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Ecology, conservation, and restoration of large carnivores in western North America

Introduction

Large carnivores operate over large spatial scales and affect and are affected by multiple ecosystem processes (e.g., predation, migration, climate, fire, etc.). Thus carnivore ecologists must deal with expansive areas and multiple scales and disciplines. For this reason, studies of top carnivores have played a significant role in fostering ecosystem approaches among managers and researchers (Minta et al. 1999). Specifically, wolves (*Canis lupus*), cougars (*Puma concolor*), and bears (*Ursus* spp.) have become important symbols for conservation and ecosystem management. Recent research has examined multiple large carnivores (Kunkel et al. 1999, Carroll et al. 2001) and multiple ecosystems in regional conservation networks (Soule and Terborgh 1999). Conservation perspectives resulting from such work can help build strategies to protect appreciable amounts of native biological diversity (Noss and Cooperrider 1994, Paquet and Hackman 1995, Soule and Terborgh 1999). Conservation strategies that focus on charismatic animals such as large carnivores have additional advantages because such a focus motivates organizations and the general public.

Even though large carnivores often are grouped for management and share many traits, some important differences affect their resiliency (Weaver et al. 1996). The most obvious split occurs between the obligatory predators (cougars, wolves, and jaguars (*Panthera onca*)) and the omnivorous facultative predators (bears). Cougars, wolves, and jaguars have higher dispersal capabilities and higher reproductive rates than bears. Wolves are social; cougars, jaguars, and bears are solitary. Cougars, being solitary, are less plastic in predatory behavior than wolves, rely on smaller prey, and are less competitive in multi-carnivore environments

(Kunkel et al. 1999). As stalking predators, cougars are more habitat-specific than coursing wolves. Brown bears (*U. arctos*) pose the most direct perceived conflict with humans, and wolves the greatest perceived conflict with livestock, so both are less socially acceptable and experience higher human-caused mortality. As a result of these varying levels of resiliency, management is easiest for cougars, more difficult for wolves, and most difficult for brown bears.

This chapter reviews and synthesizes information on large carnivores in North America as it applies to their management and their roles in biodiversity conservation in coniferous forests of North America. Treatment of basic ecology will be brief and will focus on aspects related most to management; others (Carbyn et al. 1995, Clark et al. 1999, Soule and Terborgh 1999, Demaris and Krausman 2000, Gittleman et al. 2001) have provided recent reviews of carnivore ecology. Management implications will be indicated throughout and in separate management sections. Black bears (*U. americanus*) are treated more lightly than the other species due to their more secure conservation status. Jaguars also are treated lightly due to their limited range in southwestern coniferous forests, lack of study, and current absence. This does not, however, correlate to a reduced need to consider these species in management.

Current status and ecological roles

Wolves

Historically, wolves were distributed throughout most of North America in all habitats that supported ungulates. By 1930, after decades of persecution, wolves were eliminated from the western U.S. and had declined greatly in western Canada. Wolves started a remarkable comeback in the northwestern U.S. in the 1980's. More than 400 wolves now occupy the northern Rockies as a result of natural re-colonization and re-introductions (Bangs et al. 1998). Populations are centered in the recovery areas of northwest Montana, central Idaho, and the Yellowstone ecosystem of Montana, Idaho, and Wyoming. Re-introductions of Mexican wolves (*Canis Lupus Baileyi*) were initiated in 1998 in the southwestern U.S., and approximately 30 wolves occupied the area along the New Mexico and Arizona border in 2001 (W. Brown, U.S. Fish and Wildlife Service, unpublished data).

By 1996, eight wolf packs had re-colonized northwest Montana via dispersal from Canada (Boyd and Pletscher 1999). Density of wolves in northwestern Montana is approximately 10 wolves per 1000 km^2. Annual survival rate of wolves there is about 0.80 and their finite annual rate of increase is about 1.2 (Pletscher et al. 1997). The majority of mortality there, as elsewhere, is illegal and legal kill by humans. Annual finite rates of increase for wolves in North America range from 0.4 to 2.5 (Fritts and Mech 1981, Keith 1983, Fuller 1989).

Wolves released in Yellowstone Park and Idaho have prospered remarkably. Those re-introduced to Yellowstone increased from 31 wolves soft-released (held in pens for acclimation for two months prior to release) in 1996 to 177 in 18 packs in 2000 (Smith et al. 2001). The population in central Idaho increased from 35 hard-released (released immediately to the wild) in 1996 to 191 in nine packs in 2000 (C. Mack, Nez Perce Tribe, unpublished data). At least four wolves have been confirmed to have dispersed from one recovery area to another (Yellowstone to Idaho, northwest Montana to Idaho, and Idaho to northwest Montana), and dispersing wolves have survived to reproduce outside recovery areas.

Impacts of predation

In western North America, wolves prey primarily on Elk (*Cervus elaphus*), deer (*Odocoileus* spp.), moose (*Alces alces*), and caribou (*Rangifer tarandus*). Wolves are opportunistic predators and variation in prey preferences have been reported (Huggard 1993, Weaver 1994, Kunkel 1997, Bergerud and Elliot 1998, Smith et al. 2001). Kill rates vary greatly from 2.0 to 7.2 kg per wolf per day (Ballard and Gipson 2000). Wolves generally kill animals that are vulnerable because of age, condition, or habitat and weather circumstances (Mech 1996). Wolf population density varies directly and widely with prey density (Fuller 1989).

The impact of wolf predation on ungulate populations has been much studied and debated. Impacts reported vary from slight to regulating (i.e., density-dependent; Van Ballenberghe and Ballard 1994). Potential reasons for this variation include variation in local conditions (habitat, weather, prey and predator densities, and behavior, etc.; Messier 1995) and the inherent difficulty of field studies of large carnivores that influences data collection and interpretation. There is good evidence for limiting (one factor that far outweighs others in impeding the rate of increase; Leopold 1933:39) but not regulating (density-dependent factors that keep a prey population in equilibrium) impacts of wolf predation (Gasaway et al. 1992, Messier 1994, Van Ballenberghe and Ballard 1994, Boertje et al. 1996, National Research Council 1997, Kunkel and Pletscher 1999). In northern latitudes with simpler predator–prey systems, the impacts of predation may be regulating, especially when wolves and another predator (bears) prey on one or two prey species (Messier 1994). Where wolves and deer co-exist in the northern U.S. and Canada and have been well studied, their populations have been unstable for the duration they have been examined (the last 20–40 years; Potvin et al. 1988, Fuller 1990, Hatter and Janz 1994). Given the large-scale, density-independent influences such as weather and loose regulatory feedback inherent to these northern systems, this instability is not surprising (Botkin 1990, Bergerud and Elliot 1998).

Human harvests of prey in Alaska and Canada were significantly lower where wolves were not hunted or controlled (Gasaway et al. 1992). Also, hunter success for deer and elk declined as wolves re-colonized northwest Montana and was lower than in areas wolves had not re-colonized (Kunkel and Pletscher 1999). Predator numbers declined as a result of predator-induced declines in prey and this resulted in a rebound in prey in northwest Montana. Mech and Nelson (2000) found no impact of wolf predation on harvest of white-tailed deer (*O. virginianus*) bucks in "good deer habitat" in northern Minnesota, but did find an impact in poor habitat. Additionally, doe harvest had to be eliminated. Despite increasing evidence of wolf predation limiting prey populations, the National Research Council (1997) in a summary of research on effects of wolf control on ungulate populations concluded that there was little evidence to indicate the long-term effectiveness of wolf control for increasing human harvest of prey.

Wolf re-colonization of the western U.S. will likely result in declines of local cervid populations, especially where multiple predators are present (Crete 1999, Kunkel and Pletscher 1999). Managers should expect cervid populations to remain low for extended periods where wolves, bears, cougars, and humans vie for the same prey (Gasaway et al. 1992, National Research Council 1997). Lower cervid densities may result in lower predator densities and thus slow wolf and brown bear recovery (McLellan and Hovey 1995, Boertje et al. 1996, Mladenoff et al. 1997). Depending on objectives, managers should be prepared to reduce hunting pressure on cervids to prevent potentially long-term low densities of prey in such areas (Fuller 1990, Gasaway et al. 1992, Boertje et al. 1996). Management of wolves through harvest may also be an option once wolves are delisted.

