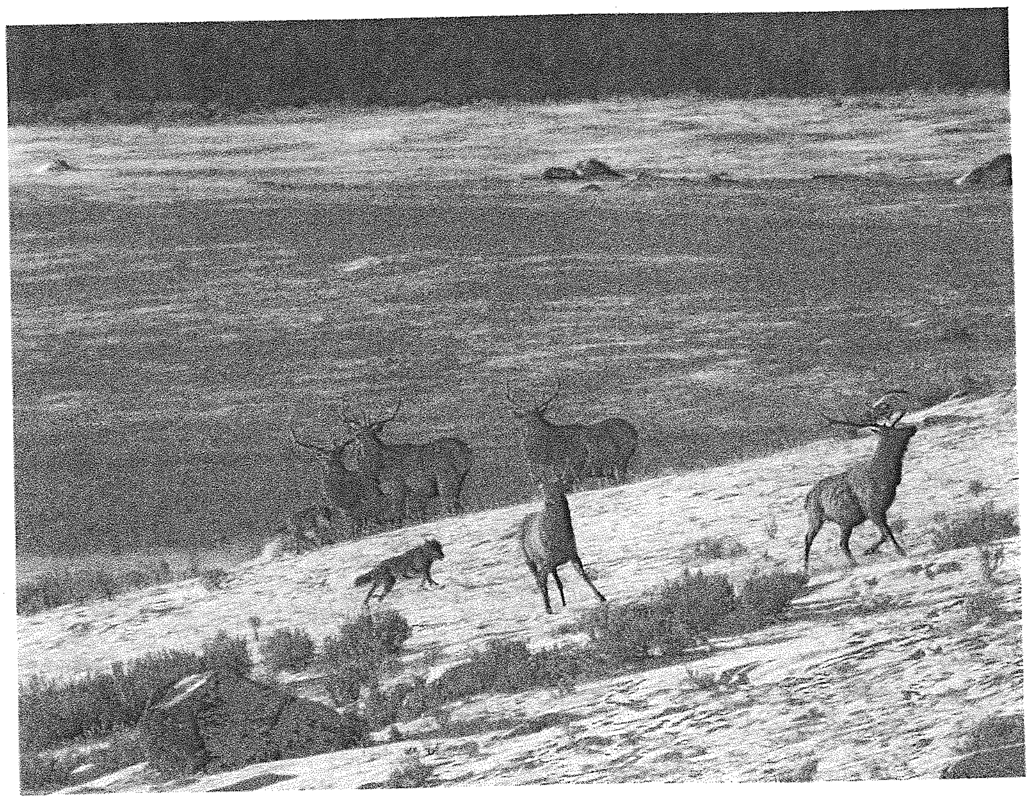

Chapter 3

The Importance of Large Carnivores

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INTRODUCTION

Aldo Leopold (1966, 190) wrote that "the last word in ignorance is the man who says of an animal or plant: 'What good is it?' To keep every cog and wheel is the first precaution of intelligent tinkering." Despite this sage advice, we have not kept every cog and wheel. Today, the scythe of extinction cuts 1,000 to 10,000 times faster than historical background rates (i.e., average historical extinction rates), and its pace is increasing (E. O. Wilson 2002). A healthy ecosystem requires a full complement of native species and biological processes such as structure and function associated with the species.

Finely tuned interactions among species, physical environments, and ecological processes form the webs of life on our planet. Ecosystems, species, and systems have evolved over time within a range of variability (Noss 1999). When cogs or wheels are lost, the variability range that species can tolerate exceeds their ability to adapt, causing secondary waves of extinction that amplify instability.

Among animals, the pollinators, seed dispersers, ecosystem engineers such as beavers, and a host of other organisms are critical to the structure and function of biological communities (Owen-Smith 1989; E. O. Wilson 1987; Buchmann and Nabhan 1996; Detling 1998). We believe self-sustaining populations of gray wolves (*Canis lupus*) within their native range indicate healthy ecosystems. When wolves are eliminated, ecological and evolutionary relationships are distorted far beyond the obvious effect of changes in the number and behavior of ungulates, their principal prey. Wolves perform important functions at and above the community level, whether through pathways of energy flow, widespread coevolutionary adaptations with other organisms (e.g., prey species, mesopredators, parasites), or by affecting standing plant biomass and production. Today, in the absence of wolves, the Southern Rocky Mountains suffer from ecological imbalances such as too many elk (*Cervus elaphus*) and the effects of their overpopulation on the flora and fauna of the region. Accordingly, restoring an ecologically viable wolf population in the Southern Rocky Mountains should restore a significant level of ecological health to the region.

Large carnivores, including wolves, are important for more than just their ecological value, however. For many people, such animals represent strong cultural and aesthetic values, and the importance of these values appears to be increasing (Kellert 1996). The strong values large carnivores invoke lead to substantial economic value as more people spend money to see carnivores in the wild and purchase related products. Simply put, large carnivores matter to a vast and growing number of people.

