Hilderbrand et al. 1999

The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears

G.V. Hilderbrand, C.C. Schwartz, C.T. Robbins, M.E. Jacoby, T.A. Hanley, S.M. Arthur, and C. Servheen

Abstract: We hypothesized that the relative availability of meat, indicated by contribution to the diet, would be positively related to body size and population productivity of North American brown, or grizzly, bears (*Ursus arctos*). Dietary contributions of plant matter and meat derived from both terrestrial and marine sources were quantified by stable-isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of hair samples from 13 brown bear populations. Estimates of adult female body mass, mean litter size, and population density were obtained from two field studies of ours and from other published reports. The populations ranged from largely vegetarian to largely carnivorous, and food resources ranged from mostly terrestrial to mostly marine (salmon, *Oncorhynchus* spp.). The proportion of meat in the diet was significantly correlated with mean adult female body mass ($r = 0.87$, $P < 0.01$), mean litter size ($r = 0.72$, $P < 0.01$), and mean population density ($r = 0.91$, $P < 0.01$). Salmon was the most important source of meat for the largest, most carnivorous bears and most productive populations. We conclude that availability of meat, particularly salmon, greatly influences habitat quality for brown bears at both the individual level and the population level.

Résumé : Nous avons posé en hypothèse que la disponibilité relative de chair animale, telle qu'évaluée d'après sa proportion dans l'alimentation, est probablement reliée directement à la taille corporelle et à la productivité de la population chez l'Ours brun ou Grizzli, *Ursus arctos*. Les contributions alimentaires respectives des matières végétales et animales provenant de sources terrestres et marines ont été évaluées par une analyse des isotopes stables ($\delta^{13}C$ et $\delta^{15}N$) dans des échantillons de poils prélevés chez 13 populations d'ours. Des estimations de la masse corporelle des femelles adultes, du nombre moyen de petits par portée et de la densité des populations ont été obtenues au cours de nos deux études sur le terrain et à partir de données publiées. Certaines populations étaient surtout végétariennes, d'autres surtout carnivores et leurs ressources alimentaires variaient de principalement terrestres à principalement marines (saumon, *Oncorhynchus* spp.). La proportion de tissu animal dans le régime était en corrélation significative avec la masse moyenne des femelles adultes (r = 0,87, P < 0,01), le nombre moyen de petits dans une portée (r = 0,72, P < 0,01) et la densité moyenne de la population (r = 0,91, P < 0,01). Le saumon était la principale source de chair animale pour les ours les plus gros, les plus carnivores et pour les populations les plus productives. Nous devons conclure que la disponibilité de matières animales, particulièrement la chair de saumon, améliore fortement la qualité de l'habitat des Ours bruns, autant pour les individus que pour les populations.

[Traduit par la Rédaction]

Introduction

The historic range of the North American brown, or grizzly, bear once spanned from the Arctic to central Mexico and from the Pacific Ocean to the Mississippi River (Servheen 1984). Expanding human populations and habitat loss reduced this range to much of Alaska, western Canada, and small areas in the contiguous 48 United States (Servheen 1984; U.S. Fish and Wildlife Service 1993). Because of the reduction in population size and range, the griz-

Received April 27, 1998. Accepted September 14, 1998.

G.V. Hilderbrand[1] and M.E. Jacoby. Department of Zoology, Washington State University, Pullman, WA 99164, U.S.A.
C.C. Schwartz[2] and S.M. Arthur.[3] Alaska Department of Fish and Game, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, U.S.A.
C.T. Robbins. Departments of Natural Resource Sciences and Zoology, Washington State University, Pullman, WA 99164, U.S.A.
T.A. Hanley. Pacific Northwest Research Station, United States Forest Service, 2700 Sherwood Lane, Suite 2A, Juneau, AK 99801, U.S.A.
C. Servheen. United States Fish and Wildlife Service, University Hall, University of Montana, Missoula, MT 59812, U.S.A.

[1]Author to whom all correspondence should be sent at the following address: Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518 U.S.A. (e-mail: Grant_Hilderbrand@Fishgame.state.ak.us).
[2]Present address: Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717, U.S.A.
[3]Present address: Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, U.S.A.

Table 1. Isotope signatures and dietary contributions for adult female North American brown bears.