Cougars

Cougars presently occupy almost all of their historic range in western North America. The cougar's solitary nature, use of remote and rugged landscapes, relatively uncommon predation on livestock, and relatively high reproductive rate helped it escape the regional extinctions that befell other large carnivores. The recovery of cougars in the West occurred in the equivalent of only three cougar lifetimes (Logan and Sweanor 2000). Cougars are currently expanding into western portions of the Great Plains.

Cougar populations were thought to be regulated through socially controlled land tenure (Hornocker 1970, Seidensticker et al. 1973). Recent research from California, however, indicates that cougars, like other carnivores, were limited in abundance primarily by the supply of food rather than land tenure (Pierce et al. 2000). Density of cougars ranges from 5.8 to 47 cougars per 1000 km^2. Annual survival rates for females average 0.80 (Logan and Sweanor 2000) with humans being the major cause of death for cougars in protected and unprotected populations. Finite annual rates of increase varied from 1.18 to 1.32 for a protected population in New Mexico (Logan et al. 1996).

Impacts of predation

Under some circumstances cougars only minimally affect prey populations. Cougars have had little direct effect on the size of elk and deer populations in the Yellowstone ecosystem (Murphy et al. 1999). Similarly, cougar populations in Idaho, Arizona, and Utah do not prevent elk or mule deer (*O. hemionus*) from increasing (Hornocker 1970, Shaw 1980, Lindzey et al. 1994). Logan et al. (1996) concluded that habitat quality and quantity, not cougars, were the ultimate limiting factors for mule deer in southern New Mexico.

Under other conditions cougars may significantly reduce prey numbers. In northwestern Montana, cougars in combination with wolves and bears limited (as defined above) white-tailed deer and elk populations (Kunkel and Pletscher 1999). In California, cougar predation caused precipitous declines in small bighorn sheep (*Ovis canadensis*) populations where few alternate prey were available (Wehausen 1996, Hayes et al. 2000). Cougars also are limiting recovery of state-endangered desert sheep (*Ovis canadensis mexicanus*) in New Mexico (Fisher et al. 1999). There is no evidence that indiscriminate control of cougars alters these trends (Evans 1983, Hurley and Unsworth 1999; but see Ernest et al. 2002); more targeted control of individual cougars appears most effective for sheep populations (Ross et al. 1997, Wright et al. 2000).

Brown bears

Brown bears currently are found in <50% of their former range in North America and <2% of their former range in the lower 48 United States. Five subpopulations exist in the contiguous United States: (1) Yellowstone ecosystem, (2) northern continental divide ecosystem in northwestern Montana, (3) Cabinet/Yaak ecosystem in northwestern Montana, (4) Selkirk ecosystem in northern Idaho, and (5) North Cascades ecosystem in northern Washington. These areas are dominated by parks and designated wilderness areas. In contrast, only about 12% of the bears are confined to protected areas in British Columbia (McLellan and Hovey 2001).

Densities of brown bear populations range from 3.9 (arctic Alaska) to 551 (southern coastal Alaska) bears per 1000 km^2 (Miller et al. 1997). Brown bears display some of the lowest reproductive rates and rates of increase among terrestrial mammals due to late sexual maturity and protracted reproductive cycles (Jonkel 1987, Eberhardt et al. 1994, Craighead et al. 1995, Hovey and McLellan 1996, Pease and Mattson 1999).

Impacts of predation

Impacts of bear predation on ungulates is mostly on neonates (Schwartz and Franzmann 1991, Kunkel and Mech 1994, Smith and Anderson 1996, National Research Council 1997, Ballard and Van Ballenberghe 1998, Bergerud and Elliot 1998). In combination with other predators, bears may limit some ungulate populations (Messier 1994, Bergerud and Elliot 1998, Kunkel and Pletscher 1999). Messier (1994) suggested that the presence of a bear species may be necessary for wolves to regulate moose at low density. Under such circumstances, reductions in bear densities may or may not benefit ungulate populations (National Research Council 1997, Ballard and Van Ballenberghe 1998).

Predation by bears on salmon (*Onchorynchus* spp.) can be intense. On Chichagof Island in southeast Alaska, over 50% of a sample of 1100 salmon carcasses showed signs of bear predation (Willson et al. 1998). On a Moresby Island stream in western British Columbia, black bears captured over 4200 salmon during the 45-day spawning period in 1993, about 74% of the salmon entering the stream (Reimchen 2000). On large Alaskan rivers with large salmon runs bears take as little as 2.5% of the run but on smaller streams they take up to 85% (Reimchen 2000). Intensive levels of predation may be responsible for the evolutionary selection of some features in salmon including body size and reproductive strategies (Willson et al. 1998, Reimchen 2000).

Black bears

The black bear is the most successful of the world's eight bear species at co-existing with humans. Black bear status in North America varies from pest to threatened (Pelton 2000). The range of the species in the western U.S. is largely associated with public lands in forested mountain terrain. Densities of black bears range from 90 (Alaska) to 1300 (Washington) per 1000 km^2 in western North America (Kolenosky and Strathearn 1987, Miller et al. 1997). Densities and demographic rates are highest in diverse early-successional forests with rich soils and in areas with relatively long foraging seasons (Schwartz and Franzmann 1991). Reproductive rates of black bears are low. If a female bear lives to age 15, she will generally produce a maximum of six litters during her lifetime (Kolenosky and Strathearn 1987). Most mortality is caused by humans and includes hunting, poaching, depredation control, and vehicle collisions. Annual survival rates of adult females average 0.87 (Pelton 2000).

Jaguars

Jaguars were probably eliminated from the northern portion of their range in southern New Mexico and Arizona early in the twentieth century (Valdez 2000). The northern portion of the range of jaguars has receded southward about 1000 km and has been reduced in area by nearly 70% (Swank and Teer 1989). Jaguar elimination resulted from the same predator control programs that reduced the other large carnivores in the West. Limited sightings of probable dispersers from the closest population in Mexico (approximately 200 km south of the US–Mexico border) have been made recently in both New Mexico and Arizona. Jaguars were classed as endangered in the U.S. in 1997, but there is presently no recovery plan in place. Densities of jaguars in tropical forests range from 30 to 70 per 1000 km^2 and likely 13 to 19 per 1000 km^2 in northwestern Mexico (Lopez Gonzales and Brown in press).

In the tropics, jaguars are usually associated with closed canopy forest and permanent water below 1200 m (Quigley and Crawshaw 1992). Jaguars used riparian forests more than expected and open forests less than expected in the Pantanal region of South America (Crawshaw and Quigley

1991). Jaguars occupy montane oak (*Quercus* spp.), oak-pine (*Pinus* spp.) forests, riparian forests, and mesquite thickets at the northwestern limit of their range (Brown 1983). Jaguars appear particularly adapted for preying on large slow mammals such as peccaries (*Tayassu* spp.), while cougars, being smaller and more agile than jaguars, are more adapted to prey on deer (*Odocoileus* spp.; Aranda 1994). This difference likely reduced competition between the two species (Aranda and Sanchez-Cordero 1996). Like other large carnivores, jaguars are opportunistic and have been recorded to prey on over 85 species (Seymour 1989). Even though jaguars presently occur primarily in the tropics, they originated in the holarctic (Kurten and Anderson 1980) and they no doubt would do well in temperate regions with ample prey (Valdez 2000).

Intraguild dynamics among carnivores

Only recently has comprehensive work examined interactions (predation, competition, kleptoparasitism) among large carnivores in ecosystems (Kunkel 1997, Murphy et al. 1998, Kunkel et al. 1999, Smith et al. 1999, 2001). Wolves and cougars both selected the white-tailed deer for prey in northwestern Montana and they selected similar classes of prey (Kunkel et al. 1999). Wolves kleptoparasitized cougar kills and killed cougars, and wolves and cougars were largely responsible for the white-tailed deer and elk population declines in northwest Montana that resulted in starvation in some cougars. These results suggested exploitation and interference competition between the two species. Exploitation competition rather than interference competition likely was responsible for the population decline in cougars because more cougars starved than were killed by wolves. Such interactions have only been examined in a few other studies worldwide. Iriarte et al. (1990) speculated that prey selection by cougars in the Americas resulted from competitive evolution with sympatric jaguars. Wolf kleptoparasitism of cougar kills may force cougars to increase their kill rate as the wolf population expands (Murphy et al. 1998).

