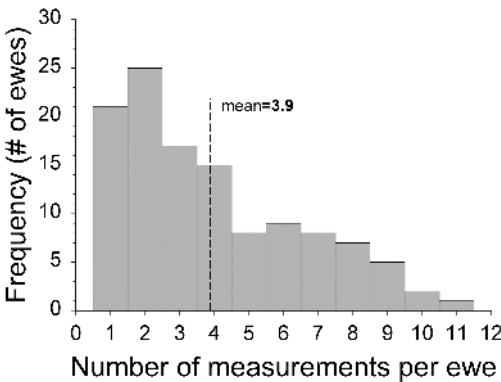


FIG. 15.1. Frequency distribution of the number of years in which individual bighorn ewes were measured for date of first ovulation. A total of 464 such measurements were obtained on 118 different ewes.

TABLE 15.1. Summary of a linear mixed model analysis of ovulation date as a function of ewe identity, ewe age, and year.

	COEFFICIENT	SD ¹	SE ¹	TEST STATISTIC ²	df	p-VALUE
Fixed effects						
Ewe age						
1 year	9.30	—	1.48	6.27	—	< 0.001
≥ 3 years	−2.53	—	0.57	−4.41	—	< 0.001
Intercept	32.55	—	0.90	—	—	—
Random effects						
Ewe identity	—	3.33	0.30	121.11	1	<< 0.001
Year	—	2.31	0.53	81.32	1	<< 0.001
Residual	—	3.45	0.13	—	—	—

¹Estimated standard deviations and errors.²Z for fixed effects and *t* for random effects.

in this sample is presented in Figure 15.2. Individual and year-specific effects may be interpreted similarly to the fixed effect coefficients. They are estimates of the individual and year-specific advance or delay in ovulation date, again measured in units of days. Figure 15.2 shows that the predicted random effects for identity are symmetrically distributed about zero. This indicates that our use of the normal as a model for the random effects distribution was appropriate.

A simple way to evaluate the overall (versus year or individual-specific) contribution of the random effects to total variation in the response variable is to compare standard deviations (see Table 15.1). For example, we can say that, roughly speaking, the average (absolute) effect of identity on ovulation date (3.3 days) exceeded that for year (2.3 days) and was comparable to the average (absolute) residual effect (3.4 days). Similarly, the average (absolute) effect of identity (3.3 days) exceeded the fixed effect attributable to development from age 2 years to the age class 3 years and older (2.5 days) but was one-third of that associated with development from 1 to 2 years of age (9.3 days).

In Table 15.1, we also present the results of the approximate test of significance for random factors. Recall that this test involves calculating log likelihoods for the model with and without the random factor of interest (here identity then year), calculating an (approximate) chi-square test statistic equal to twice the absolute difference in these likelihoods, and then dividing the associated probability by 2. Taken together, the results shown in Table

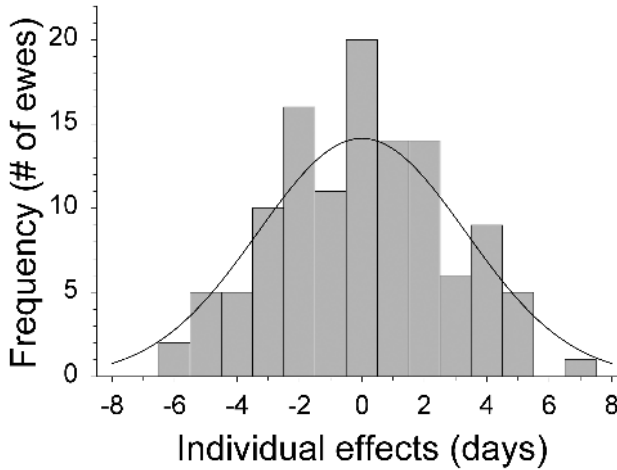


FIG. 15.2. Frequency distribution of individual effects on date of first ovulation for 118 bighorn ewes as predicted by linear mixed model regression. Histogram bins include the midpoint ± 0.5 days. The superimposed curve gives expected frequencies under the assumption that the individual effects are normally distributed with mean zero and standard deviation equal to the observed value (3.33).

15.1 provide strong evidence for large persistent individual differences in breeding date in bighorn. Excepting early development, persistent individual differences were the primary source of explained variation in ovulation date in this model, in this population, and over this time period. This is not an obvious outcome. For example, the year effects reflect the cumulative impact of temporal changes in the environment, and it would be reasonable to expect relatively large environmental influences in the case of a condition-dependent trait like breeding date.

Poisson Response Variable: Annual Male Reproductive Success

For polygynous mating systems, it may often make sense to model male reproductive success as a Poisson random variable, particularly when the expected number of offspring per male tends to be small (e.g., five or fewer). Both the number of offspring and the Poisson response variable are nonnegative counts. Moreover, although normalizing transformations, such as the square root or natural logarithm (Ott and Longnecker 2000), are often successful with count data, they will not be effective if a substantial number of the counts are zero as would be expected with a high degree of polygyny.

A Poisson generalized linear mixed model for male reproductive success

models the expected number of successful matings for the i th animal in year j , given random effects $b_{1,i}$ and $b_{2,j}$; accounting for differences among individuals and among years, respectively. The conditional mean is denoted by $\mu_{ij} = E(Y_{ij} | b_{1,i}, b_{2,j})$. It is assumed that μ_{ij} is related to the linear predictor η_{ij} through the natural logarithm of μ_{ij} ; that is, $\eta_{ij} = \log(\mu_{ij})$. The model of η_{ij} involves parameters α_0 , α_1 and α_2 , and variables x_{ij} and x_{ij}^2 observed on the i th animal in year j . Here, x_{ij} is ram age in years and x_{ij}^2 is ram age squared. This model allows the effect of age to follow a quadratic function, including one in which maximum reproductive success occurs at less than maximum age. Mathematically, the model is

$$\eta_{ij} = \alpha_0 + \alpha_1 x_{ij} + \alpha_2 x_{ij}^2 + b_{1,i} + b_{2,j}. \quad (\text{Model 2})$$

Finally, the random effects are assumed to be independent observations from normal distributions with mean 0 and standard deviations σ_1 and σ_2 . Coltman et al. (2002) used a similar regression equation to analyze annual male reproductive success but did so in a linear mixed model framework. Parameter estimates for a Poisson model may be computed using any one of several methods (Breslow and Clayton 1993, Lee and Nelder 1996, Lin and Breslow 1996, and Steele 1996). We used Steele's (1996) method.

To illustrate the application of Model (2) in estimating persistent individual differences in male reproductive success, we will use a data set composed of paternity assignments for 83 bighorn lambs conceived during nine breeding seasons (1988–1996) on the National Bison Range (Montana). Fathers for these lambs were identified by genetic exclusion using multilocus microsatellite genotypes (Hogg and Forbes 1997). Estimates of annual reproductive success were obtained for 43 rams measured in an average of 4.3 different years (range 1–9 years). When totals for all 9 years are considered, it is clear that there was large individual variation in success (Fig. 15.3). The two most successful rams fathered 21 lambs in this period, whereas almost half of the remaining 41 rams fathered none. However, some, and potentially all, of these differences could be attributable to the fact that rams were often measured at different ages and for different numbers of years. Thus, whereas the pattern in Figure 15.3 leaves open the possibility of large differences in individual quality regarding male competitive ability, it does not demonstrate or estimate such differences.

The results of a generalized linear mixed model analysis of these data using Model (2) are presented in Table 15.2 and Fig. 15.4. We can interpret the fixed and random effects on both the natural logarithm and the original count scales. The interpretation on the natural logarithm scale is the same as when a linear mixed model is used, except that the random effects are modifying the natural logarithm of the expected number of paternities rather

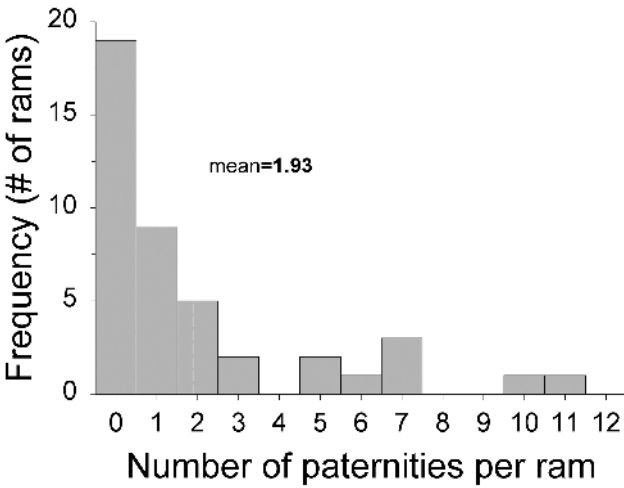


FIG. 15.3. Frequency distribution of the number of offspring conceived by 43 bighorn rams during a 9-year period (1988–1996).

than the expected number of paternities. The entries in Table 15.2 are on the natural logarithm scale. If it is desirable to examine the random effects on the original count scale, though, we compute the antilogarithm of the predicted random effects. To see the implications of this, consider that taking the antilogarithms of the left- and right-hand side of Model (2) and factoring the right-hand side yields $\mu_{ij} = \exp(\alpha_0 + \alpha_1 x_{1,ij} + \alpha_2 x_{2,ij} + b_{2,j}) \exp(b_{1,i})$.

TABLE 15.2. Summary of a generalized linear mixed model analysis of annual male reproductive success as a function of ram identity, ram age, and year. The response variable was assumed to be Poisson, given random effects for identity and year.

	COEFFICIENT	SD ¹	SE ¹	TEST		
				STATISTIC ²	df	<i>p</i> -VALUE
Fixed effects						
Ram age				15.83	2	—
Age	0.57	—	0.19	—	—	—
Age ²	−0.03	—	0.01	—	—	—
Intercept	−2.98	—	0.58	—	—	—
Random effects						
Ram identity	—	0.72	0.19	—	—	—
Year	—	0.03	0.07	—	—	—

¹Estimated standard deviations and errors.

² / for fixed effects; not available for random effects.

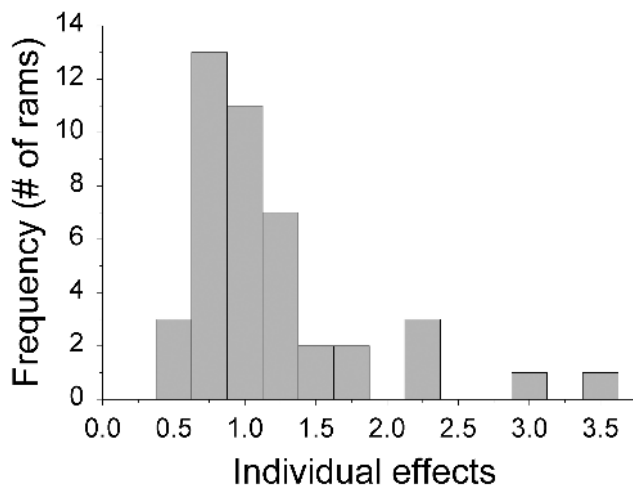


FIG. 15.4. Frequency distribution of individual effects on annual male reproductive success for 43 bighorn rams as predicted by generalized linear mixed model regression. Individual effects in this figure modify the expected number of paternities (see text). Thus a value of 1.0 indicates no effect of individual identity on reproductive success. Histogram bins include the midpoint ± 0.125 units.

This shows that $\exp(b_{1,i})$ is a multiplicative term expressing the extent to which male i differs from a typical male. Male i is typical with respect to reproductive success if $b_{1,i} = 0$, because $\exp(0) = 1$. Similarly, if $b_{1,i}$ is substantially larger than 1, then male i is regarded as more successful at reproducing than the typical male by a factor equal to its individual effect.

In our data set, annual male reproductive success was a nonlinear function of age (see Table 15.2). Maximum success occurred at 9 or 10 years of age and declined thereafter. The year random factor functioned primarily to account for annual variation in the number of lambs assigned to fathers. Because this variation was small, year effects were negligible (see Table 15.2). In contrast, individual effects varied substantially; values on the original count scale ranged from 0.51 to 3.48 (see Fig. 15.4). Thus the highest-quality male was predicted to be 3.48 times as successful as a typical male at each age (and seven times as successful as the lowest-quality individual). A formal test of significance is not available in the Poisson case. However, this level of variation in predicted individual effects is consistent with a conclusion that biologically significant differences in quality were present in this sample of rams, particularly when one considers that the multiplicative individual effects apply at each age and can therefore sum to large absolute differences in lifetime reproductive success. For example, we can estimate the difference in

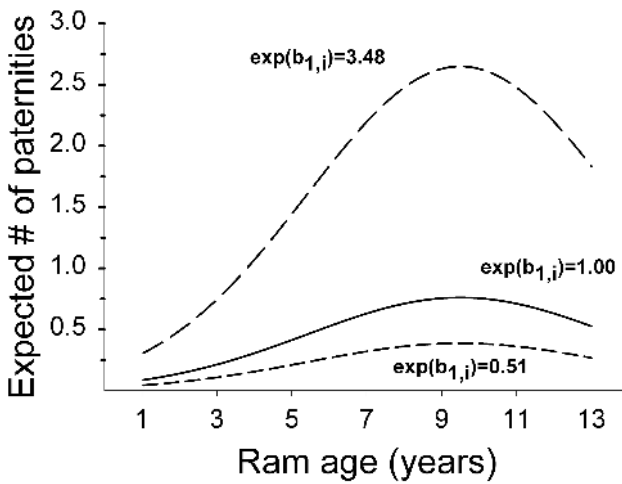


FIG. 15.5. Expected annual male reproductive success as a function of ram age for the typical [$\exp(b_{1,i}) = 1.00$], highest-quality [$\exp(b_{1,i}) = 3.48$], and lowest-quality [$\exp(b_{1,i}) = 0.51$] rams in the National Bison Range data set (Fig. 15.4). Expected success was calculated as $\mu_{ij} = \exp(-2.98 + 0.57 \times 1_{ij} - 0.03 \times 2_{ij} + b_{2,j}) \exp(b_{1,i})$ (see text for derivation). Year effects ($b_{2,j}$) were set to zero and fixed effect coefficients are from Table 15.2. The scale of the y-axis reflects the average annual number of lambs assigned paternity (9.2; SD = 1.4).

expected lifetime reproductive success for the highest- versus lowest-quality individual in this data set as the sum of the difference in annual reproductive success at each integer age (Fig. 15.5). Although the maximum difference in expected annual reproductive success was only two offspring, the difference in expected lifetime reproductive success was 16 on the assumption both individuals lived 13 years and total lamb production stayed at approximately 10 per annum (see Fig. 15.5). In the context of individual-based demographic models, multiplicative individual effects are functionally equivalent to the additive individual effects obtained in the normal case and can be readily used to increment average probabilities of paternity.

Binary Response Variable: Annual Female Reproductive Success

In this last example, we illustrate the application of the generalized linear mixed model to binary demographic data, specifically annual reproductive success among bighorn ewes. We measured female success as the number of

offspring alive in the fall of year 1 (0.5 years postpartum) when lambs are typically weaned and, alternatively, in the fall of year 2 (1.5 years postpartum) when reproductive maturity is typically reached. Bighorn litters are almost invariably singletons so these numbers are either 0 or 1 in practice. Female infertility was not distinguished from offspring mortality in these data. However, the former is uncommon relative to the latter in this population (Festa-Bianchet 1988b; Bérubé, Festa-Bianchet, and Jorgenson 1999), particularly at those ages (4–15 years) constituting the bulk of our sample. Thus, although reproductive success in this case is technically a combination of three demographic rates (fertility, fecundity, and offspring survival), differences in success among females were largely due to differences in offspring survival.

The generalized linear mixed model for annual female reproductive success models the probability of success (offspring counted alive) for the i th animal in year j , given random effects $b_{1,i}$ and $b_{2,j}$ accounting for differences among individuals and among years. The conditional probability is denoted by $\pi_{ij} = P(Y_{ij}=1 \mid b_{1,i}, b_{2,j})$. It is assumed that π_{ij} is related to the linear predictor η_{ij} through the log-odds of π_{ij} ; that is, $\eta_{ij} = \log[\pi_{ij}/(1-\pi_{ij})]$. Similar to the Poisson model of male reproductive success, η_{ij} involves parameters $\alpha_0, \alpha_1, \alpha_2$ and variables $x_{1,ij}, x_{2,ij}$ observed on the i th animal in year j . Specifically, the model is

$$\eta_{ij} = \alpha_0 + \alpha_1 x_{1,ij} + \alpha_2 x_{2,ij} + b_{1,i} + b_{2,j}, \quad (\text{Model 3})$$

where $x_{1,ij}$ is a dummy variable identifying whether the i th animal in year j is a member of the 2-year-old age class, and, similarly, $x_{2,ij}$ is a dummy variable identifying membership in the 4-year and older age class. These age classes, and the reference 3-year-old age class, generally reflect first-time mothers, second-time mothers, and veteran mothers. The random effects are assumed to be realizations from independent normal distributions with mean 0 and standard deviations σ_1 and σ_2 .

It is difficult to obtain unbiased parameter estimates for generalized linear mixed models involving binary response variables. We used Steele's (1996) method for purposes of illustration. The reader should recognize that parameter estimates obtained with this and other approximate methods should not be used for formal inference and that, without unbiased parameter estimates, formal statistical analysis of the predicted random effects is unwarranted.

The data set consisted of 574 (0.5 years) and 563 (1.5 years) measurements of reproductive success obtained from 1989 to 2000 for 127 different ewes in the Sheep River (Alberta) population. The average number of repeat

TABLE 15.3. Summary of a generalized linear mixed model analysis of annual female reproductive success (measured 0.5 and 1.5 years postpartum) as a function of maternal age, maternal identity, and year. The response variable was assumed to be Bernoulli given random effects for identity and year.

	0.5 YEARS POSTPARTUM			1.5 YEARS POSTPARTUM		
	Coefficient	SD ¹	SE ¹	Coefficient	SD ¹	SE ¹
FIXED EFFECTS						
Maternal age						
two years	-1.65	—	0.45	-1.68	—	0.66
≥ four years	0.77	—	0.29	0.74	—	0.37
Intercept	-0.45	—	0.29	-1.70	—	0.42
RANDOM EFFECTS						
Maternal identity	—	0.50	0.17	—	0.78	0.17
Year	—	0.35	0.13	—	0.67	0.20

¹Estimated standard deviations and errors.

measures per female was 4.5 (range = 1–12) at 0.5 years postpartum and 4.4 (range = 1–12) at 1.5 years postpartum. The analysis of these data using Model (3) is summarized in Table 15.3. The interpretation of the fixed and random effects in this case can be based on the log-odds model of μ_{ij} , so that $b_{1,i}$, say, expresses the difference between the i th animal and the population mean with respect to the log-odds of survival. The entries in Table 15.3 are on this scale. A simple transformation from log-odds to the probability of success scale is not available, though the following loose interpretation may be helpful. Suppose that the fixed effect portion of the linear model is 0; that is, $0 = \alpha_0 + \alpha_1 x_{1,ij} + \alpha_2 x_{2,ij} + \alpha_3 x_{3,ij}$, and $b_{2,j} = 0$. Then, $\eta_{ij} = b_{1,i}$, which implies that $\pi_{ij} = [1 + \exp(-b_{1,i})]^{-1}$. Note that if $b_{1,i} = 0$, then $\pi_{ij} = \frac{1}{2}$, and the difference $\frac{1}{2} - [1 + \exp(-b_{1,i})]^{-1}$ roughly expresses the quality of the i th female relative to the typical female in terms of the probability of reproductive success.

Cumulative relative frequencies for each set of (transformed) individual effects predicted by Model 3 are given in Figure 15.6. The general shape and horizontal location of these distributions show that the individual effects on reproductive success at 0.5 and 1.5 years were, in each case, approximately normally distributed with mean zero. Their shapes relative to each other indicate that differences in individual quality among females were markedly greater when reproductive success was measured at 1.5 versus 0.5 years (see

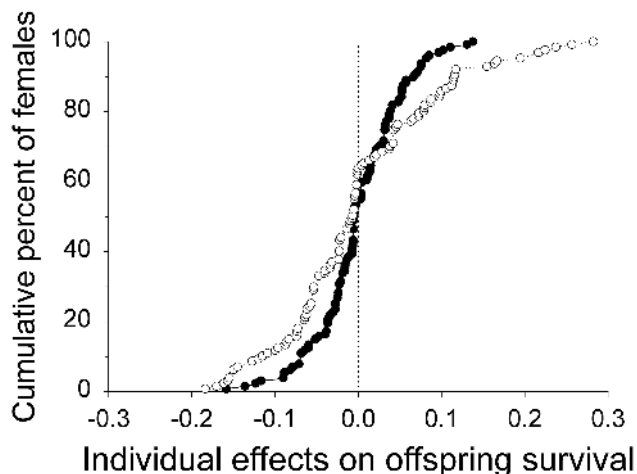


FIG. 15.6. Cumulative relative frequency of individual effects on annual female reproductive success as predicted by generalized linear mixed model regression for success measured at 0.5 (black circles) and 1.5 (white circles) years postpartum ($n = 127$ females). The (approximate) individual effects are expressed in terms of increments in the probability of success relative to the typical female (see text).

also Table 15.3). Roughly 25% of the individual effects on success at 1.5 years were greater than 0.10 or less than -0.10 , whereas only 6% of the individual effects on success at 0.5 years were this extreme (see Fig. 15.6). The same pattern was evident in the predicted year effects; between-year variation in recruitment to 1.5 years was twice that to 0.5 years (see Table 15.3). Larger predicted individual effects at 1.5 years are not easily explained as simply more time for the effects of differences in maternal quality to accumulate. Offspring were under direct maternal care in the first time period but not the second, and a substantial majority of offspring mortality in this sample (68%) occurred during the first time period.

It is more plausible that the increase signals a qualitative change, associated with the onset of winter, in the interaction between maternal differences and the environment. Climatic conditions are generally benign between birth and weaning, whereas even the largest and most vigorous lambs are relatively small and vulnerable to predation for much of this time. It makes sense that offspring mortality under these conditions would be more subject to chance (e.g., encounters with predators) and relatively independent of maternal characteristics or annual variation in seasonal climate. On the other hand, lamb survival during the first winter in this population is known to be

strongly dependent on fall body mass (Festa-Bianchet et al. 1997), perhaps because larger (fatter) lambs are better buffered against temperature extremes and less affected by poor forage quality. Thus, to the extent that mothers differ consistently with respect to the rate at which they provision lambs during gestation and prior to weaning, or in heritable traits that affect the early growth rate of offspring, one would expect the effects of maternal quality to be more telling and evident during winter (especially severe ones) even though maternal investment has ceased and fewer lambs may die. The details of this interpretation aside, the general point is that differences in individual quality, even for a fixed set of individuals, may not be equally apparent in different environments.

Practical Interpretation of Individual Effects

With these examples in mind, three points should be emphasized regarding the practical interpretation of individual effects that are intended as estimates of individual quality. First, as with any sample-based estimate, variation in the predicted individual effects reflects both sampling and process variation. Sampling variation is a function of sample size at two levels: the number of measurements per individual and the number of individuals for which repeated measurements are available. It is not possible to generalize about minimum sample sizes for a generalized linear mixed analysis of individual differences. Much will depend on the trait of interest. Relatively few repeat measures (e.g., 2–3) may be adequate for simple traits or traits that are relatively insensitive to external influences. For complex traits, or traits subject to many environmental influences, good estimates of mean within-individual performance may require substantially more repeated measurements. Similarly, we can speculate that fewer repeat measurements will be required for organisms with simple life histories (e.g., a small number of growth stages) than for those with more complex patterns of growth and development. Finally, when forced to choose between obtaining more repeat measurements and sampling more individuals, it may be helpful to consider environmental heterogeneity. Other things being equal, high spatial heterogeneity should favor larger (and more broadly distributed) samples of individuals, whereas high temporal heterogeneity may indicate a priority for larger numbers of repeat measurements (see point three following here).

Second, single, or relatively few, measurements will be common even in very long-term studies. Small individual sample sizes arise in longitudinal studies for several reasons. Some individuals may survive only one or a few time periods, whereas others will be old at the beginning of the study or born near its end. There also may be data missing. The generalized linear mixed

model predicts an individual effect for all individuals in the sample, even those measured a single time. Despite the fact that such predictions will usually be improved by more repeat measurements, it is not necessarily a good idea to exclude individuals measured fewer than some threshold number of times. To the extent that low-quality individuals survive for markedly fewer repetitions of the focal trait, such filtering may differentially remove low-quality individuals and lead to underestimation of the variance in individual quality. This type of bias may be unavoidably present if low-quality individuals often fail to survive for even one measurement of the trait. Note that individual effects predicted for relatively short-lived individuals, even when based on measurements over that individual's entire life span, should still be thought of as estimates of a quality parameter that would be better revealed by more years of data.

Finally, the distribution of individual quality is not likely to be a species- or even population-specific trait. Individual variation in performance is apt to be highly conditional on social and ecological environments. In particular, we should expect that this variation will be greater in more competitive social situations and under more severe ecological conditions (as we suggested for maternal quality in bighorn). More demanding environments may be required to expose and amplify relatively small phenotypic differences (Keller et al. 1994). This consideration may limit the generality of a given set of estimates for demographic models. However, it suggests another potential use for generalized linear mixed model analysis of fitness-related traits in conservation—that of identifying stressed populations and monitoring populations for deteriorating conditions.

Conclusions and Recommendations

The generalized linear mixed model should be considered whenever repeated measurements on recognizable individuals constitute a substantial fraction of a sample of measurements. Mixed model analysis is mandatory when, in addition, study objectives include (1) drawing conclusions about trait-specific individual effects for the population versus sample of individuals, and (2) obtaining formal estimates of the fundamental components of individual variation (e.g., individual quality).

When the latter objectives apply, field biologists, contrary perhaps to their intuition, should covet and actively seek repeated measurements on marked or otherwise recognizable individuals. The inevitability of incomplete individual records in longitudinal field studies guarantees that the average number of measurements per individual will be lower, perhaps much lower, than the number of sampling intervals (e.g., years) over which measurements have

been obtained. Thus individual sample sizes should be monitored carefully. Generally speaking, more repeat observations will be helpful.

Once repeated measurement data are in hand, it is well worth exploring normalizing transformations (if such are indicated) to stay within a linear mixed model framework. The advantages of a linear mixed model approach include well-established methods for analysis and interpretation, widely available software, and straightforward significance tests for random factors. If, however, such transformations do not work, one should not be overly concerned about the limitations of the generalized linear mixed model regarding hypothesis testing. It may still be possible to make judgments about the biological significance of a given variance in individual effects by, for example, extrapolating the lifetime or population-level consequences of the predicted effects. In addition, some insight into biological significance may often be gained by examining the extent to which fixed factor parameters (or other variance components) change when the identity random factor is dropped. Finally, if a given set of individual effects can be shown to be informative in some subsequent analysis, then we may regard this as informal evidence of biological significance. For example, a negative correlation between individual effects on annual male reproductive success and inbreeding coefficient would suggest that the predicted individual effects reflect real (genetic) differences among males.

We encourage investigators to make full use of the predicted individual effects. The further analysis of these random variables should often be rewarding. Important potential applications in conservation and behavior include (1) investigation of the genetic or ecological sources of variation in individual quality and (2) evaluations of the population-level consequences of persistent versus transient individual differences.

Summary

The generalized linear mixed model provides a powerful framework in which to formally evaluate the nature and magnitude of individual differences. We have emphasized an application in demographic models of population persistence. However, the study of individual differences and adaptive strategy in individual behavior is a central activity of behavioral ecology. Behavioral ecologists may find many conceptually distinct applications for such methods in empirical studies of behavioral strategy and, given growing interest in the population-level effects of individuality in conservation, important new applications at the interface of conservation and behavior.

The generalized linear mixed model can be applied for one or more of three reasons. First, it may be necessary to account for lack of independence

arising from repeated measurements on individuals in order to evaluate the effect of an ecological variable of interest. Second, it may be of interest to evaluate variance components for the contribution of persistent individual differences to variation in the response variable. Finally, an investigator may desire predictions of an individual quality random variable for use (like any other individual-specific measurement) in some further analysis. The latter may be the most far-reaching and unappreciated use of the generalized linear mixed model in conservation and behavior. The ways in which measurements of individual quality might be used are as various and open-ended as those for any other fundamental individual characteristic.

The power of the generalized linear mixed model comes at a cost. Repeated measurements are a requirement. This implies some system of individual recognition and the ability to relocate study individuals reliably and repeatedly. Such control may be difficult for many long-lived, wide-ranging species of conservation concern. Even when these methodological requirements can be met, there remains the challenge of sustaining studies of natural populations long enough to accumulate sufficient numbers of repeat measures. The extra effort required to surmount these obstacles should often be repaid. Although repeated measurements on known individuals are often regarded in the behavioral sciences as a hindrance to statistical inquiry (e.g., Machlis, Dodd, and Fentress 1985), the opposite is true. When analyzed in a generalized linear mixed model framework, such data improve statistical power (Diggle, Liang, and Zeger 1994) and enable a more thorough description of the nature and consequences of individual variation in natural populations.

16.

Individual Quality, Environment, and Conservation

Peter Arcese

Conservation biologists often try to recover small populations by ameliorating the causes of their decline. A first step in this process is to create ranked lists of factors known to affect population growth. Second, biologists assess which factors are amenable to management by weighing their effect on population growth against the likelihood of influencing them successfully (Boyce 1992, Caughley 1994, Beissinger and Westphal 1998, Holthausen et al. 1999, Morris et al. 1999, Noon et al. 1999). Thus, despite the fact that population growth rate in vertebrates is often most sensitive to variation in adult survival (Caswell 1978), it will sometimes be more practical to manage less influential factors, including the effects of inbreeding (Westemeier et al. 1998) or predators on offspring survival (Caro and Laurenson 1994).

Recently, it has also been suggested that detailed estimates of individual differences in phenotypic or genotypic traits that affect fitness might also be employed to model populations more precisely and manage them more successfully (Clemmons and Buchholz 1997, Connor and White 1999, Cam and Monnat 2000, Steele and Hogg, this volume). It is also discussed casually that managers might use traits of animals indicative of high fitness to select

individuals for captive breeding or translocation. In conservation, however, managers often engage in triage to allocate scarce financial and human resources (Sinclair and Arcese 1995b) and generally pursue research on new approaches only when persuasive examples exist. Because applying ideas about individual variation in fitness to conservation will require substantial effort and data (cf. Connor and White 1999, Cam and Monnat 2000), it will be essential to understand the causes of individual variation in fitness and their overall influence on population growth.

To explore this topic further, in this chapter I first review some ideas in population ecology and heterogeneity in individual quality. I then describe individual variation in annual breeding performance over 25 years in a small, unstable, and inbred population of song sparrows (*Melospiza melodia*) resident on Mandarte Island, British Columbia (Arcese et al. 1992, Keller et al. 1994). In general, I ask what value might exist in monitoring or managing one or more phenotypic traits identified as being predictive of “individual quality,” which I define here as the tendency for individual animals to perform better or worse than the population mean rate on average. I begin by reviewing some ideas about extrinsic versus intrinsic influences on individuals and populations because the former are often the focus of species recovery plans, whereas the latter include factors more often linked to heterogeneity in individual quality and behavior.

Extrinsic versus Intrinsic Influences on Individuals and Populations

Much of conservation biology focuses on the dynamics of populations and the various environmental and other extrinsic effects that limit population growth (Caughley 1994, Newton 1998). Caughley (1994) argued that the extrinsic influences of habitat loss, fire, weather, and introduced predators, competitors, and disease often have overwhelming effects on populations relative to those occurring as a consequence of intrinsic differences between individuals or, cumulatively, between populations. In contrast to extrinsic factors, intrinsic factors that influence fitness might include traits related to genotype, inbreeding, or heterozygosity, as well as phenotypic traits that vary as a consequence of maternal or developmental effects (Stearns 1992, Schlichting and Pigliucci 1998, Cam and Monnat 2000, Santos 2001).