HOW CARNIVORES AFFECT ECOSYSTEM HEALTH

When scientists discuss ecological interactions affecting abundance, distribution, and diversity across "trophic levels," or the food chain, they often talk about top-down or bottom-up control. In the ecological sense, control means a qualitative or quantitative effect on an ecosystem's structure, function, and diversity (Menge 1992).

Reducing trophic interactions to sharp categorizations of either top-down or bottom-up is counterproductive. It is clear that forces flow in both directions simultaneously and interact while doing so (Menge and Sutherland 1976; Fretwell 1987; Hunter and Price 1992; Menge 1992; Power 1992; Estes et al. 2001). While the number of trophic levels in a top-down cascade affects plant biomass, the productivity from the bottom-up also affects the number of trophic levels (Fretwell 1987; Power 1992). For example, wolves may limit the number of elk and moose (*Alces alces*) in an area and thus permit more willows to persist in a riparian area, but the amount of plant productivity also determines if enough elk and moose can survive in a region to support a population of wolves. Scientists quickly recognized the qualitative and quantitative role that food has on consumers. Until recently, however, knowledge about how carnivores affect a system remained obscure.

As a simple example, if bottom-up control dominates a system, energy moving up the food chain regulates the system. An increase in the biomass of consumers is directly related to increases in productivity of their resources. Species richness and diversity are maintained by defenses of both plants and herbivores, or because competition forces species to specialize and use discrete niches (Pianka 1974; Hunter and Price 1992; Polis and Strong 1996). Because large carnivores sit at the top of the food chain, bottom-up theories leave them with little ecological role (Estes et al. 2001). Under the bottom-up model, they receive more than they contribute. Implicitly, this can justify politically based management strategies that hold carnivore numbers artificially low, thereby "protecting" domestic livestock and increasing large-game populations to benefit sport hunters.

In a system with top-down regulation, herbivores can reduce the biomass of plants, but in turn, carnivores check the numbers of herbivores (Hairston et al. 1960; Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen and Oksanen 2000). Predation also produces indirect impacts that flow through the system far beyond the direct effect of a predator on prey. For example, too few carnivores allow ungulate numbers to increase, which changes the plant community in ways that affect diversity, abundance, and competition among many other organisms. Top-down regulation implies strong interactions among three general trophic levels: plants, herbivores, and carnivores.

At very low levels of productivity, there will be only one trophic level: plants (see Oksanen and Oksanen 2000). Factors limiting plant biomass are available resources and competition with other plants for the same resources. As productivity increases, so does plant biomass, until there is enough to support a second trophic level, the herbivorous consumers (Oksanen and Oksanen 2000). With two trophic levels, herbivore biomass increases with increasing productivity until a third trophic level can be supported, the carnivorous consumers (Oksanen and Oksanen 2000). Carnivores now limit the number of herbivores, reducing the amount of pressure that herbivores place on plants. The plants and carnivores now flourish (first and third trophic levels), whereas the herbivores (second trophic level) are held in check by carnivores.

Plants flourish under odd numbers of trophic levels, but growth is limited under even numbers. In contrast to bottom-up theory, under top-down regulation neither plant nor herbivore biomass increases linearly with increases in productivity. Instead, there will be an incremental accrual as the food chain lengthens; herbivores limit the expansion of plants and carnivores do the same to herbivores (see Oksanen and Oksanen 2000).

Sometimes a species with low biomass can have an ecological effect that is disproportionate to its abundance, as with a highly interactive species such as beavers (*Castor canadensis*) (Soulé et al. 2003a, 2005). Under top-down regulation, such species maintain diversity, although a numerically dominant species may also serve that function (Paine 1966; Estes et al. 2001). If a carnivore such as a wolf checks a prey species that is competitively superior, or changes the prey's behavior in some way, then it is erecting ecological boundaries that protect weaker competitors from competitive exclusion (Paine 1966; Terborgh et al. 1999; Estes et al. 2001). Under this paradigm, carnivores play an important role in regulating interactions, and predation can cause indirect impacts that affect flora and fauna ecologically distant from the carnivore (Terborgh 1988; Terborgh and Estes forthcoming).

THE IMPACTS OF PREDATORS ON PREY

Carnivores control prey directly and indirectly. While predation may directly reduce numbers of prey (Terborgh 1988; Terborgh et al. 1997, 2001; Estes et al. 1998; Schoener and Spiller 1999), it may also indirectly cause prey to alter their behavior so that they become less vulnerable, by choosing different habitats, different food sources, different group sizes, different times of activity, or limiting the amount of time spent feeding (Kotler et al. 1993; Brown et al. 1994; FitzGibbon and Lazarus 1995; Palomares and Delibes 1997; Schmitz 1998; Berger et al. 2001b).