Wolves and bears frequently interact at kill sites, with varying outcomes depending on number of wolves involved. One in three cougar-killed ungulates were scavenged by brown bears in the Yellowstone ecosystem during 1990–1995 and at one in eight carcasses bears displaced cougars (Murphy et al. 1998). These displacement rates were approximately twice as high as rates in the Glacier ecosystem in Montana (Murphy et al. 1998). Habitat and prey size may significantly affect these relationships (Creel 2001).

Umbrella, flagship, top-down, and keystone roles

Because regional land management is highly inefficient if done on a species by species basis (Noss et al. 1997, Simberloff 1998), conservation biologists have attempted to identify and use one or a few species as surrogates for an array of others. Such surrogates have been called indicator, umbrella, flagship, or keystone species depending on their perceived ecosystem roles and utility in addressing conservation problems (Caro and O'Doherty 1999). Definitions of surrogates have varied, and Caro (2000) urged that conservationists should define the goals of conservation projects clearly when using these terms. Power et al. (1996) defined the keystone species as one whose impacts on the community or ecosystem are large relative to the species abundance. Caro and O'Doherty (1999) argued, however, that keystones are not used as a shortcut to describe patterns or processes and have never been successfully used as surrogates, though they may be useful in choosing them (but see Simberloff 1998, Kotliar 2000). The keystone concept may be a useful tool for communicating ecological importance to the public and offsetting unfavorable public opinion of some species (Kotliar 2000). Indicator species are used as surrogates for ecosystem health or areas of high species richness (Landres et al. 1988). Umbrella species differ from indicator species in that they are used to specify the size and type of habitat to be protected rather than its location (Berger 1997). Flagship species are charismatic species used to raise awareness, build public support, or attract funding for a conservation cause (Caro and O'Doherty 1999).

Trophic cascades, top-down effects, and keystones

Removal of top carnivores can lead to a cascade of community alterations including relaxation of predation as a selective force, the irruption of herbivore populations, the spread of disease, and diminished biodiversity (Kay 1994, McShae and Rappole 1997, Wilson and Childs 1997, Berger 1998, Terborgh et al. 1999, 2001). Relaxation of predation was shown in Alaska where field experiments demonstrated that moose are sensitive to vocalizations of ravens (*Corvus corax*) and may rely on their cues to avoid wolf predation (Berger 1999). A similar relationship was absent in areas of Alaska and Wyoming where wolves and bears have been extirpated

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for 50–70 years. Evidence for diminished biodiversity related to large carnivore absence was provided by Berger et al. (2001*a*) in a comparison of densities and diversities of riparian birds in areas of high moose density (lacking large carnivores) to areas of lower moose density (human-harvested populations). Willow communities were more altered, and densities and diversity of birds were lower in the areas of higher moose density.

Removal of top predators may result in superabundant populations of herbivores and medium-sized predators. This in turn may result in reproductive failure and local extinction of plants, birds, reptile, amphibians, and rodents (Crooks and Soule 1999, Henke and Bryant 1999, Terborgh et al. 2001). Coyotes expanded their range and densities following the extirpation of wolves in the western U.S. (Johnson et al. 1996), and this may have resulted in decreased densities of red foxes (*Vulpes vulpes*; Peterson 1995) and swift foxes (*Vulpes velox*; Kitchen et al. 1999). Seven years after arrival to Isle Royale, wolves completely eliminated coyotes (Krefting 1969). On the Kenai Peninsula, Alaska (Thurber et al. 1992), northwest Montana (Arjo and Pletscher 1999), and Manitoba (Paquet 1991), however, extensive overlap of wolf and coyote home ranges occurred with little reduction in coyote density. As evidenced in large carnivore inter-relationships, habitat and prey size may significantly affect large and smaller carnivore relationships (Creel 2001). Smaller carnivores may be more vulnerable in more open habitats, and wolf and coyote co-existence may be more likely where prey size is larger and consumption by wolves is relatively less, thereby providing food for coyotes (Peterson 1995).

There is little direct evidence indicating that systems are regulated by growth and biomass of plants (bottom-up) or indicating top-down control in terrestrial systems (Gasaway et al. 1992, Crete and Manseau 1996, National Research Council 1997, Soule and Terborgh 1999, Kunkel and Pletscher 1999). Evidence for top-down control is increasing, however (Schmitz et al. 2000, Estes et al. 2001, Halaj and Wise 2001, Miller et al. 2001, Terborgh et al. 2001). On Isle Royale growth rates of balsam fir (*Abies balsamea*) were regulated by moose density, which in turn was reduced by wolf predation (McLaren and Peterson 1994). Ripple and Larsen (2000) provided evidence of a significant decline in aspen overstory recruitment after 1920 in Yellowstone and hypothesized that elimination of wolves and the resultant increase in elk numbers was largely responsible for this decline. Wolf restoration may change this trend by the resulting decrease in elk numbers and subsequent increase in aspen recruitment. An increase in aspen may also result from elk avoiding browsing in aspen stands as an antipredator response to the presence of wolves (Ripple et al. 2001). Boyce and Anderson (1999) believe however that fluctuations in vegetation and overwinter mortality will continue to cause much greater annual variation (including major perturbations) of ungulate populations in the Yellowstone ecosystem than wolves. Documenting a fortuitous natural experiment of large predator exclusion on newly created islands in Venezuela, Terborgh et al. (2001) showed that the absence of predators consistently freed certain consumers to increase many times above "normal." This unleashed a trophic cascade whose effects included severely depressed recruitment of canopy trees. Hyperabundant consumers threaten to reduce much plant and animal diversity in these species-rich forests. More opportunistic predators like wolves likely will have greater top-down effects than the more specialized cougars (McCann et al. 1998, Miller et al. 2001).

The top-down or keystone roles of less predatory carnivores (bears) are even less clear, but potentially significant in some systems. The millions of anadramous fish (primarily salmon) that spawn in freshwater streams along the Pacific coast provide a rich food resource that directly affects the biology of terrestrial consumers including bears and indirectly affects the entire food web that ties the water and land together (Willson et al. 1998). The high energy value of this food greatly affects bear reproductive success (Hilderbrand et al. 1999). Bears commonly carry these salmon back to streambanks and tens of meters inshore (Willson et al. 1998). Bears may carry up to 6.7 kg per ha of phosphorus into the terrestrial nutrient cycle, a level similar to the commercial application rate often used for forestry (Willson et al. 1998). This movement of carcasses is also a major source of nitrogen for riparian vegetation (Bilby et al. 1996, Ben-David et al. 1998).

The potential top-down or keystone role of large carnivores is still under debate (Polis and Strong 1996) and largely depends upon the definition of keystone roles (Power et al. 1996). The great complexity of trophic interactions makes the assessment of top-down versus bottom-up control very difficult, as the two processes may not be mutually exclusive and most likely act in concert. Using modeling, Powell (2001) predicted that predators and prey each control systems, but the control acts on different scales with variation in productivity of food causing more variation in herbivore population sizes than variation in predation rates. The best experiment completed examining top-down and bottom-up control in mammalian predator–prey systems indicated that control was both from the top-down and bottom-up in a lynx–hare (*Lynx lynx* and *Lepus americanus*, respectively) system in the boreal forest (Krebs et al. 1995). Both types of control should be anticipated and probably vary depending on spatial and temporal scales and the complexity of the predator–prey systems.

A shift apparently occurs from bottom-up dominance (caribou and moose) in unproductive northern tundra ecosystems to top-down (wolf and bear regulated) dominance in lower-latitude, more productive boreal ecosystems (Messier 1995, Crete and Manseau 1996). The theory of food chain dynamics predicts that trophic levels are added sequentially as primary productivity increases (Fretwell 1987). At low primary productivity, herbivores should have a strong impact on plant biomass, but predators would be absent or unable to regulate their prey (due to the migratory behavior of caribou at high latitudes resulting from low habitat productivity). With increased primary productivity, predators would be able to hold herbivores in check, and herbivores then will have only a small impact on the plant community (e.g., moose at mid-latitudes; Crete 1999). Where wolves are absent cervid biomass is five times greater. The Isle Royale example (McLaren and Peterson 1994) fits this model. The moose–wolf and caribou–wolf systems examined by Messier (1995) fitted this theory in a broad sense but departed from it when: (1) habitat quality was high enough for moose to escape regulation by wolves (predator satiation) unless another predator such as bears was also present, and (2) caribou–plant interactions are affected by multi-year time lag effects that produce recurring fluctuations in caribou numbers. The pattern of increasing cervid density with increasing biomass productivity (along the latitudinal gradient) in the absence of wolves and bears predicts that cervid abundance will significantly decrease in the western U.S. with wolf re-colonization (Crete 1999, Oksanen et al. 2001). The equilibrium biomass (<100 kg km^{-2}) of cervids in this region however will not be as low as in the moose range of the mid-latitudes because equilibrium density is higher in multi-species assemblages.