Population	N	$\delta^{13}C$	$\delta^{15}N$	Dietary contribution (%) Marine meat	Terrestrial meat	Plant matter
Admiralty Island, Alaska	9	−19.3±0.7	10.4±0.8	77±18	0.0	23±18
Arctic National Wildlife Refuge	12	−21.9±0.3	4.5±0.5	0.0	17±15	83±15
Black Lake, Alaska	10	−19.4±0.4	13.8±0.8	79±14	2±5	19±11
Brooks Range, Alaska	19	−21.9±0.3	4.7±0.9	0.0	28±19	72±19
Denali National Park	7	−23.1±0.5	3.6±0.7	0.0	4±11	96±11
Glacier National Park	7	—	3.2±0.8	0.0	3±4	97±4
Katmai National Park	18	−19.8±0.7	11.3±1.5	62±25	7±15	31±19
Kenai Peninsula, Alaska	14	−19.9±0.6	12.1±1.9	62±24	13±23	25±16
Kluane National Park	19	−23.1±0.7	3.3±0.9	0.0	2±5	98±5
Prudhoe Bay, Alaska	7	−21.9±0.4	5.5±1.0	2±5	42±34	56±31
Susitna Valley, Alaska	20	−21.5±0.3	4.3±0.9	4±6	9±13	87±13
Terror Lake, Alaska	15	−20.7±0.4	7.0±1.8	33±16	0±1	67±16
Yellowstone National Park	6	—	5.8±1.0	0.0	44±22	56±22

Note: Values are given as the mean ± 1 SD.

zly bear was listed as threatened under the U.S. Endangered Species Act in 1975 (Servheen 1984; U.S. Fish and Wildlife Service 1993). Since its listing as a protected species in the contiguous 48 United States, conservation efforts have emphasized reduction of mortality, habitat management, public education, and reintroduction of bears to selected ecosystems (Servheen 1997).

Brown bears have one of the lowest reproductive rates of any terrestrial mammal (Bunnell and Tait 1981). Because female bears give birth during hibernation, they must accumulate enough energy stores to support themselves and their offspring through this period of winter dormancy. In bears, reproductive success is directly related to body mass in the fall (Rogers 1976; Blanchard 1987; Stringham 1990*a*, 1990*b*; Schwartz and Franzmann 1991; Atkinson and Ramsay 1995; Samson and Huot 1995). The combined costs of hibernation, gestation, and lactation place large energetic demands on brown bears (Watts and Jonkel 1988; Farley and Robbins 1995).

The availability of high-quality food resources in late summer and fall is especially important for the accumulation of fat by bears for sustenance through winter dormancy (Farley and Robbins 1995; Barboza et al. 1998). Brown bears prefer lipid-rich foods and highly digestible animal parts (Gilbert and Lanner 1996). The digestible-energy content of foods consumed by bears varies from as little as 30% for some vegetation and berries to over 90% for meat (Pritchard and Robbins 1990; Welch et al. 1997). The low nutritional value of most plant matter relative to meat and the low rates of dry matter intake when bears feed on berries can limit mass gain by females, which can limit reproductive success (Welch et al. 1997). Additionally, in populations without access to high-quality food resources, both age at first reproduction and interval between litters are increased (Bunnell and Tait 1981; Rogers 1987; Stringham 1990*a*, 1990*b*). Therefore, we hypothesized that the relative availability of meat, indicated by contribution to the diet, is positively related to body size, reproductive success, and population density of brown bears.

This evaluation is timely because of (*i*) the current discussion about and potential consequences of controlling brucellosis (*Brucella abortus*) in bison (*Bison bison*) and elk (*Cervus elaphus*) in the Yellowstone ecosystem through intensive population reductions, (*ii*) the potential crash of the of cutthroat trout (*Oncorhynchus clarki*) population in Yellowstone Lake caused by introduced lake trout (*Salvelinus namaycush*) (McIntyre 1995), (*iii*) the increasing human use of wild salmon populations, and (*iv*) the reintroduction of wolves (*Canis lupus*) into brown bear habitats.

Methods

Stable isotope analyses of hair samples, which indicate the consumer's diet during the period of hair growth in summer and fall (Hilderbrand et al. 1996), were used to estimate the contribution of marine meat, terrestrial meat, and plant matter to summer and fall diets of 13 North American brown bear populations (Table 1). Dietary contribution is defined as the proportion of assimilated carbon and nitrogen derived from a particular source (i.e., marine meat, terrestrial meat, or plant matter). Thus, estimates do not indicate biomass consumed (i.e., food habits) because assimilation includes digestibility and metabolizability, which vary across dietary items (Pritchard and Robbins 1990; Hilderbrand et al. 1996). Dietary meat is defined as the sum of marine and terrestrial meat contributions.

We collected hair samples from the forelegs of anesthetized female brown bears (Telazol®, 5–10 mg/kg body mass; Taylor et al. 1989) captured via helicopter on the Kenai Peninsula and in Denali National Park, both in Alaska. Hair samples from adult females (>5 years) from the 11 other populations were obtained from state and federal wildlife agencies. Hair samples were cut to <1 mm length and rinsed with warm distilled water (40°C) followed by chloroform–methanol (2:1) to remove any impurities and surface oils. Samples were ground to a powder in liquid nitrogen and subsampled (2.0 ± 0.1 mg) after the liquid nitrogen had evaporated. Subsamples were combusted and analyzed for isotopic content using a Finnigan MAT Delta-S isotope ratio mass spectrometer (Boston University Stable Isotope Laboratory). Results are reported as ratios relative to PeeDee limestone ($\delta^{13}C$) or atmospheric nitrogen ($\delta^{15}N$) as follows:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X is $\delta^{13}C$ or $\delta^{15}N$ and R is the ^{13}C:^{12}C or ^{15}N:^{14}N ratio (Peterson and Fry 1987).