Recall, however, that both extrinsic and intrinsic factors can act simultaneously on individuals and populations. Extrinsic influences on individual fitness occur, for example, when a parasite reduces the reproductive output of its host (Smith 1981a). This extrinsic effect will impact population fitness

if it affects enough individuals to reduce the mean rate of reproduction compared to that in populations without parasites (Arcese, Smith, and Hatch 1996). Similarly, in the case of intrinsic effects, we can contrast the fitness of inbred individuals to outbred ones in the same population (Keller 1998) and also compare the fitness of populations with different mean rates of inbreeding (Gilpin and Soulé 1986). Overall, this distinction between individual and population effects is crucial to many arguments about the relevance of behavioral or other individual-based approaches to conservation. Even though we can often demonstrate substantial impacts of a particular effect on individual fitness, conservation teams will be compelled to consider ameliorating such effects only when it is also shown that their magnitude and frequency are sufficient to influence population dynamics overall (Arcese, Keller, and Cary 1997; Beissinger 1997).

Caughley's view of the predominance of extrinsic influences on conserved populations persists today. This is because very few studies have demonstrated strong links between heterogeneity in the intrinsic quality of individual animals and variation in demographic rates at the level of populations. In addition, many case studies in conservation demonstrate an overwhelming influence of extrinsic factors on population growth, especially via habitat loss (Noon and McKelvey 1996), predator introduction (Reichel, Wiles, and Glass 1992), exploitation by humans (Brashares, Arcese, and Sam 2001), and disease (Atkinson et al. 1995). Moreover, techniques for estimating individual quality and incorporating it into predictive models of populations are recently introduced to conservation and in various states of development (Conner and White 1999, Kendall and Gordon 2002, Steele and Hogg, this volume). Thus, until recently, it has generally seemed practical to assume that management will be most effective when it focuses on the amelioration of detrimental extrinsic effects, while acknowledging that a focus on individuals may be appropriate in remnant or captive populations (Caughley 1994, Beissinger and Westphal 1998, Morris et al. 1999, Noon et al. 1999). However, this view may be changing.

In particular, several studies now suggest that the dichotomy of extrinsic versus intrinsic influences on populations is too simplistic overall, and that the potential interplay of individual heterogeneity and environment is more influential on population trajectory than assumed previously. For example, in some populations, individual differences in fitness vary more or less synchronously in time as a consequence of feedback between the state of the population or environment and the quality of individual animals or their young (Cam and Monnat 2000, Coulson et al. 2001, Reid et al. in press). Summed over individuals, these shared differences in fitness have the potential to cause cohort or other group-specific differences in vital rates that may

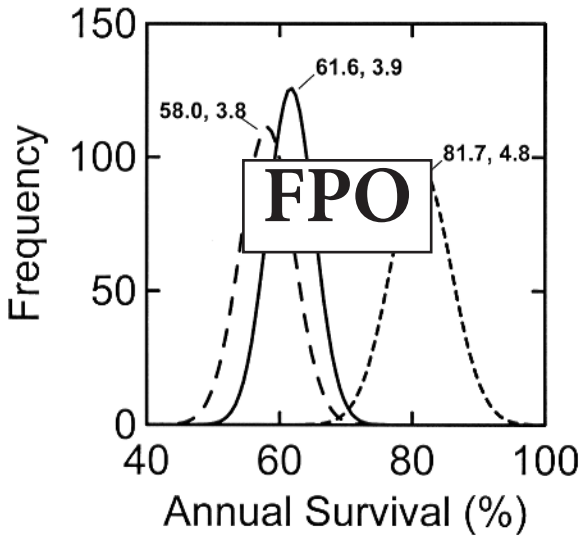


FIG. 16.1. Normal approximations of the distribution of annual survival rates in “native” (long dash) and “ F_1 hybrid” (short dash) male song sparrows (cf. Marr, Keller, and Arcese 2002:136), and for the weighted mean of the pooled estimates (solid line; based on 500 random draws given indicated mean, SD). Natives had no immigrant parents or grandparents; F_1 s produced by immigrant-native matings. Distributions represent a case wherein two classes of individuals exist in one population and survive at different rates; pooled distribution depicts the mean, SD, that might be reported by researchers and modeled by managers in the absence of data on individual heterogeneity in fitness.

in turn influence the mean expected rate of population growth (Fig. 16.1). In the Mandarte Island song sparrow population, for example, small population size and coincident inbreeding can reduce individual fitness (Keller 1998; Marr, Keller, and Arcese 2002; see Fig. 16.1) and, presumably, mean expected population size. Successful immigrants to the island, however, raised hybrid offspring that survived better than natives and constituted a substantial fraction of the smallest populations (Marr, Keller, and Arcese 2002). It is plausible, therefore, that immigration acts to increase the population’s growth rate most when it is small by raising the fraction of hybrid offspring and population fitness overall. Demonstrating that such mechanisms operate in nature argues strongly for the management of immigration in fragmented systems of populations and, perhaps, also for monitoring the average quality of individual breeders.

Covariance in fitness components among classes of individuals can also

lead to structural dependencies that affect the precision and accuracy of predictive models and the stability of populations (Engen, Bakke, and Islam 1998; Connor and White 1999; Cam and Monnat 2000; Fox and Kendall 2002; see Fig. 16.1). Among Soay sheep (*Ovis aries*), for example, weather and population density each affect population stability directly but also interact with population age structure, sex ratio, and individual fitness as a consequence of additive genetic variation in body size, parasite resistance, and feeding apparatus (Coltman et al. 1999a,b, Smith et al. 1999, Milner et al. 2000). Forchhammer et al. (2001) showed further that density-dependent and climatic conditions experienced by individuals before birth as a consequence of maternal effects, and after birth as a consequence of direct environmental influences on development, varied by cohort and resulted in persistent differences in mean fitness among cohorts. Coulson et al. (2001) suggested that differences among cohorts are sufficient to influence population growth and, in particular, to facilitate declines. Chitty (1967, 1999) also described relationships between population size and fecundity, aggressive behavior, and body size in voles (*Microtus* spp.), some of which are indirect consequences of changes in the biotic environment (Norrdahl and Korpimäki 2002).

Individual by environment interactions may also destabilize populations when inbreeding depression is expressed as a nonlinear, additive mortality during periods of severe environmental stress (Keller et al. 1994, Keller and Waller 2002; Fig. 16.2). In island-living song sparrows and large-billed ground finches (*Geospiza magnirostris*), for example, Keller et al. (1994, 2002) showed that selection was concentrated on inbred individuals during population crashes that coincided with periods of cold and drought, respectively. If selection purges populations of deleterious alleles responsible for inbreeding depression, it may also ameliorate population-level effects of inbreeding on population growth (Keller and Waller 2002). However, even rare instances of immigration may be sufficient to reestablish deleterious alleles that facilitate inbreeding depression (Keller et al. 2001, Keller and Waller 2002). Thus, where immigration occurs and inbreeding depression is expressed only under the most stressful conditions, it becomes plausible that the average level of inbreeding might rise in the period between stressors, and destabilize populations overall.

Taken together, these examples suggest that predictive models of conserved populations might capture more accurately their dynamics and predict better the influence of particular vital rates on population growth by taking into account the interplay of intrinsic and extrinsic influences via their links to individual quality (Engen, Bakke, and Islam 1998; Connor and White 1999; Coulson et al. 2001; Kendall and Gordon 2002). Such models might include parameter estimates for subpopulations of individuals that

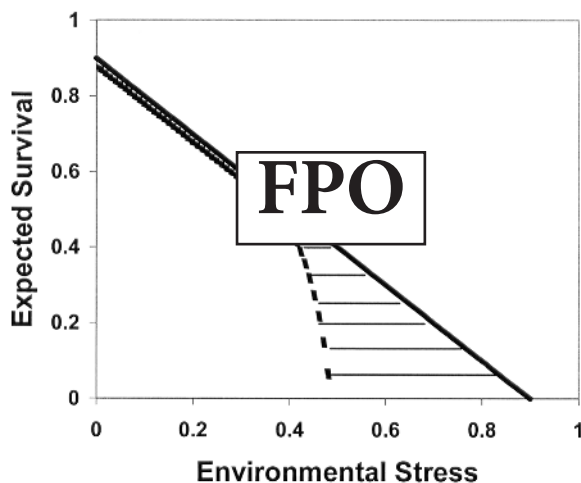


FIG. 16.2. Hypothetical relationships between the expected survival of two classes of individuals that vary intrinsically in quality, in relation to “environmental stress.” Solid line depicts a negative linear relationship wherein 90% of high-quality individuals will survive the most benign years but 0% survive very stressful conditions. Dashed line depicts the case wherein impaired individuals survive about normally in benign to moderately stressful years, but experience catastrophic mortality in more stressful years. Horizontal lines emphasize the difference in expected survival of each class in stressful years. Note that the effects of stress on the size of a population composed of these two classes of individuals will depend on the fraction in each class at the time of a stressful event, and that buildups in the fraction of impaired individuals in the population between stressful events will destabilize the population overall.

vary intrinsically in quality as a consequence of genetic, maternal, or environmental effects (Connor and White 1999, Cam and Monnat 2000; see Figs. 16.1 and 16.2). Ideally, these models should improve the efficiency of management and triage exercises by reducing uncertainty about the response of populations to alternate management proposals. Managers might also use traits indicative of individual quality to identify candidates for captive breeding, reintroduction, or translocation likely to contribute positively to population growth.

Many questions remain about the utility of focusing on heterogeneity in individual quality in conservation. In particular, we need to know (1) what are reliable indexes of individual quality, (2) which traits have large and consistent influences on fitness, (3) whether interactions between individual

quality and extrinsic factors are common features of populations, and (4) whether such interactions are often sufficient to affect population growth. I focus on the first two questions in the remainder of this chapter because identifying reliable and influential indexes of individual quality will be a first step to incorporating the concept into conservation practice.

Currencies and Repeatability of Individual Quality

References to individual quality nearly all consider measurable traits that are known or assumed to predict individual fitness (Grafen 1988, Hochachka 1993, Cam and Monnat 2000). However, a brief survey of recent literature shows that no universally applied index exists (see Table 16.1). In contrast, researchers typically adopt as candidate indexes various traits linked to survival or annual or lifetime reproductive success by statistical correlation, including the ability to defend territory (Arcese 1987), breed early (Hochachka 1993, Catry et al. 1999), or attain high social status (Dufour and Weatherhead 1998), or to maintain high body condition (Faivre et al. 2001), bilateral symmetry (Bowyer et al. 2001), immunocompetence (Hasselquist, Wasson, and Winkler 2001), or low parasite loads (Engen and Folstad 1999; see Table 16.1). This partial list is a testament to the potential of individual variation in quality to become a unifying theme in population, behavioral, and conservation ecology.

However, the diversity of candidate indexes listed here and in Table 16.1 also raises challenges to applying ideas about individual quality to conservation. These challenges arise, first, because much exploratory work will be needed in all but the most thoroughly studied species to identify and validate reliable and influential indexes of individual quality. In many cases, this work will be prohibitively expensive, time consuming, or logistically impractical. As a consequence, proposals to pursue such work will have little weight in the allocation of scarce conservation resources except where substantial data and candidate indexes already exist.

A second challenge to applying ideas about variation in individual quality to conservation involves the inconsistent definitions in the literature of quality as a fixed versus ephemeral trait of animals. Cam and Monnat (2000) point out that several different views on individual quality exist in the literature, with different implications for population dynamics and structure. Thus, whereas positive relationships between survival and reproduction are often accepted as evidence of heterogeneity in individual quality within populations (Smith 1981b, Stearns 1992), there is no consensus on whether quality is an ephemeral, static, or dynamic trait of individual animals (Cam and Monnat 2000). For example, body condition, typically expressed as mass relative to structural size, is often related positively to other direct correlates of

TABLE 16.1. Traits considered as potential indexes of individual quality in animals, with their stated or implied cause of variation.

TAXA	INDEX OF INDIVIDUAL QUALITY	ORIGIN OF EFFECT	SOURCE
BIRDS			
<i>Bucephala clangula</i>	plumage ornaments	—	Ruusila et al. 2001
<i>Sterna hirundo</i>	condition, fate, ARS	—	Becker et al. 2001
<i>Sterna hirundo</i>	age, condition	Intrinsic	Wendeln et al. 2000
<i>Pagodroma nivea</i>	body size	Intrinsic	Barbraud et al. 2000
<i>Rissa dactyla</i>	reproductive state	Intrinsic, repeatable	Cam and Monnat 2000
<i>Puffinus tenuirostris</i>	breeding frequency	Intrinsic, repeatable	Bradley et al. 2000
<i>Catharacta skua</i>	breeding date	—	Catry et al. 1999
<i>Diomedea chrysostoma</i>	ARS	Intrinsic, repeatable	Cobley et al. 1998
<i>Tyto alba</i>	plumage ornaments	Intrinsic, repeatable	Roulin et al. 1998
<i>Meleagris gallopavo</i>	spur length asymmetry	Intrinsic, repeatable(?)	Badyaev et al. 1998
<i>Dendrocopos minor</i>	clutch size, lay date, ARS	—	Wiklander et al. 2001
<i>Tachycineta bicolor</i>	immunocompetence	—	Hasselquist et al. 2001
<i>Hirundo rustica</i>	tail feather asymmetry	Intrinsic, repeatable	Shykoff and Möller 1999
<i>Manor ina melanocephala</i>	mobbing behavior	—	Arnold 2000
<i>Pica pica</i>	tail length	—	Blanco and Puente 2002
<i>Turdus merula</i>	condition, bill color, lay date	—	Faivre et al. 2001
<i>Parus caeruleus</i>	size, mite load, lay date, survival	Intrinsic, repeatable	Leech et al. 2001
<i>Parus caeruleus</i>	fecundity, parasitism, immunocompetence	Intrinsic/extrinsic	Merila and Andersson 1999
<i>Parus major</i>	plumage ornaments, carotenoids	—	Horak et al. 2001
<i>Alauda arvensis</i>	aerial display/song	—	Hedenstrom and Alerstam 1996
<i>Ficedula albicollis</i>	feather wear	—	Merila and Hemborg 2000

<i>Sturnus unicolor</i>	resource holding potential, androgens	Intrinsic	Veiga et al. 2001
<i>Sturnis vulgaris</i>	body mass, clutch size, lay date	Intrinsic/extrinsic	Christians et al. 2001
<i>Passer domesticus</i>	plumage ornaments	Intrinsic, repeatable	Gonzalez et al. 2001
<i>Passer domesticus</i>	plumage ornaments, androgens	—	Buchanan et al. 2001
<i>Melospiza melodia</i>	territory tenure	Intrinsic, repeatable	Arcese 1989
<i>Melospiza melodia</i>	repertoire size	Intrinsic, repeatable	Heibert et al. 1989
<i>Melospiza melodia</i>	lay date, clutch size, condition, ARS	Intrinsic, some repeatable	Hochachka 1993
<i>Melospiza melodia</i>	inbreeding	Intrinsic, repeatable	Keller et al. 1994
<i>Melospiza melodia</i>	heritage (immigrant, resident, hybrid)	Intrinsic, repeatable	Marr et al. 2002
MAMMALS			
<i>Microtus agrestis</i>	body condition, shape	Extrinsic via population size	Norrdahl and Korpimäki 2002
<i>M. rossiaemeridionalis</i>	body condition, shape	Extrinsic via population size	Norrdahl and Korpimäki 2002
<i>Clethrionomys glareolus</i>	body condition, shape	Extrinsic via population size	Norrdahl and Korpimäki 2002
<i>Peromyscus maniculatus</i>	breeding performance	Intrinsic/extrinsic	McAdam and Millar 1999
<i>Alces alces</i>	horn shape asymmetry	—	Bowyer et al. 2001
<i>Rangifer tarandus</i>	horn size/shape asymmetry	—	Markusson and Folstad 1997
<i>Capreolus capreolus</i>	horn size asymmetry	Intrinsic/extrinsic, repeatable	Pelabon and van Breukelen 1998
<i>Dama dama</i>	social dominance	—	Pelabon and Joly 2000
<i>Oreamnos americanus</i>	horn length asymmetry	Intrinsic, repeatable	Côté and Festa-Bianchet (2001d)
<i>Ourebia ourebi</i>	horn shape asymmetry	Intrinsic, repeatable	Arcese 1994
<i>Ovis aries</i>	parasite load	Intrinsic, repeatable	Smith et al. 1999
<i>Ovis canadensis</i>	body mass	Extrinsic, repeatable	Bérubé et al. 1999

(Continues)

TABLE 16.1. Continued)

TAXA	INDEX OF INDIVIDUAL QUALITY	ORIGIN OF EFFECT	SOURCE
INSECTS, FISH, REPTILES AND CRUSTACEANS			
<i>Ageneotettix deorum</i>			
(Acrididae)	predator avoidance	Intrinsic/extrinsic	Oedekoven and Joern 2000
<i>Gadus morhua</i>	parasitism, leukocyte, sperm count	—	Engen and Folstad 1999
<i>Gasterosteus aculeatus</i>	lateral plate asymmetry	Intrinsic/extrinsic, repeatable	Reimchen and Nosil (2001)
<i>Anolis cristatellus</i>	pushup display, condition, endurance	—	Leal 1999
<i>Carcinus maenas</i>	fighting performance	—	Sneddon and Swaddle 1999
<i>Drosophila buzzatii</i>	wing-length asymmetry	Intrinsic, repeatable	Santos 2001

Intrinsic effects are those established in the individual phenotype via developmental or genetic effects. Extrinsic effects are those acting on individuals randomly with respect to phenotype (see text); or occasionally interacting with phenotype under particular conditions. Repeatability was either a condition of the authors, implied given the trait or timeframe examined, or uncertain (—). Taxonomic emphasis reflects primarily frequency in literature. ARS: annual reproductive success.

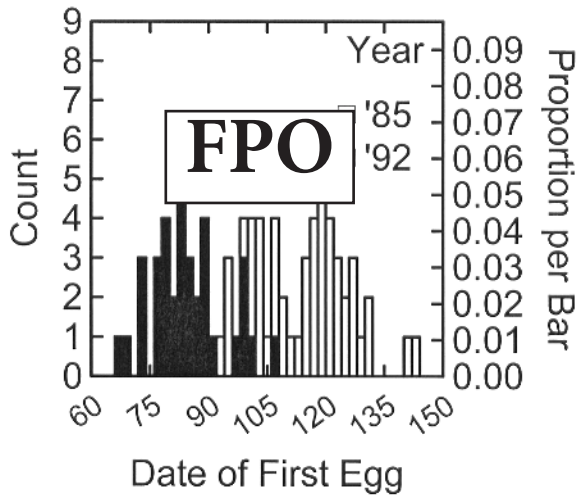


FIG. 16.3. Distribution of laying dates of first clutches by female song sparrows in a cool (1985: mean Julian date = 113, range = 93–143, $n = 56$, degree days of warming = 2719) and a warm year (1992: mean Julian date = 84, range = 66–106, $n = 36$, degree days of warming = 2074, see Methods). Identifying environmental influences on factors such as breeding date will improve models of populations wherein fitness depends on breeding date. But to apply ideas about individual heterogeneity in quality we must also know that identifiable classes of individuals lie, on average, in a similar relative position within distributions sequentially; in this case, high-quality females should appear consistently in the left tail of distributions in successive years because early breeding is related to high ARS (see text; Tables 16.2 and 16.3).

fitness such as survival or reproductive success (Sæther 1990). As a consequence, body condition is sometimes adopted as an index of individual quality (Cam and Monnat 2000; see Table 16.1). However, many fitness correlates, including body condition, also vary temporally as a function of season, environmental condition, population density, habitat quality, or food abundance (Drent and Daan 1980, Boutin 1990, Both 1998, Newton 1998). Thus the mean of condition will vary in time and space and be higher in favorable time periods or study areas as a consequence of the shared response of individual animals to environmental variation (Fig. 16.3). Some fraction of the total variance in body condition observed among individuals will be attributable solely to environmental influence. In addition, however, body condition may also vary as a consequence of maternal or developmental effects with more or less permanent influence on fitness (Norrdahl and Korpimäki 2002)

or be under genetic control and reduced, for example, in inbred lines (Wright 1978). In this case, we expect individuals of higher and lower quality to lie nearer the upper and lower tails of the distribution of body condition, respectively, when observed across time and space. Overall, it will be essential to distinguish between ephemeral versus repeatable candidate indexes of individuals' quality to apply them in conservation.

For example, it is axiomatic that as traits measured instantaneously are shown to be predictive of fitness over longer intervals, they will also become more reliable indexes of fitness. Thus high body condition may predict high survival over a period of days in a small bird or mammal; but if condition is random with respect to phenotype, it is unlikely to predict fitness over longer intervals. That is, it is unlikely to be a repeatable trait that can be used to predict individual fitness or, cumulatively, population fitness in the future. Hence, to apply ideas about individual quality to conservation, we also need to ask what particular traits can be used to identify individuals that differ repeatably in quality; that is, those individuals who lie consistently in the upper and lower tails of the fitness distribution through time (see Fig. 16.3; see also Łomnicki 1978).

For some genetic traits (inbreeding, heterozygosity) repeatability will equal 1, subject to the limits of sampling error. For phenotypic traits, however, repeatability will vary depending on a variety of factors, including their heritability and developmental stability, and any interactions of genotype, environment, and life history that affect their expression in time (Stearns 1992, Lynch and Walsh 1998, Schlichting and Pigliucci 1998). If phenotype varies as a function of environment and age, for example, an index of individual quality would require description over the lifetime of individuals, hindering their application in conservation. Candidate indexes shown to be repeatable predictors of fitness over periods of 1 to 2 years may prove unreliable over longer intervals (Catry et al. 1999, Cam and Monnat 2000).

Finally, there are also theoretical reasons to suspect that many repeatable traits will be only weakly related to fitness on average and, therefore, will not affect population growth. The heritability of traits is, on average, related negatively to their influence on fitness (Gustafsson 1986, Merila and Gustafsson 1996). If few indexes of individual quality exist that also account for a substantial fraction of variation in fitness, it will be difficult to demonstrate that variation in the population mean of individual quality will affect population growth or the precision of models which incorporate such indexes.

To summarize to this point, because potential indexes of individual quality are so diverse and because there are so few data demonstrating the magnitude of their influence on population fitness, it is difficult for conservationists to apply ideas about heterogeneity in individual quality. If developing such

indexes is desirable for managing species of concern, the majority of which lack longitudinal data on individual animals, detailed studies and subsequent “fishing expeditions” to identify useful indexes might be undertaken, but with high cost and uncertain result. Moreover, even with potential indexes identified, further research will be needed to justify their application by showing that variation in the population mean of individual quality influences population trend or model precision. So far, such demonstrations are rare. Finally, repeatability is required of indexes of individual quality if we are to apply them reliably. Traits predictive of fitness in one year but not others are unlikely to result from genetic effects or other fixed components of phenotype inherited in the broad sense as maternal effects or via developmental interactions with the environment. Traits with low repeatabilities will be poor predictors of performance across years, and of little value as indexes of individual quality.

Given these concerns, it seems prudent to explore them further in species wherein substantial data already exist, and to focus in particular on whether reliable indexes of individual heterogeneity in quality exist and are of sufficient magnitude to affect populations. To begin this exploration, I now describe further the specific goals of my current analysis, and my study site, methods, and statistical approach to identifying reliable indexes of individual quality in the song sparrow.

Individual Quality and Reproductive Output in Song Sparrows

My first goal was to identify traits indicative of individual quality via their correlation with annual reproductive success (ARS) using data from a 25-year study of the semi-isolated song sparrow population that resides year-round on Mandarte Island, British Columbia, Canada. I chose seasonal as opposed to lifetime reproductive success (LRS) as a dependent variable because many studies yield estimates of the former but few estimate the latter. Moreover, early work on components of variation in LRS in the song sparrow found relatively little evidence of repeatable individual variation in LRS (Smith 1988; Hochachka, Smith, and Arcese 1989) but some evidence of repeatability in components of ARS (Hochachka 1993). Finally, perhaps the best empirical analysis of individual heterogeneity in quality to date employed ARS as a dependent variable (Cam and Monnat 2000). My hope is that by also focusing on ARS I will facilitate the transferability of my results to species of concern, wherein data on LRS are typically unavailable. Although estimates of LRS may be desirable (Connor and White 1999) or even necessary (McNamara and Houston 1996) for resolving some questions

about individual heterogeneity in quality, the realities of research on rare species make short-term estimates of fitness more attainable in practice.

With correlates of ARS identified, I next rank extrinsic and intrinsic effects in approximate order of influence, and then calculate the repeatability of intrinsic traits identified as being predictive of ARS. I conclude my analysis by speculating briefly on how variation in the average quality of individuals in populations might be expected to influence population growth, and how interactions between the environment and individual quality might affect stability and persistence in this population.

Song sparrows are a short-lived, socially monogamous, open-nesting passerine with several traits and enemies in common with many rare and declining species of passerines, including being a popular host of the brood-parasitic brown-headed cowbird (*Molothrus ater*) and prey to a wide range of other vertebrates (Arcese et al. 2002). The Mandarte Island study population (4–72 breeding females; median = 47) is ideal for my purposes here because about 97% of birds there are hatched locally and of known age. A pedigree of social pairings allows the estimation of inbreeding coefficients of most birds (Keller 1998). Finally, the length of the study and intermittent colonization of the island by cowbirds, an important nest predator and brood parasite (Arcese, Smith, and Hatch 1996), has led to a wide range of environmental and ecological conditions over which birds of various age and inbreeding have been studied. Although many individual effects of density, environment, cowbirds, inbreeding, and age are described elsewhere for this population (Nol and Smith 1985; Keller et al. 1994; Arcese et al. 1992; Arcese, Smith, and Hatch 1996; Keller 1998; Marr, Keller, and Arcese 2002), the relative influence of these factors on ARS has not been examined. Readers are referred to these other papers for details of methods not given here.

My main data set comprised 922 female-years of data collected from 1975 to 1999, based on the onset and fate of each nesting effort by all females. Most (56%) females that breed in this population do so for only one season (Smith 1988) and no female contributed more than seven observations (0.08%) to the overall data set. Thus there was no need to control statistically for the influence of individual females on the statistical significance of results. However, some circumstances did limit which data I included in particular analyses. For example, breeding was not monitored in 1980, adults were of unknown age when the study began, and, due to a gap in the pedigree in 1980, inbreeding coefficients were calculated only for birds hatched after 1981. For all years except 1980, I estimated the total number of independent young raised by each female and the date of first laying by most females. I knew the age of most females and their mates in most cases but pooled birds ≥ 5 years of age to maintain suitable sample sizes.

Extrinsic and Intrinsic Effects in the Song Sparrow

I followed Newton (1998) by including as extrinsic factors variation in climate, population density, and the impact of natural enemies, and extended slightly his definition of intrinsic factors as demographic rates to include phenotypic and genotypic attributes of individual birds. I recognize, however, that interactions may exist between the intrinsic traits of individuals and extrinsic factors, such that inbred, infirm, aged, or other classes of individuals may perform badly when extrinsic factors are severe, but perform about as well as high-quality individuals under benign conditions (Keller et al. 1994, Sinclair and Arcese 1995b, Chitty 1999).

Because of the potential for interaction between intrinsic and extrinsic effects, I attempted to separate their relative influence on fitness in my analyses. For example, consider the mean initiation date of breeding each year, which varies as a function of “spring warming” (cumulative degree-days of warming from January through April) and influences ARS via its effect on season length and the number of broods raised (Arcese et al. 1992, unpublished results). In warm years early bud break in plants and ecdysis in arthropods are mechanistic responses to the environment that act as extrinsic influences on birds via their effects on the availability of food and nesting cover; warm temperatures also act directly on birds via the effect of temperature on the accumulation of breeding reserves (Newton 1998). Around each annual mean, however, there also exists substantial variation in individual response to variation in the environment (see Fig. 16.3). This individual response, in the absence of sampling error, represents the intrinsic component of variation between birds in their response to variation in the environment. Yet, before we can attribute these individual responses to heterogeneity in quality, we must demonstrate further that these residuals about the mean population response are repeatable overall (see following).

Statistical Methods and Terms

I used general linear models (GLM; SYSTAT 1992) to identify extrinsic and intrinsic correlates of individual variation in ARS (the total number of young raised to independence from parental care annually by a female and her mate[s]). I chose variable combinations for entry into stepwise or forced models based on earlier work but only retained models wherein all variables were judged to be statistically significant ($p \leq 0.05$). Some statistically significant effects, however, will be simply a consequence of the number of models explored; I did not correct for this effect in the exploratory models and results presented here. I provided p -values for regression coefficients based

on the t -statistic and for terms in analysis of variance (ANOVA) (e.g., age) based on the F -distribution, and all p -values for the models reported were ≤ 0.0001 . Overall, my goal was to add terms and interactions to minimize the residual sums of squares and then rank variables by their effect on ARS.

The “intrinsic traits” considered included (1) territory size (residuals of \log_{10} defended area of shrub in late April regressed on total adult breeders, see following text); (2) female age (1 to ≥ 5 yrs); (3) male age (age of female’s mate at the onset of breeding; 1 to ≥ 5 yrs); (4) breeding date (residuals date of first egg annually regressed on degree-days of warming, see introduction and following text for rationale); (5) Wright’s coefficient of inbreeding (f coefficient; after Keller 1998, Marr, Keller, and Arcese 2002); (6) fecundity as the residuals of the ANOVA of eggs laid annually versus year; and (7) efficiency as the transformed ($\log_{10} [X + 1]$) residuals of the ANOVA of the fraction of eggs laid that survived to independence versus year.

Note that fecundity and efficiency, as defined here, are each related closely to ARS and in their untransformed state should sum to equal ARS. It may be useful to think of fecundity as equaling the potential ARS of individual females in the absence of hatching failure, nest depredation, starvation, abandonment, or other factors likely to compromise the fitness of newly laid eggs. By contrast, efficiency represents the inherent viability of eggs plus the female’s alacrity in raising that initial reproductive investment to when offspring are independent of direct parental investment. It should therefore be clear, for example, that females could potentially maximize ARS by laying many eggs of poor quality and caring for them crudely, by laying fewer eggs and caring for them fastidiously, or by pursuing some combination of these tactics. I also standardized fecundity and efficiency by year to estimate the contribution of individual females as opposed to years in subsequent analyses (see e.g., Hochachka 1993).

The extrinsic traits I considered included: (1) warming as the annual degree-days of warming summed from January to April (U.S. National Oceanographic and Atmospheric Administration Meteorological Station at Olga, WA); (2) intensity of nest parasitism as the total number of eggs laid by cowbirds; and (3) population density as the total number of territorial adults present in late April each year. I used the number of cowbird eggs as an index of the extrinsic effect of enemies because cowbirds are the main cause of nest failure and because nest failure is a key factor affecting ARS (Arcese, Smith, and Hatch 1996; Arcese and Smith 1999). Overall, the number of cowbird eggs laid annually was related closely to nest failure ($r = 0.90$, $n_{\text{yrs}} = 24$), but failure was low and about constant in the 7 years when cowbirds were absent (mean percentage of nests failed annually \pm SD = 18.16 ± 3.98) versus when

they were present (mean \pm SD = 34.42 \pm 13.66). Cowbirds colonized the study region in the mid-1960s.

Although I categorized variables as intrinsic or extrinsic, some are closely related. Median annual breeding date varied widely across years (Julian day 83–126) and was earlier in warmer years ($r = 0.76$, $n = 24$ yrs). However, there was also marked variation in breeding date among individuals within years (see Fig. 16.3). Thus, to reduce the correlation between individual breeding date and spring warming in statistical models, I regressed each female's annual first laying date on annual degree-days of warming, and then used the residuals or the regression as the intrinsic response of individuals to the extrinsic effect of warming (henceforth breeding date). In addition, because territory size and density were negatively related ($r = -0.58$, $n = 898$), I regressed \log_{10} territory size on density to obtain for each individual a measure of the residual variation in territory size in each year. Other correlations between model variables were modest ($r \pm 0.40$).

I calculated the repeatabilities of traits following Lessels and Boag (1987) using data from 61 females that survived to at least 4 years of age. This method uses ANOVA to partition variance in the trait of interest (the dependent variable) among and within study subjects. Repeatability is defined as the intraclass correlation coefficient based on the variance components derived by one-way ANOVA (Lessels and Boag 1987:116). Note, however, that because repeatability is defined mathematically as:

$$r = (V_G + V_{Eg}) / V_P \quad (\text{Equation 1})$$

where V_G is the genotypic variance, V_E is the general environmental variance, and V_P is the phenotypic variance (Falconer 1981), the standardization of some traits (e.g., breeding date, territory size) for environmental variation will inflate estimates of repeatability based on these standardized variables (see also Hochachka 1993). I used standardization here to control statistically for annual variation in the population mean of the dependent variable, assuming that the remainder variance after standardization should represent primarily correlated errors due to variation among females plus random error.