Umbrellas and flagships

Because large carnivores have such large home ranges (e.g., 100–2000 km^2) and their habitat encompasses those of many other species, they have been used as umbrella species. It is debatable however whether this means large carnivores serve as umbrellas. Noss et al. (1996) and Caro and O'Doherty (1999) could find no definitive published studies documenting the level of protection afforded to other species by a conservation plan focused on large carnivores. In one of the few preliminary tests of the umbrella concept, Berger (1997) concluded that, despite their large home range, black rhinos (*Diceros bicornis*) did not serve well as an umbrella for species at the same trophic level. While there is great urgency for finding management paradigms to conserve biodiversity, the complexity of ecosystems and our lack of knowledge of them should temper our rush into specific, potentially expensive paradigms (Andelman and Fagan 2000).

In an analysis of the California coastal sage scrub, the Columbia Plateau, and all the U.S. counties, Andelman and Fagan (2000) found that surrogate species did not perform substantially better than randomly selected sets of a comparable number of species. They also found little evidence to support the claim that umbrella, flagship, or biodiversity indicator schemes (including using large carnivores) have special biological utility as conservation surrogates for protecting regional biota. Extensive reliance on surrogate species may be a poor allocation of scarce conservation resources and even the most carefully selected surrogate might prove inadequate and inefficient (Andelman and Fagan 2000). These authors urged caution in adopting umbrella or flagships until their usefulness as predictors of biological diversity and its persistence has been more fully investigated. One start at such an assessment provided evidence that the red wolves (*C. rufus*) in the southeast served as a successful flagship (Phillips 1990).

Because large carnivores are habitat generalists, protecting their habitat may not necessarily protect the habitat of some specialists. Protection of large areas though will reduce this short coming. Large carnivores primarily need sufficient prey and relatively low levels of human-caused mortality, criteria that may not necessarily meet the needs of many other species. The diverse and extensive habitat needs of brown bears, however, may make them a potentially better umbrella species than the other large carnivores. The best surrogate species are those that can be easily monitored (Caro and O'Doherty 1999): bears do not fit this criteria. According to the criteria of Caro and O'Doherty (1999), wolves are the only large carnivore that may serve as a surrogate species and then only as a flagship. In developing a comprehensive conservation strategy for carnivores in the Rocky Mountains, Carroll et al. (2001) concluded that the plan must consider several species rather than a single umbrella species. Even so, they also concluded that the viability of individual species serves as a biological "bottom-line" that allows evaluation of the effectiveness of a conservation

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strategy in a way not possible with composite indicators of ecosystem function.

Recent expansions by wolf populations provide further evidence of their tenuous role as umbrellas. Restoration of wolves in forested regions of the Great Lakes may not necessarily be a sign that the ecosystem there has been restored to some previous level of ecosystem function (Mladenoff et al. 1997). In fact, wolves may do well because the ecosystem is altered. High deer populations support large numbers of wolves, but they can also negatively affect other important aspects of forest biodiversity (DeCalesta 1994). Wolf recovery in the Great Lakes region and potentially the Yellowstone area has resulted not from restoration of the original ecosystems but from more tolerant human attitudes in combination with human-caused landscape and prey changes (high deer and elk numbers). Management of these systems may require the reduction of prey densities to reduce impacts of high prey numbers on ecosystems (Kay 1994), which would ultimately reduce carrying capacity for wolves. Alternately, wolves may be used as the management tool to reduce those prey densities and associated impacts. See Singer et al. (2003) for more information on this topic.

In some situations, restoration of a large carnivore may have negative consequences for the ecosystem. The expansion of cougars has the potential to extirpate small populations of native vertebrates (e.g., porcupines (*Erethizon dorsatum*) and desert sheep in the Great Basin; Berger and Wehausen 1991, Sweitzer at al. 1997). We must recognize that recent ecosystem changes have altered the dynamics of interacting native species in ways that threaten patterns of biodiversity (Berger and Wehausen 1991, Sweitzer at al. 1997).

Landscape management and large carnivore conservation

Forest, land, and human management

Few areas in western North America combine high biological productivity and low human impact (Carroll et al. 2001). Thus zones of human–carnivore conflict are often in areas of highly productive habitat that have above-average human use, are spatial buffers between large core habitat areas and zones of high human use, or are likely to experience increased human use in the future (Boyd 1997, Mace and Waller 1998, Merrill et al. 1999). Outside of Alaska and northwestern Canada, opportunities for creating single reserves large enough to sustain populations of large carnivores are very limited. Even in Alaska and northwestern Canada, careful management will be required to ensure the long-term persistence of large mammals. Even so, most of western North America still has relatively few people and could accommodate reserves buffered from intensive land use and interconnected by networks covering large areas (Noss 1992).

Wolves

Even though wolves are habitat generalists and ungulate densities explain more than 70% of the variation in wolf densities (Fuller 1989), some natural and anthropogenic landscape variables appear important to wolves (Singleton 1995, Boyd 1997, Kunkel and Pletscher 2000, 2001). In the Great Lakes region, wolves avoid agricultural areas and deciduous forests and favor forests with a conifer component (Mladenoff et al. 1995). Centers of wolf territories are most likely to occur in areas with road densities below 0.23 km per km^2 and nearly all wolves occur where road densities are below 0.45 km per km^2. No wolf territory was bisected by a major highway or where human population densities were >1.5 persons per km^2. Mladenoff et al. (1995) found road density to be the best predictor of wolf habitat in the Great Lakes region. Their data suggested that wolves selected areas to avoid contact with and consequent potential mortality from humans. Wolves in the Rocky Mountains, however, selected for areas with roads, probably because roads coincided with valley bottoms preferred by prey (Boyd 1997, Kunkel and Pletscher 2000), and 75% of human-caused wolf mortality was within 250 m of a road. Similarly, Trans Canada Highway 1 accounted for more than 90% of wolf mortalities in the Bow Valley, British Columbia (Paquet P., World Wildlife Fund, personal communication).

Some models have been developed to predict areas that wolves will recolonize (Singleton 1995, Boyd 1997, Kunkel 1997, Mladenoff et al. 1999) or where potential conflicts with prey (U.S. Fish and Wildlife Service 1994, Kunkel and Pletscher 1999, 2000, 2001) and livestock (Fritts et al. 1992, U.S. Fish and Wildlife Service 1994, Mech et al. 2000) will be the highest. These models are currently being refined for various regions in the Rocky Mountains. They may help managers to delineate priority areas for managing and monitoring wolves and their prey, and predict and remedy conflicts with landowners and hunters. Only two restrictions on land use have been used to promote wolf recovery in the western U.S. A 1.6-km radius area around dens is sometimes protected from intensive human use between 15 March and 1 July, and USDA Wildlife Services cannot use nonselective predator control in areas occupied by endangered wolves.

Cougars

Topographic relief or abundant vegetative cover are important habitat components for cougars (Seidensticker et al. 1973, Logan and Irwin 1985, Logan et al. 1986, Van Dyke et al. 1986, Laing and Lindzey 1991, Williams et al. 1995). Cover improves success in ambush hunting and provides protection from enemies (Kunkel 1997, Kunkel et al. 1999). Cougar dens are usually located in rock outcrops, in dense shrubfields, or under downed conifers (Murphy et al. 1999). Travel corridors used by cougars in southern California are typically drainage washes or ridges with abundant native woody vegetation that provide security from human disturbance (Beier 1995).

Logging, burning, or grazing may reduce the cover needed by cougars (Logan and Irwin 1985, Van Dyke et al. 1986, Laing and Lindzey 1991). Cougar track density decreased by 61% in timber harvest areas in southern California from 1986 to 1992 (Smallwood 1994). Logging would likely have negligible effects if logged areas were small relative to area requirements of cougars. Like other obligate carnivores, cougar habitat use and density will be affected by landscape alterations as they affect prey spatial temporal distribution, use of hiding cover, and density (Kie et al. 2003). Human activity may reduce habitat quality. Cougars in Utah shifted to nocturnal activity patterns in the presence of human disturbance and crossed less-traveled roads more than higher-use roads (Van Dyke et al. 1986).