Fig. 1. Relationship between mean body masses of adult female and adult male brown bears from 16 North American populations.

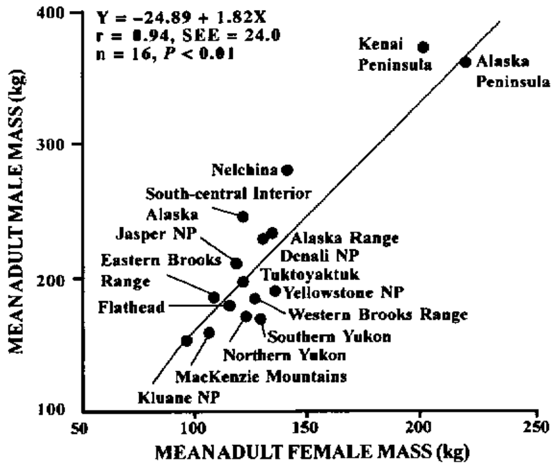
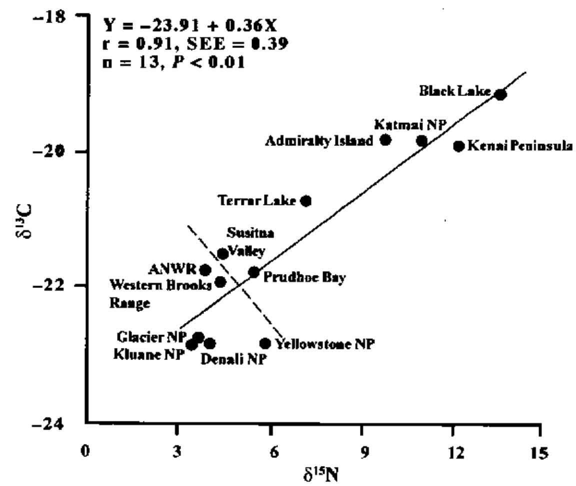


Fig. 2. Relationship between $\delta^{15}N$ and $\delta^{13}C$ signatures of hair samples from 13 North American brown bear populations. The populations above the broken line contained individuals with marine-meat dietary signatures.



The contribution of marine meat, terrestrial meat, and plant matter to brown bear diets was estimated according to Hilderbrand et al. (1996). However, as isotope signatures vary geographically (Garten 1993; Chamberlain et al. 1997), eqs. 1 and 2 of Hilderbrand et al. (1996) were modified in order to best reflect the isotope signatures of each ecosystem. Isotope signatures of the hair from large ungulates, including mule deer (*Odocoileus hemionus*), Sitka black-tailed deer (*O. hemionus sitkensis*), white-tailed deer (*O. virginianus*), elk, moose (*Alces alces*), pronghorn antelope (*Antilocapra americana*), and caribou (*Rangifer tarandus*), collected in Yellowstone National Park, Glacier National Park, the Kenai Peninsula, Admiralty Island, and the North Slope of Alaska, were used to develop herbivore base lines for each population (Barnett 1994; Ben-David et al. 1997; Jacoby 1998).

Body masses of bears captured from the Kenai Peninsula and Denali National Park populations were determined using a tripod and electronic load cell (±0.2 kg). Mean body masses, based on actual masses rather than estimates, for the other 14 populations were previously published and summarized in Blanchard (1987), Stringham (1990*b*), McLellan (1994), and McCann (1997). Adult female body masses, which were compared with litter sizes, were representative of the years during which litter size was measured and therefore may differ from the values in the above citations. When possible, the mass measurements used were those for the individuals from which hair samples were collected. If no mass measurements were available, previously published means for each population were used (Reynolds 1992; McLellan 1994; R. Sellers, personal communication). As body masses were measured at different times during the year, seasonal body mass measurements were standardized according to Stringham (1990*a*) and McLellan (1994). Mean spring litter sizes for 10 populations were obtained from Barnes and Smith (1992), Reynolds (1992), McLellan (1994), Knight et al. (1997), McCann (1997), Miller (1997), Reynolds (1997), and R. Sellers (personal communication). Density estimates for 10 populations were obtained from Knight et al. (1990), Miller and Sellers (1992), McLellan (1994), Miller et al. (1997), and Knight et al. (1997). The density of the Kenai Peninsula population was extrapolated from known densities of other populations by Del Frate (1993).

Relationships between dietary meat content, female body mass, litter size, and population density were tested using linear least squares regression analyses (Zar 1984). Density estimates for the Kenai Peninsula, Black Lake, and Yellowstone National Park populations were not included in the analyses (see the Discussion). Litter size, estimated in early spring, was chosen as the most appropriate variable for reproductive success because it should be the most sensitive to female condition in the den and therefore to the availability of food resources in the preceding year. It should also be independent of virtually all non-nutritional factors affecting bears after hibernation, such as social interactions, hunting by humans, and predation.

