Conservation Biology and Carnivore Conservation in the Rocky Mountains

REED F. NOSS,*§ HOWARD B. QUIGLEY,† MAURICE G. HORNOCKER,†
TROY MERRILL,† AND PAUL C. PAQUET‡

*7310 NW Acorn Ridge, Corvallis, OR 97330, U.S.A., email nossr@ucs.orst.edu
†Hornocker Wildlife Research Institute, University of Idaho, P.O. Box 3246, Moscow, ID 83843, U.S.A.
‡Departments of Biology and Environmental Design, University of Calgary, Calgary, Alberta T2N 1N4 Canada

Abstract: *Large carnivores need large areas of relatively wild habitat, which makes their conservation challenging. These species play important ecological roles and in some cases may qualify as keystone species. Although the ability of carnivores to control prey numbers varies according to many factors and often is effective only in the short term, the indirect effects of carnivores on community structure and diversity can be great. Perhaps just as important is the role of carnivores as umbrella species (i.e., species whose habitat area requirements encompass the habitats of many other species). Conservation areas large enough to support populations of large carnivores are likely to include many other species and natural communities, especially in regions such as the Rocky Mountains of Canada and the United States that have relatively low endemism. For example, a plan for recovery of grizzly bears (*Ursus arctos*) proposed by Shaffer (1992) covers, in part, 34% of the state of Idaho (compared to 8% covered by a U.S. Fish and Wildlife Service proposal) and would capture 10% or more of the statewide ranges of 71% of the mammal species, 67% of the birds, 61% of the amphibians, but only 27% of the reptiles native to Idaho. Two-thirds (67%) of the vegetation types in Idaho would have 10% or more of their statewide area included in the Shaffer plan. The U.S. Fish and Wildlife Service recovery zones provide a much poorer umbrella. The umbrella functions of large carnivores are expected to be poorer in regions with high endemism. The application of metapopulation concepts to large carnivore conservation has led to proposals for regional reserve networks composed of wilderness core areas, multiple-use buffer zones, and some form of connectivity. The exceptional vagility of most large carnivores makes such networks feasible in a region with low human population density, such as the Rocky Mountains, but mortality risks still need to be addressed. Roads are a major threat to carnivore recovery because of barrier effects, vehicle collisions, and increased accessibility of wild areas to poachers. Development, especially for tourism, is also becoming a threat in many parts of the region.*

Biología de la Conservación y Conservacíon de Carnivoros en las Montañas Rocallosas

Resumen: *Los carnívoros mayores requieren de extensas áreas de hábitat relativamente natural, lo cual hace de su conservación un reto. Estas especies juegan un papel ecológico importante y pueden, en algunos casos, ser consideradas como especies clave. Aunque la capacidad de los carnívoros para controlar la abundancia de sus presas varía en función de numerosos factores y a menudo solo es a corto plazo, los efectos indirectos de los carnívoros sobre la estructura y diversidad de la comunidad pueden ser grandes. Posiblemente igual importancia tiene el papel de los carniívoros como especies sombrilla (i.e., especies cuyos requerimientos de extensión del hábitat comprenden los hábitats de muchas otras especies). Es probable que áreas de conservación suficientemente grandes para mantener poblaciones de carnívoros mayores incluyan muchas otras especies y comunidades naturales, especialmente en regiones con endemismo relativamente bajo, tal como las Montañas Rocallosas. Por ejemplo, un plan de recuperación de osos pardos (*Ursus arctos*) propuesto por Schaffer (1992) abarca, en parte, el 34% del estado de Idaho (comparado con el 8% del Servicio de Pesca*

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y Vida Silvestre de los E.U.) abarcaria el 10% o más de los rangos estatales de distribución del 71% de las especies de mamiferos, 67% de aves y 61% de anfibios, pero solo el 21% de reptiles nativos de Idaho. Dos tercios (67%) de los tipos de vegetación de Idaho tendrían 10% o más de su extensión en el estado incluida en la propuesta de Schaffer. Las zonas de recuperación propuestas por el Servicio de Pesca y Vida Silvestre constituyen una sombrilla Más pequeña. Se espera que en regiones de alto endemismo la función cobertora de los carnívoros mayores es más pobre. La aplicación del concepto de metapoblación en la conservación de carnívoros mayores ha llevado a propuestas de redes regionales de reservas interconectadas de alguna manera y compuestas por zonas núcleo y zonas de amortiguamiento de usos múltiples. La vagilidad excepcional de la mayoría de los carnívoros permite dichas redes en una región con baja densidad poblacional humana, tal como las Montañas Rocallosas, aunque los riesgos de mortalidad deberán ser considerados. Los caminos son una amenaza mayor para la recuperación de carnívoros por fungir como barreras, propiciar colisiones con vehículos y facilitar el acceso a cazadores furtivos. El desarrollo especialmente para el turismo también se está convirtiendo en una amenaza en muchas partes de la región.

Introduction

Arguably, no group of organisms offers more challenges to conservation biology and conservation politics than large carnivores. These animals, in accord with how they make their living, are big and fierce. Considerable expanses of land are required to encompass even single home ranges. Areas apparently needed to maintain viable populations over centuries are so large as to strain credibility; they certainly strain political acceptance. Making the situation more difficult is the association of large carnivores with wildlands. Although they often avoid roads and developed areas, large carnivores do not necessarily prefer wilderness; rather, they are persecuted and often unable to persist in more accessible areas (Shaffer 1992; Noss & Cooperrider 1994; Mech 1995; Mattson et al., this issue).

Well aware of the sociopolitical challenges carnivore management entails, Aldo Leopold considered carnivores a critical test of society's commitment to conservation (Meine 1988, 1992). Saving a small woodlot for a rare lily is one thing; protecting millions of hectares for grizzly bears (*Ursus arctos*) is quite another. Because the life requisites of carnivores were thought to make them good indicators of complete and healthy ecosystems, early conservation scientists in North America focused on the needs of carnivores in their designs for nature reserves (e.g., Shelford 1933; Kendeigh et al., 1950–1951). The reserves envisioned in these plans were large parks surrounded by buffer zones. Shelford and his colleagues had no way of knowing what later population viability studies and models would suggest—that their recommendations for reserves, although ambitious, did not begin to encompass enough wild land for the long-term persistence of large carnivores. Reserves on the order of 1000–10,000 km^2 might suffice for a few decades (Belovsky 1987), but more than 100,000 km^2 might be required for long-term viability (Schonewald-Cox et al. 1983; Shaffer 1987; Metzgar & Bader 1992). No park or wilderness area in North America is this large. Thus, in concert with increased interest among biologists in metapopulation models, conservation proposals for large carnivores and other area-demanding species evolved from single reserves to reserve networks (Noss & Cooperrider 1994).