Bears

Bear-management strategies presented here apply primarily to brown bears. Because black bears are generally less sensitive to human disturbance than are brown bears, management for brown bears generally benefits and is adequate for black bears. Although brown bears are flexible in the habitats they use (Waller and Mace 1997) protection of certain habitats in forested mountains of the western interior is important. Bears generally select riparian areas and avalanche chutes in spring (Mace et al. 1999, McLellan and Hovey 2001). Bears track plant phenologies by moving up elevation in avalanche chutes during the summer to find the berries (*Vaccinium* spp. and *Shepherdia* spp.) that dominate their diet (McLellan and Hovey 1995). Ensuring wild or prescribed fire is important as berries are found most in open timber and open timber burns 50–70 years old at high elevations, and fire promotes regeneration of important whitebark pine seeds (*Pinus albicaulis*). Timber harvests must be carefully planned as large regenerating timber harvest blocks are rarely used in any season by bears (McLellan and Hovey 2001). Alpine insect aggregations are used by brown bears in summer and fall (Mattson et al. 1991*a*, *b*) and human disturbance to bears in these areas should be minimized.

Human presence in brown bear habitats often leads to bear–human conflicts, often with fatal consequences for bears. Human-defense kills of brown bears occur more frequently in areas of higher human populations (Mattson et al. 1996*a*). Human-habituated brown bears may use native and non-native foods near human developments and are killed more often than non-habituated bears (Mattson et al. 1996*a*). Where available, fish are critical in the summer and fall (Mattson and Reinhart 1995, Hilderbrand et al. 1999). Intense sport fishing and development along rivers and streams can exclude bears from important food sources. When this exclusion is combined with human-induced mortality, mortality of bears can exceed sustainable levels (Mattson and Reinhardt 1995, Schwartz and Arthur 1997). Limiting adult annual female mortality to <10% is key to brown bear conservation in the small, threatened populations of the lower 48 states (Wielgus et al. 1994, Mattson et al. 1996*b*, Mace and Waller 1998, McLellan et al. 1999).

Road construction and timber harvest should avoid riparian areas and avalanche chutes (Mace et al. 1999). Secure cover should be maintained near these chutes; clear-cuts and heavy thinning adjacent to avalanche chutes should be avoided. To maintain existing habitat quality, Craighead et al. (1995) recommended improving sanitation in areas in and surrounding recovery areas and establishing maximum road densities of 1 km per 6.4 km^2 ($\frac{1}{4}$–$\frac{1}{3}$ the density of current standards). Areas with road densities of >6 km per km^2 were not used by brown bears in western Montana (Mace et al. 1996). Multiple-use lands remote from human population centers may be critical for bears and must be managed for low-density and educated human use (McLellan et al. 1999). Hunters must be educated in identification of brown versus black bears and must handle ungulate carcasses in ways to avoid attracting bears. Craighead and Craighead (1991) recommended that the vegetation of the entire northern Rockies bioregion be satellite-mapped using a regionally consistent, botanically detailed hierarchy of vegetation and landform classifications. Thereby, habitat quality and quantity of bear foods could be defined from ecosystem to ecosystem and carrying capacities could be estimated. This work has recently been completed for the Selway-Bitterroot ecosystem (Merrill et al. 1999, U.S. Fish and Wildlife Service 2000).

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Accumulation of energy reserves is crucial for successful reproduction of bears (Hilderbrand et al. 1999). Litter sizes and population densities are linked to dietary meat content (Miller et al. 1997, Hilderbrand et al.1999) indicating the importance of fish and ungulate populations to bears including Yellowstone Lake cutthroat trout (*Oncorhynchus clarki*) and bison (*Bison bison*) and other ungulate carcasses in Yellowstone National Park. Bears with access to abundant meat sources had dietary meat contents generally >70% (Jacoby et al. 1999). Protection and restoration of anadromous fish runs coincident with the maintenance of safe and productive foraging areas for bears may require careful management. Such management is critical in maintaining the historic linkage between these terrestrial and aquatic systems. Restoration of salmon in the Columbian River system including central Idaho, for example, may be important for long-term viability of bears in this system (Craighead et al. 1995, Hilderbrand et al. 1999).

Craighead et al. (1995) outlined goals to achieve population recovery for brown bears in the lower 48 states. They argued that more extensive areas than outlined in the recovery plan (U.S. Fish and Wildlife Service 1993*a*) need to be ascribed with greater connectivity to reduce bear mortality and increase population potential. They recommended following the population viability analysis of Shaffer (1983, 1992) to guide recovery. Most significantly, and most controversially (Schullery 1997), Craighead et al. (1995) recommended developing "ecocenters" for bears of strategically placed food concentration centers. Based on data from bears using dumps prior to closure, Craighead et al. (1995) predicted that ecocenter networks would increase mean rates of natality and survival and carrying capacity, buffer seasonal variation in bear foods, serve to concentrate bears reducing movement into areas where risk of mortality may be high, and increase bear count reliability. They argued that current recovery areas are not large enough to support bears over the long-term and only with husbandry and extra inputs into the system can bears persist.

Brown bear population trends in the Yellowstone ecosystem have been debated (Eberhardt et al. 1994) with Pease and Mattson (1999) concluding the population has changed little since 1975. The population probably increased in whitebark pine crop mast years and declined in years when this crop failed. Mattson and Reid (1991) and Pease and Mattson (1999) cautioned that a conservative approach be maintained because the long-term habitat condition trend resulting from increasing numbers of humans in the area and the potential for global warming is likely downward. They argued that making decisions that have long-term consequences based on short-term trends would be an error, and thus it is premature to remove brown bears from the threatened list. This recommendation is presently under considerable debate (MacCracken and O'Laughlin 1998).

Livestock

Wolves

Control of wolves preying on livestock is one of the greatest management concerns for the species (Mech 1995). Concurrent with the increase in wolves and their range in Minnesota, the number of wolves killed by USDA Wildlife Services for depredation control has increased dramatically, from six in 1979 to 216 in 1997 (Mech et al. 2000). Even with >2000 wolves, the total percentage of farms in wolf range in Minnesota that suffer verified wolf predations is only about 1% per year. Wolf depredations on livestock are relatively low compared to other causes of livestock mortality, but are inordinately controversial (Bangs et al. 1998). Between 1987 and 2000, confirmed minimum livestock losses in northwest Montana totaled 82 cattle, 68 sheep and seven dogs (E. Bangs, USFWS, unpublished data). As a result, 41 wolves were killed and 32 were translocated. On average, <6% of the wolf population is annually affected by agency wolf-control actions (Bangs et al. 1998). Minimum confirmed livestock losses have annually averaged about 3.6 cattle, 27.8 sheep, and 3.8 dogs in the Yellowstone area and 9.2 cattle, 29.4 sheep, and 1.8 dogs in central Idaho. Since 1995, USFWS and the Wildlife Services have killed 18 wolves in central Idaho and 26 in the Yellowstone area because of conflicts with livestock. Since 1987, a private compensation fund administered by Defenders of Wildlife has paid livestock producers about $155 000 for confirmed or highly probable wolf-caused losses in Montana, Idaho, and Wyoming. This compares to an estimated $45 000 000 in annual losses to all causes for livestock producers in Montana alone. While losses to wolf depredation are insignificant to overall losses, losses to individual operators can be significant. It is likely that some form of compensation for losses (private or public) will always be required to ensure persistence of large carnivores in the West, and even then illegal killings of carnivores and low livestock producer support for restoration will remain (Bangs et al. 1998).

To determine best methods for managing depredations, researchers have examined the characteristics of farms experiencing depredations. Farms with chronic losses in Minnesota were larger, had more cattle, and had herds farther from human dwellings than farms with no losses (Mech

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et al. 2000). Forested public lands intermixed with private farm/ranch lands have experienced the greatest losses in the western recovery areas. The best management prescription for depredations in most cases appears to be lethal control. An analysis for Montana concluded that livestock losses and control costs could be significantly reduced by killing rather than relocating depredating wolves (Bangs et al. 1998). Non-lethal control options may be valuable in certain circumstances especially where wolf populations remain low. Non-lethal tools that will be successful will likely vary by circumstance (Mech 1995, Knowlton et al. 1999).