Results

Mean body masses of adult female and adult male brown bears were highly correlated ($P < 0.01$) and varied twofold across the species' North American range (Fig. 1; Stringham 1990*a*, 1990*b*). Adult males were, on average, 1.8 times larger than females irrespective of location. The $\delta^{13}C$ and $\delta^{15}N$ signatures of adult females were positively correlated ($P < 0.01$) because $\delta^{15}N$ increases with increasing trophic level, and both $\delta^{13}C$ and $\delta^{15}N$ increase with marine content of the diet (Hilderbrand et al. 1996). $\delta^{13}C$ and $\delta^{15}N$ values of diets ranged from very low for the interior, non-salmon-eating populations in Glacier, Kluane, and Denali National Parks to very high values for the coastal, salmon-eating Alaskan populations (Fig. 2). Yellowstone bears had the highest dietary meat contribution of all interior populations (Table 1).

Mean female body mass was positively correlated with an increasing contribution of dietary meat (Fig. 3). Coastal, salmon-eating bears were the largest and interior, vegetarian bears the smallest. Mean litter size was positively correlated with dietary meat content (Fig. 4A) and female body mass (Fig. 4B; Stringham 1990*b*; McLellan 1994). Population density was positively correlated with dietary meat contribution (Fig. 5). Most highly piscivorous coastal Alaska populations had densities as much as 55 times those of the more vegetarian interior populations. The densities of three populations (Black Lake, Kenai Peninsula, and Yellowstone National Park), however, were lower than expected. We believe that this may reflect the influence of human activities and (or) unique food conditions (see below). When coastal, salmon-eating populations (Katmai National Park, Kenai Peninsula, Black Lake, Terror Lake, and Admiralty Island)

Fig. 3. Relationship between dietary meat contribution and mean body mass of adult females from 11 North American brown bear populations.

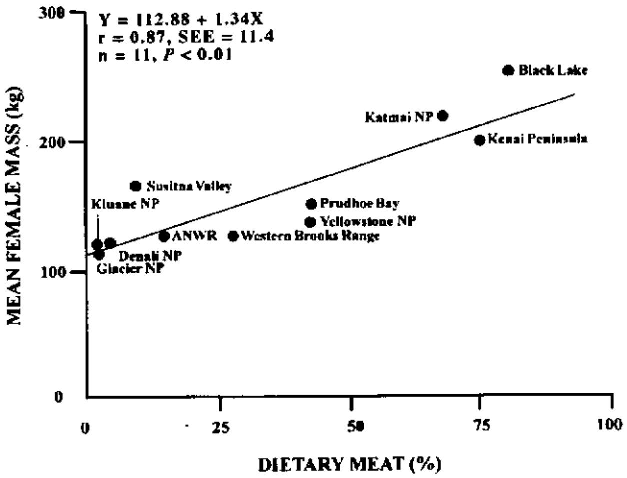


Fig. 4. (A) Relationship between dietary meat and mean litter size for brown bears from eight North American populations. (B) Relationship between mean adult female body mass and mean litter size for brown bears from eight North American populations.

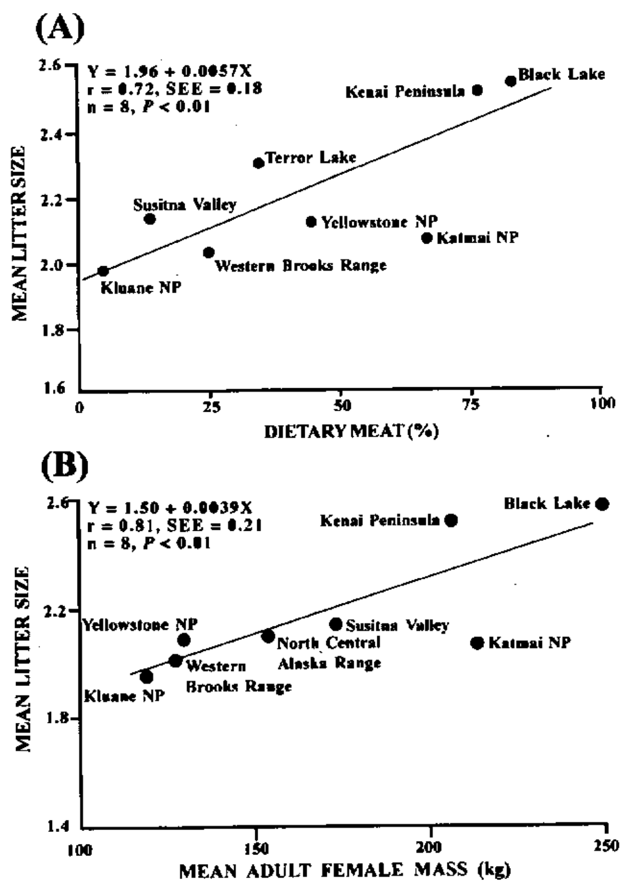
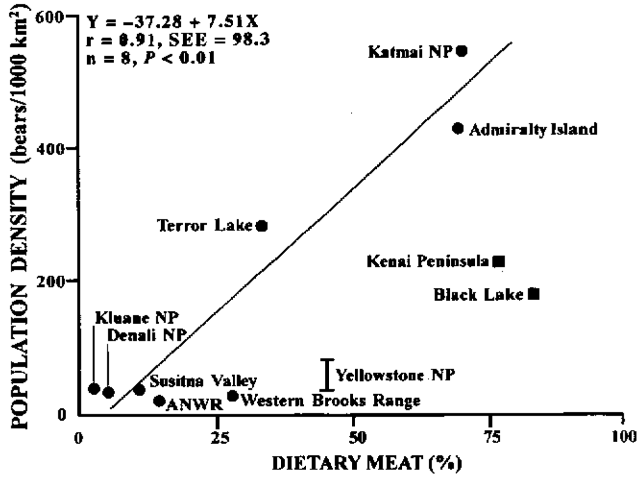