In North America, at least, a landscape that retains populations of large carnivores is often one where natural vegetation predominates, where most native species can still be found, and where ecological processes operate more or less as they have for a long time. Hence, large carnivores have been considered indicators of the health or integrity of an ecosystem (Eisenberg 1980; Noss 1995). But because some landscapes containing large carnivores are otherwise impoverished or damaged biologically, for instance from logging, a more reasonable suggestion is that landscapes with large carnivores—implying a relatively intact food web—have high *potential* for ecological integrity. In discussing the ecological roles of large carnivores, their requirements for viability, and reserve design, we draw our examples from around the world but focus on the Rocky Mountains of the United States and Canada. We present a brief case study for a subregion of the Rockies in the state of Idaho.

Carnivores as Tools for Conservation

The current vogue among land management agencies in the United States and Canada is "ecosystem management," a concept that has been defined in several, often conflicting ways. Ecosystem management is enlightened to the extent that management decisions are based on ecological principles and biocentric values, but the concept may also be used politically to justify increased exploitation (Grumbine 1992, 1994; Noss & Cooperrider 1994; Stanley 1995). Regardless of the conceptual merit of ecosystem management, ecosystems are complex, and they generally cannot be managed directly. Ecosystems can be identified as vegetation types or habitats, can be mapped, and can be evaluated in terms of current area and extent of change from historical conditions (Crumpacker et al. 1988; Scott et al. 1993; Noss et al. 1995). But managing an ecosystem requires attention to specific, measurable indicators of the composition, structure, and function of that system (Franklin et al. 1981; Noss 1990, 1995). Those indicators can be monitored and, to some extent, managed. Although the concept of "management indicator species," whereby a single species is assumed to represent the status of all others associated with the same habitat, has been largely discredited (Landres et al. 1988; Noss 1990), there is merit in the broader idea that the status of certain ecologically pivotal species is indicative of the integrity of an ecosystem. Much is known about the biology of many carnivore species, and their influence on community structure is often great. Resource management agencies are better prepared organizationally to deal with vertebrate species requirements and habitat characteristics than whole ecosystems and their processes. It is also significant that big animals inspire people—agency staff as well as the general public—in a way that mycorrhizal fungi and hydroperiods never will. Thus, large carnivores are useful focal species for conservation planning.

Ecological Roles of Carnivores

Ecological studies of large carnivores in northern North America suggest they are capable of controlling their own numbers through social behavior (Hornocker 1969, 1970; Seidensticker et al. 1973; Beecham 1983; Hornocker & Bailey 1986), but their numbers can respond to changes in prey abundance (Fuller 1989; Quigley et al. 1989). In some cases, such as wolves (*Canis lupus*) at high latitudes (Bergerud & Ballard 1988), predators have been shown to regulate prey populations. Their ability to control prey numbers in natural systems is often only short term, however, and it typically depends on harsh environmental factors, such as deep snow or reduced availability of nutritious forage, that increase the vulnerability of prey (Nelson & Mech 1981; Fuller 1991; Koehler & Hornocker 1991; Huggard 1993). Where natural predators have been eliminated or severely reduced, dramatic increases in herbivore populations are more likely than they would be in the presence of large carnivores (Ballard et al. 1987; Warren 1991). Much of the evidence is circumstantial, however, and habitat factors are generally considered most important in regulating prey numbers (Peek 1980; Ozoga & Verme 1982; Seagle & McNaughton 1992).

Whether mammalian carnivores are true keystone species that control the diversity of lower trophic levels (Paine 1969) is debatable. Probably in some cases they are keystone species and in others they are not (Mills et al. 1993). Although direct, experimental evidence of keystone predator influences exists for other taxa (Connell 1971; Inouye 1980), such data are scarce for large mammalian carnivores. Many indirect effects of predation on community structure and diversity have been proposed, however, and research has documented differences within systems from which large predators have been removed or are missing (Glanz 1982; Emmons 1984; Soulé et al. 1988; Terborgh 1988; Leigh et al. 1993). A recent study on Isle Royale, Michigan (U.S.A.), found strong evidence of top-down control of a food chain by large carnivores. Growth rates of balsam fir (*Abies balsamea*) were regulated by moose (*Alces alces*) density, which in turn was controlled by wolf predation (McLaren & Peterson 1994). When the wolf population declined for any reason, moose reached high densities and suppressed fir growth. This top-down "trophic cascade" regulation is apparently replaced by bottom-up influences only when stand-replacing disturbances such as fire or large windstorms occur at times when moose density is already low (McLaren & Peterson 1994).

Large mammalian carnivores may help control populations of medium-sized, opportunistic predators in landscapes with some degree of habitat fragmentation. Soulé et al. (1988) suggested that heavy predation on birds' nests in some canyons in southern California was due to the absence of coyotes (*Canis latrans*) from those canyons, which in turn allowed populations of "opportunistic mesopredators" such as gray foxes (*Urocyon cinereoargenteus*) and feral cats (*Felis catus*) to increase. Citing other examples of apparent mesopredator release, Soulé et al. (1988) concluded that it is a general phenomenon and that "smaller omnivores and predators undergo population explosions, sometimes becoming four to 10 times more abundant" when large, dominant predators are extirpated. In Yellowstone National Park (Wyoming, U.S.A.), coyotes expanded in population after extirpation of wolves and assumed many of the ecological characteristics and functions of wolves, including pack formation and predation on large ungulates (R. Crabtree, personal communication). Coyotes have not entirely fulfilled the functions of the extirpated (and now reintroduced) wolf, however, because they are less effective predators of large ungulates. Research in Spain (Palomares et al. 1995) suggests that the Iberian lynx (*Felis pardina*), although it preys on European rabbits (*Oryctolagus cuniculus*), controls smaller predators such as Egyptian mongooses (*Herpestes ichneumon*), and by so doing permits increased densities of rabbits. In many regions, fragmented landscapes that have lost their large carnivores have unusually high populations of opportunistic predators, often resulting in substantial predation on eggs and nestlings of forest songbirds (Wilcove et al. 1986). In most of these cases, however, cause and effect have not been unequivocally established.

The ecological roles of less predatory carnivores, such as grizzly bears and black bears (*Ursus americanus*), are not clearly defined. As omnivores and (relative) habitat generalists, the direct influences of these animals on other organisms and ecosystem processes are difficult to quantify. Their seasonal and periodic predation on other vertebrates certainly can affect those populations at least locally, and bears likely play an important role in dispersing the seeds of many "soft mast" plants such as *Rubus* species.