Extrinsic Effects on Annual Reproductive Success

Population density, parasitism, and warming were each related negatively to ARS and accounted together for about 16% of variance in ARS across years and individuals (Table 16.2). Tested individually, density, parasitism, and warming accounted for only 11, 10, and 1% of variance in ARS, respectively. Cowbirds were absent in 7 years and laid fewer eggs and spent fewer days on

TABLE 16.2. Extrinsic effects on annual reproductive success estimated in the Mandarte Island song sparrow population over 25 years

EFFECT	COEFFICIENT	STANDARD ERROR	STANDARD COEFFICIENT
Constant	11.7590	1.3906	0.000
Warming	−0.0027	0.0006	−0.262
Parasitism	−0.2560	0.0526	−2.040
Density	−0.0188	0.0028	−0.234
Warming × Parasitism	0.0001	0.00002	1.913

Degree-days of warming, parasitism, and density, and an interaction term, accounted for about 16% of variation in annual reproductive success (ARS) ($r^2 = 0.16$, $F_{4,917} = 43.02$). Parasitism may depress ARS more in cool years because breeding commenced later, and more nests were exposed to cowbirds. Statistics include the estimated regression coefficient, its standard error, and the standardized coefficient. All coefficients had p -values < 0.001 .

the island when density was low (Smith and Arcese 1994). Thus the similar explanatory power of parasitism and density in simple regression, and lack of additivity in the GLM, was due partly to a positive correlation between them.

It is also likely, however, that density and parasitism each had independent negative effects on ARS. At high density, the breeding habitat was more finely divided among birds, making reductions in available food and nest sites automatic. Parasites also reduce ARS by removing eggs from nests, in addition to causing nests to fail (Arcese and Smith 1999). Thus it is noteworthy that sparrows with supplemental food nested earlier, had more eggs, suffered less brood parasitism and nest failure, and raised about four times more young than controls (Arcese and Smith 1988). Overall, these results indicate that high density and parasitism each impinged on the reproductive potential of individual birds by making them less able to feed themselves or their young, and/or less able to defend their nests against cowbirds. Consequently, individual heterogeneity in intrinsic traits related to the acquisition, utilization, or defense of food could drive individual variation in ARS.

Intrinsic Effects on Annual Reproductive Success

I explored the effects of age, inbreeding, territory size, breeding date, fecundity, and efficiency by examining the significance of each variable added to the preceding extrinsic model (Table 16.3). Although I was able to fit each variable to improve the extrinsic model, I found that age, inbreeding, territory size, breeding date, and fecundity each had little influence as compared

TABLE 16.3. Effect of intrinsic variables on annual reproductive success measured among song sparrows

EFFECT	MODEL				
	COEFFICIENT	STANDARD ERROR	r^2	F	df
Inbreeding	-3.6720	1.2827	0.19	31.32	5,692
Breeding date	-0.0366	0.0051	0.20	40.25	5,787
Territory size	1.0130	0.2885	0.18	38.75	5,892
Eggs	0.1568	0.0214	0.20	46.86	5,915
Efficiency	13.6409	0.3714	0.64	330.44	5,912
	F	df			
Female age	11.28	4,828	0.22	95.68	8,828
Male age	3.71	4,818	0.19	107.96	8,818

Intrinsic variables were added sequentially to the extrinsic model of Table 16.1. Standardized coefficients were not comparable across models and thus not listed. Female and male age were added as categorical effects. All coefficients had p -values < 0.001 except inbreeding ($p = 0.004$) and male age ($p = 0.005$).

to efficiency (see Table 16.3). Efficiency accounted for 48% of total variation in ARS among years and females in simple regression. Efficient females were those that hatched a high fraction of eggs laid and lost few eggs or young to predators, because starvation, abandonment, and other incidental causes of nest failure and egg loss were rare (Arcese and Smith 1988, Hatch 1996). By contrast, females with high fecundity were primarily those with many re-laying attempts annually, which were associated with high rates of nest failure and the laying of replacement clutches. Females with the highest average ARS laid intermediate numbers of eggs.

Interactions among Intrinsic Effects

Various qualities of individual females are likely to contribute to their ability to raise young efficiently. Keller (1998) noted that low ARS in inbred females was related to poor hatching success as a result of infertility or arrested development. However, I found only weak predictors of efficiency in fecundity (partial $r^2 = 0.044$, $p < 0.001$), female age (partial $r^2 = 0.032$, $p < 0.001$) and inbreeding (partial $r^2 = 0.014$, $p < 0.001$), with about 9% of variation accounted for overall ($r^2 = 0.09$, $F_{6,682} = 52.46$, $p < 0.0001$).

Female age was the next best explanatory variable added to the extrinsic model (see Table 16.3). Age was shown earlier by Nol and Smith (1985) to be related to an initial increase and then plateau in ARS. Thus I expected that age might also affect other intrinsic variables related to ARS. In particular, breeding date was related weakly to age ($r^2 = 0.02$, $F_{4,718} = 4.12$, $p = 0.002$), but the fraction of variation accounted for was increased by the inclusion of inbreeding ($r^2 = 0.07$, $F_{5,597} = 29.80$, $p < 0.001$) and then territory size into the model ($r^2 = 0.09$, $F_{6,585} = 43.03$, $p < 0.001$). This final model suggested that breeding was earliest in relatively outbred 2-year-olds on larger than average territories. Although territory size was also related weakly to the age of the female's mate ($r^2 = 0.03$, $F_{4,804} = 5.67$, $p < 0.001$), other intrinsic effects were unrelated to territory size, and male age was unrelated to breeding date. Thus territory size influenced ARS mainly via its positive effect on breeding date. Finally, inbreeding was also related weakly to breeding date ($r^2 = 0.03$, $F_{1,608} = 21.83$, $p < 0.001$) and efficiency (see earlier), but not to territory size or fecundity.

Interactions among Intrinsic and Extrinsic Effects

The extrinsic effects of nest parasitism and its interaction with warming had the strongest influence on ARS (Table 16.4). Years of high parasitism were associated with poor ARS, but these effects were ameliorated in warm years because more nesting attempts were completed before cowbirds arrived. Density and warming each had less influence than efficiency or fecundity, but more influence than breeding date. These seven variables accounted for 76% of variation in ARS (see Table 16.4).

Although inbreeding was excluded from the final model, it was related negatively to efficiency and parasitism and positively to breeding date (see Table 16.4). Thus inbred females generally bred later, were less efficient, and lived in years with fewer cowbirds. Overall, however, I found no evidence of strong statistical interactions between the intrinsic traits of individuals and extrinsic effects on ARS. In particular, the effect of inbreeding did not depend strongly on other extrinsic effects modeled statistically here. Earlier analyses of survival in this population not only suggest that the magnitude of inbreeding depression was increased during periods of extreme environmental stress (Keller et al. 1994) but also acknowledge that post hoc analyses of observational data must be interpreted cautiously due to the lack of experimental control. A recent experimental study also failed to find a positive association of inbreeding depression and environmental stress in *Drosophila* (Fowler and Whitlock 2002).

TABLE 16.4. Coefficients of the best-fitting statistical model of annual reproductive success for song sparrows that bred on Mandarte Island from 1975 to 1999.

EFFECT	COEFFICIENT	STANDARD ERROR	STANDARD COEFFICIENT
Constant	10.9196	0.8103	0.0000
Parasitism	-0.2066	0.0315	-1.6556
Efficiency	14.2627	0.3442	0.7522
Fecundity	0.2311	0.0146	0.3079
Density	-0.0190	0.0017	-0.2331
Warming	-0.0023	0.0003	-0.2199
Breeding date	-0.0116	0.0031	-0.0754
Warming \times Parasitism	0.00007	0.00001	1.5296

$r^2 = 0.76$, $F_{7,785} = 345.25$, $p \leq 0.0001$; all coefficients < 0.0002 . Inbreeding was correlated weakly to the variables, in the order listed above: $r = 0.06$, -0.17 , 0.01 , 0.19 , 0.00 , -0.11 .

Repeatability of Traits and Candidate Indexes of Quality

I calculated the repeatabilities of each intrinsic trait predictive of ARS in my final model, which included efficiency, fecundity, and breeding date. Of these traits, however, only fecundity and breeding date were repeatable (Table 16.5). This finding presents a predicament in my search for reliable indicators of individual quality because efficiency was the only intrinsic trait with marked influence on ARS. Fecundity and breeding date each accounted for only about 4% of variation in ARS with extrinsic effects accounted for (see Tables 16.2 and 16.3). Thus, whereas breeding date and fecundity each represent statistically defensible indexes of quality, neither has an effect size to recommend it strongly as a candidate for inclusion in a population model, or as the focus of management to improve the performance of wild or captive populations. Overall, therefore, despite “explaining” 76% of variation in ARS over 25 years (see Table 16.4), I did not identify an index of individual quality likely to have a strong influence on population growth.

The fact that efficiency was not repeatable suggests further that factors affecting egg and offspring survival acted randomly with respect to female phenotype. Indeed, it was shown elsewhere that a key factor affecting variation in reproductive output on Mandarte Island was the rate of total nest failure, which itself depends on the intensity of nest parasitism by cowbirds (Arcese, Smith, and Hatch 1996; Arcese and Smith 1999). Hochachka (1993) estimated the repeatability of nest failure at 0.01. Given that the rate of nest failure experienced by individual females was not repeatable, it is unsurprising that efficiency was also unrepeatable.

TABLE 16.5. Repeatabilities of three intrinsic traits predictive of annual reproductive success for 61 female song sparrows that survived to at least 4 years of age, 1975–1999 (see Statistical Methods and Terms).

TRAIT	REPEATABILITY	<i>F</i>	df	<i>P</i>
Efficiency	0.01	1.03	60, 183	> 0.4
Fecundity	0.26	2.38	60, 183	< 0.0001
Breeding date	0.27	2.27	60, 154	< 0.0001

My inability to find an influential index of individual quality is somewhat surprising given earlier work on this population showing marked inbreeding depression in several fitness-related traits (Keller 1998; Marr, Keller, and Arcese 2002). Keller (1998) estimated that the expected LRS of eggs from full-sib matings ($f = 0.25$) is about 45% less than for eggs of outbred matings. LRS is affected primarily by longevity in song sparrows (Smith 1988; Hochachka, Smith, and Arcese 1989). This suggests that a closer focus on LRS and longevity as dependent variables in my current analysis might have yielded more positive results if small individual differences measured annually accumulate over an individual's life span. Alternatively, because the modal life span of breeding female song sparrows on Mandarte Island is 1 year (Smith 1988), and the fraction of the population consisting of highly inbred individuals is usually small (Keller et al. 1994), the cumulative effects of individual quality on LRS and population fitness as related to inbreeding may also be small relative to the components of variance attributable to extrinsic causes.

A further explanation for my lack of success may be that small, short-lived species like song sparrows are simply more susceptible to extrinsic factors than larger, long-lived species (Stearns 1992, Newton 1998). Some of the best examples of phenotypic traits that affect ARS come from studies of long-lived species (Cam and Monnat 2000; Festa-Bianchet, Jorgenson, and Réale 2000; Forchhammer et al. 2001; Reid et al. in press). Finally, traits not examined here, such as those related to morphology (Schluter and Smith 1986), social status (Arcese and Smith 1985), or territory defense (Arcese 1987) might qualify as indexes of quality. Data for these traits are sparse and unevenly distributed by year.

Individual Quality and Song Sparrow Conservation

Key threats to rare and endangered subspecies of the song sparrow in the United States and Mexico include the classical ones of habitat loss and predator introduction (Marshall and Dedrick 1994, Arcese et al. 2002), fitting

Caughley's (1994) declining population paradigm. Once populations are brought to a small size, however, we might expect intrinsic traits of individuals related to genotype or phenotype to become more influential. Low fertility, symptomatic of inbreeding depression, has been observed in subspecies (Sogge and van Riper 1988) and inbred individuals isolated on islands (Keller 1998). Marked variation in ARS and survival by age is also noted among birds on Mandarte Island (Nol and Smith 1985, unpublished results). Including these variables in predictive population models of focal populations may improve decisions about competing management options. Formal modeling will be required to test this idea further and, specifically, to determine if the potential increase in understanding warrants the time and resources required to monitor the age, inbreeding level, and/or fertility of individuals in managed populations. Given my current results, however, it is probably true that indexes of individual quality have their best potential for application in the management of captive or wild populations where extrinsic effects have been ameliorated.

Conclusions and Recommendations

I began by asking what value might exist in monitoring or managing one or more traits predictive of individual quality. The potential reasons for doing so include predicting more accurately the response of populations to alternative management options and identifying better those animals likely to contribute most to the growth of captive and wild populations. My results suggest that reliable indexes of individual quality in the song sparrow have relatively little influence on individual fitness as compared to the extrinsic effects of weather, habitat, and enemies such as brood parasites and nest predators. Overall, this supports Caughley's (1994) suggestion that a focus on extrinsic effects will prove most practical in the majority of cases where managers intervene to conserve populations and species. Confirming these suggestions, however, requires further work to partition the components of variation in population growth among intrinsic and extrinsic effects, and to test further for potential interactions between intrinsic and extrinsic effects that might destabilize populations overall (see Fig. 16.2).

In the wider context of conservation applications it also remains possible that the small, repeatable differences in quality identified here, such as those related to fecundity, breeding date, and inbreeding (see Tables 16.3 and 16.5) could be shown to account for a larger fraction of variation in fitness and population growth in longer-lived species. In some ungulates, for example, it is clear that maternal effects and environmental conditions early in life affect survival and LRS (Festa-Bianchet, Jorgenson, and Réale 2000; Forchhammer

et al. 2001), and that individual differences in fitness can influence population dynamics when cohorts vary in the mean of influential vital rates (Coulson et al. 2001). Thus further work to estimate the cumulative effect of individual variation in quality on population growth, stability, or persistence in long-lived species seems warranted, especially where long-term studies have already accumulated detailed data amenable to exploratory analysis. Indeed, the further development of ideas about individual quality to conservation is most suited to common and intensively studied species, many of which are of little specific interest in conservation, and is unsuited to rare species wherein detailed data on individual fitness are not practically collected. Thus further progress in this area probably relies on researchers that focus on intensively studied populations and have a proclivity for integrating classical approaches to evolutionary, behavioral, and population ecology to improve conservation practice.

Whether managers ever focus on indexes of individual quality depends on their demonstrated influence on populations and their ease of observation in live animals. Perhaps the ideal condition is where reliable external badges of individual quality are described and validated as influential indexes of fitness. One interesting and controversial potential index involves bilateral symmetry (Palmer 2000, Santos 2001). In artiodactyls, for example, horn length and shape symmetries have been related to harem size, social status, and annual and lifetime reproductive success (see Table 16.1). Overall, however, the strength and direction of relationships vary markedly (Kimball, Ligon, and MerolaZwartjes 1997; Dufour and Weatherhead 1998; Palmer 2000; Santos 2001; references in Table 16.1), and such indexes remain elusive despite their obvious appeal. Even when candidate indexes of individual quality are identified by their correlation to fitness (see Table 16.1), much work will be necessary to show further that the magnitude of their effect on individuals, and their pervasiveness within populations, justifies their potential application in population management. So far, convincing demonstrations that offer clear lessons for management have not appeared.

Summary

Conservation biologists and managers often try to identify factors influential of population growth, and then devise tactics to ameliorate deleterious effects to reverse population declines. Traditionally, such exercises focus on extrinsic factors, such as those related to the environment, habitat, predators, and competitors because many examples of their potential effect on populations exist (Caughley 1994, Newton 1998). However, as populations decline to small size or are brought into captivity where extrinsic influences are

minimized, it has also been suggested that identifying the intrinsic traits that influence individual and population fitness should provide additional levers with which to model populations more precisely and manage them more successfully. It has also become apparent that, in a few species, the intrinsic traits of individuals interact with extrinsic factors to influence survival, reproductive success, and population growth. Recent examples include inbreeding and phenotype–environment interactions that influence survival and destabilize populations (Keller et al. 1994, 2001, Forchhammer et al. 2001, Coulson et al. 2001). These and other observations suggest that the extrinsic–intrinsic dichotomy is too simplistic. The identification of reliable indexes of individual quality may improve predictions of population response to alternate management tactics by identifying which individuals are likely to contribute more to population growth.

One approach to characterizing individual quality has been to identify phenotypic indexes of the relative fitness of individuals in populations. However, little has been done to estimate the repeatability of these indexes, the magnitude of their impact on individual fitness, or their cumulative impact on populations. Overall, the idea that easily observable indexes of individual quality exist and are sufficiently reliable as a basis for management decisions is an attractive one, but it is also fraught with practical and theoretical problems that will probably limit its application in conservation. In particular, demonstrating convincing interactions between individual variation in fitness and population trends in the wild will require very large data sets, careful analysis, and, in many cases, experimentation. Here, I described statistically factors accounting for approximately 76% of the observed variation in the annual reproductive success of female song sparrows over 25 years, but I was unable to detect a reliable index of individual quality likely to be markedly influential of population growth. It remains possible that a closer focus on survival, LRS, or species with a longer life span will provide more convincing examples of the application of individual quality to conservation. At this point, however, the application of these ideas to conserved populations remains uncertain.

Part V

Conclusion

17.

Where Do We Go from Here?

Marco Festa-Bianchet

The preceding chapters examined how animal behavior may (or may not) contribute to wildlife management and to the conservation of biodiversity. Human activities have affected the abundance and distribution of many species and drastically altered ecosystems, sometimes in radical ways through habitat destruction, other times in more subtle ways by altering species compositions or changing the sex/age structure of populations. Although much of the emphasis was on current conservation problems and on some spectacular failures to use available knowledge of animal behavior, most chapters also related some success stories or pointed to ways to reduce our future impact on biodiversity. In this concluding chapter I offer a few reflections about how the study of animal behavior may make a greater contribution to conservation in the future.

I suggested in chapter 1 that the main contribution of animal behavior to conservation likely lies in improving the management of populations. Most of the chapters support this viewpoint. Joel Berger and collaborators (chapter 9) also point out the community implications of some behaviors. Several chapters are also concerned with how artificial barriers affect connectivity between different habitat patches or seasonal ranges. In addition, mating behavior can dramatically affect the pattern of genetic diversity within a population, especially in the small populations that are typical of endangered

species. It is clear that animal behavior should always be taken into consideration by wildlife managers interested in either protecting populations or exploiting them in a sustainable way. Although knowledge of population ecology and habitat requirements is very important to managing populations, in many cases behavior is the primary force responsible for changes in number, sex/age structure, or genetic diversity.

Two themes emerged repeatedly in this book: the importance of individual behavioral differences and the limited ability of animals to modify their behavior to deal with humanmade alterations to their environment. Individual differences are important because they affect how animal populations react to human developments or to conservation strategies. Conservation biologists must seek to preserve those individual differences. Individual differences in behavior are also important in predicting how animals may react to humanmade changes in their environment. For example, Steele and Hogg's discussion in chapter 15 about persistent individual differences in timing of estrus is clearly important in predicting the impact of climate change. It is not unreasonable to suspect that if winters continue to become shorter in the Northern Hemisphere, those bighorn ewes that tend to come into estrus earlier (and therefore give birth earlier) will be advantaged over those that typically conceive a few days later, given that in the study population the timing of birth has a strong effect on lamb survival (Festa-Bianchet 1988b).

We still know very little, however, about how genetic diversity and individual differences in behavior, both genetically derived and environmental, affect individual reproductive performance and ultimately population dynamics. Recent advances in population ecology show that differences in survival and reproductive parameters among sex/age classes are strong enough to affect population growth radically (Coulson et al. 2001), and it is likely that future research will also underline the importance of differences among cohorts and genotypes (Gaillard, Festa-Bianchet, and Yoccoz 2001). Clearly, a greater understanding of the role of individual differences in population dynamics would be of great utility in predicting how wildlife populations may react to human impacts.

Some chapters explored the role of learning in modifying animal behavior, and others emphasized the potential for behavior to evolve under natural or artificial selection. This knowledge could be put to good use in some cases; for example, in favoring the development of behaviors that reduce wildlife conflicts with humans. I pointed out in chapter 12 that numerous behavioral differences exist between the European and North American populations of several species, and that some of those differences may be due to the greater impact of humans on evolution of European than of North American animals (Martin and Clobert 1996).

In a few special cases, greater knowledge of animal behavior may point to management strategies to discourage or modify behaviors that increase the negative effects of humans on wildlife, such as aggressiveness in large carnivores, or crop raiding by herbivores. Increasingly, negative conditioning is used as an alternative to killing or transplants to discourage aggressive or other undesirable behaviors by bears in Canadian national parks. Knowledge of marine turtle swimming behavior was instrumental in the development of turtle excluding devices to decrease the number of turtles killed as bycatch during fishing operations (chapter 4). Similarly, studies of behavior of wildlife near major roads are useful in determining the best location and characteristics of underpasses and overpasses to reduce roadkills (Clevenger and Walther 2000).

As remarked in many of the chapters, however, conservation will benefit much more from the modification of those human activities that lead to habitat destruction or species loss, than from seeking to modify animal behavior. For example, a short-term management solution to dog-killing behavior by cougars may be an aversive-conditioning technique to make attempted killing of domestic pets a very unpleasant experience. If successful, aversive conditioning may give the appearance that the problem has been solved. I suggest, however, that the real problem is not the killing of domestic dogs, but the suburbanization of cougar habitat in much of western North America. Preventive management is much more likely to be successful than remedial management: wildlife habitat is often not compatible with residential developments. Animals do not need wildlife managers to improve their lot, but people need wildlife managers to limit their negative impact on animal populations.

Many of the contributing authors, after discussing the science of animal behavior, pointed out how the application of scientific knowledge to conservation requires cooperation with other scientists, land managers, and elected officials. It is remarkable how many of the authors of chapters in this book either collaborate actively with conservation or management agencies, have been employed by such agencies, or are otherwise directly involved in wildlife conservation. For example, Morris Gosling led a successful program to eradicate exotic mammals from Britain; Joel Berger and John Hogg are employed by conservation nongovernmental organizations (NGOs) in the United States; Jon Swenson has worked as a wildlife manager in both the United States and Norway; and I currently chair the Committee on the Status of Endangered Wildlife in Canada. Many other chapter authors have volunteered time and expertise to assist in the solution of conservation problems. Research in animal behavior is most effectively translated into improvements in conservation when it involves a cooperative effort among academic

researchers, government officials, and, often, environmental NGOs or land-use groups.

Cooperation with government agencies that control land use and wildlife management is particularly important for studies of animal behavior that seek to understand the relationships between individual variation, natural and artificial selection, and population dynamics under different management regimes. These studies require a long-term commitment because they must take environmental variability into account (Gaillard et al. 2000). Several chapters in this book underline the value of long-term studies of marked individuals to advance our knowledge of animal behavior and then to better prepare us to apply such knowledge to wildlife conservation. Typically, large-scale management experiments can only be conducted with the cooperation and support of the government agencies that control the land base. Long-term studies of specific populations require a secure long-term access to a study area, and it is often through the committed partnership of government departments that a secure access can be obtained.

A picture of a female mountain goat, her yearling daughter and male kid graces the cover of this book. The picture was taken at Caw Ridge, Alberta, where, with my students and collaborators, I've been studying mountain goats since 1988. Nanny #64 was tagged as a yearling in 1990 and as I write these words she's somewhere on Caw Ridge with her new male kid, probably being watched by a graduate student. During 14 years of research on mountain goats, we have learned a lot about their behavior. Many of our findings have practical implications for the management of this species. We have shown that goats are highly susceptible to helicopter harassment (Côté 1996), and our work has led to changes in guidelines for helicopter use over mountain goat habitat in many North American jurisdictions. Our findings about individual differences in female reproductive success (Côté and Festa-Bianchet 2001a,b,c) have been taken into account in the formulation of management plans for this species. Most of the financial support for the mountain goat research has come from the Natural Sciences and Engineering Research Council of Canada, but the study would have been impossible without the collaboration and support of the Alberta Fish and Wildlife Division. Clearly, this is an example of a very desirable partnership for wildlife conservation, and it is very similar to the arrangements existing, for example, between Jean-Michel Gaillard and the Office Nationale de la Chasse in France, Jack Hogg and the National Bison Range in the United States, Joel Berger and several American conservation and wildlife management agencies, or Jon Swenson and wildlife management agencies in Norway and Sweden.

Cooperative research efforts involving university-based researchers,

government agencies, and NGOs also provide excellent opportunities for training graduate students. Long-term studies allow access to databases that can be incorporated in graduate student projects to address fundamental questions in animal behavior and conservation. Working alongside academics, government biologists, and a variety of other professionals also provides students with experience in both the fundamental and the applied aspects of research in animal behavior, and allows the development of skills that will be very useful in their future career. A conservation biologist that is able to consider the economic and political implications of alternative management strategies will be much more effective than one that knows the biology very well but has had no exposure to the realities of conservation. There is a need for conservation biologists because of human activities driven by economics and politics.

Research on animal behavior is often seen as a purely academic exercise. When right-wing politicians complain about government funding of fundamental research, they often cite titles of research in animal behavior as examples of wasted money. Yet, in this book we have demonstrated the importance of knowledge of animal behavior for wildlife conservation. Students of animal behavior have not been very effective in communicating the practical importance of their research. As pointed out in many chapters, the onus is on behavioral ecologists to communicate with other biologists and land-use managers to ensure that their research results are applied to conservation. Clearly, all conservation biologists and wildlife managers need to do a better job of communicating the economic value of conservation because so many members of the general public still see environmental protection as an alternative to economic development, not as a way to ensure greater economic opportunities (much less survival!) in the future (Lewis and Alpert 1997, Chichilnisky and Heal 1998, Armsworth and Roughgarden 2001). Cooperation with economists is essential to ensuring that a proper valuation of biodiversity is incorporated in economic and political analyses. In many cases, we are wasting biodiversity because we are unaware of its value.

Finally, I call attention to the enormously important role played by the media in our society. If we want to get our ideas across to the general public, we have to be able to do so in a way that can be easily understood by most people. Students of animal behavior are in a particularly enviable position in terms of communicating with the general public (compared to, say, students of inbreeding or extinction risk) because behavior is possibly the best characteristic of wildlife that can be used to communicate a message of conservation through the mass media—nature shows typically involve animals doing something. With this opportunity, however, comes a great responsibility: although it can be made suitable for a general audience, the message must have its basis in scientific evidence.

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Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania

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Abstract: Tanzania holds most of the remaining large populations of African lions (*Panthera leo*) and has extensive areas of leopard habitat (*Panthera pardus*), and both species are subjected to sizable harvests by sport hunters. As a first step toward establishing sustainable management strategies, we analyzed harvest trends for lions and leopards across Tanzania's 300,000 km² of hunting blocks. We summarize lion population trends in protected areas where lion abundance has been directly measured and data on the frequency of lion attacks on humans in high-conflict agricultural areas. We place these findings in context of the rapidly growing human population in rural Tanzania and the concomitant effects of habitat loss, human-wildlife conflict, and cultural practices. Lion harvests declined by 50% across Tanzania between 1996 and 2008, and hunting areas with the highest initial harvests suffered the steepest declines. Although each part of the country is subject to some form of anthropogenic impact from local people, the intensity of trophy hunting was the only significant factor in a statistical analysis of lion harvest trends. Although leopard harvests were more stable, regions outside the Selous Game Reserve with the highest initial leopard harvests again showed the steepest declines. Our quantitative analyses suggest that annual hunting quotas be limited to 0.5 lions and 1.0 leopard/1000 km² of hunting area, except hunting blocks in the Selous Game Reserve, where harvests should be limited to 1.0 lion and 3.0 leopards/1000 km².

Keywords: harvests, *Panthera leo*, *Panthera pardus*, population trends, sport hunting

Efectos de la Cacería Deportiva sobre Poblaciones de Leones y Leopardos en Tanzania

Resumen: Tanzania mantiene la mayoría de las poblaciones remanentes de leones Africanos (*Panthera leo*) y tiene extensas áreas de hábitat de leopardo (*Panthera pardus*), y ambas especies son sujetas a cosechas considerables por cazadores deportivos. Como un primer paso hacia el establecimiento de estrategias de manejo sustentable, analizamos las tendencias de cosecha de leones y leopardos en los 300,000 km² de bloques de cacería de Tanzania. Sintetizamos las tendencias poblacionales de leones en áreas protegidas donde la abundancia de leones ha sido medida directamente, así como datos sobre la frecuencia de ataques de leones sobre humanos en áreas agrícolas altamente conflictivas. Ubicamos estos resultados en el contexto de la población humana en rápido crecimiento en Tanzania rural y los efectos concomitantes de la pérdida de hábitat, el conflicto humanos-vida silvestre y las prácticas culturales. Las cosechas de leones han declinado 50% en Tanzania entre 1996 y 2008, y las áreas de cacería con las cosechas iniciales más altas sufrieron las declinaciones más pronunciadas. Aunque cada parte del país está sujeto a alguna forma de impacto antropogénico por habitantes locales, la intensidad de la cacería deportiva fue el único factor significativo en el análisis estadístico de las tendencias poblacionales de leones. Aunque las cosechas de leopardos fueron más estables, regiones fuera de la Reserva de Caza Selous con las cosechas iniciales de leopardos más altas también mostraron las declinaciones más pronunciadas. Nuestros análisis cuantitativos sugieren que las

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cuotas anuales de cacería se limiten a 0.5 leones y 1.0 leopardo/1000 km² de área de cacería, excepto los bloques de cacería en la Reserva de Caza Selous, donde las cosechas deben limitarse a 1.0 león y 3.0 leopardos/1000 km².

Palabras Clave: cacería deportiva, *Panthera leo*, *Panthera pardus*, cosechas, tendencias poblacionales

Introduction

Although habitat loss and retaliatory killing are generally considered the primary threats to large felids across Africa (Ray et al. 2005; IUCN 2006; Bauer et al. 2008), hunting can also deplete animal populations (e.g., Milner-Gulland et al. 2003; Fryxell et al. 2010), especially in felids in which sexually selected infanticide is common (e.g., Whitman et al. 2004; Caro et al. 2009). For example, excessive trophy hunting appears to have caused large-scale declines in African lions (*Panthera leo*), American cougars (*Felis concolor*), and possibly African leopards (*Panthera pardus*) (Packer et al. 2009). Across seven countries (lions) and 11 U.S. states (cougars), jurisdictions with the highest sport-hunting harvests per 1000 km² of habitat subsequently showed the steepest proportional declines in harvests. The growing use of dogs to hunt leopards in Zimbabwe, and declining leopard harvests in Zambia and Zimbabwe (Purchase & Mateke 2008; Balme 2009; Packer et al. 2009; Balme et al. 2010) have also raised concerns about leopard management and trophy hunting.

Tanzania has an extensive network of national parks (38,365 km², including Ngorongoro Conservation Area), game reserves (102,049 km²), and game-controlled areas (202,959 km²), and has more lions than any other country in Africa. Four of the continent's six largest remaining populations of lions occur in Tanzania in the Serengeti, Maasai Steppe, Selous, and western Tanzania (Fig. 1). Leopards are common throughout Tanzania, and the country has been granted one of the highest export quotas for leopard trophies by CITES. In addition, Tanzania is the most popular destination for sport hunting of lions and leopards (<http://www.unep-wcmc.org/citestrade/>) in the world. An average of 243 wild lion trophies were exported per year between 1996 and 2006. In Zimbabwe and Zambia 96 and 55 trophies/year, respectively, were exported, and no other country exported more than 20 per year (Packer et al. 2009). Tanzania also exported an average of 303 wild leopard trophies/year, whereas Zimbabwe exported 300 per year and no other country exported more than 100 per year.