As wolves adapt to travel through relatively settled and open areas, opportunities for conflicts will increase as wolf populations increase. One partial solution to this is zoning to separate wolf habitat from wolf-free areas (Mech 1995). Zoning at large scales (among states; U.S. Fish and Wildlife Service 1993*b*) simplifies management. The primary disadvantage of large-scale zoning is that wolves would not be allowed to live in some areas where they could persist. Smaller-scale zoning would be more complex, but would allow wolves to live in many more enclaves. Even though dispersing wolves would likely face higher probabilities of mortality in the small-scale zoning management paradigm, there would be enough populations of wolves in such a meta-population for persistence to be likely (Mech 1995, Haight et al. 1998). Biologically, wolves could occupy parts of almost all regions of the western U.S. For this to occur, however, there must be acceptance by the public to control problem wolves (Mech 1995).

Cougars

In northwestern North America, rates of cougar predation on livestock are generally low. In Montana from 1984 to 1993, only 8.2 predation incidents occurred annually (Montana Fish, Wildlife and Parks 1996). Claims for compensation in Alberta for cougar kills averaged 4.4 per year from 1974 to1987. For every cougar claim, there were five wolf, 13 bear, and 42 coyote claims over a similar period (Pall et al. 1988). Selective removal of offending individuals is usually a more effective response than other management actions, especially translocation (Ruth et al. 1998). The complete elimination of cougars from problem regions in New Mexico has been attempted three times – twice to protect domestic sheep and once for wild sheep. None of these efforts resulted in a reduction in predation (Evans 1983).

Brown bears

Brown bear depredation on livestock is highly variable among years and areas. Livestock losses from brown bears in the Yellowstone ecosystem averaged 35 cattle and 29 sheep per year (Gunther et al. 1998). Losses averaged eight cattle and 17 sheep per year in the northern continental divide ecosystem (U.S. Fish and Wildlife Service 2000). Management of brown bears that prey on livestock must be more conservative than that for wolves or cougars because of the bear's relatively low reproductive rates. Bears must be provided more leeway than cougars or wolves before direct management actions are taken. Like wolves and cougars, bears that are relocated experience low survival and high return rates to capture sites (Blanchard and Knight 1995). Relocation has been most successful for subadult females. Similar to their wolf program, Defenders of Wildlife pays compensation to ranchers suffering losses of livestock to brown bears. More recently, this program and innovative initiatives by other conservation organizations have expanded to start purchasing grazing permits on public lands and retiring them where chronic conflicts with large carnivores occur. These initiatives hold great potential for reducing many livestock/wildlife conflicts on public lands.

Jaguars

Significant habitat loss and consequent loss of prey base is increasingly forcing jaguars to co-exist with humans and livestock in fragmented areas. The most urgent problem facing jaguar populations is indiscriminate killing of jaguars where conflicts with humans occur. Most research examining livestock predation by jaguars comes from Central and South America where livestock management is often less controlled and where non-lethal methods to manage depredations are less available and known than in North America. As a result, depredation rates there are relatively higher than rates for other large carnivores in North America. Cattle constituted a major part of the jaguar diet in studies conducted on ranches in seasonally flooded savannah woodland in the Venezuelan llanos (Hoogesteijn et al. 1993). Jaguar-caused mortality to calves ranged from 6% on a well-managed ranch to 31% on a smaller ranch in a more agriculturally developed region. Research conducted in Belize, however, indicated that healthy adult male jaguars can range close to livestock without causing problems (Rabinowitz 1986). Formation of protected areas within a network of ranches and ranches with easements may reduce mortality

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to jaguars but also allow ranching to remain viable (Lopez Gonzalez and Brown in press).

Landscape effects on carnivore hunting success

Structure and pattern of landscapes can affect the hunting success of carnivores, or alternately, the vulnerability of their prey and thus management of these landscapes can impact carnivores and their prey. Bergerud (1988) postulated that part of the decline of woodland caribou in British Columbia was due to forest harvest practices that concentrated caribou in small patches that were easily accessible and searched by wolves. Prior to the arrival of Europeans, lightning-caused and Indian-caused fires produced more open habitats in many portions of the Rockies (Barrett and Arno 1982). Control of fire in the Rocky Mountains has advanced forest succession which has resulted in an increase in stalking cover for predators (Barrett and Arno 1982). This has potentially altered predator–prey dynamics in certain situations in favor of wolves and cougars. Similar human-caused shifts in balance (disequilibriums) have been hypothesized for declines in bighorn sheep (Berger and Wehausen 1991), moose, and caribou (Bergerud 1981, 1988, but see Kunkel and Pletscher 2000).

Human harvest of carnivores

Due to their threatened and endangered status, wolves and brown bears are not harvested outside of Alaska and Canada. In Alaska, current regulations require wolves and bears that are harvested to be inspected and sealed. The wolf is the only big game animal in Canada that is hunted year-round, has no bag limits in many areas, and does not require a hunting license (Hayes and Gunson 1995). Harvests for wolves are liberal because of concerns for impacts of wolves on big game and because estimates of harvest rates necessary to reduce wolf population densities are >40% (Keith 1983).

Because of the low reproductive rates of brown bears, an overall female mortality of <1–16% (depending on other demographic parameters) was necessary to sustain populations (Eberhardt 1990, McLellan et al. 1999). Sustainable harvest rates range from 2% (Yukon) to 6% (Montana) per year (Miller et al. 1997). Bears in poor habitat can only support the most limited adult female mortality rates; so, harvest rates must be very conservative. Harvest rates of >30% of adult males resulted in a decline of a small brown bear population in Alberta (Wielgus and Bunnell 1994) apparently because of the immigration of subadult male brown bears after mortality of adult males and the resulting infanticide (Wielgus and Bunnell 1995, Swenson et al. 1997). The effects of harvest of males on cub survival remain controversial, but Swenson et al. (1997) concluded that harvesting one adult male brown bear corresponded to harvesting 0.5–1.0 adult females.

Legal harvest is usually the greatest source of mortality for cougars (Murphy 1983, Logan et al. 1986, Anderson et al. 1992, Ross and Jalkotzy 1992). In unhunted cougar populations or where cougar depredation on livestock is substantial, control actions may be the greatest source of human-caused mortality (Cunningham et al. 1995). The strong dispersal capability of cougars leading to immigration may help ameliorate the effects of mortality where cougar habitat is contiguous and exceeds 2200 km^2 (Beier 1993) and where travel corridors allow free exchange of dispersers among subpopulations (Lindzey et al. 1992, Logan et al. 1996, Murphy et al. 1999). Research and management, and especially population data for cougars, are often inadequate for managing harvests and thus harvest should be conservative. Harvest of male cougars should not exceed 8%, and hunting of females should be restricted (Logan et al. 1996).

Social systems of all the large carnivores must be taken into consideration in harvest programs, because harvest may disrupt the social system of a species and result in counterintuitive or greater than expected effects (Swenson et al. 1997). There may be significant differences between the behavior of populations of exploited and of non-exploited carnivores and this may impact population trajectories (Seidensticker et al. 1973, Hornocker and Bailey 1986, Kitchen et al. 2000*a*, *b*, Wright et al. 2000; but see Meier et al. 1995).

Restoration and conservation over large landscapes

Restoration priorities and techniques

Given the tenuous status of brown bears and wolves in the lower 48 United States and the mandate of the U.S. Federal Endangered Species Act to restore species over a significant portion of their range, restoration is critical for conservation of these species. We should work to restore large carnivores because of the key role they play in ecosystems and should strive to conserve the suite of adaptations of large carnivores to the environmental conditions and prey assemblages in which they live (Wikramanayake et al. 1998). Suitable habitats for wolves and brown bears exist in many places in the West, but, because of high mortality encountered by wolves and bears moving to these areas, re-introductions may be necessary (but see Boyd and Pletscher 1999). Because re-introductions are expensive, often fail, and are very high profile, managers should follow re-introduction guidelines of the International Union for the Conservation of Nature (IUCN; IUCN 1998) and others (Reading and Clark 1996) when considering a re-introduction. The biological feasibility of establishment of the species must be assessed in the area being considered for a re-introduction, and local public support must be established. The monitoring and management programs to be put into place after re-establishment are also critical to success.

Re-introductions of wolves from Canada have apparently been successful in the short term in Yellowstone and central Idaho. Success in the mid-term also seems likely as wolves may reach criteria for downlisting by 2002 (E. Bangs, USFWS, personal communication). Captive-reared Mexican wolves (*C. l. baileyi*) also were re-introduced into eastern Arizona in 1998 in an attempt to establish a wild population of >100 wolves (Parsons 1998). The population was classified as experimental non-essential, and by 2000 54 wolves had been re-introduced, and 30 in five packs were free-ranging (W. Brown, USFWS, unpublished data). Only two pairs have failed to reproduce. To date, five depredations on cattle have occurred and five wolves have been illegally killed.