Carnivores as Umbrellas

Carnivores have pragmatic value as conservation tools, even in cases in which their ecological role is unknown or apparently minor. For many of the central research areas of conservation biology—population viability analysis, reserve design, landscape ecology—the spatial scale of concern increases directly with the body size and trophic status of the species. Because large carnivores require so much land, their habitat requirements encompass those of many other species. In the Rocky Mountains, for example, individual, annual home ranges are on the order of 150 km^2 for black bears (Amstrup & Beecham 1976; Beecham & Rohlman 1994), more than 400 km^2 for mountain lions (puma, *Puma concolor*; Seidensticker et al. 1973), and nearly 900 km^2 for grizzly bears (Blanchard & Knight 1991; see also Weaver et al., this issue). Even wolverines (*Gulo gulo*), which generally weigh less than 20 kg, use more than 400 km^2 (Hornocker & Hash 1981). The only social large carnivore in the region, the gray wolf, uses from 250 to over 2000 km^2 per pack territory (Pletscher et al. 1991; Ream et al. 1991; Paquet 1993); territories are usually in the smaller end of that range after pack dynamics stabilize, but they tend to be higher in more topographically extreme landscapes with less usable habitat. Other terrestrial vertebrates in the Rocky Mountain region, even large herbivores such as moose and elk (*Cervus elaphus*), require much less space than large carnivores.

It is commonly assumed that a conservation plan focused on large carnivores will protect most other species (e.g., Foreman 1992). That is, large carnivores are "umbrella species" and provide a "coattail effect" (Soulé 1985) for species with more modest area requirements. Conservation biologists must evaluate claims of coattail effects critically. We could find no definitive, published studies documenting the level of protection afforded to other species by a conservation plan focused on large carnivores or, for that matter, any other ostensible umbrella species. It seems reasonable that large carnivores, with their enormous area requirements, should function as umbrellas, but it is unlikely that any umbrella will shelter all other species.

Whether or not carnivores function effectively as umbrellas depends on the biogeographic characteristics of the region and the extent to which the optimal habitats for carnivores overlap biodiversity hot spots or, more generally, habitats required by other species. In chaparral canyons in southern California, for example, where endemism is high, 62.5% of the available area is needed to represent all bird, mammal, and plant species (Ryti 1992). Plants (collectively) are the best umbrellas in this region; reserves representing all plants would capture 96% of the vertebrates (Ryti 1992). A conservation plan designed in this region for a large carnivore, the mountain lion, would likely protect fewer species. A simulation model incorporating demographic and environmental stochasticity for cougars in southern California showed that 1000–2000 km^2 of habitat would be needed to maintain a mountain lion population with a 98% probability of persistence for 100 years (Beier 1993). The ideal habitat, however, including corridors, would not encompass all the endemic plant sites and other areas of high value for biodiversity (California Natural Diversity Data Base, unpublished data). Most large carnivores are habitat generalists, relatively speaking, and do not select sites based on biodiversity values; what they need most is sufficient prey and security from human persecution.

On the other hand, in northern temperate regions with comparably low species richness and endemism, setting aside areas big enough for large carnivores might very well protect most other species. In the Rocky Mountains of Canada and the U.S., the several species of large carnivores collectively use a wide variety of habitats. For example, wolves mostly occupy—or are expected to occupy after population recovery—broad, wooded, and semi-wooded river valleys (Fritts et al. 1994). Mountain lions are more effective predators in wooded and semi-wooded areas of moderate to extreme topographic relief at mid-elevations (Hornocker 1970; Seidensticker et al. 1973; Ruth & Hornocker, unpublished report). In combination with the variety of mostly wooded habitats used by black bears (Beecham & Rohlman 1994) and the diverse habitats required by grizzly bears, including alpine meadows (Craighead et al. 1982; Mattson et al. 1991), carnivore habitat spans most of the spectrum of natural communities in the region.

No reserve proposal for large carnivores has been mapped for the Rocky Mountains, although Paquet and Hackman (1995) outlined a general strategy. In addition, Shaffer (1992) offered an alternative recovery plan, including a rough map, for the grizzly bear that considerably expands the area currently designated as the recovery zone by the U.S. Fish and Wildlife Service. (Shaffer's plan is more ambitious than the government plan, largely because his assumptions about population viability were more conservative and he worked under fewer political constraints; Shaffer 1992; U.S. Fish and Wildlife Service 1993.) We conducted an umbrella function analysis for Idaho as a subregion of the Rocky Mountains because it is the first state in the region with a completed gap analysis (Scott et al. 1993). Shaffer's proposed grizzly bear recovery zones cover 34% of Idaho, in addition to por-

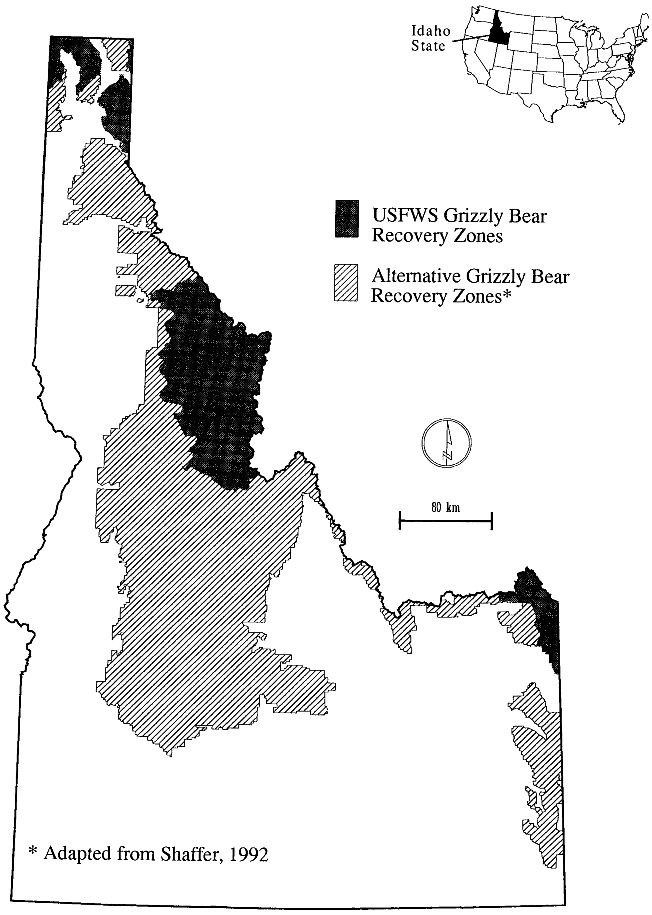

Figure 1. Historically the grizzly bear ranged over most of Idaho (Mattson, unpublished data). Official recovery zones for the bear proposed by the U.S. Fish and Wildlife Service are restricted to areas currently or recently (ca. 1950s) occupied by grizzly bears. The alternative recovery zones proposed by Shaffer (1992) encompass most of the U.S. Forest Service lands within the historic range of the bear. Both proposals extend zones into other states (not shown).