Fig. 5. Relationship between dietary meat contribution and population density for brown bears from eight North American populations. Populations from Black Lake, Kenai Peninsula, and Yellowstone National Park were not included in the statistical analysis (see the Discussion). The range of densities for Yellowstone National Park represents available estimates.



were excluded from regression analyses, adult female body mass ($r = 0.43$), litter size ($r = 0.57$), and population density ($r = 0.49$) were all positively correlated with dietary meat contribution, but none of these relationships were significant.

Discussion

Coastal populations with access to abundant, spawning salmon consist of larger individuals that achieve greater reproductive success than interior populations, which eat mostly plant matter and terrestrial meat (Stringham 1980; Bunnel and Tait 1981). Several interior populations have access to ungulate neonates and winter-killed carrion during spring (Adams et al. 1995; Green et al. 1997; Mattson 1997; Young and McCabe 1997) and viscera left by hunters or animals weakened during the fall rut (McLellan and Hovey 1995; Mattson 1997). However, the availability of meat is much less in interior regions than in coastal areas with abundant salmon runs. The importance of access to an abundant, high-quality food resource such as salmon is evident in all three parameters: body size (Figs. 1 and 3), reproductive success (Fig. 4), and population density (Fig. 5; Miller et al. 1997).

Bear populations can be divided into two distinct groups on the basis of population density: (1) populations with access to an abundant and reliable source of meat (i.e., salmon) in the fall, characterized by densities >190 bears/1000 km^2, and (2) populations that lack an abundant and reliable source of meat in the fall, characterized by densities <50 bears/1000 km^2 (Fig. 5). Two possible reasons for the greater ecological importance of salmon relative to terrestrial meat are (1) different nutrient requirements and metabolism in spring versus fall and (2) major differences in the availability (quantity or vulnerability) of terrestrial meat versus salmon. Mass gain by adult female brown bears that eat meat in spring is approximately 70% lean body mass (i.e., protein and water), whereas mass gain in the fall is approximately 80% fat (Hilderbrand 1998). Deposited fat is more important than lean body mass in meeting the costs of cub production that are incurred during winter dormancy (Farley and Robbins 1995). Therefore, abundant late-summer and fall salmon are more useful for the accumulation of the lipid reserves necessary for successful hibernation and cub production than are meat resources in spring, which primarily replenish lost body reserves (Hilderbrand 1998).

The three populations with a substantially lower density than would be predicted from the relative meat content of their diet (Black Lake, Kenai Peninsula, and Yellowstone National Park; Fig. 5) illustrate different constraints on brown bear populations. The Black Lake population is moderately hunted, probably reducing the density below what would be expected on the basis of available food resources (Sellers 1994). This reduction in density likely contributes to the large individual size (D. Sellers, personal communication). The Kenai Peninsula population is also hunted and is in an area of expanding residential and commercial development, increased recreational activity, and logging. Bears have been excluded from some salmon runs by intense sport fishing and development along rivers and streams, and recently, combined mortality due to hunting and kills made in defense of life and property have exceeded sustainable harvest estimates (Schwartz and Arthur 1997). Additionally, the current population estimate (Del Frate 1993) is an extrapolation from measurements from other populations and is probably conservative. As bears are restricted to increasingly fewer fishing sites, greater competition and risk of predation could prevent smaller bears and females with offspring from exploiting spawning salmon, which could lead to increased mortality (Schoen and Beier 1990; McLellan 1994; Mattson and Reinhart 1995). Thus, while some adults, particularly lone bears, continue to eat a lot of salmon, the salmon intake of the population as a whole is restricted by the number of feeding sites. Ultimately, research must be done to establish the relationships between the density of spawning salmon streams and bear access, the temporal, spatial, and biomass characteristics of spawning runs, and bear density.