Lions and leopards throughout Africa are subject to widespread loss of habitat, prey depletion, and human-animal conflicts that are associated with rapid human population growth (e.g., Ray et al. 2005; Woodroffe & Frank 2005; IUCN 2008). In Tanzania, human population growth has been particularly high along the borders of the wildlife areas (Fig. 2a), and deforestation has accelerated in the past 15 years (Packer et al. 2009) with

concomitant declines in herbivore populations (Stoner et al. 2007). Thus, there is an urgent need for quantitative analysis to establish sustainable harvest practices, while taking care to disentangle the impacts of trophy hunting from these other anthropogenic factors. Trophy-hunting quotas for lions and leopards have never been based on rigorous quantitative analysis of harvest patterns in any country (Packer et al. 2009).

Data on lion population trends in Tanzania are available from long-term studies conducted in a small number of protected areas where trophy hunting is not permitted (e.g., Kissui & Packer 2004; Packer et al. 2005a), but no comparable population data exist for leopards. The population status of both species is unknown in all of the country's hunting blocks. Nevertheless, three factors allow Tanzania's trophy harvests to be used as indirect measures of population trends (Packer et al. 2009). First, hunting companies invest enormous effort into locating lions and leopards, and most animals are shot at baited stations. Male lions frequently scavenge (Schaller 1972) and are thus especially susceptible to baiting. Second, clients must purchase a "21-day safari package" to be granted permission to hunt lions or leopards in Tanzania. Sales have grown by 60% over the past decade, and overall quotas for lions and leopards have also risen (Fig. 2b). Third, a substantial proportion of Tanzania's lion trophies in 2006–2008 consisted of subadult males (see Fig. 5 in Packer et al. 2009), which is a sign of over-exploitation (e.g., Allendorf & Hard 2009). Therefore, any decline in harvest likely reflects declining population size.

We assessed whether trophy hunting has had measurable effects on the abundance of lions and leopards in Tanzania. We tested whether hunting areas with the highest harvest levels subsequently showed signs of overhunting. Additionally, we used data from long-term studies of lions conducted in Tanzania's phototourism areas to examine whether any of these largely unhunted populations have been affected by trophy hunting. We also evaluated the potential effects of other anthropogenic factors, such as conversion of natural vegetation to agriculture, human population density and growth, the presence of ritual and retaliatory killings, and proximity of wildlife habitat to human-occupied areas.

Methods

Continuous, long-term records of individual lions have been collected in 2700 km² of Serengeti National Park since 1966 (Packer et al. 2005a), in the 250-km² floor of

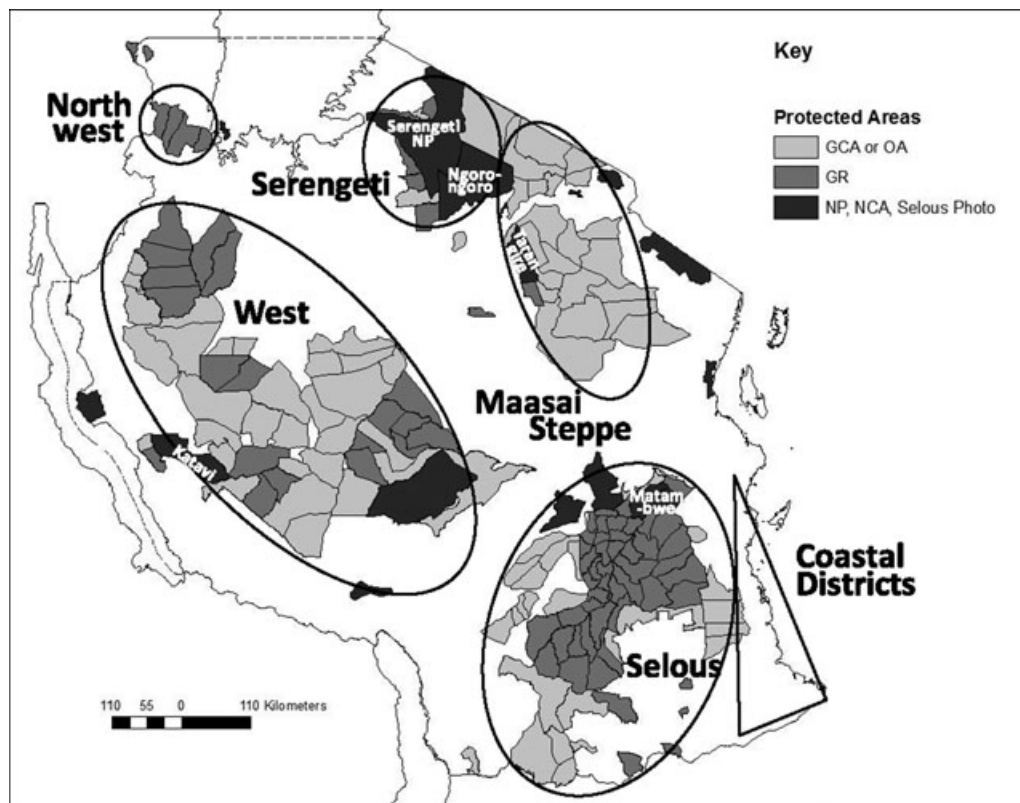


Figure 1. Map of protected areas and hunting areas in Tanzania (ellipses, major ecosystems within the country). No settlements are allowed in game reserves (GR) and national parks (NP); only pastoralist Maasai are allowed to reside in Ngorongoro Conservation Area (NCA); and settlements are permitted in game controlled (GCA) and open areas (OA). Trophy hunting is prohibited inside national parks and the Ngorongoro Conservation Area.

Ngorongoro Crater since 1963 (Kissui & Packer 2004), and in 2000-km² of Tarangire National Park since 2003. Comparable short-term studies of individual lions were conducted in 600–850 km² areas of the Matambwe Phototourism Area of Selous Game Reserve in 1996 and 1999 (Spong 2002) and in 2007–2008. We did not consider data from a 1992 study by Creel and Creel (1997) because of the small size of the area they covered (90 km² vs. 725 km² in subsequent studies) and because of atypically high lion density in their lakeshore study area.

Female lions in Serengeti, Tarangire, and Matambwe were fitted with radio collars and located and observed two to eight times per month. We used these data to determine the group membership of each pride. Ngorongoro Crater is primarily open grassland; thus, individual lions could be located opportunistically. Our estimates of lion density in Katavi National Park came from Caro (1999), who surveyed 80 km of ground-based transects twice annually since 1995 and controlled for variations in visibility along the width of each transect in his surveys. Cases of lion attacks on humans are reported to District Game Offices throughout the country (Packer et al. 2005b). We updated data from districts with the highest number of lion attacks in the country over the past two decades (Lindi, Masasi, Mkuranga, Mtwara, Ruangwa,

Rufiji, and Tunduru districts) to extend the analysis to 2008.

The CITES office at the Division of Wildlife Headquarters in Dar es Salaam provided data on quotas and harvests of lions and leopards in each hunting block, as well as the national totals of clients and 21-day safaris. We analyzed the harvest data at two scales: individual hunting blocks and seven geographically discrete regions. Hunting blocks are leased by the Tanzanian government and range in size from 141 to 8440 km² (mean [SD] = 1695 km² [1339], $n = 168$). We restricted our block-level analysis to the 45 blocks in the Selous Game Reserve because the German Technical Assistance agency, Gesellschaft für Technische Zusammenarbeit (GTZ), had spent considerable development funds on record keeping in the Selous (Baldus & Cauldwell 2004; Caro et al. 2009; Leader-Williams et al. 2009) and because records were available from an average of 87% of the Selous blocks each year (vs. only 69% in the rest of the country). In the regional analysis, we considered seven discrete areas: Maasai steppe (22 blocks), northwestern Tanzania (4 blocks), greater Serengeti (8 blocks bordering Serengeti National Park), western Tanzania (42 contiguous blocks), Selous Game Reserve (45 blocks), a set of blocks near Selous Game Reserve first hunted in 2002 (14 blocks), and a set of

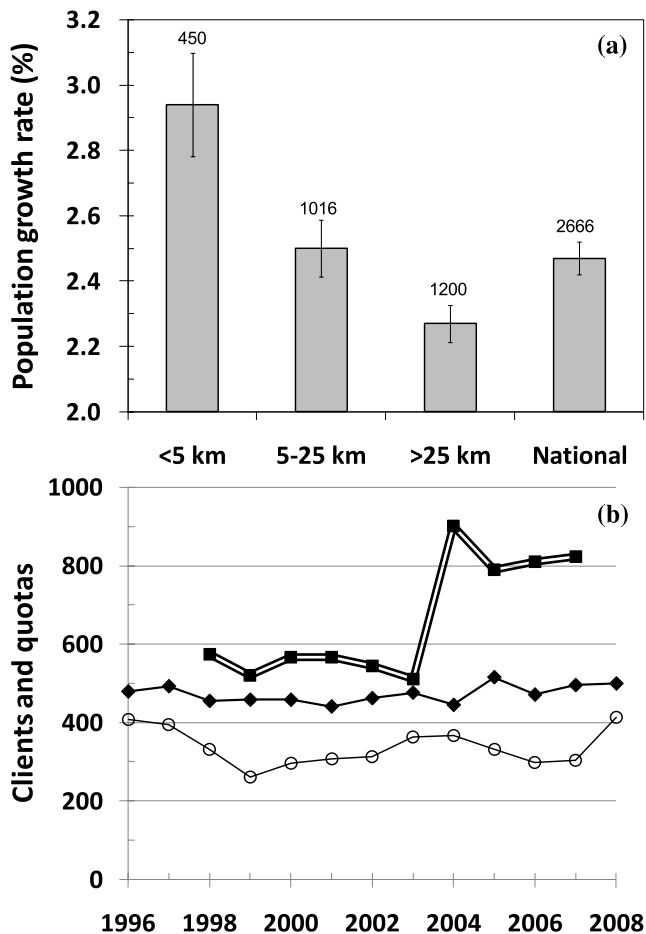


Figure 2. Human population growth and demand for lion and leopard trophies in Tanzania. (a) Annual population growth from 1988 to 2002 in wards located each distance from national parks and game reserves (numbers above bars, number of wards; lines, SE). Wards <5 km from protected areas grew faster than those 5–25 or >25 km away ($p < 0.001$). (b) Total number of 21-day safaris (double line, solid squares) and total quotas for lions (solid diamonds) and leopards (open circles) across all of Tanzania's hunting blocks.

blocks near Selous hunted since 1996 (7 blocks). For each hunted area, we defined the initial hunting intensity as the average annual number of animals harvested per 1000 km² in 1996–1999. We then calculated the harvest regression coefficient for 1996 through 2008. The annual rate of change in lion harvest was the regression coefficient divided by the initial intensity. Because the rate of change approaches zero at high initial intensities, we log-transformed all data sets where initial intensities exceeded 3 trophies·1000 km⁻²·year⁻¹.

We estimated potential habitat loss with data from 1997 on land conversion to agriculture within or adjacent to each wildlife area (FAO 2002). We used data from the

national census (Tanzanian National Bureau of Statistics 2002) to measure human population density in 2002 and the rate of human population growth in each ward between 1988 and 2002). Ward-level growth rates were calculated from photographs of 1988 ward-boundary maps stored at the National Bureau of Statistics in Dar es Salaam. For most areas, quantitative data were not available for prey loss, extent of retaliatory killing, ritual killing, or disease, so we noted only presence or absence of each factor (Table 1) and whether felids living in phototourism areas were affected by trophy hunting (e.g., Tarangire lions regularly move into hunting blocks from the national park). As a measure of overall exposure to anthropogenic effects of local people, we distinguished between hunting blocks that were completely surrounded by other hunting blocks and blocks that abutted non-wildlife areas and were thus located along an “edge.” Proportion of edge is the total area of edge blocks in a particular ecosystem divided by the total hunted area in that ecosystem.

For the analysis of the regional trophy harvests, we constructed a priori candidate models to test the effects of hunting intensity, agriculture, human population density, human population change, and “edge effects” (Table 2). We sought the best model(s) to account for harvest trends in each species. Statistics were run in PROC REG in SAS (version 9.1, SAS Institute 2002). We performed model selection with Kullback–Leibler (K–L) information-theoretic approach with Akaike's information criterion corrected for small sample size (AIC_c) (Burnham & Anderson 2002; Anderson & Burnham 2002). For each candidate model, we used the residual sum of squares (RSS) to calculate the values for AIC_c: $\Delta AIC_c = (AIC_i - \min AIC)$, where min AIC is the minimum AIC value of all models, ω_i is the Akaike weight (weight of evidence that model i is the best approximating model given the data and the set of candidate models) (Burnham & Anderson 2002).

Mean harvest intensities and harvest trends were tested for normality by regressing the residuals against normal probability curves. We detected no significant deviations or evidence of kurtosis.

Results

Across the five long-term lion studies in nonconsumptive protected areas, lion numbers remained the same in one population (Matambwe), increased in one population (Serengeti), and decreased in three populations (Tarangire, Katavi, and Ngorongoro), and the frequency of lion attacks on humans also declined in the agricultural areas of coastal Tanzania (Fig. 3).

The Serengeti and Ngorongoro lions suffered from severe disease outbreaks (Table 1). Whereas the Serengeti population recovered quickly (Packer et al. 2005a), the

Table 1. Summary of threats to Tanzania's lion and leopard populations.

Ecosystem and site	Type of area	Size of ecosystem (km ²)	Survey area (km ²)	Years	Lion population or harvest trend ^a (r ² , p)	Lion harvest/1000 km ² /yr 1996–1999 ^b	Leopard harvest trend ^a (r ² , p)	Leopard harvest/1000 km ² /yr 1996–1999	Proportion agriculture in 1997 (%)	Human population density per km ² in 2002	Human population growth 1988–2002 (%)	Prey loss ^c	Retaliatory lion killing ^b	Ritual killing Disease	Proportion edge
Greater Serengeti															
Ngorongoro Crater	photo tourism	250	250	1989–2009	−0.23 0.027	N			0	9.77	9.53	N	Y	N	N
SE Serengeti National Park	photo tourism	25,000	2,700	1989–2009	+0.74 <0.001	Y			0.67	13.35	3.59	Y	Y	Y	Y
Serengeti blocks (8)	trophy hunting	25,000	11,597	1996–2008	−0.44 0.026	2.06	−0.25 ns	2.30	6.89	11.14	3.72	Y	Y	Y	100%
Maasai Steppe															
Tarangire National Park	photo tourism	52,836	2,000	2003–2009	−0.64 0.031	Y	−0.15 ns	1.36	0	15.52	2.95	Y	Y	N	Y
Maasai Steppe blocks (24)	trophy hunting	52,836	50,036	1996–2008	−0.04 ns.	0.54			16.9	9.04	4.96	Y	Y	N	69%
Greater Selous															
Matambwe Photo-Area	photo tourism	90,089 ^c	725	1997–2009	−0.20 ns.	Y	+0.05 ns	2.45	0.02	2.95	1.26	Y	Y	N	Y
Selous game reserve blocks (45)	trophy hunting	90,089	44,244	1996–2008	−0.51 0.006	2.62			2.01	2.51	1.06	Y	Y	N	34%
Selous: old blocks (7)	trophy hunting	90,089	13,774	1996–2008	−0.10 ns.	1.36	+0.13 ns	0.64	17.1	13.05	2.40	Y	Y	Y	100%
Selous: new blocks (16)	trophy hunting	90,089	17,295	2002–2008	−0.41 0.119	2.00	−0.03 ns	1.72	12.5	7.60	1.43	Y	Y	Y	100%
Western Tanzania															
Katavi National Park	photo tourism	143,138	4,300 ^d	1995–2009	−0.50 0.016	Y			0.40	4.35	2.97	Y	Y	Y	Y
Western blocks (54)	trophy hunting	143,138	121,551	1996–2008	−0.57 0.004	1.42	−0.10 ns	1.08	5.08	6.61	4.15	Y	Y	Y	76%
Northwest Tanzania															
Northwestern blocks (4)	trophy hunting	4,240	3,995	1996–2008	−0.45 0.034	2.26	−0.11 ns	4.11	2.45	28.43	4.34	Y	Y	N	100%
Southeast Tanzania															
Coastal districts	agriculture	58,704	58,704	1990–2008	±0.24 0.05 ^e	Y			42.9	32.62	2.51	Y	Y	N	Y

^aTrends are based on annual lion surveys in the photo tourism areas and on lion and leopard harvests in the hunting areas over the years specified in each row.^bAbbreviations: N, no threat; Y, threat present.^cTotal area of photo tourism areas: 2996 km².^dArea repeatedly surveyed (80 km of ground transects).^eNumber of lion attacks on humans, r² and p are for the quadratic term.

Table 2. Akaike information criterion (AIC) test of the contribution of each variable to lion-harvest trends and leopard-harvest trends in six sport-hunting areas.*

Model	K	AIC _c	ΔAIC_c	ω_i
Lion harvest				
lion trophy hunting	2	-46.64	0.00	0.922
null model	1	-39.31	7.33	0.024
proportion edge	2	-38.02	8.62	0.012
lion trophy hunting + proportion edge	3	-37.65	8.99	0.010
proportion agriculture	2	-37.43	9.21	0.009
Leopard harvest				
log leopard trophy hunting	2	-37.85	0.00	0.637
null model	1	-35.37	2.48	0.184
proportion agriculture	2	-33.29	4.56	0.065
log leopard trophy hunting + proportion edge	3	-31.93	5.92	0.033
Human population change	2	-31.81	6.04	0.031

* The model with the lowest AIC and highest Akaike weight (ω_i) values is the best model, although any model with a ΔAIC value of <2 would be considered a plausible alternative. Models with ΔAIC greater than the null model can be disregarded (Burnham & Anderson 2002) ($K = df$). All the same variables were tested for both species, but only the top five models for each are reported.

abundance of Ngorongoro Crater lions remained below carrying capacity due to recurrent epizootics (Kissui & Packer 2004). This population also suffered mortality from Maasai herders (Kissui et al. 2009).

The Matambwe and Serengeti study populations were exposed to modest levels of trophy hunting, whereas the Tarangire population spent 4–6 months of the year outside the National Park, where they are subject to high levels of retaliatory killing in response to cattle depredation (Kissui 2008) and to trophy hunting. In contrast, Katavi lions were relatively sedentary, and their numbers were low as a result of high trophy harvests in the surrounding hunting blocks (Kiffner et al. 2009).

Lion harvests declined significantly in four of seven hunting areas across the country: the northwest, the west, around Serengeti National Park, and inside Selous Game Reserve (Fig. 4; Table 1). Record keeping was most thorough inside the Selous Game Reserve and provided the best opportunity for a block-by-block analysis. The “retention scheme” in Selous also provided higher levels of antipoaching and infrastructure development than any other hunting area in the country (Baldus & Cauldwell 2004; Leader-Williams et al. 2009), so we considered hunting trends in this area separate from other areas.

Lion harvests inside the Selous Game Reserve declined most steeply in blocks that experienced the highest legal harvest per 1000 km² in 1996–1999 (Fig. 5a). Human settlement is not permitted inside Tanzanian Game Reserves, so none of these blocks suffered any loss of habitat from agriculture or deforestation. Lion harvests did not decline more rapidly in the “edge” blocks of the Selous than in blocks that were completely surrounded by other hunting blocks. In the remaining six hunting areas, regions with the highest initial trophy harvests per 1000 km² again showed the steepest proportional declines in harvest (Fig. 5b). No other variable (e.g., agriculture, human population density, etc.) had a statistically significant effect (Table 2).

In contrast to lions, leopard harvests have not shown statistically significant harvest trends in any of the seven hunting areas (Fig. 4). Nevertheless, harvests in the north-west declined by about 10% per year since 1996, and harvests around Serengeti declined 5% per year. Within the Selous Game Reserve, hunting harvests declined more steeply in the blocks with the highest harvest level in 1996–1999, but this trend was not significant (Fig. 5c). Across the rest of the country, the proportional decline in leopard harvest was significantly higher in areas with the highest initial harvests (Fig. 5d), and trophy hunting was the only important variable (Table 2).

Reports by hunting operators and tour guides inside Selous indicate leopard abundance has increased in the past 5 years. Selous hunting blocks with the highest average lion harvests in 1996–2008 showed the largest increases in leopard harvests (Packer et al. 2009).

Discussion

Trophy hunting appears to have been the primary driver of a decline in lion abundance in the country’s trophy-hunting areas and is likely affecting lion abundance in Katavi National Park and possibly Tarangire National Park. In contrast, lion abundance was unchanged in two of the three phototourism areas that are only minimally affected by trophy hunting; lion abundance has fallen in Ngorongoro Crater even though the area is protected from hunting. We lacked independent estimates for leopard population trends, but trophy hunting may have similarly driven a decline in leopard abundance in several areas outside Selous. In contrast to the conclusions of IUCN (2006) and Bauer et al. (2008), reports, we were unable to detect any consistent impact from habitat loss or human–carnivore conflict in hunting areas, although retaliatory killing was substantial in several of the protected areas.

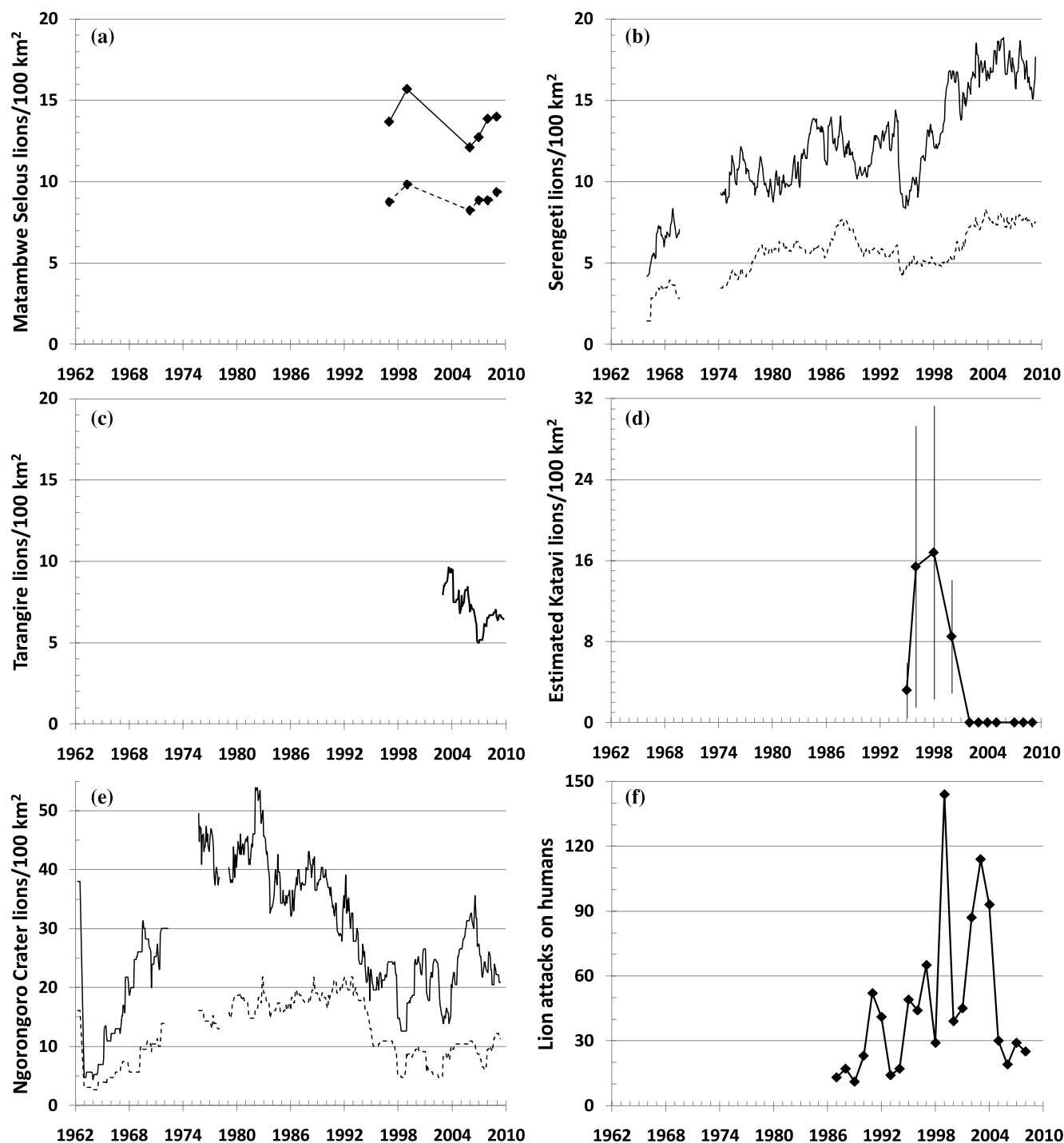


Figure 3. Long-term data on lion population density in (a) Matambwe Phototourism Area, Selous Game Reserve, (b) Serengeti National Park, (c) Tarangire National Park, (d) Katavi National Park (SE), and (e) Ngorongoro Crater and on (f) the number of lion attacks in Lindi, Masasi, Mkuranga, Mtwara, Ruangwa, Rufiji, and Tunduru districts (reported to the Tanzanian Wildlife Authorities) (solid lines, total population density; dotted lines, adult density; diamonds, annual surveys; lines without diamonds, continuous observations).

Trophy Hunting

In Tanzania the Selous Game Reserve is the largest contiguous hunting area uninhabited by humans and is thus

the area most exclusively affected by trophy hunting (Caro et al. 2009). The simulation models of Whitman et al. (2004) predicted that removing 10% of ≥ 4 year-old-male lions each year would cause an eventual 50%

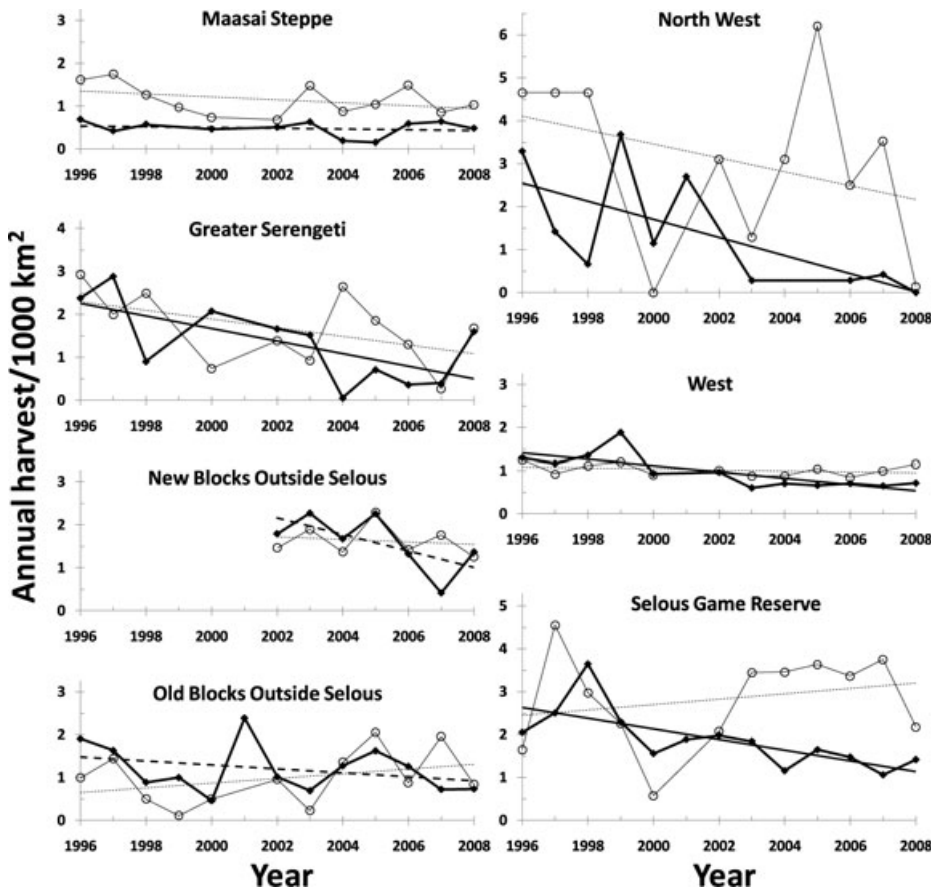


Figure 4. Average number of lions (heavy lines, diamonds) and leopards harvested (thin lines, circles) in major hunting areas (solid regression line, statistically significant declines between 1996 and 2008; dashed regression line, not significant).

decline in the total population. The average annual harvest in Selous was 2.62 males per 1000 km² in 1996–1999, which would have comprised 9.4% of 27.9 adult males per 1000 km² in the Matambwe phototourism sector. In the Katavi-Rukwa ecosystem, an average of 10.8 males were shot each year between 1996 and 2008, a period when an estimated average of 38 adult males occupied the entire area (Caro 2008; Kiffner et al. 2009), making annual harvests about 28.4% of males. Thus it is plausible that trophy hunting has reduced the lion population inside Katavi National Park, as suggested by Kiffner and colleagues (2009). High lion harvest around Zimbabwe's Hwange National Park has had measureable effects on the population inside the Park (Loveridge et al. 2007, 2009), whereas seasonal movements of lions originating from Tarangire National Park may have helped sustain harvests in nearby hunting blocks—an effect that counters extensive human population growth and habitat loss in the Maasai Steppe.

At least three factors may be responsible for stability of leopard harvests. First, widespread declines in lion abundance could have released leopards from interspecific competition (Crooks & Soulé 1999), and leopards seem to have benefited from declining lion numbers in Selous Game Reserve (Packer et al. 2009), although we have only anecdotal reports that leopards have increased in the Selous. Second, about 30% of Tan-

zania's documented leopard trophies are female (Spong et al. 2000). Packer et al. (2009) showed that cougar populations can theoretically withstand higher levels of harvest of females than males, and the same pattern should occur in any other polygynous species with sexually selected infanticide. Third, hunting companies might have put more effort into shooting leopards as lions became more difficult to locate in their hunting blocks.

Loss of Habitat and Prey

As seen elsewhere (Wittemyer et al. 2008), human population growth is highest in wards located <5 km from Tanzania's wildlife protected areas (Fig. 2a). Tanzania has lost >37% of woodland and forest habitat since 1990 (Packer et al. 2009), and bushmeat poaching has increased throughout the country (Jambiya et al. 2007), further reducing the prey base for lions and leopards. Bushmeat poachers operate within Katavi National Park (Caro 2008), the western edge of the Serengeti ecosystem (Sinclair et al. 2008), and in most hunting areas around the country (Caro & Andimile 2009). In northern Serengeti National Park, lions were largely extirpated in the 1980s by poachers setting snares for herbivores (Sinclair et al. 2003). Matambwe lions have died after eating poisoned carcasses set out to kill crocodiles in Selous. Conversion of rangeland to agriculture in the Maasai Steppe

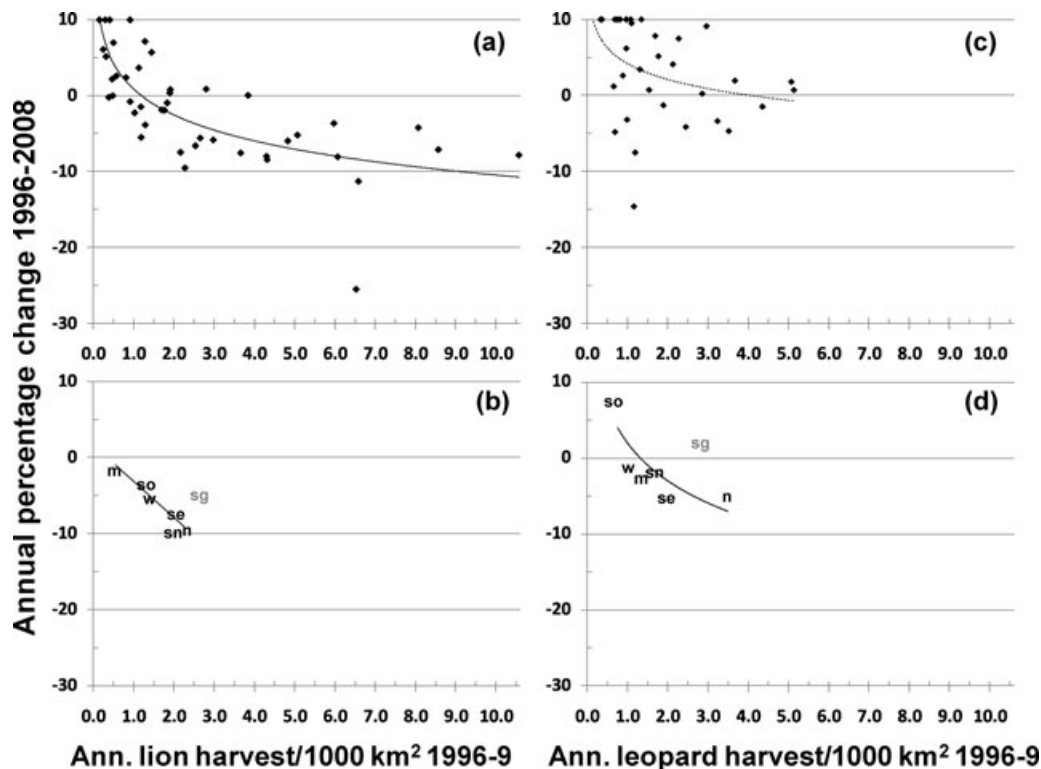


Figure 5. Proportional change in harvest of lions and leopards versus average harvest in 1996–1999: (a) lion harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = 0.57$, $n = 44$ blocks, $p < 0.0001$) and (b) lion harvests in the six ecosystems outside of Selous ($r^2 = 0.87$, $n = 6$ ecosystems, $p = 0.0064$) (M, Maasai Steppe, 24 blocks; n, northwestern Tanzania, 4 blocks; SE, Serengeti, 8 blocks; SN, new blocks outside Selous, 16 blocks; SO, old blocks outside Selous, 7 blocks; W, western Tanzania, 54 blocks; SG, Selous Game Reserve, 45 blocks [plotted for comparison]); (c) leopard harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = -0.11$, $n = 32$ blocks, $p = 0.0600$); (d) leopard harvests in the six ecosystems outside Selous ($r^2 = -0.71$, $n = 6$ ecosystems $p = 0.0345$) (Selous again plotted for comparison).

has blocked several migratory routes of Tarangire's wildebeest and zebra populations, which has likely forced lions to rely more on livestock when outside the park (Kahurananga & Silkiluwasha 1997). Tanzanian districts with the highest number of lion attacks on humans have the lowest abundance of natural prey (Packer et al. 2005b), and villages with the most lion attacks on humans have lower richness of prey species than neighboring villages without attacks (Kushnir et al. 2010).