tions of adjacent states, compared to 8% in the proposal of the U.S. Fish and Wildlife Service (Fig. 1). The grizzly bear originally inhabited virtually all of Idaho (D. Mattson, unpublished data). We used a geographic information system (GIS) to overlay the proposed recovery zones of Shaffer and of the U.S. Fish and Wildlife Service on the distributions of Idaho vegetation and vertebrate species. The proportion of terrestrial vertebrate species whose ranges are captured by Shaffer's (1992) proposed network is much greater than that captured by the U.S. Fish and Wildlife Service proposal (Tables 1 & 2). Two-thirds (67%) of the vegetation types in Idaho would have 10% or more of their statewide area included in the Shaffer plan (T. Merrill, unpublished data available on request). But although many habitats and species groups are well covered by the grizzly bear umbrella, others,

Table 1. Comparison of the number of terrestrial vertebrate species with greater than 10% of their predicted statewide distribution based on the Idaho gap analysis[a] within U.S. Fish and Wildlife Service (USFWS) recovery zones and alternative recovery zones.[b]

Class	*USFWS zones (%)*	*Alternative zones (T)*	*State total species*
Amphibians	6 (46)	8 (61)	13
Reptiles	1 (5)	6 (27)	22
Birds	81 (35)	156 (67)	233
Mammals	40 (40)	71 (71)	100
Total	128 (35)	241 (65)	215

[a] *Scott et al. 1993.*
[b] *Shaffer 1992.*

such as reptiles, are poorly represented (Tables 1 & 2; Figs. 2 & 3). Adding consideration of the habitat requirements of other carnivore species to a reserve proposal would be expected to improve the umbrella function. An analysis of vertebrate species distributions in the central Rocky Mountains of Canada showed that protecting the optimal habitats of grizzly bears, lynx (*Felis lynx*), and wolf would conserve the best available habitat for 403 of 407 additional terrestrial vertebrate species (P. Paquet, unpublished report).

Ideally a conservation plan will be based on multiple criteria, incorporating large carnivores as well as other reserve selection indicators. These indicators include vegetation types and/or physical habitats (the goal being representation of all types), occurrences of rare species and communities, centers of endemism and species richness, critical watersheds for aquatic taxa, and sites sensitive to development (Usher 1986; Noss 1992, 1993*a*, 1995; Pressey et al. 1993; Scott et al. 1993; Noss & Cooperrider 1994). The utility of large carnivores as umbrella species often is greatest during the reserve-design and landscape-zoning phases of conservation, after the sites with the highest biodiversity values and those needed for complete representation of habitats have been identified. At this point the conservation planner must look to the particular elements at greatest risk of being lost from the region if human activities are unrestricted. Among the most vulnerable species, if not already extirpated, are the large carnivores. By considering the needs of large carnivores, which typically have the largest area

Table 2. The same comparison as in Table 1 but with ubiquitous species[a] and peripheral species[b] not included.

Class	*USFWS zones (%)*	*Alternative zones (T)*	*State total species*
Amphibians	4 (50)	5 (63)	8
Reptiles	0 (0)	2 (15)	13
Birds	66 (52)	100 (79)	126
Mammals	32 (47)	51 (75)	68
Total	102 (47)	158 (73)	215

[a] *Predicted distribution > 80% of state.*
[b] *Predicted distribution < 5% of state.*

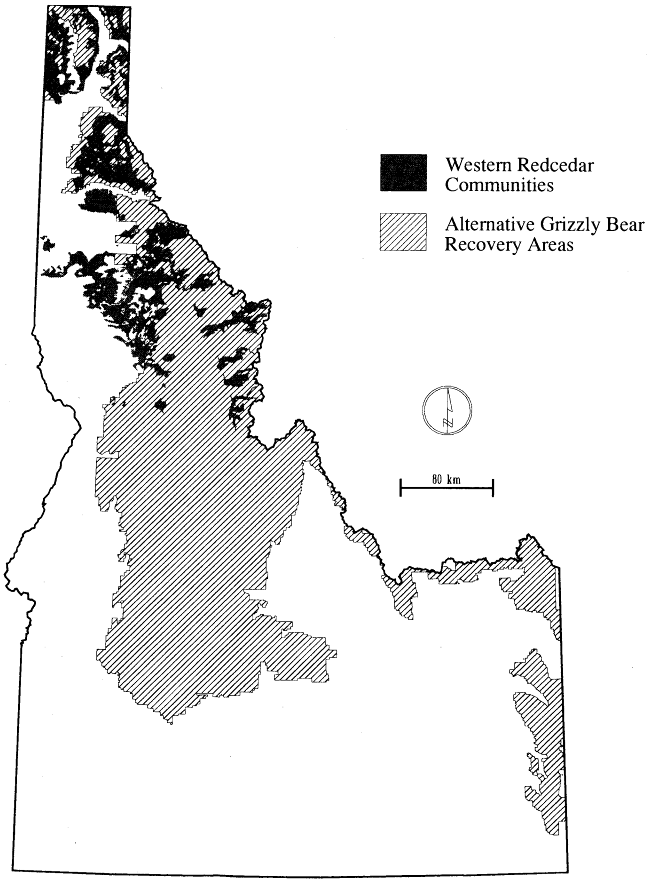

Figure 2. Western red cedar communities occur at low to middle elevations in moist areas of Idaho. Proposed recovery zones for grizzly bears (Shaffer 1992) provide a good "umbrella" for these communities, which are threatened by logging.

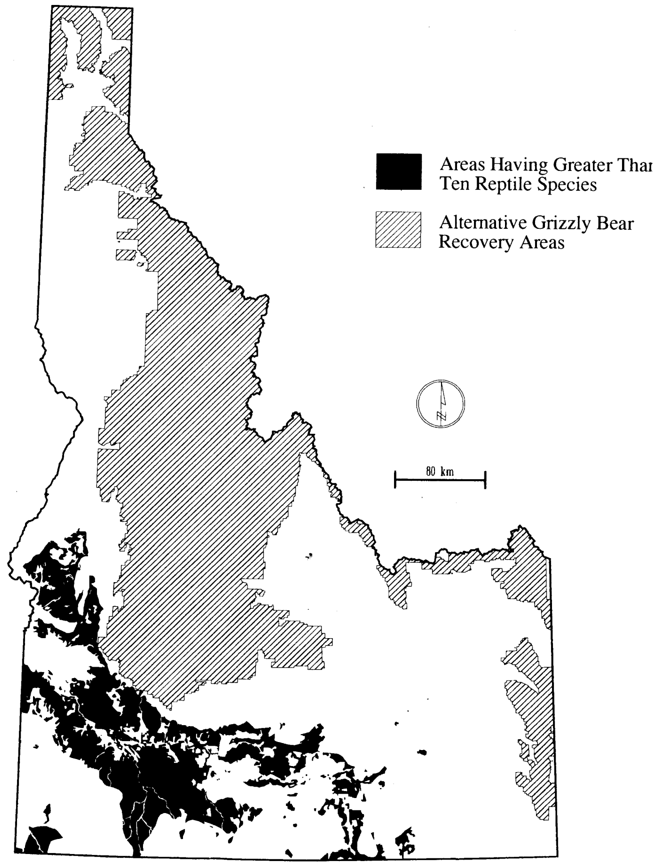

Figure 3. Areas of high reptile species richness (>10 species) in Idaho are not well captured by the grizzly bear umbrella.

requirements and longest dispersal distances of all native fauna, the planner has an objective basis for determining the optimal size of reserve networks, the optimal length and width of landscape linkages, allowable road density, and permissible human uses in various zones.