The Yellowstone population is likely an example of an interior population with similar problems. The low density of this population relative to that predicted by the dietary meat contribution may be due to any or all of five possibilities: (1) the population estimates are low, (2) the population density is being depressed unnaturally by man, (3) meat resources, particularly ungulates and army cutworm moths (*Euxoa auxiliaris*) (Mattson et al. 1991*a*, 1991*b*), are more difficult to exploit efficiently than salmon, owing to spatial and temporal distribution patterns, (4) relatively little nutritious plant matter is available, so even relatively small amounts of dietary meat provide a disproportionate amount of total nutrients, and (5) the inconsistent availability of ungulate carcasses and whitebark pine seeds (*Pinus albicaulis*) across years (Mattson 1997) makes cub-rearing success highly variable. Hypotheses 3, 4, and 5 are supported by the lack of significant berry production in Yellowstone National Park relative to virtually all other ecosystems farther north where brown bears occur (Mattson et al. 1991*a*), and the small body masses of both adult male and adult female bears in Yellowstone National Park relative to those of salmon-eating bear populations (Figs. 1 and 3). We hypothesize that any reduction in available meat (i.e., ungulates, army cutworm moths, and cutthroat trout) and whitebark pine seeds would have a greater impact in Yellowstone than in other ecosystems where other nutritious alternative foods are available.

Availability of meat and (or) berries during the fall is an important management consideration in ecosystems targeted for brown bear reintroductions, such as the Bitterroot Ecosystem in central Idaho (Servheen 1984; U.S. Fish and Wildlife Service 1996). Historically, this area supported salmon (Fulton 1968, 1970) that were heavily used by brown bears when available (Hilderbrand et al. 1996). In the Bitterroot Ecosystem, the brown bear is now extinct, and the salmon nearly so. Recovery of salmon in that ecosystem could transform a reintroduced, low-density population of brown bears characterized by small individuals and low productivity to one of much higher density and with larger bears. However, salmon recovery will require a very long-term effort.

In conclusion, abundant meat resources positively affect body size, reproductive success, and population density of brown bears. Thus, purposeful management of such meat resources for bears will benefit both interior and coastal populations. As wildlife management agencies increasingly practice ecosystem management in which predators are a valued component, defining harvestable surpluses of ungulates and fish has important implications for the availability of these nutritional resources to large carnivores like brown bears, as well as to the rest of the freshwater and terrestrial ecosystem (Kline et al. 1990; Bilby et al. 1996; Ben-David et al. 1997). We conclude that the availability of dietary meat, especially salmon during late summer and fall, has a major influence on habitat quality for brown bears at both the individual level and the population level.

Acknowledgements

The authors thank biologists R. Ernst, T. Spraker, G. Del Frate, T. Bailey, J. Keay, and S. Farley and pilots R. Johnston, C. Lofsted, V. Lofsted, K. Solloy, J. DeCreeft, L. Nichols, T. Cambier, J. Larivee, K. Butters, D. Glaser, and D. Miller for their assistance in collecting samples from the Kenai Peninsula and Denali National Park. Hair samples from other populations were graciously provided by R. McCann (Kluane National Park), S. Miller (Susitna Valley), H. Reynolds (Brooks Range, Arctic National Wildlife Refuge), R. Shideler (Prudhoe Bay), R. Sellers (Katmai National Park, Black Lake), R. Smith (Terror Lake), K. Titus (Admiralty Island), K. Gunther, M. Haroldson, and D. Moody (Yellowstone National Park), and K. Aune and T. Manley (Glacier National Park). V. Barnes, Jr., B. Gilbert, K. Gunther, R. McCann, S. Miller, H. Reynolds, L. Rogers, R. Sellers, R. Shideler, R. Smith, and an anonymous reviewer provided constructive and insightful comments. Isotopic analyses were conducted by Robert Michener, Boston University Stable Isotope Laboratory. Funding was provided by the Intermountain and Pacific Northwest Forest and Range Experiment Stations of the U.S. Forest Service, U.S. Fish and Wildlife Service, U.S. Park Service, Alaska Department of Fish and Game Federal Aid to Wildlife Restoration, Projects W-24-3, W-24-4, and W-24-5, National Fish and Wildlife Foundation, and Raili Korkka Brown Bear Endowment.

References

Adams, L.G., Singer, F.J., and Dale, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. J. Wildl. Manage. **59**: 584–594.

Atkinson, S.N., and Ramsay, M.A. 1995. The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct. Ecol. **9**: 559–567.

Barboza, P.S., Farley, S.D., and Robbins, C.T. 1998. Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus* and *U. arctos*). Can. J. Zool. **75**: 2129–2136.

Barnes, V.G., Jr., and Smith, R.B. 1992. Survival and productivity of female brown bears on Kodiak Island, Alaska. Kodiak Brown Bear Research and Habitat Maintenance Trust, U.S. Fish and Wildlife Service, Kodiak, Alaska.