Although rapid human population growth and high human population density in several areas would seem likely to have contributed to declining harvests (Table 1), lion and leopard harvests have been stable in the Maasai Steppe and in the older hunting areas around Selous, despite widespread conversion of land to agriculture and high human population density (Table 1). Thus, losses of habitat and prey do not explain changes in lion and leopard harvests in hunted areas (Table 2). These effects may be obscured, however, by the seasonal influx of lions from nearby National Parks (as for the Maasai Steppe) and by limitations in our data (data on agriculture were from 1997, and the last Tanzanian census was in 2002).

Retaliation

Retaliatory killing mostly affects lions; local communities seldom succeed in retaliating against stock-killing leopards (Kissui 2008). Retaliatory killing likely occurs in every area, but has been prominent in Tarangire, Ngorongoro Crater, and districts along the coast that have high levels of attacks on humans. Around Tarangire and in most of the Ngorongoro Conservation Area, Maasai kill lions in direct proportion to the number of cattle lost to lions (Kissui 2008; Ikanda & Packer 2008). Across the nation, the number of lion attacks on humans increased dramatically in the late 1990s (Packer et al. 2005b), possibly as a result of extensive flooding during the El Niño rains of 1998. Retaliatory lion killing in coastal districts intensified in 2004–2005, and few cases of attacks on humans have been reported in the past few years (Fig. 3f). Members of Tanzania's largest ethnic group, the agropastoralist Sukuma, kill lions in response to livestock depredation (Abrahams 1967). The Sukuma have recently settled in wildlife areas (Brandstrom 1985; Paciotti et al. 2005) and may have reduced lion

abundance in several hunting areas. Sukuma poisoned 22 lions in 2005–2006 in one block near the Selous (R. Shalom, personal communication). Sukuma have also killed lions in Maswa Reserve (adjacent to the Serengeti) and in the Katavi–Rukwa ecosystem. Nevertheless, the number of lions killed by sport hunters has been stable in the Maasai Steppe, despite intensive retaliatory killing of lions from the Tarangire National Park. Thus, retaliation is unlikely to be the major cause of the overall decline in lion harvests in hunting areas (Table 2).

Ritual Killing

Leopards are not killed in rituals. Maasai kill lions for ritual purposes (*Ala-mayo*), but such incidents are uncommon in the Serengeti–Ngorongoro ecosystem (~2 per year) relative to retaliatory killing (3–4 per year) (Ikanda & Packer 2008) and trophy harvests (11.5 per year). Ritual killing appears to be rare in Tarangire compared with retaliatory killing (Kissui 2008). The Datoga rituals are similar to those of the Maasai (Wilson 1952; Klima 1965), and, like the Sukuma, they have recently settled in wildlife areas in central and western Tanzania. Lion killings by the Datoga have been documented north of the Selous and in the West, but precise impacts on lions are difficult to evaluate. Sukuma conduct ritual killings in western Tanzania, the extent of which is unknown.

Disease

Diseases of lions have been studied only in Serengeti and Ngorongoro Crater, and no quantitative data are available on diseases of leopards in Tanzania. Severe drought led to fatal infections of canine distemper virus and babesia in Serengeti lions in 1994 and Ngorongoro Crater lions in 2001 (Munson et al. 2008), and the Ngorongoro Crater lions also suffered from two undiagnosed epizootics in 1994 and 1998 (Kissui & Packer 2004) (Figs. 3b & e). The Ngorongoro Crater population appears to be immunocompromised by a high degree of inbreeding (Kissui & Packer 2004); a similar situation in South Africa's Hluhluwe iMfolozi Park was ameliorated by translocating unrelated animals into the park population (Trinkel et al. 2008). Thus, chronic vulnerability to disease largely results from inbreeding in small, isolated lion populations, and disease outbreaks are unlikely to have contributed to the persistent population declines in any of the hunting areas.

Harvest for Body Parts and Edge Effects

Although lion teeth and claws have long been sold in local markets and Sukuma use lion parts as medicine, there are so far no reports of lion bones being exported from Tanzania as substitutes for tiger bones in traditional Chinese medicines.

Hunting areas located adjacent to human-dominated areas did not have larger declines in lions or leopards than

hunting areas that were buffered from human-dominated areas, suggesting that the overall effects of local people have been less severe than the effect of sport hunting.

Recommendations

Sport hunters are extremely efficient in locating their quarry, lion and leopard trophy hunting specifically targets adult males, and each male replacement has profound effects on the reproduction of multiple females. Tanzania currently allows about 500 lions and 400 leopards per year to be killed for sport in an area of 300,000 km² (1.67 lions and 1.33 leopards/1000 km²). The proportion of male lions removed by trophy hunters in the mid- to late 1990s was unsustainable (28%/year in some areas).

Lion hunting should not exceed 1.0 lions/1000 km² in the Selous Game Reserve (Fig. 5a), whereas an upper limit of 0.5 lions/1000 km² should be imposed for the rest of the country (Fig. 5b). Within the Selous, leopard harvests increased 2%/year despite an annual average offtake of 2.9 leopards/1000 km² (Fig. 5c); thus, an upper limit of 3.0 leopards/1000 km² would be prudent. In the rest of the country, leopard quotas should not exceed 1.0 leopard/1000 km² (Fig. 5d). If these recommendations were adopted, national quotas would total about 180 lions and 400 leopards/year. These numbers still exceed current harvest levels, but, if they were adopted, hunting effort would be distributed more evenly across the country.

A strict age minimum would help ensure safe harvest levels despite uncertainties about local population sizes (Whitman et al. 2004, 2007). Restricting harvest to male lions that are ≥5 years old may be sufficient to minimize the population impacts of trophy hunting, even if every ≥5-year-old male was removed every year (Whitman et al. 2004, 2007). Lion ages can be reliably estimated in field conditions (Whitman & Packer 2007), and Mozambique's Niassa Reserve has successfully implemented a 6-year age minimum for hunted lions (Begg & Begg 2009), and a few Tanzanian hunting companies have voluntarily set a 6-year age minimum. A safe minimum age for leopards may be 7 years (Packer et al. 2009). Age-assessment criteria, however, are not yet available for leopards, and it is unknown whether leopard ages can be estimated reliably in the field.

Lions and leopards are CITES-listed species; thus, every precaution should be taken to prevent harvesting that could cause populations to decline. We therefore recommend, first, that Tanzania reduce quotas to 0.5 lion (or 1.0 in Selous) and 1.0 leopard (or 3.0 in Selous)/1000 km². Comparable statistical analysis should be performed in other range states, as sustainable offtake rates are likely to vary between countries. Second, professional hunters and clients in every range state should be educated as to

how to estimate ages of lions (Whitman & Packer 2007). Third, the age of each trophy lion should be independently validated by post-mortem photographs illustrating physical features that indicate age (e.g., nose coloration) and tooth x-rays (pulp cavities enclose by year 4 in lions) and physical measurement of tooth wear (Whitman & Packer 2007). Fourth, underage trophy lions should not be exported. Fifth, similar age-assessment criteria and export policies should also be developed for leopards.

Trophy hunting has been considered essential for providing economic incentives to conserve large carnivores (e.g., Baker 1997; Hurt & Ravn 2000; Child 2004; Lindsey et al. 2006; Dickson et al. 2009). Nevertheless, successful conservation clearly requires that hunting harvests not exceed sustainable levels.

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Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania

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Abstract: Tanzania holds most of the remaining large populations of African lions (*Panthera leo*) and has extensive areas of leopard habitat (*Panthera pardus*), and both species are subjected to sizable harvests by sport hunters. As a first step toward establishing sustainable management strategies, we analyzed harvest trends for lions and leopards across Tanzania's 300,000 km² of hunting blocks. We summarize lion population trends in protected areas where lion abundance has been directly measured and data on the frequency of lion attacks on humans in high-conflict agricultural areas. We place these findings in context of the rapidly growing human population in rural Tanzania and the concomitant effects of habitat loss, human-wildlife conflict, and cultural practices. Lion harvests declined by 50% across Tanzania between 1996 and 2008, and hunting areas with the highest initial harvests suffered the steepest declines. Although each part of the country is subject to some form of anthropogenic impact from local people, the intensity of trophy hunting was the only significant factor in a statistical analysis of lion harvest trends. Although leopard harvests were more stable, regions outside the Selous Game Reserve with the highest initial leopard harvests again showed the steepest declines. Our quantitative analyses suggest that annual hunting quotas be limited to 0.5 lions and 1.0 leopard/1000 km² of hunting area, except hunting blocks in the Selous Game Reserve, where harvests should be limited to 1.0 lion and 3.0 leopards/1000 km².

Keywords: harvests, *Panthera leo*, *Panthera pardus*, population trends, sport hunting

Efectos de la Cacería Deportiva sobre Poblaciones de Leones y Leopardos en Tanzania

Resumen: Tanzania mantiene la mayoría de las poblaciones remanentes de leones Africanos (*Panthera leo*) y tiene extensas áreas de hábitat de leopardo (*Panthera pardus*), y ambas especies son sujetas a cosechas considerables por cazadores deportivos. Como un primer paso hacia el establecimiento de estrategias de manejo sustentable, analizamos las tendencias de cosecha de leones y leopardos en los 300,000 km² de bloques de cacería de Tanzania. Sintetizamos las tendencias poblacionales de leones en áreas protegidas donde la abundancia de leones ha sido medida directamente, así como datos sobre la frecuencia de ataques de leones sobre humanos en áreas agrícolas altamente conflictivas. Ubicamos estos resultados en el contexto de la población humana en rápido crecimiento en Tanzania rural y los efectos concomitantes de la pérdida de hábitat, el conflicto humanos-vida silvestre y las prácticas culturales. Las cosechas de leones han declinado 50% en Tanzania entre 1996 y 2008, y las áreas de cacería con las cosechas iniciales más altas sufrieron las declinaciones más pronunciadas. Aunque cada parte del país está sujeto a alguna forma de impacto antropogénico por habitantes locales, la intensidad de la cacería deportiva fue el único factor significativo en el análisis estadístico de las tendencias poblacionales de leones. Aunque las cosechas de leopardos fueron más estables, regiones fuera de la Reserva de Caza Selous con las cosechas iniciales de leopardos más altas también mostraron las declinaciones más pronunciadas. Nuestros análisis cuantitativos sugieren que las

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cuotas anuales de cacería se limiten a 0.5 leones y 1.0 leopardo/1000 km² de área de cacería, excepto los bloques de cacería en la Reserva de Caza Selous, donde las cosechas deben limitarse a 1.0 león y 3.0 leopards/1000 km².

Palabras Clave: cacería deportiva, *Panthera leo*, *Panthera pardus*, cosechas, tendencias poblacionales

Introduction

Although habitat loss and retaliatory killing are generally considered the primary threats to large felids across Africa (Ray et al. 2005; IUCN 2006; Bauer et al. 2008), hunting can also deplete animal populations (e.g., Milner-Gulland et al. 2003; Fryxell et al. 2010), especially in felids in which sexually selected infanticide is common (e.g., Whitman et al. 2004; Caro et al. 2009). For example, excessive trophy hunting appears to have caused large-scale declines in African lions (*Panthera leo*), American cougars (*Felis concolor*), and possibly African leopards (*Panthera pardus*) (Packer et al. 2009). Across seven countries (lions) and 11 U.S. states (cougars), jurisdictions with the highest sport-hunting harvests per 1000 km² of habitat subsequently showed the steepest proportional declines in harvests. The growing use of dogs to hunt leopards in Zimbabwe, and declining leopard harvests in Zambia and Zimbabwe (Purchase & Mateke 2008; Balme 2009; Packer et al. 2009; Balme et al. 2010) have also raised concerns about leopard management and trophy hunting.

Tanzania has an extensive network of national parks (38,365 km², including Ngorongoro Conservation Area), game reserves (102,049 km²), and game-controlled areas (202,959 km²), and has more lions than any other country in Africa. Four of the continent's six largest remaining populations of lions occur in Tanzania in the Serengeti, Maasai Steppe, Selous, and western Tanzania (Fig. 1). Leopards are common throughout Tanzania, and the country has been granted one of the highest export quotas for leopard trophies by CITES. In addition, Tanzania is the most popular destination for sport hunting of lions and leopards (<http://www.unep-wcmc.org/citestrade/>) in the world. An average of 243 wild lion trophies were exported per year between 1996 and 2006. In Zimbabwe and Zambia 96 and 55 trophies/year, respectively, were exported, and no other country exported more than 20 per year (Packer et al. 2009). Tanzania also exported an average of 303 wild leopard trophies/year, whereas Zimbabwe exported 300 per year and no other country exported more than 100 per year.

Lions and leopards throughout Africa are subject to widespread loss of habitat, prey depletion, and human-animal conflicts that are associated with rapid human population growth (e.g., Ray et al. 2005; Woodroffe & Frank 2005; IUCN 2008). In Tanzania, human population growth has been particularly high along the borders of the wildlife areas (Fig. 2a), and deforestation has accelerated in the past 15 years (Packer et al. 2009) with

concomitant declines in herbivore populations (Stoner et al. 2007). Thus, there is an urgent need for quantitative analysis to establish sustainable harvest practices, while taking care to disentangle the impacts of trophy hunting from these other anthropogenic factors. Trophy-hunting quotas for lions and leopards have never been based on rigorous quantitative analysis of harvest patterns in any country (Packer et al. 2009).

Data on lion population trends in Tanzania are available from long-term studies conducted in a small number of protected areas where trophy hunting is not permitted (e.g., Kissui & Packer 2004; Packer et al. 2005a), but no comparable population data exist for leopards. The population status of both species is unknown in all of the country's hunting blocks. Nevertheless, three factors allow Tanzania's trophy harvests to be used as indirect measures of population trends (Packer et al. 2009). First, hunting companies invest enormous effort into locating lions and leopards, and most animals are shot at baited stations. Male lions frequently scavenge (Schaller 1972) and are thus especially susceptible to baiting. Second, clients must purchase a "21-day safari package" to be granted permission to hunt lions or leopards in Tanzania. Sales have grown by 60% over the past decade, and overall quotas for lions and leopards have also risen (Fig. 2b). Third, a substantial proportion of Tanzania's lion trophies in 2006–2008 consisted of subadult males (see Fig. 5 in Packer et al. 2009), which is a sign of over-exploitation (e.g., Allendorf & Hard 2009). Therefore, any decline in harvest likely reflects declining population size.

We assessed whether trophy hunting has had measurable effects on the abundance of lions and leopards in Tanzania. We tested whether hunting areas with the highest harvest levels subsequently showed signs of overhunting. Additionally, we used data from long-term studies of lions conducted in Tanzania's phototourism areas to examine whether any of these largely unhunted populations have been affected by trophy hunting. We also evaluated the potential effects of other anthropogenic factors, such as conversion of natural vegetation to agriculture, human population density and growth, the presence of ritual and retaliatory killings, and proximity of wildlife habitat to human-occupied areas.

Methods

Continuous, long-term records of individual lions have been collected in 2700 km² of Serengeti National Park since 1966 (Packer et al. 2005a), in the 250-km² floor of

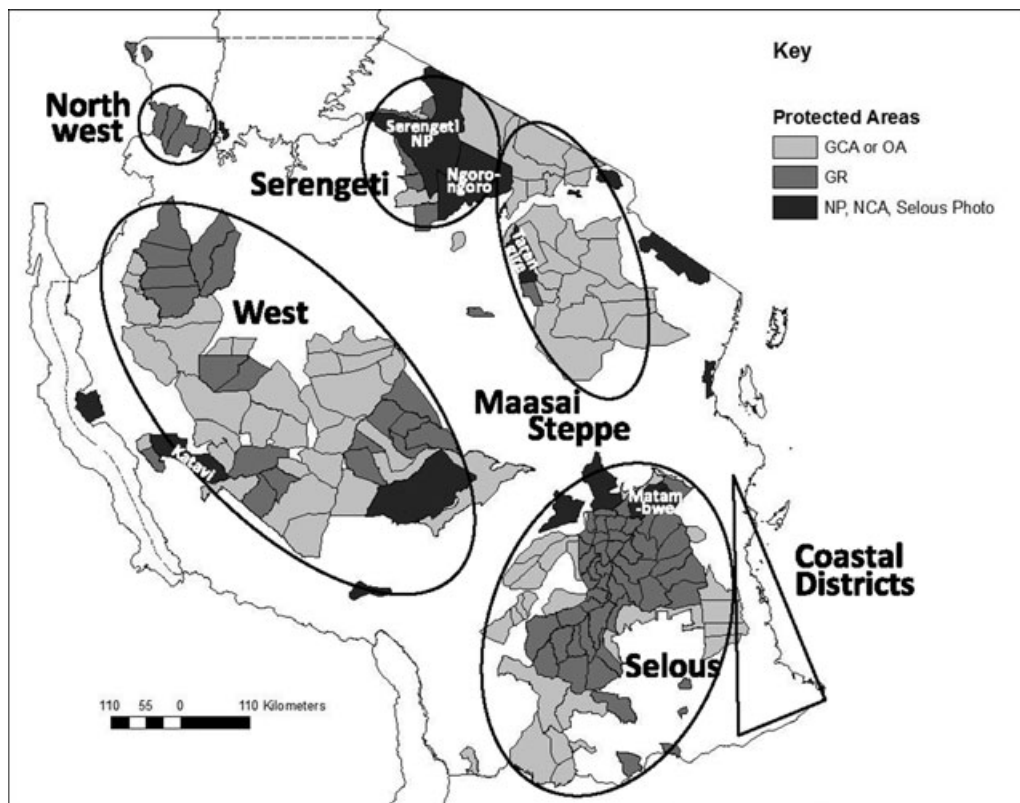


Figure 1. Map of protected areas and hunting areas in Tanzania (ellipses, major ecosystems within the country). No settlements are allowed in game reserves (GR) and national parks (NP); only pastoralist Maasai are allowed to reside in Ngorongoro Conservation Area (NCA); and settlements are permitted in game controlled (GCA) and open areas (OA). Trophy hunting is prohibited inside national parks and the Ngorongoro Conservation Area.

Ngorongoro Crater since 1963 (Kissui & Packer 2004), and in 2000-km² of Tarangire National Park since 2003. Comparable short-term studies of individual lions were conducted in 600–850 km² areas of the Matambwe Phototourism Area of Selous Game Reserve in 1996 and 1999 (Spong 2002) and in 2007–2008. We did not consider data from a 1992 study by Creel and Creel (1997) because of the small size of the area they covered (90 km² vs. 725 km² in subsequent studies) and because of atypically high lion density in their lakeshore study area.

Female lions in Serengeti, Tarangire, and Matambwe were fitted with radio collars and located and observed two to eight times per month. We used these data to determine the group membership of each pride. Ngorongoro Crater is primarily open grassland; thus, individual lions could be located opportunistically. Our estimates of lion density in Katavi National Park came from Caro (1999), who surveyed 80 km of ground-based transects twice annually since 1995 and controlled for variations in visibility along the width of each transect in his surveys. Cases of lion attacks on humans are reported to District Game Offices throughout the country (Packer et al. 2005b). We updated data from districts with the highest number of lion attacks in the country over the past two decades (Lindi, Masasi, Mkuranga, Mtwara, Ruangwa,

Rufiji, and Tunduru districts) to extend the analysis to 2008.

The CITES office at the Division of Wildlife Headquarters in Dar es Salaam provided data on quotas and harvests of lions and leopards in each hunting block, as well as the national totals of clients and 21-day safaris. We analyzed the harvest data at two scales: individual hunting blocks and seven geographically discrete regions. Hunting blocks are leased by the Tanzanian government and range in size from 141 to 8440 km² (mean [SD] = 1695 km² [1339], $n = 168$). We restricted our block-level analysis to the 45 blocks in the Selous Game Reserve because the German Technical Assistance agency, Gesellschaft für Technische Zusammenarbeit (GTZ), had spent considerable development funds on record keeping in the Selous (Baldus & Cauldwell 2004; Caro et al. 2009; Leader-Williams et al. 2009) and because records were available from an average of 87% of the Selous blocks each year (vs. only 69% in the rest of the country). In the regional analysis, we considered seven discrete areas: Maasai steppe (22 blocks), northwestern Tanzania (4 blocks), greater Serengeti (8 blocks bordering Serengeti National Park), western Tanzania (42 contiguous blocks), Selous Game Reserve (45 blocks), a set of blocks near Selous Game Reserve first hunted in 2002 (14 blocks), and a set of

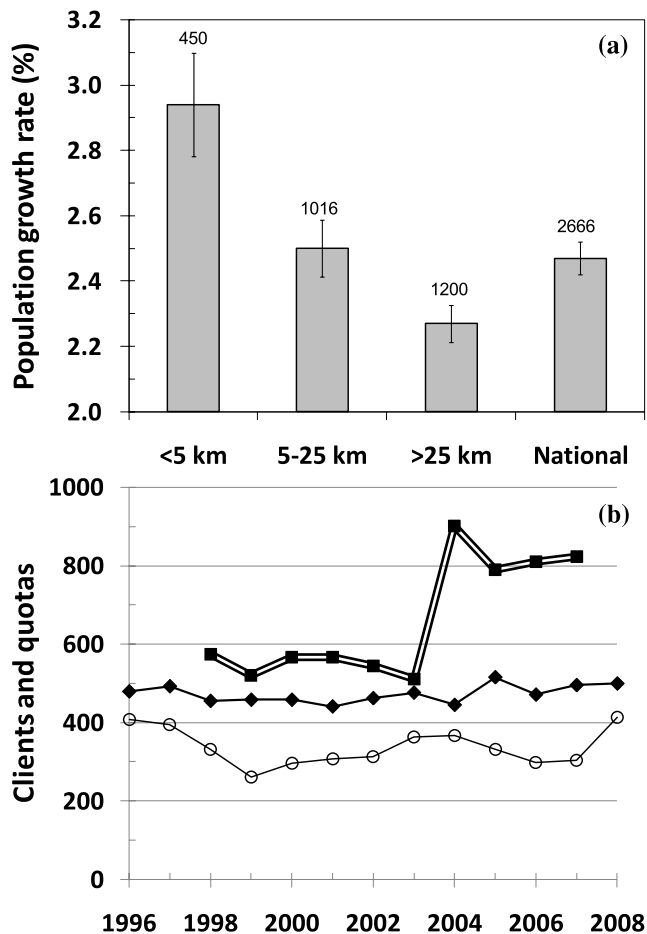


Figure 2. Human population growth and demand for lion and leopard trophies in Tanzania. (a) Annual population growth from 1988 to 2002 in wards located each distance from national parks and game reserves (numbers above bars, number of wards; lines, SE). Wards <5 km from protected areas grew faster than those 5–25 or >25 km away ($p < 0.001$). (b) Total number of 21-day safaris (double line, solid squares) and total quotas for lions (solid diamonds) and leopards (open circles) across all of Tanzania's hunting blocks.

blocks near Selous hunted since 1996 (7 blocks). For each hunted area, we defined the initial hunting intensity as the average annual number of animals harvested per 1000 km² in 1996–1999. We then calculated the harvest regression coefficient for 1996 through 2008. The annual rate of change in lion harvest was the regression coefficient divided by the initial intensity. Because the rate of change approaches zero at high initial intensities, we log-transformed all data sets where initial intensities exceeded 3 trophies·1000 km⁻²·year⁻¹.

We estimated potential habitat loss with data from 1997 on land conversion to agriculture within or adjacent to each wildlife area (FAO 2002). We used data from the

national census (Tanzanian National Bureau of Statistics 2002) to measure human population density in 2002 and the rate of human population growth in each ward between 1988 and 2002). Ward-level growth rates were calculated from photographs of 1988 ward-boundary maps stored at the National Bureau of Statistics in Dar es Salaam. For most areas, quantitative data were not available for prey loss, extent of retaliatory killing, ritual killing, or disease, so we noted only presence or absence of each factor (Table 1) and whether felids living in phototourism areas were affected by trophy hunting (e.g., Tarangire lions regularly move into hunting blocks from the national park). As a measure of overall exposure to anthropogenic effects of local people, we distinguished between hunting blocks that were completely surrounded by other hunting blocks and blocks that abutted non-wildlife areas and were thus located along an “edge.” Proportion of edge is the total area of edge blocks in a particular ecosystem divided by the total hunted area in that ecosystem.

For the analysis of the regional trophy harvests, we constructed a priori candidate models to test the effects of hunting intensity, agriculture, human population density, human population change, and “edge effects” (Table 2). We sought the best model(s) to account for harvest trends in each species. Statistics were run in PROC REG in SAS (version 9.1, SAS Institute 2002). We performed model selection with Kullback–Leibler (K–L) information-theoretic approach with Akaike's information criterion corrected for small sample size (AIC_c) (Burnham & Anderson 2002; Anderson & Burnham 2002). For each candidate model, we used the residual sum of squares (RSS) to calculate the values for AIC_c: $\Delta AIC_c = (AIC_i - \min AIC)$, where min AIC is the minimum AIC value of all models, ω_i is the Akaike weight (weight of evidence that model i is the best approximating model given the data and the set of candidate models) (Burnham & Anderson 2002).

Mean harvest intensities and harvest trends were tested for normality by regressing the residuals against normal probability curves. We detected no significant deviations or evidence of kurtosis.

Results

Across the five long-term lion studies in nonconsumptive protected areas, lion numbers remained the same in one population (Matambwe), increased in one population (Serengeti), and decreased in three populations (Tarangire, Katavi, and Ngorongoro), and the frequency of lion attacks on humans also declined in the agricultural areas of coastal Tanzania (Fig. 3).

The Serengeti and Ngorongoro lions suffered from severe disease outbreaks (Table 1). Whereas the Serengeti population recovered quickly (Packer et al. 2005a), the

Table 1. Summary of threats to Tanzania's lion and leopard populations.

Ecosystem and site	Type of area	Size of ecosystem (km ²)	Survey area (km ²)	Years	Lion population or harvest trend ^a (r ² , p)	Lion harvest trend ^a (r ² , p)	Leopard harvest trend ^a (r ² , p)	Leopard harvest/1000 km ² /yr 1996–1999	Proportion agriculture in 1997 (%)	Human population density per km ² in 2002	Human population growth 1988–2002 (%)	Prey loss ^b	Retaliatory lion killing ^b	Ritual killing Disease	Proportion edge
Greater Serengeti															
Ngorongoro Crater	photo tourism	250	250	1989–2009	–0.23 0.027	N			0	9.77	9.53	N	Y	N	N
SE Serengeti National Park	photo tourism	25,000	2,700	1989–2009	+0.74 <0.001	Y			0.67	13.35	3.59	Y	Y	Y	Y
Serengeti blocks (8)	trophy hunting	25,000	11,597	1996–2008	–0.44 0.026	2.06	–0.25 ns	2.30	6.89	11.14	3.72	Y	Y	Y	100%
Maasai Steppe															
Tarangire National Park	photo tourism	52,836	2,000	2003–2009	–0.64 0.031	Y		1.36	0	15.52	2.95	Y	Y	N	Y
Maasai Steppe blocks (24)	trophy hunting	52,836	50,036	1996–2008	–0.04 ns	0.54	–0.15 ns		16.9	9.04	4.96	Y	Y	N	69%
Greater Selous															
Matambwe Photo-Area	photo tourism	90,089 ^c	725	1997–2009	–0.20 ns	Y			0.02	2.95	1.26	Y	Y	N	Y
Selous game reserve	trophy hunting	90,089	44,244	1996–2008	–0.51 0.006	2.62	+0.05 ns	2.45	2.01	2.51	1.06	Y	Y	N	34%
blocks (45)															
Selous: old blocks (7)	trophy hunting	90,089	13,774	1996–2008	–0.10 ns	1.36	+0.13 ns	0.64	17.1	13.05	2.40	Y	Y	Y	100%
Selous: new blocks (16)	trophy hunting	90,089	17,295	2002–2008	–0.41 0.119	2.00	–0.03 ns	1.72	12.5	7.60	1.43	Y	Y	Y	100%
Western Tanzania															
Katavi National Park	photo tourism	143,138	4,300 ^d	1995–2009	–0.50 0.016	Y			0.40	4.35	2.97	Y	Y	Y	Y
Western blocks (54)	trophy hunting	143,138	121,551	1996–2008	–0.57 0.004	1.42	–0.10 ns	1.08	5.08	6.61	4.15	Y	Y	Y	76%
Northwest Tanzania															
Northwestern blocks (4)	trophy hunting	4,240	3,995	1996–2008	–0.45 0.034	2.26	–0.11 ns	4.11	2.45	28.43	4.34	Y	Y	N	100%
Southeast Tanzania															
Coastal districts	agriculture	58,704	58,704	1990–2008	±0.24 0.05 ^e	Y			42.9	32.62	2.51	Y	Y	N	Y

^aTrends are based on annual lion surveys in the photo tourism areas and on lion and leopard harvests in the hunting areas over the years specified in each row.

^bAbbreviations: N, no threat; Y, threat present.

^cTotal area of photo tourism areas: 2996 km².

^dArea repeatedly surveyed (80 km of ground transects).

^eNumber of lion attacks on humans, r² and p are for the quadratic term.

Table 2. Akaike information criterion (AIC) test of the contribution of each variable to lion-harvest trends and leopard-harvest trends in six sport-hunting areas.*

Model	K	AIC_c	ΔAIC_c	ω_i
Lion harvest				
lion trophy hunting	2	-46.64	0.00	0.922
null model	1	-39.31	7.33	0.024
proportion edge	2	-38.02	8.62	0.012
lion trophy hunting + proportion edge	3	-37.65	8.99	0.010
proportion agriculture	2	-37.43	9.21	0.009
Leopard harvest				
log leopard trophy hunting	2	-37.85	0.00	0.637
null model	1	-35.37	2.48	0.184
proportion agriculture	2	-33.29	4.56	0.065
log leopard trophy hunting + proportion edge	3	-31.93	5.92	0.033
Human population change	2	-31.81	6.04	0.031

*The model with the lowest AIC and highest Akaike weight (ω_i) values is the best model, although any model with a ΔAIC value of <2 would be considered a plausible alternative. Models with ΔAIC greater than the null model can be disregarded (Burnham & Anderson 2002) ($K = df$). All the same variables were tested for both species, but only the top five models for each are reported.

abundance of Ngorongoro Crater lions remained below carrying capacity due to recurrent epizootics (Kissui & Packer 2004). This population also suffered mortality from Maasai herders (Kissui et al. 2009).