Population Viability Considerations

The upsurge of interest in population viability that occurred approximately a decade ago centered on the dynamics of single populations. More recent work has focused on loosely connected systems of local populations (metapopulations, considered generally). Our concern is the suite of characteristics large carnivores possess that influence their viability in single or spatially subdivided populations and as members of guilds. We are also concerned with how estimates of viable populations translate to estimates of optimal reserve network size and configuration. A definition of viability is not essential for this general discussion, but a 100- to 500-year horizon with risk of extinction below 5% seems reasonable (Shaffer 1987; Beier 1993).

Population viability can be related to demographic, genetic, and environmental factors, any or all of which can be modeled to examine their effects on the persistence of populations. The relative importance of these factors has been argued extensively (Lande 1988), and their influence on population viability can be expected to differ between situations. In most cases, these factors interact with each other; for example, inbreeding depression has demographic as well as genetic consequences (Mills & Smouse 1994). Among the population-specific factors that determine viability are reproductive rate, survivorship, and genetic effective population size. The large carnivore species in the Rocky Mountains are of concern to conservationists precisely because their values for these characteristics (especially reproductive rate and effective population size) are generally low compared to other vertebrate species, which leads to high estimates for the population sizes necessary to assure persistence. For example, annual female reproductive rates for grizzly bears in the region range from 0.75 (Craighead et al. 1974; Wielgus et al. 1994) to 0.46 (Wielgus & Bunnell 1993); values for mountain lions (Beier 1993; Lindzey et al. 1994) and black bears (Beecham 1980; Bunnell & Tait 1981; Rogers 1987) from the same region and elsewhere are approximately twice those for grizzly bears but still low for vertebrates generally. Female reproductive rates for wolves can be almost 10 times those of grizzly bears (Fuller 1989; Pletscher et al. 1991), but usually only a single alpha female and alpha male in each pack breed (see also Weaver et al., this issue). In addition, first-year survival of wolves is relatively low (Fuller 1989). Survival-rate data for black bears, mountain lions, and grizzly bears are sketchy (but see Eberhardt 1990).

Genetic influences on the viability of small populations are complicated, and research in this area is evolving quickly (Schonewald-Cox et al. 1983; Lande & Barrowclough 1987; Lande 1988, 1995; Seal 1992; Mills & Smouse 1994). Among the critical factors is the genetic effective population size, N_e. Of the characteristics of non-ideal populations that tend to decrease the ratio of N_e to N (Harris & Allendorf 1989), at least four are evident in the large carnivore species of the Rocky Mountains: overlapping generations, unequal number of breeding males and females, non-Poisson variance in distribution of offspring surviving to adulthood, and nonrandom mating. For black bears N_e has been determined as less than 70% of N (550/810; Chepko-Sade & Shields 1987), whereas N_e for grizzly bears can be as low as 24% of N (Harris & Allendorf 1989; Craighead & Vyse 1996). The N_e for wolves in the Central Canadian Rockies is about 33% of N (P. Paquet, unpublished data).

The role of environmental variation in the viability of large carnivores is little understood, although weather effects have been implicated in some cases (Rogers 1976; Nelson & Mech 1981; Fuller 1991). Demographic and genetic considerations alone, accentuated by low population densities, suggest that immense areas are needed to assure persistence. Population densities of carnivores in the Rocky Mountains are low largely because so much of the total area is rough, inhospitable terrain. Often usable habitat is linear and restricted to lower-elevation valley bottoms, especially in the northern part of the region and in winter when snow depth restricts movement. Using estimated average densities for grizzly bears in the northern Rocky Mountains of the U.S. (4 bears/259 km^2) and the 1:4 ratio of N_e to N estimated by Harris and Allendorf (1989), Metzgar and Bader (1992) calculated that 129,500 km^2 of wildland would be needed to maintain an N_e of 500, the official recovery goal for the species. Wolves in our focal region may require 4 to 10 times the area of grizzly bears—that is, from 518,000 to 1,295,000 km^2—given current estimates of N_e and population density (P. Paquet, unpublished data).

A partial solution to this problem of extreme space requirements is to examine carnivore population viability in the framework of metapopulations; exchange between populations can reduce tremendously the size of each local population required. Population subdivision also may reduce the total population size required because the action of environmental variation as an extinction force is reduced when populations are spread across space (Goodman 1987; Shaffer 1987). Large carnivores typically show a subdivided population structure, with long-distance movements of individuals and genes among local populations (Craighead & Vyse 1996; Fritts & Carbyn 1995; Forbes & Boyd 1996). Thus, the 129,500 km^2 potentially required to maintain 2000 grizzly bears need not be protected in one piece but rather across a broad region, so long as some interchange occurs among populations. Many metapopulation structures are possible, with the classic model of interacting subpopulations in approximate balance between colonization and extinction probably rare in nature (Harrison 1994). In the Rocky Mountains, population dispersion for large carnivores—at the present time and after recovery efforts for the grizzly bear and wolf in the United States have been successful—will likely be a combination of patterns. Interactions among species, human land uses and behaviors, and other factors make prediction of future distributions risky.

A striking characteristic of large carnivores is their strong dispersal capabilities. Dispersal distances of 50 to 100 km are not unusual (Rogers 1987; Blanchard & Knight 1991; Pletscher et al. 1991; Lindzey et al. 1994), and distances of hundreds of kilometers have been recorded for wolves (Fritts 1983; Ballard et al. 1987; Mech et al. 1995; Boyd et al. 1996). Long-distance dispersal offers exceptional opportunities for population interchange, reducing estimates of local population sizes required for persistence and increasing the level of optimism for recovery. In mammalian carnivores, however, generally only the males disperse widely. Hence, opportunities for demographic rescue will be limited when the number of breeding females is the critical factor in a declining population, which is often true for grizzly bears (Craighead & Vyse 1996). Citing the remarkable dispersal capacities of wolves, Fritts and Carbyn (1995:26) believe that theoretical treatments of population viability have "created unnecessary dilemmas for wolf recovery programs by overstating the required population sizes." But they concede that maintaining opportunities for safe dispersal is crucial. Based on research showing multiple, unrelated founders and high genetic variation in wolves naturally recolonizing northern Montana, Forbes and Boyd (1996) conclude that "wolves will best flourish in the Rocky Mountains if public tolerance and legal protection allow continued natural migration throughout the region."