One of the best areas, both biologically and socially, to restore wolves in the western U.S. is the southern Rockies. A population and habitat viability analysis recently completed for wolf re-introduction into the southern Rockies concluded that biologically the area could support over 2000 wolves (Phillips et al. 2000). Wolf restoration in the southern Rockies could result in a population connected from Alaska to Mexico and meet endangered species recovery requirements of restoring the species to a significant portion of their historic range.

Establishment of a brown bear population has never been attempted via re-introduction, although augmentations have been conducted (Servheen et al. 1995). Subadult female brown bears were successfully translocated from British Columbia to the Cabinet–Yaak ecosystem in northwest Montana to augment that population (Servheen et al. 1995). The re-introduction into the Bitterroot ecosystem in central Idaho of an experimental population of brown bears has been approved by the US Fish and Wildlife Service (2000) and translocation from British Columbia was scheduled to begin in 2002. Assuming a 4% growth rate, recovery of bears in this ecosystem (280 bears) might then occur within

50 years. A Citizen Management Committee would be responsible for management of bears. Integrating stakeholders closely in the development of management objectives and strategies and even in the design and implementation of research increases the positive investment of people most likely to affect bear survival and increases the likelihood that their concerns will be addressed in a constructive preventative manner (Gregory and Keeney 1994, Wondolleck et al. 1994, Mattson et al. 1996*a*, *b*). Impacts of re-introduced bears on ungulates, livestock, humans, and land use in the Bitterroot ecosystem were predicted to be minimal (U.S. Fish and Wildlife Service 2000). The southern Rockies (San Juan ecosystem) has been recommended for further evaluation as another brown bear re-introduction site (U.S. Fish and Wildlife Service 1993*a*, Craighead et al. 1995), and the southwest also deserves consideration.

The high rate of deforestation, settlement, and conversion to livestock ranching are the major threats to jaguar populations in many regions (Valdez 2000). As a result, jaguars have probably lost significant elements of their genetic diversity. Re-introduction in the southwest U.S. should be considered because establishment of a population by natural re-colonization is unlikely, and because a population in the southwest may be necessary to ensure the persistence of jaguars in the northern portion of their range especially as habitat pressures mount in northwestern Mexico.

Connectivity

Wolf re-colonization in northwestern Montana and southeastern British Columbia occurred through natural dispersal (Boyd and Pletscher 1999). Average dispersal distance of female wolves in northwest Montana was 78 km, which fell within the range of mean dispersal distance of females wolves from various studies in North America (65–144 km; Boyd and Pletscher 1999). Annual mean survival rate of dispersing wolves (64%) was lower than for resident wolves (88%; Pletscher et al. 1997). Colonizing wolves moved over large-scale landscapes rather than defined corridors, and the majority of colonizations occurred outside protected areas but originated from them (Boyd and Pletscher 1999). This phenomenon demonstrates the importance of refuges for population resistance and resilience in the face of management mistakes, fragmentation, or natural stochastic events (McCullough 1996).

In areas of low human population density such as southern New Mexico and Montana, cougars are able to disperse across large areas (females averaged 13.1 km and males 116.1 km in New Mexico; Montana Fish, Wildlife and Parks 1996, Sweanor et al. 2000). In areas of high human density, such as southern California, dispersal success has been poor, and subpopulations have become isolated with little chance of rescue (Beier 1993, 1995). Even so, cougars were able to use low-quality corridors for dispersal in these areas (Beier 1995). In areas of extremely fragmented habitat and high human density, corridors should be created along natural travel routes that contain ample woody cover. They should include underpasses with roadside fencing, lack artificial lighting, and have less than one dwelling unit per 16 ha (Beier 1995).

Simulation modeling indicated that a habitat area of 1000–2200 km^2 is needed to support a cougar population without immigration (15–20 cougars) in southern California with >98% probability of persistence for 100 years (Beier 1993). With the immigration of one female and three males per decade, areas of 600–1600 km^2 are needed. Such areas are a minimum and do not ensure long-term (centuries) persistence. From his modeling, Beier (1993) concluded that natural catastrophes of moderate severity do not appear important to cougar persistence. These models should be interpreted with caution as analytic models and simulation models incorporating density independence produced much larger minimum areas necessary for cougars.

Brown bear populations required protection of areas of 4000 and 50 000 km^2 in size to have a 50% and 90% chance, respectively of surviving (Woodroffe and Ginsberg 1998). Juvenile male brown bears dispersed 45–105 km from maternal home ranges through relatively "friendly" habitats in the Yellowstone ecosystem (Blanchard and Knight 1991). Populations isolated by these or greater distances in less friendly habitat would probably not benefit from corridors as traditionally conceived (Mattson et al. 1996*a*). Rather, movement would depend upon the establishment and survival of adult females in the intervening habitat, that would function as a sequence of demographic stepping stones (linkage zones). Connectivity then depends on creating habitats in these areas where females can survive (Mattson et al. 1996*a*). The distance between each of the three large brown bear recovery areas in the northern Rockies (Yellowstone, Selway–Bitterroot, and northern continental divide, each >20 000 km^2) is <300 km. Minimally disturbed habitat sufficient to support small populations of large carnivores currently exists in intermediate locations between these cores and could be conserved through the establishment of conservation areas and enhanced through the modification of current barriers and prohibition of new barriers (Craighead et al. 1999). No single size, configuration, or suite of attributes exists for designing protected areas for large carnivores, but Mattson et al. (1996*a*) described a framework and conceptual model (largely incorporating the role of humans) for addressing these issues for brown bears. Carroll et al. (2001) also identified habitats in an area southeast of Wells–Gray Provincial Park in British Columbia and north-central Idaho that are high-quality for carnivores and are unprotected, and thus are priority conservation areas in the Rocky Mountain region. Soule and Terborgh (1999:65–209) offer an excellent synthesis of conservation design including core protected areas.

Little is known about the habitat needs of jaguars in Arizona and New Mexico. More than 3200 km^2 of protected habitat was estimated to be required to support a minimum population of 50 jaguars in the Pantanal region of South America (Quigley and Crawshaw 1992). A protected area of 6600 km^2 in eastern Sonora would support an estimated 60–100 jaguars (Lopez Gonzalez and Brown in press).

Source-sink dynamics

Humans are usually the single greatest cause of large carnivore mortality, and most of this occurs when carnivores stray beyond reserve boundaries (Pletscher et al. 1997, Woodroffe and Ginsberg 1998, McLellan et al. 1999). Border areas around reserves are often population sinks and will be more significant in small reserves where perimeter:area ratios are high and among species that range widely (Woodroffe and Ginsberg 1998). Reserve size was a better predictor of large carnivore disappearance than was population size, and thus stochastic processes were less important than human mortality. Management should focus on maximizing reserve size and reducing persecution in reserve buffer zones (Woodroffe and Ginsberg 1998). Bears that may spend only a short time outside of protected areas due to the attractiveness of resources there may be quite vulnerable to mortality (Mattson et al. 1996*a*, Samson and Huot 1998).

Although wolves have successfully re-colonized many places outside protected areas in Montana (Boyd and Pletscher 1999), some areas appear to be sinks. Wolves have repeatedly established themselves along the east front of the Rockies in Montana and southern Alberta but have been killed or removed due to livestock predation. In areas like these with open landscapes and high densities of livestock, wolves may never be able to sustain populations over the long-term. In this landscape, cougars and

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bears have had greater success because they generally have fewer conflicts with livestock, are less visible, and use these areas only seasonally (bears).