The Matambwe and Serengeti study populations were exposed to modest levels of trophy hunting, whereas the Tarangire population spent 4–6 months of the year outside the National Park, where they are subject to high levels of retaliatory killing in response to cattle depredation (Kissui 2008) and to trophy hunting. In contrast, Katavi lions were relatively sedentary, and their numbers were low as a result of high trophy harvests in the surrounding hunting blocks (Kiffner et al. 2009).

Lion harvests declined significantly in four of seven hunting areas across the country: the northwest, the west, around Serengeti National Park, and inside Selous Game Reserve (Fig. 4; Table 1). Record keeping was most thorough inside the Selous Game Reserve and provided the best opportunity for a block-by-block analysis. The “retention scheme” in Selous also provided higher levels of antipoaching and infrastructure development than any other hunting area in the country (Baldus & Cauldwell 2004; Leader-Williams et al. 2009), so we considered hunting trends in this area separate from other areas.

Lion harvests inside the Selous Game Reserve declined most steeply in blocks that experienced the highest legal harvest per 1000 km² in 1996–1999 (Fig. 5a). Human settlement is not permitted inside Tanzanian Game Reserves, so none of these blocks suffered any loss of habitat from agriculture or deforestation. Lion harvests did not decline more rapidly in the “edge” blocks of the Selous than in blocks that were completely surrounded by other hunting blocks. In the remaining six hunting areas, regions with the highest initial trophy harvests per 1000 km² again showed the steepest proportional declines in harvest (Fig. 5b). No other variable (e.g., agriculture, human population density, etc.) had a statistically significant effect (Table 2).

In contrast to lions, leopard harvests have not shown statistically significant harvest trends in any of the seven hunting areas (Fig. 4). Nevertheless, harvests in the northwest declined by about 10% per year since 1996, and harvests around Serengeti declined 5% per year. Within the Selous Game Reserve, hunting harvests declined more steeply in the blocks with the highest harvest level in 1996–1999, but this trend was not significant (Fig. 5c). Across the rest of the country, the proportional decline in leopard harvest was significantly higher in areas with the highest initial harvests (Fig. 5d), and trophy hunting was the only important variable (Table 2).

Reports by hunting operators and tour guides inside Selous indicate leopard abundance has increased in the past 5 years. Selous hunting blocks with the highest average lion harvests in 1996–2008 showed the largest increases in leopard harvests (Packer et al. 2009).

Discussion

Trophy hunting appears to have been the primary driver of a decline in lion abundance in the country’s trophy-hunting areas and is likely affecting lion abundance in Katavi National Park and possibly Tarangire National Park. In contrast, lion abundance was unchanged in two of the three phototourism areas that are only minimally affected by trophy hunting; lion abundance has fallen in Ngorongoro Crater even though the area is protected from hunting. We lacked independent estimates for leopard population trends, but trophy hunting may have similarly driven a decline in leopard abundance in several areas outside Selous. In contrast to the conclusions of IUCN (2006) and Bauer et al. (2008), reports, we were unable to detect any consistent impact from habitat loss or human–carnivore conflict in hunting areas, although retaliatory killing was substantial in several of the protected areas.

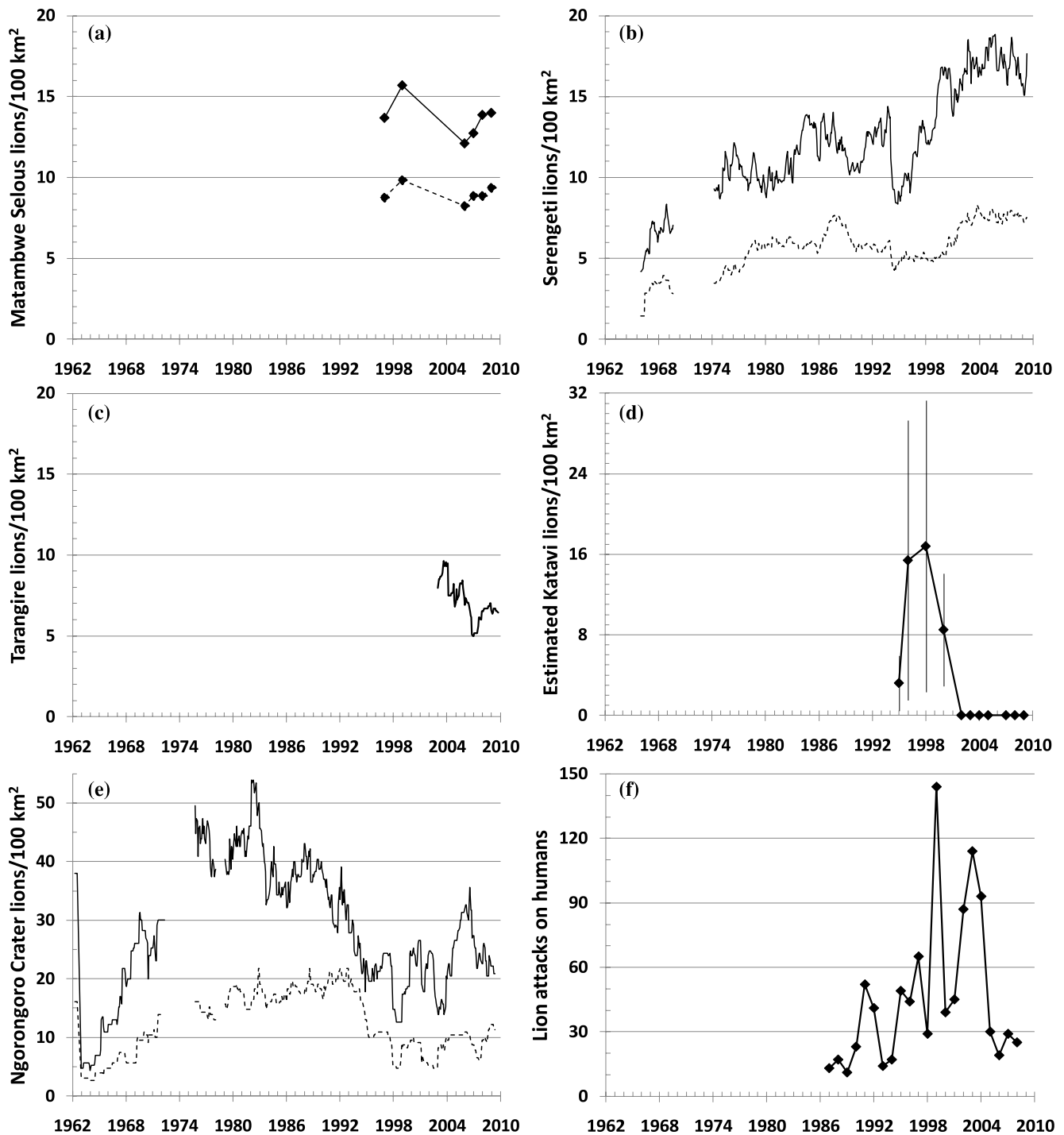


Figure 3. Long-term data on lion population density in (a) Matambwe Phototourism Area, Selous Game Reserve, (b) Serengeti National Park, (c) Tarangire National Park, (d) Katavi National Park (SE), and (e) Ngorongoro Crater and on (f) the number of lion attacks in Lindi, Masasi, Mkuranga, Mtwara, Ruangwa, Rufiji, and Tunduru districts (reported to the Tanzanian Wildlife Authorities) (solid lines, total population density; dotted lines, adult density; diamonds, annual surveys; lines without diamonds, continuous observations).

Trophy Hunting

In Tanzania the Selous Game Reserve is the largest contiguous hunting area uninhabited by humans and is thus

the area most exclusively affected by trophy hunting (Caro et al. 2009). The simulation models of Whitman et al. (2004) predicted that removing 10% of ≥ 4 year-old-male lions each year would cause an eventual 50%

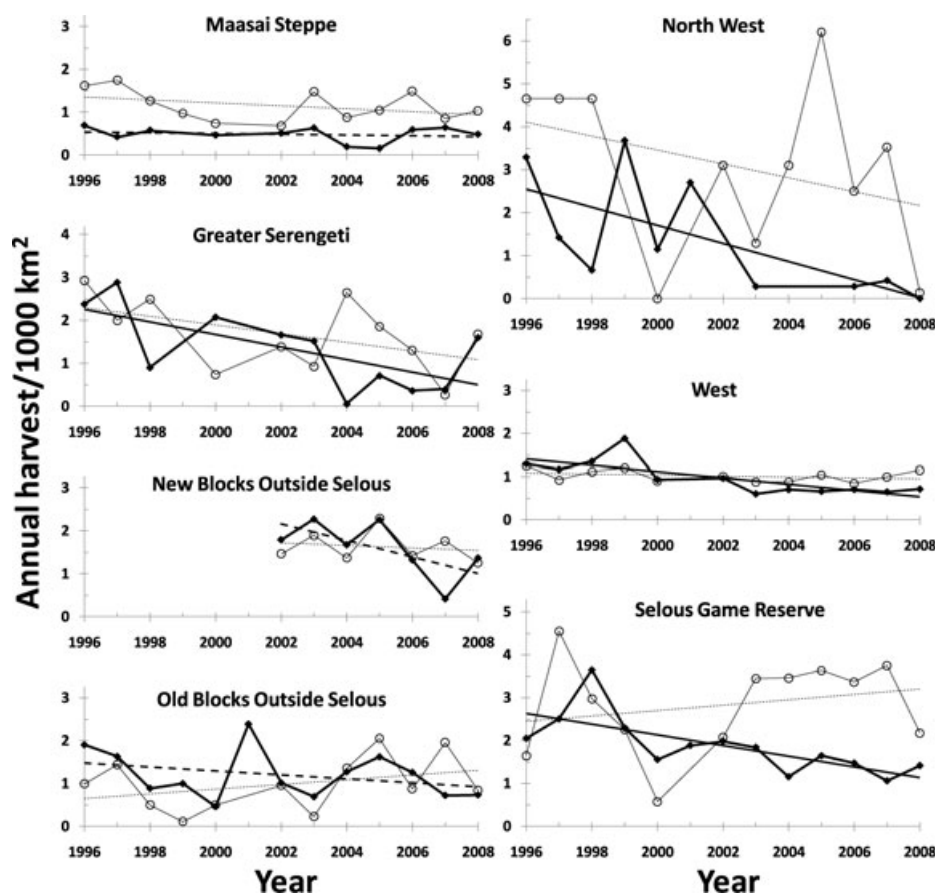


Figure 4. Average number of lions (heavy lines, diamonds) and leopards harvested (thin lines, circles) in major hunting areas (solid regression line, statistically significant declines between 1996 and 2008; dashed regression line, not significant).

decline in the total population. The average annual harvest in Selous was 2.62 males per 1000 km² in 1996–1999, which would have comprised 9.4% of 27.9 adult males per 1000 km² in the Matambwe phototourism sector. In the Katavi–Rukwa ecosystem, an average of 10.8 males were shot each year between 1996 and 2008, a period when an estimated average of 38 adult males occupied the entire area (Caro 2008; Kiffner et al. 2009), making annual harvests about 28.4% of males. Thus it is plausible that trophy hunting has reduced the lion population inside Katavi National Park, as suggested by Kiffner and colleagues (2009). High lion harvest around Zimbabwe's Hwange National Park has had measureable effects on the population inside the Park (Loveridge et al. 2007, 2009), whereas seasonal movements of lions originating from Tarangire National Park may have helped sustain harvests in nearby hunting blocks—an effect that counters extensive human population growth and habitat loss in the Maasai Steppe.

At least three factors may be responsible for stability of leopard harvests. First, widespread declines in lion abundance could have released leopards from interspecific competition (Crooks & Soulé 1999), and leopards seem to have benefited from declining lion numbers in Selous Game Reserve (Packer et al. 2009), although we have only anecdotal reports that leopards have increased in the Selous. Second, about 30% of Tan-

zania's documented leopard trophies are female (Spong et al. 2000). Packer et al. (2009) showed that cougar populations can theoretically withstand higher levels of harvest of females than males, and the same pattern should occur in any other polygynous species with sexually selected infanticide. Third, hunting companies might have put more effort into shooting leopards as lions became more difficult to locate in their hunting blocks.

Loss of Habitat and Prey

As seen elsewhere (Wittemyer et al. 2008), human population growth is highest in wards located <5 km from Tanzania's wildlife protected areas (Fig. 2a). Tanzania has lost >37% of woodland and forest habitat since 1990 (Packer et al. 2009), and bushmeat poaching has increased throughout the country (Jambiya et al. 2007), further reducing the prey base for lions and leopards. Bushmeat poachers operate within Katavi National Park (Caro 2008), the western edge of the Serengeti ecosystem (Sinclair et al. 2008), and in most hunting areas around the country (Caro & Andimile 2009). In northern Serengeti National Park, lions were largely extirpated in the 1980s by poachers setting snares for herbivores (Sinclair et al. 2003). Matambwe lions have died after eating poisoned carcasses set out to kill crocodiles in Selous. Conversion of rangeland to agriculture in the Maasai Steppe

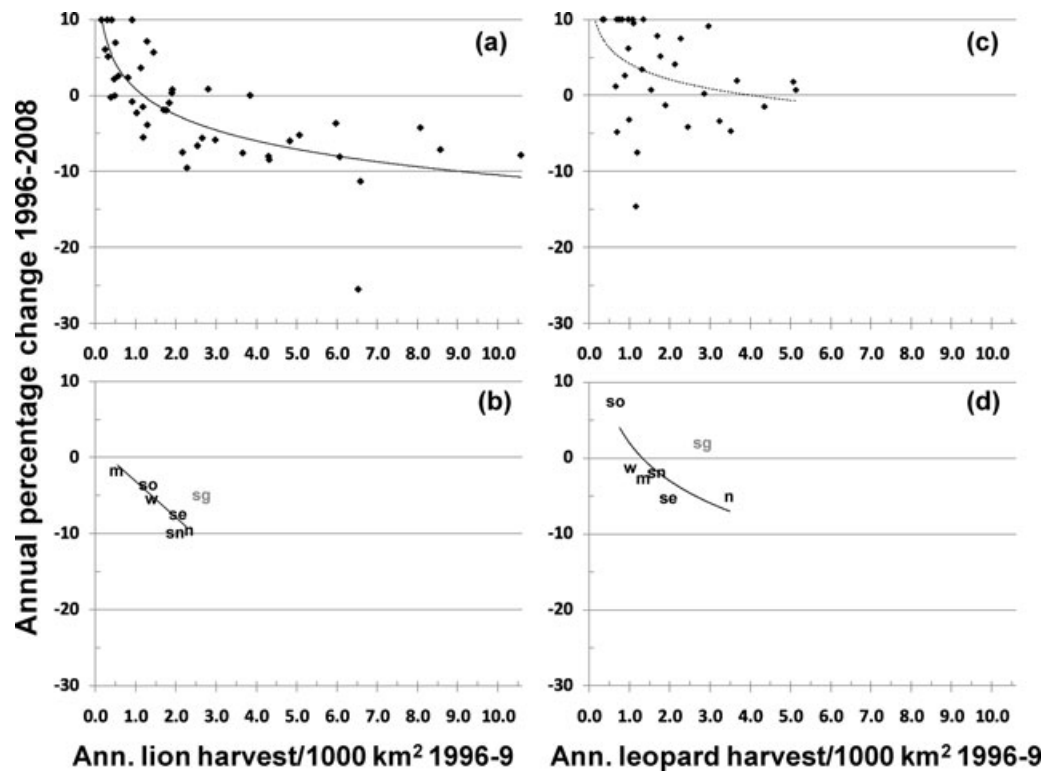


Figure 5. Proportional change in harvest of lions and leopards versus average harvest in 1996–1999: (a) lion harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = 0.57$, $n = 44$ blocks, $p < 0.0001$) and (b) lion harvests in the six ecosystems outside of Selous ($r^2 = 0.87$, $n = 6$ ecosystems, $p = 0.0064$) (M, Maasai Steppe, 24 blocks; n, northwestern Tanzania, 4 blocks; SE, Serengeti, 8 blocks; SN, new blocks outside Selous, 16 blocks; SO, old blocks outside Selous, 7 blocks; W, western Tanzania, 54 blocks; SG, Selous Game Reserve, 45 blocks [plotted for comparison]); (c) leopard harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = -0.11$, $n = 32$ blocks, $p = 0.0600$); (d) leopard harvests in the six ecosystems outside Selous ($r^2 = -0.71$, $n = 6$ ecosystems $p = 0.0345$) (Selous again plotted for comparison).

has blocked several migratory routes of Tarangire's wildebeest and zebra populations, which has likely forced lions to rely more on livestock when outside the park (Kahurananga & Silkiluwasha 1997). Tanzanian districts with the highest number of lion attacks on humans have the lowest abundance of natural prey (Packer et al. 2005b), and villages with the most lion attacks on humans have lower richness of prey species than neighboring villages without attacks (Kushnir et al. 2010).

Although rapid human population growth and high human population density in several areas would seem likely to have contributed to declining harvests (Table 1), lion and leopard harvests have been stable in the Maasai Steppe and in the older hunting areas around Selous, despite widespread conversion of land to agriculture and high human population density (Table 1). Thus, losses of habitat and prey do not explain changes in lion and leopard harvests in hunted areas (Table 2). These effects may be obscured, however, by the seasonal influx of lions from nearby National Parks (as for the Maasai Steppe) and by limitations in our data (data on agriculture were from 1997, and the last Tanzanian census was in 2002).

Retaliation

Retaliatory killing mostly affects lions; local communities seldom succeed in retaliating against stock-killing leopards (Kissui 2008). Retaliatory killing likely occurs in every area, but has been prominent in Tarangire, Ngorongoro Crater, and districts along the coast that have high levels of attacks on humans. Around Tarangire and in most of the Ngorongoro Conservation Area, Maasai kill lions in direct proportion to the number of cattle lost to lions (Kissui 2008; Ikanda & Packer 2008). Across the nation, the number of lion attacks on humans increased dramatically in the late 1990s (Packer et al. 2005b), possibly as a result of extensive flooding during the El Niño rains of 1998. Retaliatory lion killing in coastal districts intensified in 2004–2005, and few cases of attacks on humans have been reported in the past few years (Fig. 3f). Members of Tanzania's largest ethnic group, the agropastoralist Sukuma, kill lions in response to livestock depredation (Abrahams 1967). The Sukuma have recently settled in wildlife areas (Brandstrom 1985; Paciotti et al. 2005) and may have reduced lion

abundance in several hunting areas. Sukuma poisoned 22 lions in 2005–2006 in one block near the Selous (R. Shalom, personal communication). Sukuma have also killed lions in Maswa Reserve (adjacent to the Serengeti) and in the Katavi-Rukwa ecosystem. Nevertheless, the number of lions killed by sport hunters has been stable in the Maasai Steppe, despite intensive retaliatory killing of lions from the Tarangire National Park. Thus, retaliation is unlikely to be the major cause of the overall decline in lion harvests in hunting areas (Table 2).

Ritual Killing

Leopards are not killed in rituals. Maasai kill lions for ritual purposes (*Ala-mayo*), but such incidents are uncommon in the Serengeti-Ngorongoro ecosystem (~2 per year) relative to retaliatory killing (3–4 per year) (Ikanda & Packer 2008) and trophy harvests (11.5 per year). Ritual killing appears to be rare in Tarangire compared with retaliatory killing (Kissui 2008). The Datoga rituals are similar to those of the Maasai (Wilson 1952; Klima 1965), and, like the Sukuma, they have recently settled in wildlife areas in central and western Tanzania. Lion killings by the Datoga have been documented north of the Selous and in the West, but precise impacts on lions are difficult to evaluate. Sukuma conduct ritual killings in western Tanzania, the extent of which is unknown.

Disease

Diseases of lions have been studied only in Serengeti and Ngorongoro Crater, and no quantitative data are available on diseases of leopards in Tanzania. Severe drought led to fatal infections of canine distemper virus and babesia in Serengeti lions in 1994 and Ngorongoro Crater lions in 2001 (Munson et al. 2008), and the Ngorongoro Crater lions also suffered from two undiagnosed epizootics in 1994 and 1998 (Kissui & Packer 2004) (Figs. 3b & e). The Ngorongoro Crater population appears to be immunocompromised by a high degree of inbreeding (Kissui & Packer 2004); a similar situation in South Africa's Hluhluwe iMfolozi Park was ameliorated by translocating unrelated animals into the park population (Trinkel et al. 2008). Thus, chronic vulnerability to disease largely results from inbreeding in small, isolated lion populations, and disease outbreaks are unlikely to have contributed to the persistent population declines in any of the hunting areas.

Harvest for Body Parts and Edge Effects

Although lion teeth and claws have long been sold in local markets and Sukuma use lion parts as medicine, there are so far no reports of lion bones being exported from Tanzania as substitutes for tiger bones in traditional Chinese medicines.

Hunting areas located adjacent to human-dominated areas did not have larger declines in lions or leopards than

hunting areas that were buffered from human-dominated areas, suggesting that the overall effects of local people have been less severe than the effect of sport hunting.

Recommendations

Sport hunters are extremely efficient in locating their quarry, lion and leopard trophy hunting specifically targets adult males, and each male replacement has profound effects on the reproduction of multiple females. Tanzania currently allows about 500 lions and 400 leopards per year to be killed for sport in an area of 300,000 km² (1.67 lions and 1.33 leopards/1000 km²). The proportion of male lions removed by trophy hunters in the mid- to late 1990s was unsustainable (28%/year in some areas).

Lion hunting should not exceed 1.0 lions/1000 km² in the Selous Game Reserve (Fig. 5a), whereas an upper limit of 0.5 lions/1000 km² should be imposed for the rest of the country (Fig. 5b). Within the Selous, leopard harvests increased 2%/year despite an annual average offtake of 2.9 leopards/1000 km² (Fig. 5c); thus, an upper limit of 3.0 leopards/1000 km² would be prudent. In the rest of the country, leopard quotas should not exceed 1.0 leopard/1000 km² (Fig. 5d). If these recommendations were adopted, national quotas would total about 180 lions and 400 leopards/year. These numbers still exceed current harvest levels, but, if they were adopted, hunting effort would be distributed more evenly across the country.

A strict age minimum would help ensure safe harvest levels despite uncertainties about local population sizes (Whitman et al. 2004, 2007). Restricting harvest to male lions that are ≥5 years old may be sufficient to minimize the population impacts of trophy hunting, even if every ≥5-year-old male was removed every year (Whitman et al. 2004, 2007). Lion ages can be reliably estimated in field conditions (Whitman & Packer 2007), and Mozambique's Niassa Reserve has successfully implemented a 6-year age minimum for hunted lions (Begg & Begg 2009), and a few Tanzanian hunting companies have voluntarily set a 6-year age minimum. A safe minimum age for leopards may be 7 years (Packer et al. 2009). Age-assessment criteria, however, are not yet available for leopards, and it is unknown whether leopard ages can be estimated reliably in the field.

Lions and leopards are CITES-listed species; thus, every precaution should be taken to prevent harvesting that could cause populations to decline. We therefore recommend, first, that Tanzania reduce quotas to 0.5 lion (or 1.0 in Selous) and 1.0 leopard (or 3.0 in Selous)/1000 km². Comparable statistical analysis should be performed in other range states, as sustainable offtake rates are likely to vary between countries. Second, professional hunters and clients in every range state should be educated as to

how to estimate ages of lions (Whitman & Packer 2007). Third, the age of each trophy lion should be independently validated by post-mortem photographs illustrating physical features that indicate age (e.g., nose coloration) and tooth x-rays (pulp cavities enclose by year 4 in lions) and physical measurement of tooth wear (Whitman & Packer 2007). Fourth, underage trophy lions should not be exported. Fifth, similar age-assessment criteria and export policies should also be developed for leopards.

Trophy hunting has been considered essential for providing economic incentives to conserve large carnivores (e.g., Baker 1997; Hurt & Ravn 2000; Child 2004; Lindsey et al. 2006; Dickson et al. 2009). Nevertheless, successful conservation clearly requires that hunting harvests not exceed sustainable levels.

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What is an apex predator?

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Large ‘apex’ predators influence ecosystems in profound ways, by limiting the density of their prey and controlling smaller ‘mesopredators’. The loss of apex predators from much of their range has led to a global outbreak of mesopredators, a process known as ‘mesopredator release’ that increases predation pressure and diminishes biodiversity. While the classifications apex- and meso-predator are fundamental to current ecological thinking, their definition has remained ambiguous. Trophic cascades theory has shown the importance of predation as a limit to population size for a variety of taxa (top–down control). The largest of predators however are unlikely to be limited in this fashion, and their densities are commonly assumed to be determined by the availability of their prey (bottom–up control). However, bottom–up regulation of apex predators is contradicted by many studies, particularly of non-hunted populations. We offer an alternative view that apex predators are distinguishable by a capacity to limit their own population densities (self-regulation). We tested this idea using a set of life-history traits that could contribute to self-regulation in the Carnivora, and found that an upper limit body mass of 34 kg (corresponding with an average mass of 13–16 kg) marks a transition between extrinsically- and self-regulated carnivores. Small carnivores share fast reproductive rates and development and higher densities. Large carnivores share slow reproductive rates and development, extended parental care, sparsely populated territories, and a propensity towards infanticide, reproductive suppression, alloparental care and cooperative hunting. We discuss how the expression of traits that contribute to self-regulation (e.g. reproductive suppression) depends on social stability, and highlight the importance of studying predator–prey dynamics in the absence of predator persecution. Self-regulation in large carnivores may ensure that the largest and the fiercest do not overexploit their resources.

The ecological role of large predators is expressed by their classification as ‘apex predators’; a term used to denote their elevated position on the trophic ladder. Apex predators are primarily known for their role as inhibitors of population irruptions of prey and smaller predators, an effect that cascades throughout ecological communities and promotes biodiversity. The keystone role of apex predators as ecosystem regulators is now firmly embedded in ecological theory (Estes et al. 2011, Ripple et al. 2014). Medium-sized predators, termed ‘mesopredators’, also drive community structure through a variety of pathways, including predation on small prey (Roemer et al. 2009). Apex predators limit the density of mesopredators so that total predation pressure is contained (Ripple et al. 2014). The loss of apex predators removes this inhibiting factor, resulting in ‘mesopredator release’ (Crooks and Soulé 1999, Prugh et al. 2009).

‘Apex predator’, ‘mesopredator’ and ‘mesopredator release’ are terms that have set the tone for our understanding of a wide range of ecological processes (Estes et al. 2011). However, the categorization of predators remains ambiguous. Within each ecosystem the largest extant predators are often classed as apex predators even if these same species are considered typical mesopredators elsewhere. For example, cats

and foxes fall easily into the mesopredator group (Crooks and Soulé 1999), but as introduced species on islands they are often the largest mammal present and are therefore classed as apex predators (Rayner et al. 2007, Bergstrom et al. 2009, Roemer et al. 2009). The mesopredator release concept in itself was developed from the study of the coyote *Canis latrans* as an apex predator (Crooks and Soulé 1999), a species frequently placed in the mesopredator group when in the presence of wolves *Canis lupus* (Prugh et al. 2009, Ripple et al. 2013). Some regions contain a rich guild of large predators making it difficult to determine where to draw the line between apex- and meso-predators (Prugh et al. 2009). Indeed, some of the world’s iconic apex predators coexist with larger and fiercer predators (Palomares and Caro 1999), and many of the world’s largest predators are now extinct. Is the gray wolf therefore a mesopredator in the presence of larger carnivores?

Predators of all sizes harass, kill and scare predators smaller than themselves: tigers dominate wolves (Miquelle et al. 2005), wolves exclude coyotes (Ripple et al. 2013), coyotes control foxes (Crooks and Soulé 1999), foxes kill cats (Glen and Dickman 2005), cats suppress rats (Rayner et al. 2007), and rats displace mice (Wanless et al. 2007).

Predators of all sizes can also induce trophic cascades: pumas promote tree recruitment by controlling deer (Ripple et al. 2014), sea otters recover kelp forests by eating herbivorous sea urchins (Estes et al. 2011), cats maintain island productivity by suppressing rabbits (Bergstrom et al. 2009), plants benefit when fish reduce dragonfly predation on pollinating insects (Knight et al. 2005), and nutrient cycling is influenced by the stress response of herbivorous grasshoppers to hunting spiders (Hawlena and Schmitz 2010).

Despite these similarities there appears to be little functional redundancy between large and small predators. The loss of the largest of predators has had a disproportionately disruptive influence on ecosystem structure and function (Ripple et al. 2014); a process coined ‘trophic downgrading’ (Estes et al. 2011). Defining predator status comparatively within each system is problematic because it implies that mesopredators can step into the role of apex predators as these disappear from the landscape. Studies suggest the opposite: mesopredators are not effective replacements for apex predators (Prugh et al. 2009). Size may in fact be a reliable predictor of a predator’s ecological status, reflecting differences in evolutionary pressures and adaptation. A mesopredator may therefore remain a mesopredator even in systems devoid of larger predators, and an apex predator need not be the single largest.

What then distinguishes apex predators from mesopredators? One fundamental consequence of size is that large predators are relatively safe from predation (Promislow and Harvey 1990). In the absence of an effective extrinsic source of predation, there can be two main mechanisms limiting population growth: 1) the decline in the abundance of their prey (a bottom-up force), and 2) an internal mechanism of self-regulation (a socially mediated force). Although ecologists have traditionally supported the bottom-up view (Hayward et al. 2007), trophic cascades theory highlights the role of top-down regulation in population dynamics. It would be surprising if top-down forcing influences all but the largest. Indeed, studies frequently find negative rather than positive correlations between apex predators and their prey (Estes et al. 2011), hinting that apex predator may not be bottom-up driven. While habitat productivity is not ruled out as a contributing factor to population density (Carbone and Gittleman 2002, Jedrzejewski et al. 2007), large predators may be unique in maintaining their own populations at sustainable levels.

Body mass may be a good predictor of apex- and meso-predator status, because it directly influences the rate of extrinsic predation pressure, thus indirectly influencing life-history traits. Across mammals both juvenile and adult mortality rates increase as body mass declines, and higher mortality is associated with r-selected life-history variables (Promislow and Harvey 1990). Among carnivores, increasing body size is associated with dietary requirements for larger prey (Carbone et al. 2007) and lower densities relative to prey biomass (Carbone and Gittleman 2002). Evolutionary pressures that influence body mass may give rise to similar adaptations in different taxonomic groups, and the emergence of a ‘self-regulating ecomorph’ (Flueck 2000).

Most large predator populations are subjected to lethal control (Ripple et al. 2014) and therefore studies of stable

predator populations are rare. Several recent studies have pointed to the importance of considering the condition of social stability in large predators when analyzing predator–prey interactions (Wallach et al. 2009, Cariappa et al. 2011, Ordiz et al. 2013, Cubaynes et al. 2014). Evidence of social interactions that may enable self-regulation has emerged from studies of large predators including bears, large cats, large canids and large otters (Supplementary material Appendix 1 Table A1). These studies offer examples where social interactions, rather than resource availability, drive mortality and fecundity, limit population density and stability, and influence the expression of life history traits that slow population growth rates (Table 1). Where human-caused mortality is low, large predators may therefore retain relatively constant population densities despite differences in resource availability.

Here we investigate the hypothesis that predators above a certain weight threshold are self-regulating, while smaller predators require extrinsic regulation by a larger predator (Fig. 1). We conducted an analysis of life-history traits that may contribute to self-regulation in the Carnivora (hereafter carnivores). We selected the carnivores because trophic cascades effects have been consistently demonstrated for several members of this group (Ripple et al. 2014). We found that carnivores above a threshold mass have life-history traits conducive to self-regulation.

Methods

We conducted a review of life-history traits of terrestrial and semi-terrestrial species, belonging to twelve carnivore families, for which sufficient information was available ($n = 121$, Supplementary material Appendix 1 Table A2). We selected eleven variables representing four major life-history traits, which we considered likely to contribute to self-regulation, and analyzed them in relation to upper limit body mass (ULBM) and average body mass (ABM). Data was sourced from encyclopedias (e.g. Encyclopedia of Life), online databases (e.g. Carey and Judge 2002, de Magalhaes and Costa 2009, IUCN), life-history journals (e.g. Mammalian Species) and other peer-reviewed sources.