Landscape Design and Management

The overwhelming message from population viability studies of large carnivores is that conservation planning must be undertaken at vast spatial scales and must consider connectivity among local populations. The traditional method of selecting, designing, and designating discrete nature reserves—an approach that still dominates much of conservation biology—will not suffice for large carnivores, except in those rare cases where reserves of many thousands of square kilometers can be established. The sites chosen by means of popular reserve selection algorithms are usually rather small, sprinkled across a vast region, and unlikely to meet the needs of wide-ranging animals. If maintaining viable populations of species that have large home ranges and are vulnerable to human activities is an objective, then the conservation planner must grapple with the design and management of entire landscapes. Thus, a zoning approach has come to dominate conservation strategies for large carnivores (Noss & Harris 1986; Noss 1992; Mech 1995; Paquet & Hackman 1995). Zoned landscapes should include refugia that are strictly protected, but they will often be dominated by multiple-use lands.

A working model for regional reserve networks (Fig. 4) was provided by Noss (1992, 1995), building on previous work on biosphere reserves (United Nations Educational, Scientific, and Cultural Organization 1974; Dasmann 1988), multiple-use modules (Harris 1984; Noss & Harris 1986; Noss 1987*a*), and landscape ecology (Forman & Godron 1981, 1986; Noss 1983; Urban et al. 1987; Forman 1995). The central elements of this design—central in the sense that they are of highest conservation value and are often irreplaceable—are the core areas. Core areas are selected on the basis of multiple criteria (e.g., representation, biodiversity hotspot analysis) and are managed for natural or wilderness values. They are generally roadless or have very low road density, and they therefore offer security to species sensitive to human persecution and harassment.

Most biologists acknowledge that core areas for wide-ranging species such as carnivores should be large (e.g., Soulé & Simberloff 1986), but precisely how large is impossible to say without case-specific information on habitat quality and distribution, prey populations, management practices, and other human activities (Noss 1996). In any case, the landscape context is at least as important as internal habitat quality to the viability and defensibility of core areas (Noss & Harris 1986; Noss & Cooperrider 1994; Fritts & Carbyn 1995; Paquet & Hackman 1995; Peres & Terborgh 1995). Thus, old questions about how large a single reserve must be, either to maintain species richness (the island biogeography model; MacArthur & Wilson 1963, 1967) or to maintain populations of particular target species (a population viability model; Shaffer 1981; Soulé 1987), have largely given way to new questions regarding the optimal scale of the entire network of conservation lands, their relationship to surrounding lands, how lands in all categories are actually managed, and whether the overall management

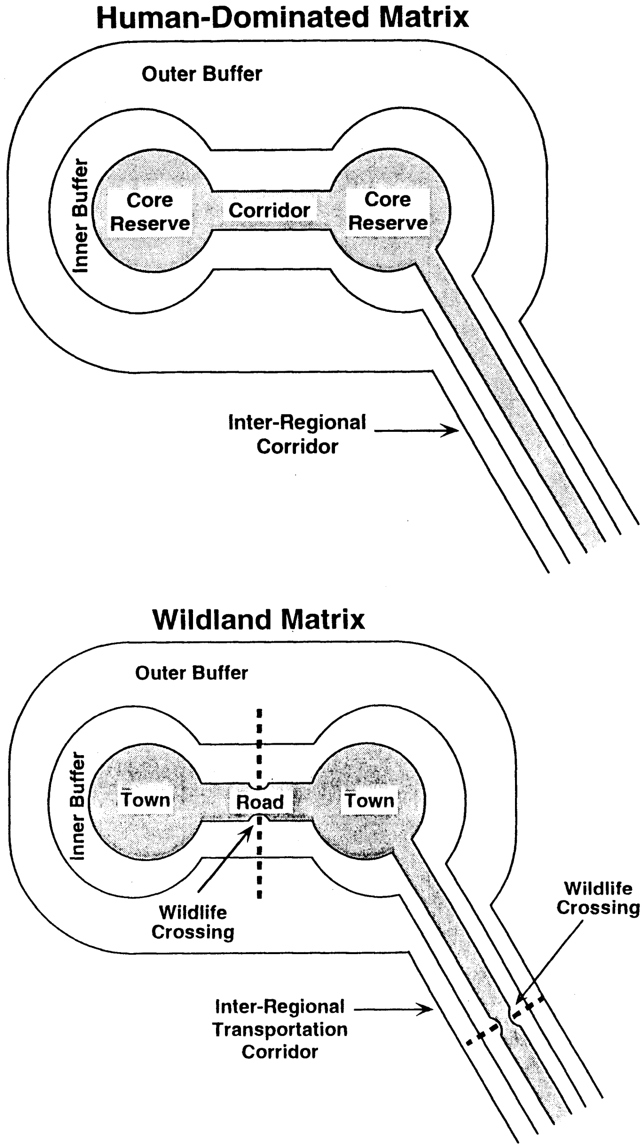

Figure 4. A model reserve network for a human-dominated region, consisting of core reserves, connecting corridors or linkages, and multiple-use buffer zones. Outer buffer zones would allow a wider range of compatible human activities than inner buffer zones. In this example an interregional corridor connects the system to a similar network in another natural region. Adapted from Noss (1992). An inverted network model, which applies to wildland-dominated regions (Wildland Matrix). In this case the matrix is wildland and the core areas are towns or other settlements connected by transportation corridors. Buffer zones are used to establish a gradient of human uses, more intense toward the settlements and diminishing toward the wildland matrix. Wildlife crossings (underpasses, overpasses, tunnels, etc.) are constructed to allow wildlife to pass safely beneath or over roads or other transportation corridors.

regime is capable of maintaining ecological integrity (Noss 1995, 1996).

Landscape design necessarily involves much more than reserves. Buffer zones (now often known by more politically correct terms such as ecosystem management zones, adaptive management areas, managed-use zones, or zones of cooperation) and the surrounding landscape matrix may be as important as reserves to the long-term viability of wide-ranging species, if for no other reason than because reserves will usually not be large and numerous enough to assure long-term viability. The third major element in this model, connectivity, can be provided either through relatively discrete habitat corridors or through buffer or matrix lands that permit safe movement among reserves or provide for a continuously distributed population. For large carnivores, connectivity is mainly an issue of circumventing barriers to animal movements (e.g., highways or developed areas) and minimizing human-caused mortality (e.g., from vehicles, hunting, or trapping).