Research needs

Large carnivores have been relatively well studied, with wolves among the most studied mammals in the world. The studies of brown bears in the Yellowstone ecosystem and wolves on Isle Royale and northern Minnesota have been some of the longest and most intensive research work done on populations of mammals. Murphy et al. (1999), however, were unaware of a single study of cougar population dynamics that spanned even one full interval of major fluctuation in primary prey. We know much of what we need to manage and restore large carnivores in western North America. Following the declining-population paradigm of Caughley (1994:236), we have deduced why populations of large carnivores have declined and are working to remove the agents of decline. Making this point, Mattson et al. (1996*b*) reported that since the early 1970's, more than 85% of all weaned and older radio-collared brown bears in the Rocky Mountains died because they were killed by people. Further, successful re-introductions of wolves have shown that, for that large carnivores, the cause of decline was successfully deduced and removed. Research now should be focused at continued monitoring of these re-introductions following the scientific method (Caughley 1994). What is primarily lacking for long-term conservation of carnivores is the will to make the sacrifices necessary to live with them. Co-operation and dialogue among all groups including non-governmental organizations and local citizens is essential to moving forward. Research into how best to attain this co-operation is important (Mattson et al. 1996*b*, Ehrlich 2002). Mattson et al. (1996*b*:1221–1223) and Mattson and Craighead (1994:121–125) recommended several new approaches to research, management, and policy measures for moving forward. Craighead et al. (1995) could find no major conservation problem that had been initially recognized and then solved by government agencies without pressure from a critical public. Some of the most progressive research and management of large carnivores is being done by private organizations (e.g., Craighead et al. 1995, Logan et al. 1996, Murphy et al. 1999, Soule and Terborgh 1999:15, Phillips et al. 2000, Berger et al. 2001*b*, Carroll et al. 2001, Sanderson et al. 2002). As stressed by Soule and Terborgh (1999:15), "conservation on the ground must replace the repetitive cycle of conferences, reports, recommendations of governments and ineffective treaties."

Despite all the work that has been done on large carnivores, we have almost no evidence upon which to assess the surrogate value of large carnivores. Restoration of large carnivores is relatively expensive and, in some cases because of this and other reasons, it might not be a conservation priority. We must assess how efficient restoration of large carnivores is for conservation of biodiversity. More research in this area, especially experimental, is needed. Natural expansion and re-introduction of populations of large carnivores into areas where they have been absent provide great opportunities to do this research (Huggard 1993, Kunkel 1997, Phillips et al. 2000, U.S. Fish and Wildlife Service 2000, Berger et al. 2001, Smith et al. 2001). Re-introductions should be designed as experiments to test these hypotheses, and adaptive management principles should be followed. Data on the demographics and behavior of prey and other carnivores, vegetation trends, and species richness prior to, during, and after re-colononization or re-introduction need to be obtained. More research and meta-analysis of data where large carnivores currently exist should be conducted to assess their umbrella, flagship, and keystone roles.

Further research is needed to assess the impacts of human harvest (sport and control harvest) on large carnivore populations, population structure, prey populations, and the impact of this on ecosystems. Sustainable rates of removals for depredating jaguars need to be examined. Further understanding of compensatory versus additive impacts of predation and how competition among carnivores affects this is needed, especially in southern multiple-predator, multiple-prey systems. More innovative work is needed on non-lethal control methods to reduce depredation on livestock. Innovative ways that allow local people, livestock and large carnivores to co-exist are needed, especially for jaguars in northwest Mexico.

Biological requirements to maintain connectivity (linkages) among isolated populations of large carnivores, especially brown bears, are little known. Analyses of how much degradation is too much and how to monitor for degradation must be completed before degradation proceeds (Doak 1995). The role of cover in mitigating impacts of human development on bear occupancy and movement are poorly documented. There is no research concerning the minimum required size of linkage zones or at what level they become ineffective for brown bears (Servheen et al. 2001). Further, classified and validated maps of brown bear habitat are generally non-existent. Despite these shortcomings, many of the basic requirements for connectivity are known, and the larger problem of politically and socially acceptable ways to mitigate for loss of habitat remains.

More research on population monitoring using non-invasive approaches is necessary. These techniques hold great potential for large carnivores, which are notoriously difficult or expensive to monitor (Beier and Cunningham 1996, Kohn and Wayne 1997, Miller et al. 1997, Becker et al. 1998, Woods et al. 1999, Mills et al. 2000). Whitebark-pine nuts are an important food for brown bears in the southern portion of their range, but their availability has decreased markedly in recent years due to whitebark-pine blister rust (*Cronartium ribicola*). Management solutions for blister rust need to be found (Servheen 1998) because brown bear mortality in the Yellowstone area is determined by whitebark-pine seed crop size (Pease and Mattson 1999). Determining jaguar distribution and ecology in northern Mexico should be a research priority. Long-term coordinated research and management between Mexico and the U.S. will be required to conserve jaguars in the region. Planning across the complete biological range of jaguars (and all large carnivores) so that all conservation efforts can be placed in the context of the species' biology is important (Sanderson et al. 2002).

Summary

Because of conflicts with humans, large carnivores have been extensively persecuted over the last century, and their populations and range have declined markedly. Recently, however, natural re-colonization and reintroductions of wolves have increased their populations significantly in the northern Rockies. Large carnivores, especially where they occur together, can at times limit and potentially regulate prey populations. However, there is little evidence that control efforts applied toward large carnivores are effective at significantly increasing prey densities over the long term.

At some scales and in some ecosystems, large carnivores likely have topdown regulatory impacts: empirical evidence for this remains slight but is increasing. Largely because research has been inadequate to date, little evidence exists for the umbrella roles of large carnivores. Theoretically, large carnivores serve in some capacity as surrogate species for conservation, especially flagships, and we should exploit this for the carnivores' own sake and larger conservation goals.

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Wolves have the potential to occupy many areas, provided that protected source populations exist nearby and wolves are actively managed to reduce conflicts with livestock to obtain a modicum of local support. Because of their greater use of more remote landscapes, cougars are easier to manage and maintain in most western landscapes than are wolves. Reducing human–brown bear conflicts is essential to brown bear persistence. In many cases this simply means reducing numbers of humans in bear habitats through management prescriptions such as road restrictions. Humans must be educated on how to minimize conflicts with bears in bear habitat and be willing to practise this. Larger tracts of habitat with little or no human impacts need to be established and maintained in the lower 48 states of the U.S. and connectivity among these habitats is essential, as is connectivity to more pristine Canadian habitats. Restoration of bears to former habitats is also important to ensure the long-term persistence in the lower 48 states. Building local support and involvement for this restoration is essential for its success.

Large carnivores have and will continue to serve as an important catalyst for conservation. They play important roles in ecosystems, and restoration should be pursued in as many areas as possible. Human encroachment and human-caused mortality are the most significant problems in large carnivore conservation. We must work aggressively to counter these impacts. Conserving animals that are capable of killing us and that need large, wild spaces requires great commitment on the part of biologists, activists, land managers, and political leaders, and also requires much tolerance from the people who live, work, and play in carnivore habitat (Noss 1996). We should recognize that because large carnivores do, in some cases, serve as effective flagships and thus attract greater support and attention, funds that are available for wolves, bears, jaguars, and cougars might not be available for work on other less "charismatic" conservation priorities. Therefore, we should take advantage of this and work to ensure that, while restoring large carnivores, we serve as large and significant a conservation goal as possible.

There is much reason for optimism. Dramatic changes in public attitudes toward carnivores have occurred in just a few decades (Kellert et al. 1996). New partnerships among diverse interests are being formed to conserve and restore wildlands and large carnivores (Rasker and Hackman 1996, e. g., citizens brown bear initiative: U.S. Fish and Wildlife Service 2000). Ultimately, the survival of large carnivores and the wildlands they occupy might simply depend on how much we can resolve conflicts among ourselves and adopt more tolerant and less acquisitive lifestyles (McDougal et al. 1988, Daly and Cobb 1989, Mattson et al. 1996*b*). Contrary to conventional wisdom about the cost of wilderness protection to local resource-based economies, recent work indicates that the protection of wilderness habitat that sustains large carnivores does not have a detrimental effect on local economies (Rasker and Hackman 1996). Economic growth is apparently stimulated by environmental amenities (Rasker and Hackman 1996). Much of the world looks to North America for leadership in conservation. Even so, North America needs to look around the world and learn from those countries where an ecosystem approach has been in use for a long time; where local human populations are recognized as part of the ecosystem; where controlled use is an option once basic ecological values are assured; and where co-operation across cultural, ideological, and political boundaries is a reality (Weber and Rabinowitz 1996). Some of the poorest countries are making the greatest contributions to conserving large carnivores. Rwanda and Botswana have placed >10% of their land in protected areas while the US has only 4% protected (World Resources Institute 1994, Weber and Rabinowitz 1996).

Biologists have an obligation and responsibility to help protect and preserve the species we are working on by going beyond data collection and serving the larger cause of finding solutions at local levels, as well as national and international levels (Schaller 1996). We must "fight for what remains and restore what has been squandered . . . because to save carnivores and their environment is as important to their future as it is to ours" (Schaller 1996).

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