Barnett, B.A. 1994. Carbon and nitrogen isotope ratios of caribou tissues, vascular plants, and lichens from northern Alaska. M.S. thesis, University of Alaska, Fairbanks.

Ben-David, M., Hanley, T.A., Klein, D.R., and Schell, D.M. 1997. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. Can. J. Zool. **75**: 803–811.

Bilby, R.E., Fransen, B.R., and Bissson, P.A. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. **53**: 164–173.

Blanchard, B.M. 1987. Size and growth patterns of the Yellowstone grizzly bear. *In* Bears—Their Biology and Management: Proceedings of the Seventh International Conference on Bear Research and Management, Williamsburg, Va., 21–26 February 1986, and Plitvice Lakes, Yugoslavia, 2–5 March 1986. *Edited by* P. Zager. International Association for Bear Research and Management, Washington, D.C. pp. 99–107. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, U.S.A.]

Bunnell, F.L., and Tait, D.E.N. 1981. Population dynamics of bears — implications. *In* Dynamics of large mammal populations. *Edited by* C.W. Fowler and T.D. Smith. John Wiley & Sons, Inc., New York. pp. 75–98.

Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W., and Graves, G.R. 1997. The use of isotopic tracers for identifying populations of migratory birds. Oecologia, **109**: 132–141.

Del Frate, G.G. 1993. Brown bear survey — inventory activities, Units 7 and 15 Kenai Peninsula. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Project W-23-4, Juneau.

Farley, S.D., and Robbins, C.T. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can. J. Zool. **73**: 2216–2222.

Fulton, L.A. 1968. Spawning areas and abundance of chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River Basin — past and present. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 571. pp. 1–26.

Fulton, L.A. 1970. Spawning areas and abundance of steelhead trout, coho, sockeye, and chum salmon in the Columbia River Basin — past and present. U.S. Natl. Mar. Fish. Serv. Spec. Sci. Rep. Fish. No. 618. pp.1–37.

Garten, C.T., Jr. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch watershed. Ecology, **74**: 2098–2113.

Gilbert, B.K., and Lanner, R.M. 1996. Energy, diet selection and restoration of brown bear populations. *In* Proceedings of a Symposium: Management of Small and Relictual Bear Populations, presented at the Ninth International Conference on Bear Research and Management, Grenoble, France, 19–22 October 1992. Museum of Natural History, Grenoble, France. pp. 232–240.

Green, G.I., Mattson, D.J., and Peek, J.M. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. J. Wildl. Manage. **61**: 1040–1055.

Hilderbrand, G.V. 1998. Studies of the nutritional ecology of brown bears. Ph.D. thesis, Washington State University, Pullman.

Hilderbrand, G.V., Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K., and Servheen, C. 1996. Use of stable isotopes to determine diets of living and extinct bears. Can. J. Zool. **74**: 2080–2088.

Jacoby, M.E. 1998. Resource partitioning in North American grizzly/brown and black bears. M.S. thesis, Washington State University, Pullman.

Kline, T.C., Jr., Goering, J.J., Mathisen, O.A., Poe, P.H., and Parker, P.L. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. δ^{15}N and δ^{13}C evidence in Sashin Creek, southeastern Alaska. Can. J. Fish. Aquat. Sci. **47**: 136–144.

Knight, R.R., Blanchard, B.M., and Mattson, D.J. 1990. Yellowstone grizzly bear investigations. Report of the Interagency Study Team, 1987, U.S. National Park Service, Bozeman, Mont.

Knight, R.R., Blanchard, B.M., and Haroldson, M.A. 1997. Yellowstone grizzly bear investigations. Annual Report of the Interagency Grizzly Bear Study Team, Bozeman, Mont.

Mattson, D.J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biol. Conserv. **81**: 161–177.

Mattson, D.J., and Reinhart, D.P. 1995. Influence of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. Can. J. Zool. **73**: 2072–2079.

Mattson, D.J., Blanchard, B.M., and Knight, R.R. 1991*a*. Food habits of Yellowstone grizzly bears, 1977–1987. Can. J. Zool. **69**: 1619–1629.

Mattson, D.J., Gillin, C.M., Benson S.A., and Knight, R.R. 1991*b*. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. Can. J. Zool. **69**: 2430–2435.

McCann, R. 1997. Kluane National Park grizzly bear research project — year end report 1996. Prepared for Parks Canada by the Centre for Applied Conservation Biology, University of British Columbia Press, Vancouver.

McIntyre, J.D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout. *In* The Yellowstone Lake crisis: confronting a lake trout invasion. *Edited by* J.D. Varley and P. Schullery. Yellowstone Center for Resources, Yellowstone National Park, Wyoming. pp. 28–33.

McLellan, B.C. 1994. Density-dependent population regulation of brown bears. *In* Bears—Their Biology and Management: International Conference on Bear Research and Management Monogr. Ser. No. 3. pp. 15–37.