The model portrayed in Fig. 4a could be applied at virtually any spatial scale, from woodlots in an agricultural landscape linked by fencerows (Merriam 1988) to a network of wilderness areas linked by landscape-scale corridors across regions (Noss 1992). The broad-scale model is most relevant to large carnivores, although an intermediate-scale model could contribute to at least short-term persistence of the more reclusive carnivores (e.g., mountain lions or, in some cases, wolves) in intensively used landscapes (Maehr 1990; Beier 1993; Mech 1995). Less reclusive and more aggressive animals, such as grizzly bears, normally have little chance of surviving in intensively used landscapes because of conflicts with humans (Zager & Jonkel 1983; LeFranc et al. 1987; Wielgus et al. 1994). The model in Fig. 4b can be applied at watershed to regional scales in cases where the matrix remains wildland. The two models could be hybridized in regions with gradients from intensive use to wildland.

Key hypotheses (or assumptions) behind the model proposed in Fig. 4a are as follows: (1) a system of reserves linked by movement corridors will be a whole greater than the sum of its parts because, whereas no single reserve can support a viable population, a network of reserves may do so; (2) at least some dispersing individuals will be able to move safely from one reserve to another; (3) extinctions of populations in reserves can be reversed through recolonizations; (4) buffer zones will help protect sensitive species from frequent contact with people and provide supplemental habitat; and (5) compatible human uses can be found for most zones. For the inverted model in Fig. 4b, it is necessary only that the matrix remain wild (i.e, minimal human access) and that highways or railways do not impose serious mortality risks or barriers.

Hypothesis 1 is supported by the abundant evidence that many wild species have a subdivided population structure (Fahrig & Merriam 1994). This structure may not be a classic metapopulation, however, in which extinction and colonization are in equilibrium (Harrison 1991, 1994). Rather, it may be more of a source-sink system in which some subpopulations produce abundant offspring, which then disperse into landscapes of lower quality or higher risk where they fail to survive or reproduce (Pulliam 1988). The source-sink model may apply well to wolves, which have high reproductive potential and generate abundant dispersing individuals that settle in landscapes of variable quality (Mech 1995; Mladenoff et al. 1995; Boyd et al. 1996). Although mortality may be high and reproductive success low in fragmented landscapes, populations may persist there as long as the source population keeps producing colonizers.

A population structure that is becoming increasingly common is one in which the entire regional population is fragmented so badly that little or no successful dispersal and interchange occurs between subpopulations. In this scenario, local extinctions signal bit-by-bit extinction of the regional population or the entire species (Harrison 1994). In developed regions carnivores may occur in small remnant populations that gradually "wink out" over time as a result of demographic, genetic, or environmental stochasticity. Examples of small populations of large carnivores winking out on their own are hard to find, however; rather, extirpations are usually related to direct killing by humans. In any case, local populations can be united to form a whole greater than the sum of its parts only if hypotheses 2 and 3 are correct, that dispersing individuals pass safely from one local population to another and local extinctions are reversed through recolonization.

Hypotheses 4 and 5, regarding the effectiveness of buffer zones and compatibility of human uses, have not been well evaluated empirically. We might expect that buffer zones would not only help shield sensitive species from human harassment, but they might also shield human settlements from depredation by wildlife (Noss & Harris 1986). We know of no definitive tests of this idea. Given current human attitudes toward predators in the Rocky Mountains (Kellert et al., this issue), the need to protect these animals from persecution is obvious, but it is also apparent that protection will ultimately require a major shift in human values and cannot rely only on such measures as reserve establishment, zoning, and road closures.

A difficult issue, scientific as well as practical, in large carnivore conservation is connectivity—whether individual animals can move safely through the landscape. The connectivity question must be considered at many different scales. Conservation planners must be concerned with movements within home ranges, with dispersal between home ranges or between populations, and, in cases where source populations are farther apart than normal dispersal distances, with maintaining resident individuals or continuous populations across regions (Noss 1991, 1992; Beier & Loe 1992; Noss & Cooperrider 1994). Alternately, long-distance connectivity could be accomplished by translocation of individuals among populations, an action that might accomplish genetic management objectives (Hedrick 1995). It falls short of fulfilling the goal of self-sustaining populations, however, and it would also depend on a long-term commitment of substantial funds. For these reasons we consider the translocation option inferior to maintaining or restoring natural linkages in the Rocky Mountains.

Large carnivores require connections for movement on a daily to seasonal basis within their home ranges. Grizzly bears commonly use ridgetops, saddles between peaks, and riparian networks for travel (LeFranc et al. 1987); they avoid crossing clearcuts and other large openings (D. Mattson, personal communication). Black bears in the Rocky Mountains use wooded northern slopes for travel and riparian areas for feeding (Beecham & Rohlman 1994), although elsewhere riparian areas are important travel corridors for this species (Kellyhouse 1980; Mollohan 1982). Black bears are also known to avoid areas more than 25 m from cover and rarely use young clearcuts (Lindzey & Meslow 1977; Young & Beecham 1983; Beecham & Rohlman 1994). These movement patterns may be learned behaviors, and ecological factors that determine the availability and quality of movement corridors (e.g., distribution of prey and denning sites, climate) often vary seasonally and annually. Thus, movement corridors are dynamic, not fixed features of the landscape. In the central Canadian Rockies, valley bottoms are both primary habitat and movement corridors for carnivores, but these are unfortunately the same parts of the landscape preferred by humans for travel and utility corridors, towns, and recreational developments. In summer carnivores make greater use of montane valleys, passes, and even alpine habitats for movement (P. Paquet, unpublished data). Collectively, these data suggest that in most cases connectivity will best be provided by broad, heterogeneous linkages, not narrow, strictly defined corridors.

In an increasing number of landscapes, animal movements require crossing roads. As traffic on roads increases, so does the mortality risk to carnivores. For example, roadkill is the single greatest known source of mortality for the Florida black bear (*U. a. floridana*) and Florida panther (*P. c. coryi*), as it is for virtually every other large mammal in Florida (Harris & Gallagher 1989). One might expect roadkill to be a significant mortality source in highly developed regions such as Florida, but not in a wildland region such as the Rocky Mountains. Thus, data showing that roadkill is the largest known mortality source for wolves in the Canadian Rockies and, even more so, in the national parks of this region (P. Paquet, unpublished data) is alarming. One obvious way to reduce roadkill is to modify the road or railway such that animals can cross safely under or over it. For example, underpasses constructed on Interstate 75 in southern Florida to reduce roadkills of panthers are now being used regularly by panthers and many other vertebrates (Foster & Humphrey 1995). In Banff National Park, Alberta, individual wolves and packs vary greatly in use of highway underpasses. Underpasses act as filters, allowing some individuals to cross but not others (P. Paquet, unpublished data).