Human hunting can have pronounced effects on the expression of life history traits (Haber 1996, Milner et al. 2007) and few populations have escaped this impact (Ripple et al. 2014). We therefore chose upper limit values for most variables (Supplementary material Appendix 1 Table A2) to account for the potential of individuals in undisturbed

Table 1. Evidence that social interactions enable self-regulation in large carnivores. For each Family we summarize the number of studies supporting the propositions that social interactions, rather than resource availability: drive mortality and fecundity (A), limit density (B), affect population stability (C), and affect the expression of life history traits that slow population growth rates (D). The proportion of studies is shown in brackets, with some studies supporting more than one proposition. Summarized from studies compiled in the Supplementary material Appendix 1 Table A1.

Proposition	Ursidea	Felidea	Canidea	Mustelidea	Total
A	8 (89%)	2 (18%)	4 (27%)	3 (60%)	17 (43%)
B	2 (22%)	8 (73%)	7 (47%)	1 (20%)	18 (45%)
C	4 (44%)	3 (27%)	5 (33%)	1 (20%)	13 (33%)
D	7 (78%)	2 (18%)	2 (13%)	0	11 (28%)

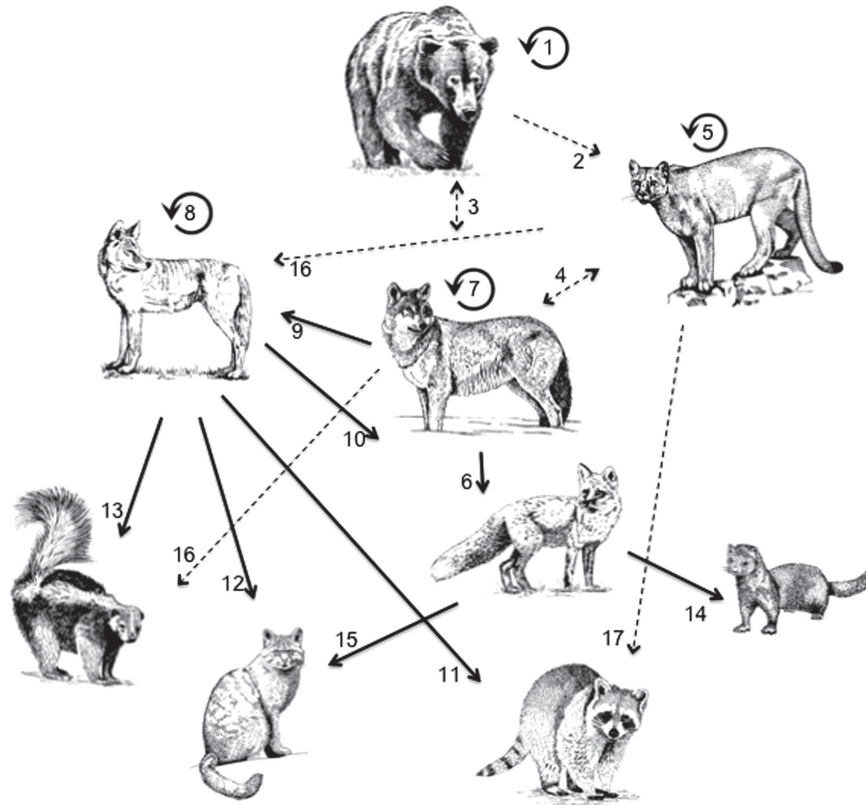


Figure 1. Apex- and meso-predator status are fixed ecological categories: apex predators are self-regulated and smaller predators are extrinsically regulated. Antagonistic interactions (dashed arrows) and top-down forces (thick arrows) exist within and across both groups, but the ability to self-regulate (circular arrows) is unique to large predators. Citations for interactions are: 1, 5, 7, 8 – Supplementary material Appendix 1 Table A1; 2 - Murphy et al. 1998; 3, 4, 16, 17 - Palomares and Caro 1999, Gunther and Smith 2004, Jimenez et al. 2008; 6 - Letnic et al. 2011; 9 - Ripple et al. 2013; 10–13 - Crooks and Soulé 1999; 14 - Carlsson et al. 2010; 15 - Glen and Dickman 2005. Artwork by J. Parkhurst.

populations to grow large, mature, form social bonds, hold territories and provide uninterrupted care for their young. The relation of life-history traits with ULBM and ABM showed similar trends (ULBM and ABM values are correlated $r = 0.97$, $p < 0.0001$), and we chose to present ULBM results because this variable is less likely to be influenced by human activity.

Variables

Reproductive strategy (r/K)

We hypothesized that self-regulating carnivores would employ a K-strategy (i.e. slow life-history) and invest more energy in fewer offspring compared to extrinsically-regulated carnivores. Five variables were assessed for this trait: 1) age at weaning, 2) age at independence (and dispersal), 3) age at sexual maturity, 4) lifespan and 5) population reproductive rate (accounting for reproductive suppression of some females).

The age at weaning and independence provide measures of parental care. To account for relative parental investment, both variables were also analyzed in relation to lifespan and reproductive rate (e.g. age at independence / lifespan / number of offspring / year). We modified the reproductive rate variable to account for social carnivores that limit the reproduction of some females (offspring / year / average number

of breeding females in a group / average number of sexually mature females in a group).

Family planning

The limitation of offspring production below the species' maximum reproductive potential is referred to here as 'family planning', and we expected this trait to contribute to self-regulation. We used two binary variables: 1) female reproductive suppression and 2) infanticide. Female reproductive suppression occurs in social species in which dominant females exclude other sexually mature females from breeding, or litters of subordinates are killed or abandoned.

Female territoriality

Territoriality is considered an important mechanism for spacing individuals or groups and limiting population density (Cariappa et al. 2011). We focused on females because territorial males may occupy the home range of several females and reproduce with all of them (e.g. felids and bears). We included a binary variable 'female territoriality' and a continuous subset variable 'female density'.

For the subset of female-territorial carnivores, we recorded the median female territory size and the average number of females in a social group to calculate an estimate of 'female density' (group size / territory size). We used the median value

because territory size may vary widely in relation to habitat conditions. To account for the differences in body mass we calculated an estimate of carnivore biomass by adjusting the density to standardized metabolic needs (group size / territory size \times ABM^{0.75}, Gittleman and Harvey 1982). Data were obtained for 55 (of 69) female-territorial carnivores.

Cooperative behavior

Cooperative behaviors may be features of self-regulating species and associated with the ability to secure large territories and large prey (Creel and Macdonald 1995). We used cooperative hunting, and two forms of cooperative care: 1) paternal care and 2) alloparental care, as measures of cooperative behaviors, all as binary variables. Carnivores were included in both categories if their social structure was flexible and inclusive of both forms (e.g. red fox *Vulpes vulpes*, Cavallini 1996).

Data analysis

We used a principal components (PC) analysis (SPSS 20), of the eleven variables for which full datasets were available ($n = 73$ species), to identify groups of strongly interacting variables (Jolliffe 2002) across the Carnivora and discretely for each Family and mass group. We compared the main PCs, and each of the individual variables, with log-transformed body mass. We then fit a piecewise regression to identify a threshold in the relationships (Toms and Lesperance 2003), using the segmented package in R (Muggeo 2008). Variables were log-transformed to meet the assumption of constant variance in residuals. Binary variables were tested using a piecewise logistic regression (Toms and Lesperance 2003). We tested the threshold significance using a Davies test (Davies 1987, Piepho and Ogutu 2003). The subset variables female density and female biomass were correlated separately with the strongest PCs and with body mass. We compared the relationship between parental care and parental investment with body mass separately.

Results

The first three PCs cumulatively accounted for 70% of the variation in the dataset (Table 2). Reproductive strategy

Table 2. Scores of the eleven life-history variables in the top three models of the principal component analysis (PCA).

Variables	PC1 (33.6%)	PC2 (25%)	PC3 (11.7%)
Lifespan	0.854	0.184	-0.091
Age at sexual maturity	0.852	0.190	0.048
Age at weaning	0.814	0.174	-0.204
Age at independence	0.770	0.359	0.039
Female reproduction suppression	-0.388	0.800	-0.051
Reproductive potential	-0.601	-0.424	-0.152
Paternal care	-0.487	0.580	-0.238
Alloparental care	-0.328	0.824	-0.216
Cooperative hunting	-0.222	0.513	-0.326
Infanticide	0.044	0.631	0.558
Territoriality (female)	-0.266	0.163	0.832

variables were most strongly associated with the first PC axis (PC1), which is representative of the fast-slow (r-K) life history continuum. The piecewise regression identified a threshold in the relationship between PC1 and ULBM at 33.85 kg (ABM 13–16 kg), with a 95% confidence interval (CI) between 18.16–63.12 kg (Davies test: $p < 0.001$, Fig. 2A). The second PC axis (PC2) was formed by the socially complex behaviors (e.g. ‘family planning’ and alloparental care) on one side, and high reproductive rates on the other, with no significant threshold identified. Female territoriality only appeared as a significant variable in PC3 (Table 2). In no case was a significant threshold detected for the individual variables included in the PCA.

Across the full carnivore mass range, both PC1 and PC2 were positively correlated with body mass (Pearson’s correlation LogULBM: PC1, $r = 0.73$, $p < 0.001$; PC2, $r = 0.38$, $p < 0.01$). There was no correlation between PC3 and body mass (NS). Large carnivores (ULBM ≥ 34 kg) had mostly positive PC1 values (70%) and about half (55%) had positive PC2 values, reflecting a K-strategy and a tendency towards socially complex reproductive behaviors. Small carnivores (ULBM < 34 kg) had predominantly negative PC1 (73%) and PC2 (69%) values, corresponding with an r-strategy and more solitary or biparental social groups (Fig. 2B). Both within and between taxonomic families, large carnivores had consistently higher PC1 and PC2 values (Fig. 2C). However, while small carnivore families were clustered together, each family of large carnivores was distinctly placed along the two axes (e.g. bears had the highest PC1 values and large canids had the highest PC2 values).

Female territoriality was ubiquitous and common across the Carnivora (71% of species), but within the subset of carnivores that are female-territorial, female density was negatively correlated with body mass (Spearman’s $r = -0.77$, $p < 0.001$; Fig. 3A) and with PC1 ($r = -0.41$, $p < 0.01$). Female biomass (female density controlled for standardized metabolic needs) was also negatively related with body mass ($r = -0.48$, $p < 0.001$, Fig. 3B), but not with PC1 (NS). Thresholds were detected for both density (71.95 kg, 95% CI 6.67–775.88) and biomass (73.70 kg, 95% CI 4.52–1199.91), but neither threshold was significant (Davies test: $p = 0.691$ and $p = 0.913$, respectively).

Large carnivores invest more time and a larger portion of their lifetime in each offspring, relative to small carnivores. Parental care (age at weaning and independence) and parental investment (parental care controlled for lifespan and reproductive rate) were positively correlated with body mass (parental care: by weaning, $r = 0.38$, $p < 0.001$, by independence $r = 0.52$, $p < 0.001$; parental investment: by weaning $r = 0.33$, $p < 0.001$, by independence $r = 0.24$, $p < 0.001$). Thresholds were detected for parental investment (by independence: 11.87 kg, 95% CI 3.43–41.02, Davies test: $p = 0.1$; by weaning 14.0 kg, 95% CI 5.64–34.78, Davies test: $p = 0.004$), but only the threshold for weaning was significant (Fig. 4).

Discussion

Life history traits that may influence population regulation differ between large and small carnivores, lending support

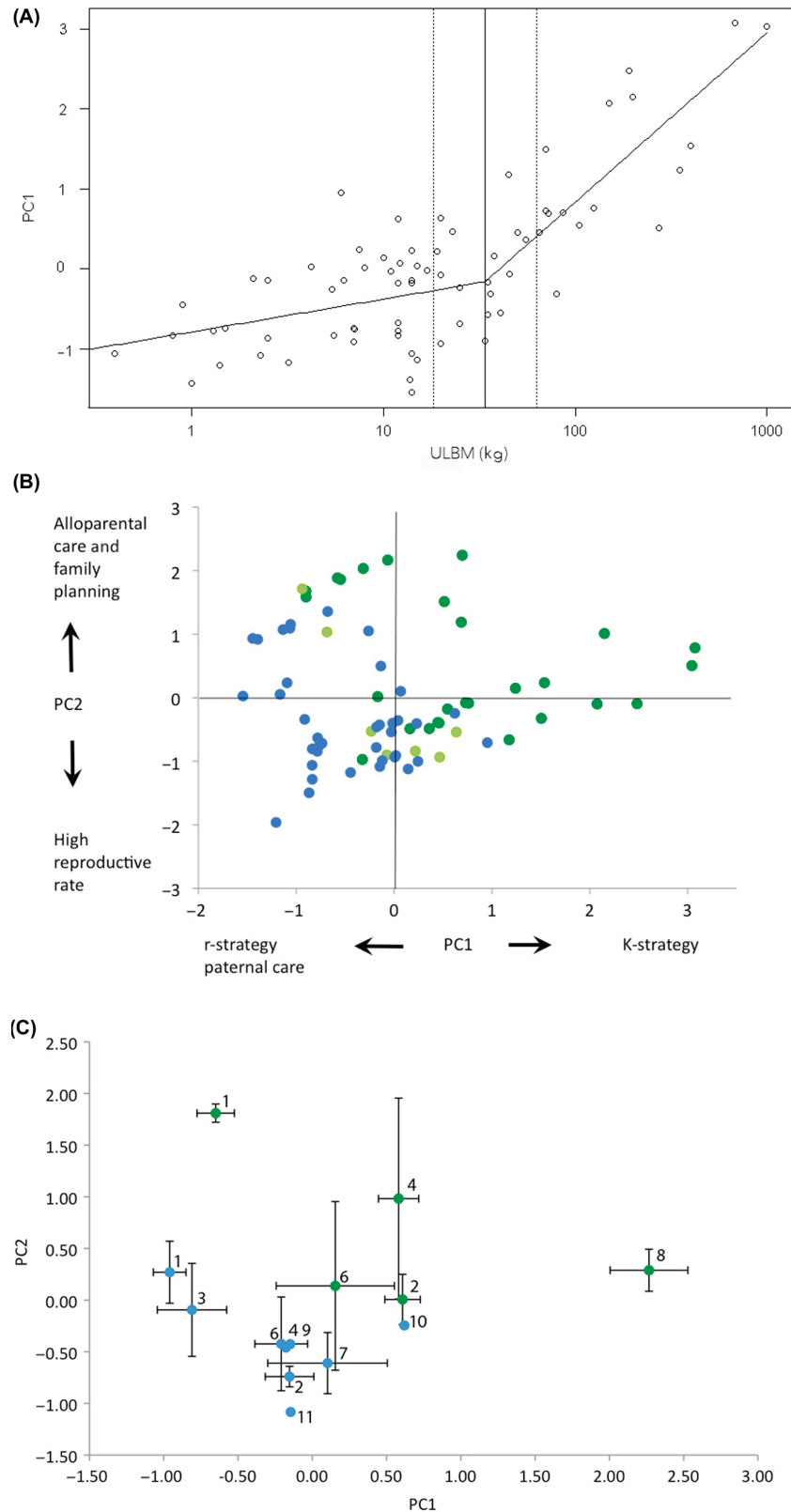


Figure 2. Relationship between the two strongest principal components (PC) and upper limit body mass (ULBM). (A) Relation of PC1 to log transformed ULBM with the estimated threshold identified at 34 kg (full line), with a 95% confidence interval of 18–63 kg (dashed lines). (B) Position of carnivores on the first two PC axes. (C) Position of family and mass groups on the two major axes (average \pm SE), separated at 34 kg. Blue circles are identified as typical mesocarnivores (ULBM < 18 kg), light green circles (in B) denote carnivores that fall within the lower threshold confidence zone (ULBM 18–34 kg) and dark green circles are identified as apex carnivores (ULBM \geq 34 kg). 1 = Canidae, 2 = Felidae, 3 = Herpestidae, 4 = Hyaenidae, 6 = Mustelidae, 7 = Procyonidae, 8 = Ursidae, 9 = Ailuridae (red panda, *Ailurus fulgens*), 10 = Eupleridae (fossa *Cryptoprocta ferox*), 11 = Viverridae (common genet, *Genetta genetta*).

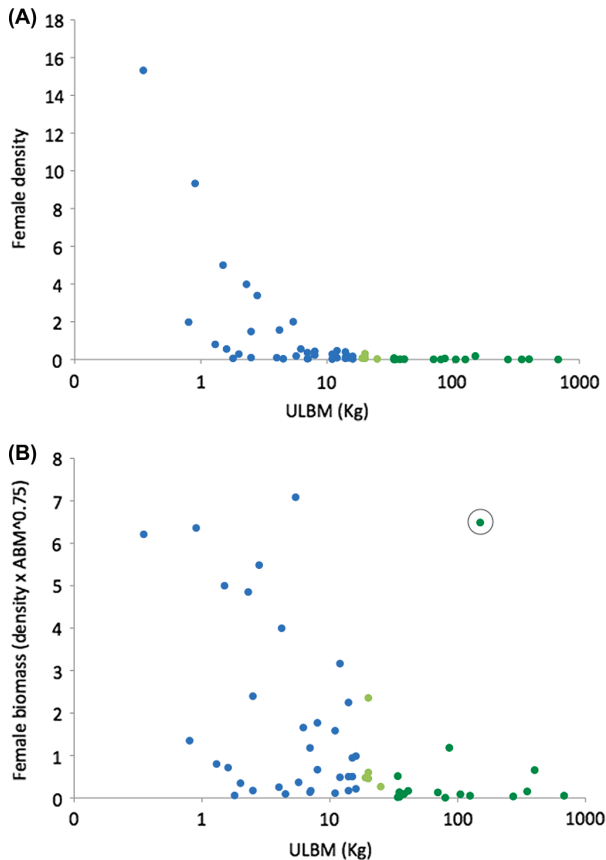


Figure 3. Density (A) and biomass (B) of territorial female carnivores relative to ULBM. The giant panda, an outlier, is circled in (B). Blue circles are identified as typical mesocarnivores (ULBM < 18 kg), light green circles denote carnivores that fall within the lower threshold confidence zone (ULBM 18–34 kg) and dark green circles are identified as apex carnivores (ULBM ≥ 34 kg).

to the proposition that apex- and meso-predator status are fixed. In this analysis of terrestrial and semi-terrestrial carnivores, an ULBM of 18–34 kg (ABM 13–16 kg) marked a transition between extrinsically regulated meso-carnivores and self-regulating apex carnivores. This threshold is similar to the commonly used ABM of 15 kg to distinguish meso-carnivores from apex-carnivores (Prugh et al. 2009, Ripple

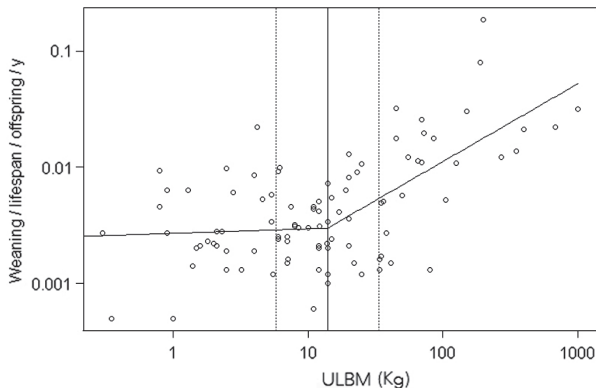


Figure 4. Relationship between parental investment (age at weaning controlled for lifespan and reproductive rate) and body mass with the estimated threshold identified at an ULBM of 14 kg (full line), with a 95% confidence interval of 6–35 kg (dashed lines).

et al. 2014), but is slightly lower than previous studies that found a dietary threshold at an ABM of 20 kg (Carbone et al. 2007). Our analysis also helps clarify the ecological position of carnivore species whose status is ambivalent (e.g. coyotes are recognized here as apex predators).

Large carnivores probably self-regulate because they typically invest more in fewer offspring, suppress the reproduction of mature females and commit infanticide ('family planning'), are socially cooperative and hold sparsely populated territories (Fig. 2–4). Mesocarnivores on the other hand are unlikely to self-regulate and are instead adapted to extrinsic-regulation pressure, as suggested by a higher reproductive rate, lower investment in each offspring, scarcity of 'family planning' and the potential to attain higher densities. Differences between large and small carnivores persist when controlling for standardized metabolic needs and group size (Fig. 3), and for lifespan and reproductive rate (Fig. 4). These life-history traits are often shared more closely within mass groups than within taxonomic groups (Fig. 2C).

Reproductive strategy, the main contributor to the first PC axis, was the most important trait defining carnivore status. Extended parental care and heavier investment in each offspring were particularly characteristic of apex carnivores. Within apex carnivores K-traits and parental investment increase relative to body mass at a faster rate than in mesocarnivores (Fig. 2A, 4). Thus apex carnivores increase their K-traits as body mass increases but this does not consistently occur in the mesocarnivore group. Predation pressure on mesocarnivores of all sizes may be consistently selecting for r-traits.

'Family planning', an important contributor to the second PC axis, was also characteristic of apex carnivores, particularly in canids. Infanticide is often associated with reproductive suppression of sexually mature females, and 65% of carnivores that exclude some females from breeding perform infanticide. In these species the dominant females kill the young of the subordinate females in their social group. Where infanticide is used to restrict the reproduction of females, it most likely acts to limit the size of social groups and ultimately population density. Overall, 52% of carnivores that practice infanticide do not suppress the reproduction of females. In these cases infanticide occurs when a rival male displaces the resident breeding male, and the sire's offspring are killed to gain reproductive advantage (sexually-selected infanticide). Male-driven infanticide has a substantial influence on population density and demography of bears and large felids (Supplementary material Appendix 1 Table A1). Male-driven infanticide may in some cases select for larger groups. In banded mongoose, reproductive suppression is selected against because pup survival increases when more females in each group reproduce due to male infanticide (Cant 2000).

Female reproductive suppression is clearly an important regulation mechanism in social carnivores, occurring in most large canids (88–100%) and large hyenas (67%) (Supplementary material Appendix 1 Table A2). It may however also function indirectly in solitary predators. For example, Ordiz et al. (2008) found that an adult female brown bear was less likely to produce cubs if her nearest neighbor already had cubs. They argued that this could be considered a form of reproductive suppression, probably caused by resource competition among female bears living close to each other.

In apex carnivores, female territoriality contributes to self-regulation by maintaining low densities (Fig. 3, Supplementary material Appendix 1 Table A1), but on its own territoriality is not a significant predictor of predator status (Table 2). Territoriality is unlikely to contribute to self-regulation if territories shrink in response to increased densities, as has been observed in several small carnivore populations (Cavallini 1996, Benson et al. 2006). Flexibility in territorial behavior is probably advantageous for smaller carnivores that have to adjust their space use in relation to the threat of larger carnivores (Cavallini 1996), while territorial stability is important for large predatory carnivores to buffer patchy or variable resources and for protection from dangerous conspecifics (Supplementary material Appendix 1 Table A1).

Cooperative behaviors were more pronounced in large carnivores (Table 2). The predisposition for cooperative hunting is in line with a tendency towards hypercarnivory in large carnivores (Carbone et al. 2007). While cooperative hunting of large prey is not unique to large carnivores (some ant species hunt prey thousands of times their size, Dejean et al. 2010), nor is it obligate (not all large carnivores are carnivorous), the most complex forms of cooperative hunting have been observed primarily in large carnivores (MacNulty et al. 2009, Bailey et al. 2013).

Alloparental care was more common in the large carnivore group, and was associated with ‘family planning’ in the second PC (Fig. 2B). In large social carnivores therefore, the association of alloparental care with female reproductive suppression and infanticide provides a high carer:offspring ratio. Paternal rearing, on the other hand, was affiliated with an r-strategy and with small carnivores in the first PC (Fig. 2B). In both solitary and biparental carnivores, female breeding is unrestricted. An r-strategy without ‘family planning’ is a condition conducive to high reproductive output and is more common in mesocarnivores: 48% of small carnivores versus 7% of large carnivores have negative PC1 values and are solitary or biparental.

The results of our study were robust despite the high level of ‘noise’ in the dataset. The quality of life history knowledge varies between species and traits: research effort is biased towards a small number of carnivores (Ripple et al. 2014); much data are derived from captive animals; and data sourced from wild populations may be equally biased due to anthropogenic effects (Milner et al. 2007). Additionally, life-history traits vary with habitat conditions (Carbone and Gittleman 2002, Jedrzejewski et al. 2007). While these biases are unlikely to be confounding in this study, we do expect that advances in life history studies of wild populations with minimal anthropogenic effects (particularly predator control) will help clarify the mechanisms regulating population size.

Our analysis identified a threshold at approximately 34 kg (ULBM), but there are several reasons not to consider this weight overly prescriptive. Firstly, the threshold mass that differentiates apex- from meso-predators is likely to vary between taxonomic groups. In this study the threshold mass was strongly influenced by three families that contributed the highest number of species: the canids, felids and mustelids. Defining a threshold mass at the Order level was necessary in order to obtain a sufficient sample size, but it may obscure differences between families. For example, the ≤ 12 kg fossa

Cryptoprocta ferox, the largest member of the Eupleridae and Madagascar’s largest carnivore, shares traits with apex carnivores (Fig. 2C). The threshold mass is also likely to be much higher in the pinnipeds whose large body mass is an adaptation to their marine habitat where they are subjected to predation from even larger predators. Secondly, the threshold mass identified can also be influenced by the traits investigated and by sample size. Here, parental investment showed a threshold at a lower position (14 kg) than the eleven variables combined in PC1 (ULBM 34 kg), possibly due to the larger sample size of the former, and the absence of many medium-sized carnivores in the latter. Lastly, it remains unclear whether habitat size influences predator status and self-regulation. Several islands are too small to support large carnivores but do contain medium-sized carnivores, which our analysis suggests are mesopredators. Whether plasticity in the expression and evolution of life-history traits can enable mesopredators to self-regulate and function as apex predators on small islands remains unknown.

The ecological roles of large carnivores vary greatly, and only some function ecologically as ‘apex predators’. Large carnivores that are primarily vegetarian will have ecological effects that differ from those that are carnivorous. Despite this, self-regulation within large predators may provide a distinct ecological function. For example, apex carnivores are less likely to become ‘invasive’. A notable case is the contrasting ecologies of the red fox and the dingo *Canis dingo*, two canids that migrated to Australia. The fox, a mesopredator, correlates positively with resource availability, and in the absence of regulation by dingoes reaches high densities and can drive the extinction of their prey. By contrast the dingo, an apex predator, forms stable population densities across a wide productivity gradient when socially stable, and contributes significantly to the preservation of Australia’s biodiversity (Wallach et al. 2009, Letnic et al. 2011).

Identifying whether predators are primarily self- or extrinsically- regulated requires long-term studies of socially stable populations. Human persecution of predators is a major influence not only on their numbers, but also on their social structure (Haber 1996, Wallach et al. 2009, Ordiz et al. 2013). In turn, social stability determines predator–prey dynamics, and the relative importance of bottom–up and top–down forces driving population size.

Influence of social stability on life-history

The expression of self-regulation in apex carnivores stems from social interactions, and is therefore subject to the condition of social stability. Reproductive strategy (r/k) variables are responsive to conditions of population density, demographics and stability. In apex carnivore populations subjected to human hunting, age at sexual maturity (and primiparity) declines, reproductive rate increases, parental care shortens and demography skews towards juveniles. In non-exploited populations of large canids, offspring often remain within their natal group for several years, delaying primiparity and reducing litter production (Haber 1996). Social stability generally acts to promote the expression of K-traits by slowing down population turnover rates (Supplementary material Appendix 1 Table A1).

Social traits that limit densities are similarly dependent upon a condition of social stability, and hunting influences carnivore densities beyond the loss of the individuals killed. Female reproductive suppression is a social phenomenon, and in hunted populations social groups are fragmented, resulting in more alpha pairs and thus more breeding females (Haber 1996, Bryan et al. 2014). Social stability also influences infanticide rates and its role in populations. Human hunting reduces female-driven infanticide associated with social regulation (Canidea), but increases male-driven infanticide related to reproductive competition (Ursidae and Felidae, Supplementary material Appendix 1 Table A1).

Cooperative behaviors require a state of social stability to develop and are often lost in populations subjected to culling. For cooperative-hunting carnivores, group size and composition are important factors contributing to the hunting success of large and dangerous prey (Creel and Macdonald 1995, MacNulty et al. 2009, Mukherjee and Heithaus 2013). Increased sociality in large canids, for example, is associated with delayed independence and dispersal (Bekoff et al. 1981) and higher pup survival (Stahler et al. 2013). In apex carnivores subjected to hunting, the loss of cooperative behaviors increases mortality rates beyond the individuals directly culled (Haber 1996).

Territoriality can only act to limit population density if territories are large and stable. The breakdown of territory boundaries may contribute to higher densities by increasing immigration rates and reducing spacing behaviors. This has been shown to occur in several large carnivores (Supplementary material Appendix 1 Table A1), but also in the European badger (McDonald et al. 2008), a small carnivore with 'apex' characteristics.

Reduced expression of self-regulation traits in socially disrupted populations can lead to both increases and declines in population density (Supplementary material Appendix 1 Table A1). For example, attempts to control dingoes with poison-baiting and shooting, can inadvertently result in higher population densities, while protected populations tend to be stable (Wallach et al. 2009). Similarly, banning wolf hunting resulted in the establishment of kin-based packs but not in higher densities (Rutledge et al. 2010). Population dynamics may vary widely between those that are socially stable and those that are disrupted. This is relevant to studies that attempt to interpret the effect of productivity on apex predators. Cariappa et al. (2011) argued that wolf populations are limited through social interactions (self-regulated) rather than prey availability alone. They showed that although wolf density can be positively correlated with ungulate biomass, a threshold limit to density is more strongly supported for wolf populations protected from hunting. Similarly, Cubaynes et al. (2014) found that the socially stable wolf population of Yellowstone National Park is primarily limited by intraspecific aggressive interactions rather than by prey availability.

Unfortunately socially stable apex predator populations are rare (Ordiz et al. 2013). Human hunting is threatening 87% of large carnivore species worldwide (ABM of > 15 kg) and most populations are decreasing (Ripple et al. 2014). Life-history traits associated with self-regulation may increase the sensitivity of carnivores to exploitation. High population size alone is an insufficient measure of population

health (Wallach et al. 2009, Ordiz et al. 2013). Carnivores subjected to hunting undergo markedly different population dynamics. There are few studies that have investigated how the loss of individual animals influences populations, and fewer still that have determined the drivers of population density in protected populations. We are only recently beginning to appreciate the profound importance of large carnivores for the health of ecosystems. Apex predators may keep the proverbial 'balance of nature' not only by limiting the populations of those they hunt, but also by limiting themselves. Whether humanity can achieve a similar feat is an important question to consider.

Are we apex primates?

Our earliest ancestors were prey species most likely top-down regulated by large carnivores (Rose and Marshall 1996), but we have evolved into the fiercest predator on the planet, free of extrinsic top-down regulation and are arguably apex predators in our own right. In the words of Louis C. K. "we got out of the food chain" (Oh My God, HBO, 2013). And yet, after surpassing a population size of 7 billion in 2012, triggering a sixth mass extinction and severely depleting non-renewable resources, one would hesitate to argue that humans are self-regulating. Current human society appears to be a classic case of mesopredator release, destined to end in a Malthusian collapse (Ehrlich and Ehrlich 2013). However, when we consider that self-regulation in apex carnivores is dependent upon a state of social stability, we can reflect upon our own condition as that of a socially disrupted apex primate. And social instability can be redressed.

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Supplementary material (available online as Appendix oik.01977 at <www.oikosjournal.org/readers/appendix>). Appendix 1.