McLellan, B.N., and Hovey, F.W. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Can. J. Zool. **73**: 704–712.

Miller, S.D. 1997. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration Study 4.26, Juneau.

Miller, S.D., and Sellers, R.A. 1992. Brown bear density on the Alaska Peninsula at Black Lake, Alaska. Reports on Cooperative Interagency Brown Bear Studies on the Alaska Peninsula, Alaska Department of Fish and Game, Juneau.

Miller, S.D., White, G.C., Sellers, R.A., Reynolds, H.V., Schoen, J.W., Titus, K., Barnes, V.G., Jr., Smith, R.B., Nelson, R.R., Ballard, W.B., and Schwartz, C.C. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark–resight techniques. Wildl. Monogr. No. 133. pp. 1–55.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

Pritchard, G.T., and Robbins, C.T. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Can. J. Zool. **68**: 1645–1651.

Reynolds, H.V., III. 1992. Grizzly bear population ecology in the western Brooks Range, Alaska. Progress Report to the National Park Service, Alaska Department of Fish and Game, Fairbanks.

Reynolds, H.V., III. 1997. Effects of harvest on grizzly bear population dynamics in the northcentral Alaska Range. Federal Aid in Wildlife Restoration, Research Final Report, Study 4.25, Alaska Department of Fish and Game, Juneau.

Rogers, L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans. N. Am. Wildl. Nat. Resour. Conf. **41**: 431–438.

Rogers, L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. No. 97. pp. 1–72.

Samson, C., and Huot, J. 1995. Reproductive biology of female black bears in relation to body mass in early winter. J. Mammal. **76**: 68–77.

Schoen, J., and Beier, L. 1990. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Federal Aid in Wildlife Restoration Study 4.17, Alaska Department of Fish and Game, Juneau.

Schwartz, C.C., and Arthur, S.A. 1997. Cumulative effects model verification, sustained yield estimation, and population viability management of the Kenai Peninsula, Alaska brown bear. Federal Aid in Wildlife Restoration Study 4.27, Alaska Department of Fish and Game, Juneau.

Schwartz, C.C., and Franzmann, A.W. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr. No. 113. pp. 1–58.

Sellers, R.A. 1994. Dynamics of a hunted brown bear population at Black Lake, Alaska. Alaska Department of Fish and Game, Juneau.

Servheen, C. 1984. The status of the grizzly bear and the interagency grizzly bear recovery effort. *In* Proceedings of the 64th Annual Conference of the Western Association of Fish and Wildlife Agencies, July 16–19, 1984, Victoria, B.C. pp. 227–234.

Servheen, C. 1998. The grizzly bear recovery program: current status and future considerations. Ursus, **10**. In press. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, U.S.A.]

Stringham, S.F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. *In* Bears—Their Biology and Management: Proceedings of the Fourth International Conference on Bear Research and Management, Kalispell, Mont., 21–24 February 1977. *Edited by* C.J. Martinka and K.L. McArthur. Bear Biology Association, Tonto Basin, Ariz. pp. 337–349. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, U.S.A.]

Stringham, S.F. 1990*a*. Black bear reproductive rate relative to body weight in hunted populations. *In* Bears—Their Biology and Management: Proceedings of the Eighth International Conference on Bear Research and Management, Victoria, B.C., 20–25 February 1989. *Edited by* L.M. Darling and W.R. Archibald. International Association for Bear Research and Management, Washington, D.C. pp. 425–432. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, U.S.A.]

Stringham, S.F. 1990*b*. Grizzly bear reproductive rate relative to body size. *In* Bears—Their Biology and Management: Proceedings of the Eighth International Conference on Bear Research and Management, Victoria, B.C., 20–25 February 1989. *Edited by* L.M. Darling and W.R. Archibald. International Association for Bear Research and Management, Washington, D.C. pp. 433–443. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, U.S.A.]

Taylor, W.P., Reynolds, H.V., III, and Ballard, W.B. 1989. Immobilization of grizzly bears with tiletamine hydrochloride and zolazepam hydrochloride. J. Wildl. Manage. **53**: 978–981.

U. S. Fish and Wildlife Service. 1993. Grizzly Bear recovery plan. U.S. Department of the Interior, Fish and Wildlife Service, Missoula, Mont.

U. S. Fish and Wildlife Service. 1996. Grizzly bear recovery in the Bitterroot Ecosystem: draft Environmental Impact Statement. U.S. Department of the Interior, Fish and Wildlife Service, Missoula, Mont.

Watts, P.D., and Jonkel, C. 1988. Energetic cost of winter dormancy in grizzly bear. J. Wildl. Manage. **52**: 654–656.

Welch, C.A., Keay, J., Kendall, K.C., and Robbins, C.T. 1997. Constraints on frugivory by bears. Ecology, **78**: 1105–1119.

Young, D.D., and McCabe, T.R. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. J. Wildl. Manage. **61**: 1056–1066.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J.