When planning for dispersal, such as movement of subadult animals out of the parental home range, larger spatial scales must be considered than when planning for movement within home ranges. As reviewed earlier, dispersal distances of large carnivores often exceed 100 km. Reported distances may give the impression that individual carnivores can easily find their way across hundreds of kilometers of terrain. In some situations and for highly mobile species such as wolves (Mech 1995; Forbes & Boyd 1996), this may be true. But conservationists should not place too much faith in the ability of carnivores to traverse large areas without incident. Such an impression ignores the threats of highways, legal and illegal hunting, and the increasing fragmentation of the regional landscape from urban, resort, and agricultural development and resource extraction activities. One reproductively successful migrant per generation may suffice to mitigate problems related to loss of alleles through drift (Allendorf 1983). But bolstering small and vulnerable populations through demographic rescue effects (Brown & Kodric-Brown 1977) is probably one of the more crucial functions of connectivity for carnivores, which may often exist in complex source-sink population mosaics. Furthermore, the degree of fragmentation imposed by existing and planned future developments in the Rocky Mountains (Shaffer 1992; Paquet & Hackman 1995) could potentially prevent even one successful migration between demes per generation, at least for grizzly bears and wolverines.

With these ideas in mind, biologists have recommended the retention or restoration of wide habitat linkages between population centers for large carnivores. Interregional corridors suggested for grizzly bears in the Rocky Mountains would link bear population centers some 250 km apart—for example, from the Greater Yellowstone Ecosystem to the Northern Continental Divide Ecosystem (U.S. and Canada) or to the wildlands of central Idaho (Picton 1986; Noss 1992; Shaffer 1992). Because such distances exceed normal, though not maximum, dispersal distances for the bear, the linkages ideally would be managed to maintain within them a low-density population or at least some resident individuals. This may be especially important for female bears, which do not disperse nearly as far as males (Craighead & Vyse 1996). Models suggest that such populations, even if they are technically sinks, could provide useful connections between source populations (Howe et al.

1991). In such cases genes might flow in both directions through the population in the corridor, and corridor width could be based on home-range diameters of the target species (Bennett 1990; Harrison 1992; Noss 1992). For example, the grizzly bear has an average lifetime home range of approximately 3885 km^2 in the greater Yellowstone region (Mattson & Reid 1991); thus, a 44.25-km-wide corridor would be needed to encompass a rectangular home range twice as long as wide (Noss 1992). Topography, however, will preclude a single, wide corridor in many areas of the Rocky Mountains; in such cases networks of protected dendritic drainages may be a more reasonable approach to connectivity. In either situation linkages do not fit the common conception of corridors. Much of the debate about corridors in the conservation biology literature (e.g., Simberloff & Cox 1987; Noss 1987*b*; Simberloff et al. 1992) revolves around a picture of corridors as linear conduits, along which an animal moves from point *A* to point *B*. This simplistic view of connectivity applies to few species (Noss 1993*b*).

The most difficult aspect of the conservation of large carnivores is their need for large areas relatively inaccessible to humans. Road access, often measured by open road density, is widely documented to be a useful measure of habitat suitability for large carnivores: as road density increases, habitat suitability declines (Brody 1984; Thiel 1985; Mattson et al. 1987; McLellan & Shackleton 1988; Mech et al. 1988). The major threat from roads noted in these studies is not roadkill but rather shooting and trapping, legal or illegal. In many cases the animals use roads, particularly unpaved and lightly traveled roads, as travel corridors, which brings them into contact with humans (LeFranc et al. 1987). Although some recent studies report wolves using landscapes with higher road densities than previously thought possible (Fuller et al. 1992; Mech 1995), these cases seem to be exceptions. Fuller et al. (1992:48) noted that "in general, wolves occurred where both road density and human density were low," and that "because of the nature of observers' activities, many records (a few of which may have been of large dogs) were obtained on or adjacent to roads and thus biased towards areas with relatively higher densities of roads and humans." Furthermore, although Mech (1995) emphasized the adaptability of wolves to agricultural and populated landscapes in Minnesota and Wisconsin, Mladenoff et al. (1995) found that mean road density is much lower in pack territories (0.23 km/km^2) than in random nonpack areas (0.74) or in the region overall (0.71). Few areas within any pack territory exceeded a road density of 0.45 km/km^2, and no areas exceeded 1.0. The wolf population is still recolonizing northern Wisconsin and is not saturated, so it may be expected to expand into areas of higher road density in the future. But Mladenoff et al. (1995) caution that the status of the wolf is precarious there and that much of the region may be a population sink because of direct human-caused mortality in accessible areas and because disease and parasites, which are a threat to pup survival and reproductive potential (Mech & Goyal 1993), are higher in developed landscapes. We can expect similar threats in developed landscapes of the Rocky Mountains.

Conclusion

The findings from conservation biology suggest that the conventional model of nature reserves—discrete and isolated entities in a human-dominated landscape—does not apply well to animals such as large carnivores. For several reasons the discrete reserve model should be replaced by a more realistic model that spans many zones and intensities of land use (Harris 1984; Noss & Harris 1986). First, opportunities for creating single reserves big enough to sustain viable populations of large carnivores are extremely limited. Second, and perhaps surprisingly, most of western and northern North America is still lightly inhabited by humans and well suited to a model in which reserves are buffered from intensive land uses and interconnected into functional networks that span huge areas (Noss 1992). Third, reserves play vital roles in these networks, but so does the surrounding semi-natural matrix. The regional landscape must be considered and managed as a whole.

A few biologists and many politicians seem ready to discard the idea of reserves altogether and to manage the entire rural landscape for multiple uses (logging, agriculture, livestock production, mining, tourism, etc.). This theme appears repeatedly in ecosystem management proposals by state, provincial, and federal government agencies, many of which seem to assume that science can determine how ecosystems function and that humans possess or can develop the technology needed to manage ecosystems wisely (Noss & Cooperrider 1994; Stanley 1995). But opening up all wildlands to multiple, extractive uses would almost certainly doom large carnivores in many regions because—among other reasons—resource production generally requires road access, which often leads to high mortality of carnivores (Mattson et al., this issue). A model in which roadless reserves are embedded in and linked by zones with low road density and in which outer zones accommodate a variety of compatible human uses is well supported by existing information on carnivore biology and, we hope, should eventually be sociopolitically feasible.

The scale of network to be considered in large carnivore conservation is controversial. Mech (1995), for example, believes that large-scale networks linking major regions (Noss 1992) are impractical and unnecessary. At least for wolves in the Great Lakes region, Mech (1995) favors small-scale zoning whereby small refuges (e.g., about 100 km^2) persist in a matrix of agricultural or other populated land and lethal control of wolves is applied as needed when wolves stray into no-wolf zones, or even within refuges if wolf populations become too high. We acknowledge that such a model might be the only viable one, in the short term, if large carnivores are to survive in developed regions (Primm & Clark, this issue). But managing for an increasingly fragmented distribution of any species is risky (Theberge 1983). In regions such as the Rocky Mountains, moreover, there still remains the opportunity to restore truly self-sustaining carnivore populations. Conservation biologists and policy makers should accept the challenge.

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