Hunter Effort and Success Rates of Hunting Bears with Hounds in Virginia

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HUNTER EFFORT AND SUCCESS RATES OF HUNTING BEARS WITH HOUNDS IN VIRGINIA

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Abstract: Hunting black bears (*Ursus americanus*) with hounds is viewed by many as unethical, and in 5 of 7 states where the issue was brought to public ballot, bear hunting with the use of hounds was closed. In Virginia, hunting bears with hounds is traditional and the favored method of hunting. We documented hunting effort and success using 3 survey methods. We accompanied houndsmen on 190 hunts during training and firearm seasons. We documented 241 hunts using mail surveys and we documented 828 hunts using hunter diaries. Virginia's houndsmen chased bears in $\leq 74\%$ of hunts and harvested bears in $\leq 17\%$ of hunts. Depending on survey method, bears were treed in 24–44% of hunts. Both the number of houndsmen and hounds ranged from 8–11/party and chases lasted 2–5 hours. Houndsmen exerted 8 hours of effort/hunt, although hounds actively hunted only half as many hours (4.2 hrs/hunt). Houndsmen were able to ascertain the gender of 67% of treed bears. Field surveys were useful, as they gave biologists first-hand knowledge of this method of hunting and removed some of the bias associated with hunter recall. Although the hunter diary and mail survey contained recall bias, they provided larger sample sizes and allowed us to survey large geographic regions. The mail survey received a higher response rate than the hunter diary; however, success rates documented in field surveys and the hunter diary were more consistent than in the mail survey.

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Key words: black bear, chased, effort, harvested, hounds, houndsmen, success, survey, treed, *Ursus americanus*, Virginia

The use of hounds to hunt bears is controversial in some parts of the United States (Elowe 1990). Voters, with the urging of animal rights advocates in Colorado, Oregon, Washington, and Massachusetts, have successfully limited bear hunting by closing black bear hunting seasons, outlawing hunting bears over bait or with hounds, or banning hunting bears in the spring when sows are accompanied by small cubs. However, they did not close bear hunting seasons in Idaho and Michigan.

Hunting bears with hounds is traditional for Virginia hunters who hunt exclusively bears. Hunters can also hunt bears by stalking them, but hunting bears over bait is illegal (Virginia Department of Game and Inland Fisheries 1996). Bears can also be harvested incidental to the white-tail deer (*Odocoileus virginianus*) and wild turkey (*Meleagris gallopavo*) seasons with the purchase of a big game license. Bears can be harvested during the month-long deer archery season in October and in the last week of the deer firearm season in November. During the late deer rifle and muzzleloader season, deer hunters can take bears (in certain counties) during the last 2 weeks of December. The late deer rifle and muzzleloader season and late turkey season overlaps with the bear firearm season. Houndsmen and still hunters can harvest bears during the bear firearm season, which occurs during December. In 1992, houndsmen gained a month-long hound training season in September. During the training season, houndsmen are not allowed to carry a firearm or harvest a bear.

Harvest data from Virginia Department of Game and Inland Fisheries documented success rate by method of hunt. In 1995, 13% of 602 bears harvested were killed by bow hunters, 34% were killed by deer hunters during the rifle season and the deer muzzleloader season, and 52% were killed by houndsmen and still hunters in the bear firearm season. In 1996, bow hunters killed 9%, deer hunters reported taking 28%, and houndsmen and still hunters registered 63% of a harvest of 623.

Mail surveys have been used to document harvest rates and sex ratio in the harvest (DuBrock et al. 1978, Peyton 1989, Litvaitis and Kane 1994), but few have documented effort and success of houndsmen. Our primary objectives were to determine hunting effort and success rates of houndsmen during the hound training season and the bear firearm season so that the effect of houndsmen on Virginia's bear population could be better documented.

STUDY AREAS

Our 2 study areas were located in western Virginia and bordered West Virginia. The southwest (SW) study area includes portions of Craig, Giles, and Montgomery counties. The northwest (NW) study area is located in Rockingham and Augusta counties. Both study areas are located in the ridge and valley region of the Appalachian mountain range (Bailey 1976), with elevations ranging from 488 to 1,378 m. Human population densities in these areas range between 16.32 and 129.50 people/km² (Southern Appalachian Man and the Biospheres 1996). Road densities range from 1.17 km/km² on the SW study area to 0.73 km/km² on the NW study area (J. O'Hear, U. S. Forest Service, Blacksburg, Virginia, USA, personal communication, 2000).

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The SW study area encompasses 1,526 km² in the Blacksburg and New Castle ranger districts of the George Washington and Jefferson National Forests (GW & JNF; Fig. 1). This portion of the GW & JNF has many small private inholdings dispersed throughout. Important tree species in the SW study area were white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), black oak (*Q. velutina*), and northern red oak (*Q. rubra*) (J. Overcash, U.S. Forest Service, Blacksburg, Virginia, USA, personal communication, 1996).

The NW study area was an 840-km² area in the Dry River and Deerfield ranger districts of the GW & JNF (Fig. 1). The NW study area is nearly contiguous national forest land. In the NW study area dominant tree species were eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), chestnut oak, pitch pine (*Pinus rigida*), white oak, black oak, northern red oak, yellow poplar (*Liriodendron tulipifera*), and eastern white pine (*P. strobus*) (Godfrey 1996, Higgins 1997).

METHODS

We conducted field surveys during the 1995 and 1996 hound training and bear firearm seasons by accompanying hunting parties on both study areas as they pursued bears with hounds. These field surveys documented their hunting effort and success rates. Hunting effort was the number of hunters participating in the hunt, the number

of hounds involved in each chase, and the length of each chase. During any given hunt, when a bear was chased more than once or more than 1 bear was chased, the successive chases were referred to as the second chase of the hunt. We described hunter success in terms of bears chased (first and second bear), bears treed (first and second bear), and in the bear firearm season, bears harvested (first and second bear). A treed bear was a bear that climbed a tree to escape the dogs and remained in the tree long enough for hunters to approach close and observe it. Hunters almost exclusively harvested bears that were treed and rarely harvested bears as they crossed roads or trails. We also recorded the sex of bears that were treed or harvested and whether the bear was marked (i.e., radiocollared, ear tagged, lip tattooed). The Cooperative Alleghany Bear Study (CABS) provided information and held meetings to inform hunters that bears were being radiocollared and that it was legal to harvest a radiocollared bear.

In 1995, we sent a mail survey to bear hunters to complement the data collected while accompanying hunters in the field. Hunters were randomly selected from either the 1993 and 1994 bear harvest data (still hunters and opportunistic hunters were included in the harvest data), Virginia Bear Hunters Association (VBHA) membership, or hunters that CABS personnel accompanied during the hound training season and bear firearm season. Surveys were sent out during the first, third, and fifth weeks of the bear firearm season, and we mailed reminders 2 weeks after each mailing to nonrespondents (Dillman 1978). We

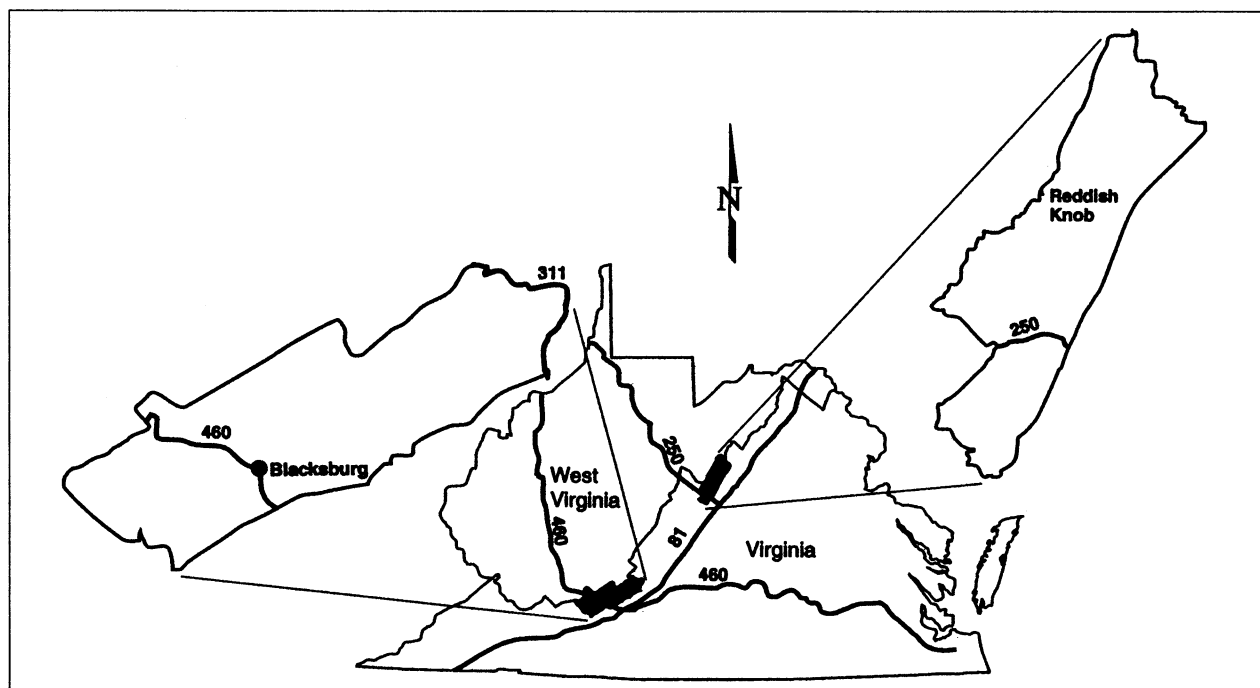


Fig. 1. Northwest and southwest study areas of the Cooperative Alleghany Bear Study, Virginia, USA.

asked hunters to describe their most recent hunt and asked for the same information that was collected in the field surveys.

After preliminary analysis of the mail survey of bear hunters, we determined that hunting effort throughout the season needed to be better documented. Thus, a diary was developed for the 1996 bear firearm season. In an attempt to select only houndsmen for the diary, only bear hunters that harvested a bear in the general bear season in December of 1995 were sampled. In addition, VBHA members and houndsmen that CABS personnel accompanied during the hound training season and bear firearm season were sampled. We mailed letters to hunters asking them to volunteer to complete a Hound Hunter Diary, then mailed diaries 1 week before the start of the bear firearm season to participating hunters. A reminder letter was sent to hunters who had not returned their diaries 1 week after the season closed.

We used the Wilcoxon rank sum test to evaluate differences in hunting effort between the NW and SW study areas, between 1995 and 1996 seasons, and between the hound training season and bear firearm season. The χ^2 goodness of fit and Fisher's exact test were used to test for differences in hunter success. A significance level of 0.05 for these tests was selected *a priori*.

RESULTS

1995 and 1996 Bear Hunter Field Surveys

We documented 190 hunts by 13 hunting parties in 2 study areas in 1995 and 1996 (Table 1). On average, 8 houndsmen and 11 hounds participated in each of the hunts that we documented in 1995 and 1996 and the average length of chase was 1.5 hours (Tables 2–4).

Hunting Effort from Field Surveys

Average number of hunters ranged from 4.5 (1995, SW, training season) to 12.3 (1996, NW, firearm season). Number of hounds averaged 2.5 (1995, SW, firearm season) to 12.3 (1996, SW, firearm season) hounds in each chase (a chase is defined as each separate attempt to chase a bear during one day of hunting effort). Length of a chase averaged 0.7 hours (1996, NW, firearm season) to 1.9 hours (1995, NW, training season; 1995, SW, firearm season, 1996; SW, training season; Table 2).

We documented differences in hunting effort between seasons, study areas, and years. During 1995 in the SW study area, the mean number of hounds and the length of the first chase in the hound training season and the bear firearm season did not differ ($P = 0.10$). However, more hunters participated in the kill season ($P = 0.05$). On the NW study area, all measures of effort for the hound train-

Table 1. Number of hunts and bears treed from field surveys by 13 hunting parties on the southwest (SW) and northwest (NW) study areas of the Cooperative Alleghany Bear Study, Virginia, 1995–96.

Area, Result	Hunts	
	1995	1996
SW, number of hunts	41	41
treed	12	18
NW, number of hunts	65	43
treed	29	9
Total hunts	106	84
		190

ing season were similar to those for the bear firearm season ($P = 0.13$ – 0.65).

In 1995, more hunters participated in hunts on the NW study area than on the SW study area during both the hound training season ($P = 0.0001$) and bear firearm season ($P = 0.006$; Table 2). However, there was no difference in the number of hounds participating in the first or the second chase ($P = 0.15$ – 0.74) or in the length of each chase ($P = 0.11$ – 0.49) between the 2 study areas (Table 2).

In 1996, hunting effort within seasons and between study areas did not differ ($P = 0.11$ – 0.97 ; Table 2). Similarly, hunting effort in the hound training season was similar to that in the bear firearm season on both study areas (SW, $P = 0.07$ – 1.0 ; NW, $P = 0.35$ – 0.88), although more hunters participated in hunts on the SW study area during the 1995 firearm season. Hunting effort during the hound training season was the same in 1995 and 1996 ($P = 0.10$ – 0.93) on both study areas, although more hunters participated in hunts on the SW study area during the 1996 hound training season ($n = 6.7$, $P = 0.01$). We did not detect differences between years during the bear firearm seasons of 1995 and 1996 ($P = 0.27$ – 1.0). Hunting effort in 1995 and 1996 was not combined because we were interested in documenting between-year differences.

Hunter Success from Field Surveys

On average, bears were chased in 65% of hunts; 24% of bears chased were treed, and a bear was harvested in 5% of all hunts (Tables 3, 5). Our field surveys indicated that the range of success in chasing a bear was 33% (1995, SW, firearm season, second bear) to 83% (1995, NW, training season, second bear) of all hunts and treed on 0% (1995, SW firearm season, second bear; 1996, NW firearm season, second bear) to 63% (1995, NW, firearm season, second bear) of all attempted chases (Table 4). Bears were harvested from 0% (1995, SW, second bear; 1996, NW, first and second bear) to 40% (1996, SW, second bear) of all chases during the firearm seasons. Hunting success (chasing or treeing a bear) during the hound training season was not different from hunting success during the bear firearm season in 1995 or in 1996 ($P = 0.06$ – 1.0). However, in 1996 houndsmen on the NW study area had a higher chance of chasing a bear in the hound training

Table 2. Comparison of hunting effort from field surveys during the hound training and the bear firearm (kill) seasons between the southwest (SW) and northwest (NW) study areas of the Cooperative Alleghany Bear Study, Virginia, 1995–96.

Season year, study area	Hunter effort									
	Hunters/hunt		Number of hounds				Length (hrs.)			
			First chase		Second chase ^a		First chase		Second chase ^a	
	Hunts	\bar{x} (SD)	Hunts	\bar{x} (SD)	Hunts	\bar{x} (SD)	Hunts	\bar{x} (SD)	Hunts	\bar{x} (SD)
Hound training										
1995 SW	24	4.5 (2.8)	25	6.6 (5.4)	9	7.4 (4.4)	25	1.0 (1.5)	8	1.3 (1.5)
NW	44	10.0 (5.8)	44	7.9 (5.4)	25	7.2 (5.7)	44	1.5 (1.7)	24	1.9 (1.9)
P^b		0.0001		0.32		0.74		0.11		0.42
1996 SW	29	6.7 (3.3)	29	8.0 (5.2)	8	11.4 (8.3)	29	1.9 (2.5)	8	0.8 (0.9)
NW	34	8.5 (4.3)	34	9.3 (8.6)	8	9.0 (7.2)	34	1.5 (1.9)	8	1.1 (2.0)
P^b		0.11		0.92		0.49		0.67		0.55
Bear Firearm										
1995 SW	15	6.6 (3.3)	16	8.4 (4.4)	2	2.5 (2.1)	14	1.9 (1.9)	2	—
NW	21	11.7 (5.9)	21	6.2 (5.4)	9	9.8 (8.4)	21	1.6 (2.2)	8	0.9 (1.0)
P^b		0.006		0.15		—		0.49		—
1996 SW	12	6.8 (3.9)	12	12.3 (7.7)	5	9.6 (4.5)	12	1.3 (1.5)	5	0.8 (1.3)
NW	9	12.3 (11.1)	9	8.1 (7.9)	5	7.0 (4.2)	9	1.6 (2.1)	5	0.7 (1.0)
P^b		0.15		0.20		0.35		0.97		0.82

^a Second chase starts after the bear trees and is chased again, or a different bear is chased.^b Wilcoxon rank sum test.

season ($P = 0.02$). In the 1995 hound training season, hunting success was the same between study areas ($P = 0.20$ – 1.0), with the exception of higher success in chasing the first bear on the NW study area ($\chi^2 = 4.22$, $P = 0.04$; Table 3). In the 1995 bear firearm season, hunting success did not differ between study areas ($P = 0.25$ – 1.0 ; Table 3), although hunters treed more bears on the NW study area ($P = 0.008$; Table 3). In the 1996 hound training and bear firearm season, hunters had higher overall success of chasing a bear (first and second bears chased included in calculation) in the firearm season on the NW study area ($P = 0.04$; Table 4); all others did not differ between study areas ($P > 0.10$; Table 3). We found no between-year differences in hunting success during the hound training season ($P = 0.08$ – 1.0) or the bear firearm

season ($P = 0.07$ – 1.0) on either study area, although more bears were treed in 1996 on the SW study area during the firearm season ($P = 0.02$).

Characteristics of Harvested Bears from Field Surveys

In the 1995 bear firearm season, we accompanied hunters on 37 hunts. A single male bear weighing 77 kg (live weight) was harvested on the SW study area. The 3 bears harvested during our field surveys in the NW study area were males and averaged 87 kg (live weight). In 1995, three bears were harvested in the SW study area during field surveys; they averaged 102 kg. The one female harvested was 8 years old, weighed 72 kg, and had 4 cubs when handled in March of 1996. The hunters did not

Table 3. Comparison of hunting success from field surveys during the hound training and the bear firearm (kill) seasons between the southwest (SW) and northwest (NW) study areas of the Cooperative Alleghany Bear Study, Virginia, 1995–96.

Season year, study area	Hunter Success					
	Chased		Treed		Harvested	
	First bear n (%)	Second bear ^a n (%)	First bear n (%)	Second bear ^a n (%)	First bear n (%)	Second bear ^a n (%)
Hound training						
1995 SW	25 (48)	10 (60)	25 (28)	10 (30)	—	—
NW	44 (73)	24 (83)	44 (23)	24 (29)	—	—
P^b	0.04	0.20	0.63	1.00	—	—
1996 SW	29 (62)	8 (63)	29 (24)	8 (38)	—	—
NW	34 (71)	8 (75)	34 (9)	8 (13)	—	—
P^b	0.48	1.00	0.17	0.57	—	—
Bear Firearm						
1995 SW	16 (63)	3 (33)	16 (13)	3 (0)	16 (6)	3 (0)
NW	21 (67)	8 (63)	21 (33)	8 (63)	21 (5)	8 (25)
P^b	0.79	—	0.25	—	1.00	—
1996 SW	12 (75)	5 (80)	12 (42)	5 (60)	12 (8)	5 (40)
NW	9 (56)	5 (40)	9 (56)	5 (0)	9 (0)	5 (0)
P^b	0.40	0.52	0.67	0.17	1.00	0.44

^a Second chase starts after the bear trees and is chased again, or a different bear is chased.^b Fisher's exact test.

observe cubs with the bear when she was harvested the following December. No bears were harvested when we accompanied hunters in the NW study area in 1996.

1995 Mail Survey

We mailed 762 surveys to bear hunters in 1995; 30 were undeliverable and 532 (73%) hunters returned their surveys. Of the 532 respondents, 241 (45%) were bear hunters who used hounds to hunt bears in the 1995 bear firearm season. Only hunters who used hounds ($n = 241$) were included in the analyses.

As reported from the mail survey, the average hunting party consisted of 10.4 hunters and, on average, 8.4 hounds participated in the first chase (Table 4). Bears were chased in 53% of hunts; 31% of bears chased were treed, and a bear was harvested in 14% of all hunts (Table 5). During these chases, a bear escaped from the original tree and ran to a second tree 21% of the time. The average length of the first chase was 4.6 hours (Table 4). Treed bears were 46% male and 16% female; 38% could not be identified by sex.

A second chase occurred in 27 of the 241 hunts (11%) with an average of 9 hounds involved in each of the second chases. The average length of the second chase was 3.7 hours and the bear was treed 9% of the time. When a second bear was chased, 27% of the bears that were treed were males, 15% were females, and the sex of 58% was not determined. During the second chase a bear was harvested 19% of the time (Table 5).

1996 Bear Hunter Diary

Letters were mailed to 611 houndsmen asking them to volunteer to complete a hunter diary; 102 houndsmen volunteered to participate. Twenty-three percent of Virginia Bear Hunters Association members ($n = 67$) and 11% of houndsmen not affiliated with VBHA ($n = 35$) that harvested a bear in 1995 volunteered to complete a diary. The response rate was 59% (60 diaries). Five of the 102 diaries were not used because the hunters were unable to hunt that year.

According to the diaries, the average hunting party in 1996 consisted of 10.5 hunters, and, on average, 7.5 hounds were used in the first chase (Table 6). Hunters spent, on average, 8 hours on each hunt, and hounds chased or tracked a bear an average of 4.2 hours. The average time the first bear was actively pursued by hounds was 2.4 hours. A bear was chased during 74% of all hunts, and in 44% of all hunts a bear was treed (Table 5). The first bear chased was treed twice in 9% of the hunts and the second bear was treed twice in 8% of the hunts. Two hundred and forty-three (67%) of 361 treed bears were identified by sex (65% male; Table 6).

A second bear was chased on 139 (17%) of 828 hunts. On average, 10 hunters and 8 hounds were involved in the second chase (Table 4). The average time a second bear was actively pursued by hounds was 2.6 hours. A bear was chased 96% of the time that a second chase was attempted, and in 49% of all hunts a bear was treed in the second chase (Table 5). Forty-six of 68 treed bears (68%) were identified by sex (72% male; Table 6). A bear was

Table 4. Comparison of hunting effort between field surveys, mail surveys, and bear hunter diary, Virginia, 1995 and 1996.

		Hunter effort								
		First chase				Second chase ^a				
	<i>n</i> ^b	Average hunters/hunt	<i>n</i> ^b	Average no. of hounds	<i>n</i> ^b	Average length (hr)	<i>n</i> ^b	Average no. of hounds	<i>n</i> ^b	Average length (hr)
Field surveys ^c	188	8.3	190	11.3	187	1.5	188	8.0	69	3.0
Mail surveys	241	10.4	241	8.4	241	4.6	27	9.0	26	3.7
Hunter diary	761	10.5	821	7.5	796	2.4	138	8.0	132	2.6

^a Second chase starts after the bear trees and is chased again, or a different bear is chased.

^b Sample size (*n*) represents number of hunts and not all hunters reported all information.

^c Results from training and firearm seasons combined.

Table 5. Comparison of hunting success between field surveys, mail surveys, and bear hunter diary, Virginia, 1995 and 1996.

	Hunter success					
	Chased		Treed		Harvested	
	First bear % (<i>n</i> ^b)	Second bear ^a % (<i>n</i> ^b)	First bear % (<i>n</i> ^b)	Second bear ^a % (<i>n</i> ^b)	First bear % (<i>n</i> ^b)	Second bear ^a % (<i>n</i> ^b)
Field surveys ^c	65 (190)	69 (71)	24 (190)	31 (71)	5 (58)	19 (21)
Mail surveys	53 (241)	11 (241)	31 (241)	9 (241)	14 (241)	19 (26)
Hunter diary	74 (828)	96 (139)	44 (828)	49 (138)	17 (828)	21 (140)

^a Second chase starts after the bear trees and is chased again, or a different bear is chased.

^b Sample size (*n*) represents number of hunts and not all hunters reported all information.

^c Results from training and firearm seasons combined.

Table 6. Sex of bears that were treed during the 1996 bear firearm season as reported in sixty 1996–97 bear hunter diaries, Cooperative Alleghany Bear Study, Virginia.

	<i>n</i> ^a	Male (%)	Female (%)
First bear treed	243	65.0	35.0
Second bear treed ^b	46	71.7	28.3
First bear chased and harvested	140	76.4	23.6
Second bear chased and harvested ^b	34	79.4	20.6

^a Not all hunters reported all information.

^b Second chase starts after the bear trees and is chased again, or a different bear is chased.

harvested by 17% of those that attempted a first chase and by 21% of those that attempted a second chase (Table 5). Overall, a bear was harvested in 20% of all hunts (includes first and second chases); males comprised 76% of the bears harvested from the first chase and 79% of the bears harvested from the second chase (Table 6).

Comparison of Three Survey Methods

Reports of hunting effort were consistent across the 3 different surveys, with the exception of length of first chase; estimates from the mail survey were 2 to 3 times longer than reported by other methods (Table 4). The higher estimate for length of first chase may be due to recall error. However, reported hunter success rates were less consistent (Table 5). Fewer first bears were reported harvested in field surveys than in the mail surveys or the hunter diaries, and fewer second bears were reported chased and treed in mail surveys.

DISCUSSION

Field surveys indicated there were virtually no differences in hunting effort or hunting success between seasons, study areas, and years, although in some instances this may be a function of sample size. DuBrock et al. (1978) surveyed bear hunters in Virginia to characterize bear hunting with hounds. They found that, on average, hunters that owned hounds owned 4 hounds, had 11 hunters in their hunting party, and used between 2 and 35 hounds in a bear chase. The DuBrock et al. (1978) findings are consistent with this study.

We found some limitations in documenting effort through field surveys and the 1995 mail survey. For instance, we did not document hunting effort in terms of the length of time hunters spent hunting, only length of time bears were chased. The length of chase should be considered as a measure of hound effort and not a measure of the actual length of time a bear was chased. Hounds rarely encounter a bear immediately after they are released on a track. Length of chase may index how long a bear was chased, but is likely an overestimate. Allen (1984) reported that in Maine, chases initiated by hounds locating

a track lasted 3.5 hours. This was consistent with the estimates from the 1995 mail survey but longer than chases documented in the field surveys and the 1996 bear hunter diary.

The use of hounds to hunt bears does not guarantee that a bear will be treed. Elowe (1990) reported that hounds in Massachusetts successfully treed a bear 30% of the time. Hounds released on radiocollared bears in Wisconsin were unable to tree a bear in 8 chases (Massopust and Anderson 1984). In Maine, bears were treed in 9 of 22 chases (41%) when the bear was first located by radiotelemetry. When chased from baits, bears were treed in 4 of 16 chases (25%), and when chased from tracking, they were treed in 14 of 43 chases (32%; Allen 1984). Willey (1980) used hounds in Vermont to capture bears, and in 38 days of chasing only 10 bears were treed. These treeing rates were consistent with those observed in this study (range = 24–44%).

Field surveys documented that houndsmen harvested a bear in the SW study area in 6% and 8% of hunts and in the NW study area in 5% and 0% of hunts in 1995 and 1996, respectively. These houndsmen harvested 14% of the bears that they successfully chased and 24% of the bears that treed. The harvest rates of houndsmen that were accompanied by CABS personnel were consistent with the harvest rates reported in Michigan (17%) and New Hampshire's (18.6%) harvest surveys (Peyton 1989, Litvaitis and Kane 1994). However, harvest rates documented in the 1995 hunter survey and 1996 hunter diary were higher than in Michigan and New Hampshire. Houndsmen that returned mail surveys harvested 25% of the bears they chased and 40% of the bears that were treed. Houndsmen that completed a hunter diary harvested 23% of the bears they chased and 39% of the bears that treed. The low success rate (percent of bears chased that were harvested) in terms of harvest may reflect the selectivity of houndsmen (Willey 1972, Poelker and Hartwell 1973, Hardy 1974, DuBrock et al. 1978, Peyton 1989, Litvaitis and Kane 1994).

Houndsmen claim to select against females, but the mail survey indicated that 40% of houndsmen did not or could not identify sex of the treed bear. In Virginia, we observed a harvest that is skewed toward males (Higgins 1997), most likely because houndsmen select older, larger bears in an effort to select against females or harvest a trophy animal.

The general public often assumes that the use of hounds gives a hunter an unfair advantage (Elowe 1990). Not only does the hound aid the hunter, but the hound exerts the most effort. In an attempt to quantify this facet of "fairness", the 1996 bear hunter diary was implemented. We determined fairness by documenting effort of Virginia's houndsmen, hounds, and bears. Prior to the

implementation of the hunter diary, we only documented length of time hounds spent pursuing a bear. The 1996 bear hunter diary specifically asked hunters what time they started hunting and what time they finished hunting, what time hounds were released and what time hounds finished chasing or tracking a bear, and length of time a bear was chased. Although these estimates are subjective, they are the best we have documented thus far. Hunters exerted the most effort (8 hrs) in terms of time spent in the woods (looking for tracks before releasing hounds and looking for hounds once the chase finished), and hounds actively hunted (4.2 hrs) half as many hours as hunters. Bears were chased by hounds for only half as many hours as hounds actually hunted (2.4 hrs; hounds may be released on a bear's track hours after the bear had been there).

Response rate in the 1995 mail survey was high (73%) and may indicate hunters' interest in the management of bears. Such high responses are common; many bear hunters in Arkansas (75–85%), Michigan (75%), and New Hampshire (72%) also responded to hunter surveys (Pharris and Clark 1987, Peyton 1989, Litvaitis and Kane 1994). The lower response rate of the 1996–97 bear hunter diary (59%) may be due to the extra time and commitment that a hunter diary requires (S. McMullin, Virginia Polytechnic Institute and State University, personal communication, 1997). The majority of respondents from the 1995 mail survey and 1996 bear hunter diary came from hunters who hunted within the northwest and southwest study areas, or were members of the VBHA. The high response rate of these hunters may be a result of the effort CABS personnel made in establishing a working relationship with the members of the VBHA and with hunters who hunt within the study areas of CABS.

The bear hunter diary appeared to be a reliable means of documenting hunting effort and success. It had the largest sample size of the 3 methods used and it documented hunter effort throughout the season. However, it had a lower response rate than the mail survey. Only 17% of houndsmen asked to complete a hunter diary volunteered to do so and only 60% of these houndsmen returned completed diaries. Therefore, <10% of Virginia's houndsmen were represented in the results of the hunter diary. The success rates documented in field surveys and the hunter diary were more consistent than in the mail survey, again lending greater reliability to field surveys and the diary. Field surveys were valuable as well, and they avoided hunter bias because CABS personnel collected the data. Additionally, the field survey allowed biologists to interact with hunters and experience hunting bears with hounds. However, only 13 hunting parties provided data for the field surveys.

Hunting bears with hounds is a tradition in Virginia. Virginia may eventually be targeted by groups whose intent is to close bear hunting with the use of hounds, thus knowledge of houndsmen effort and success rates may be useful in addressing the issue of fairness. Virginia houndsmen were moderately successful; between 11% and 20% harvested bears. Similar harvest rates have been documented in other states that use hounds to hunt bears (Peyton 1989, Litvaitis and Kane 1994). Data from this study documented that on average houndsmen successfully chased a bear in approximately 70% of all hunts, treed approximately 40% of these bears, and harvested 32% of the bears that were treed. Since houndsmen were relatively successful in chasing a bear, it appears that using hounds is a distinct advantage for encountering bears. However, the low harvest rates suggests that hunters may be selective and that hounds are not used strictly to ensure that a bear is harvested. It is more likely that houndsmen enjoy working with their hounds, as do duck hunters, upland game bird hunters, and rabbit hunters.

MANAGEMENT IMPLICATIONS

Animal rights groups have increased the public's awareness of the methods used to hunt bears and have given the public cause to question the ethics of certain aspects of hunting bears. Many state agencies have switched from managing bears as a nuisance animal to managing them as a game species. However, documentation of methods used to hunt bears has been limited. The current licensing structure (1997) in Virginia allows any hunter that purchases a big game hunting license (deer, bear, turkey tag) to harvest a bear. In December, bears can be taken with the use of hounds, still hunting during late deer muzzleloader season, and during the turkey season; however, method of take is not documented at check stations. As a result, the Virginia Department of Game and Inland Fisheries includes all bears harvested in December in their estimate for hound hunter harvest rates. Thus, the percent of bears taken by houndsmen in Virginia each year is likely over-estimated. For Virginia to more clearly and accurately depict the effect of hunting bears with the use of hounds, method of take could be included on game check station check cards. To aid in identifying the number of bear hunters who use hounds in Virginia, hunters could be required to purchase a separate bear hunting license. The bear hunting license could also have a query for the method used to hunt bears (i.e., hounds, incidental, or still hunting). As a result, the number of houndsmen that hunt bears and the success rates of Virginia's houndsmen can be more accurately depicted from harvest data.

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