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Source: *Conservation Biology*, Vol. 10, No. 4 (Aug., 1996), pp. 964-976

Published by: Wiley for Society for Conservation Biology

Stable URL: <http://www.jstor.org/stable/2387133>

Accessed: 16-12-2016 20:59 UTC

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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 caracayús (*Gulo gulo*) son aparentemente más sus-*

Paper submitted February 15, 1996; revised manuscript accepted April 22, 1996.

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 un hunted 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 (*Equis-*

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.

Acknowledgments

We thank T. Clark, J. Copeland, T. Fuller, D. Mattson, K. Murphy, and I. Ross for stimulating discussions and constructive reviews of the manuscript, as well as D. Casey and P. Curlee for their editorial assistance.

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