If a predator preys on a wide range of species, its presence may cause all prey species to reduce their respective niches and thus may reduce competition among those species. Removing the predator dissolves the ecological boundaries that check competition. As a result, prey species may compete for limited resources, and superior competitors may displace weaker competitors, thus leading to less diversity through competitive exclusion (see Paine 1966; Terborgh et al. 1997; Henke and Bryant 1999). The impact of carnivores extends beyond the objects of their predation. By changing distribution, abundance, and behavior of herbivores, carnivores have far-reaching effects. For example, because herbivores eat seeds and plants, predation on herbivores influences the structure of the plant community (Terborgh 1988; Terborgh et al. 1997, 2001; Estes et al. 1998). The plant community, in turn, influences distribution, abundance, and competitive interaction within groups of birds, mammals, and insects.

We briefly introduced the idea above that plants suffer or thrive when there are even or odd numbers of trophic levels, respectively. Direct evidence for this is the overexploitation (through the fur trade) of sea otters (*Enhydra lutris*) in the North Pacific for their fur (see Estes 1996; Estes et al. 1978, 1989, 1998; Estes and Duggins 1995). This system evolved with three trophic levels: carnivorous sea otters, herbivorous macroinvertebrates such as sea urchins, and kelp forests. Following the decline of sea otters, marine invertebrate herbivores increased in number and devastated kelp forests, thus reducing the food chain from three levels to two. This in turn produced a cascade of indirect effects, including reducing diversity among a host of fish, shorebird, invertebrate, and raptor species (see Estes 1996; Estes et al. 1978, 1989, 1998; Estes and Duggins 1995).

Gradual recovery of the sea otter in recent years has restored the third trophic level. Invertebrate grazers then declined, and the kelp forests and associated fauna recovered (Estes et al. 1978, 1989, 1998). When killer whales (*Orcinus orca*) entered the area, they imposed a fourth trophic level (Estes et al. 1998). The killer whales reduced numbers of sea otters, allowing the invertebrate grazers to increase, and that reduced the biomass of the kelp forest. At a 2001 presentation in Denver, Colorado, J. A. Estes emphasized the importance of long-term studies; he stated that analyzing any five-year block of time from their thirty years of data would produce different results.

Similarly, Krebs, Boonstra, et al. (2001) synthesized forty years of studies on the snowshoe hare (*Lepus americanus*) cycle. Some ecology textbooks highlight the observed ten-year oscillation as a predator-prey cycle between Canada lynx (*Lynx canadensis*) and hare. Studies by Krebs, Boonstra, et al. (1995) and Krebs, Boutin, et al. (2001), however, revealed that one can only understand the process by analyzing all three trophic levels. Krebs, Boutin, et al. wrote (2001, 34), "The hare cycle is caused by an interaction between predation and food supplies, and its biological impacts ripple across many species of predators and prey in the boreal forest." When examining these interactions, Krebs, Boutin, et al. (2001) stated that the dominant factor regulating the hare cycle was predation. Cycle dynamics did not change with the addition of nutrients, and the immediate cause of death in 95 percent of the hares was predation. Furthermore, lynx were not the only predator of hares. Other predators included coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), great-horned owls (*Bubo virginianus*), smaller raptors, and small mammals, particularly red squirrels (*Tamiasciurus hudsonicus*) and ground squirrels (Krebs, Boutin, et al. 2001). Absent lynx, the hare cycle continued unchanged because of "compensation," in this case increased predation by these other predators (Stenseth et al. 1998).

Both the sea otter and snowshoe hare investigations demonstrate the importance of long-term studies and accentuate the need to investigate predator-prey interactions over more than just two trophic levels, let alone examining the interactions between only one species of predator and one species of prey.

In Venezuela, Terborgh et al. (1997, 2001) took advantage of a hydroelectric project that formed Lago Guri, a reservoir 120 km (74 mi.) long and up to 70 km (43 mi.) wide with islands scattered throughout. After seven years of isolation on the islands, nearly 75 percent of the vertebrate species have disappeared; the islands are too small to support populations of jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Terborgh et al. 1997, 2001). The few animal species remaining are hyperabundant and have had devastating effects on the plant communities. On these islands there is little regeneration of the canopy trees (Terborgh et al. 1997, 2001).

In another example, researchers working on grasslands in Texas found that nine months after coyote removal, rodent species' richness and diversity declined compared to that of areas with coyotes (Henke and Bryant 1999). Twelve months after coyote removal, the Ord's kangaroo rat (*Dipodomys ordii*) was the only rodent species captured on the study area (Henke and Bryant 1999). Removing coyotes eliminated the ecological boundaries among species of rodents, and the Ord's kangaroo rat was a superior competitor, increasing in number and displacing other rodent species.

Wolves are a highly interactive species. Long-term monitoring data from the boreal forest of Isle Royale indicate that predation by wolves on moose plays a role in ecosystem function by changing the number and behavior of moose (McLaren and Peterson 1994). The number and movements of moose then affects the balsam fir (*Abies balsamea*) forest (and other woody plants) by regulating seedling establishment, sapling recruitment, sapling growth rates, litter production in the forest, and soil nutrient dynamics (Pastor et al. 1988; Post el al. 1999 and references within).

When the wolf population declined, moose reached high densities and suppressed fir growth. This top-down trophic cascade regulation is apparently replaced by bottom-up influences only when forest stand–replacing disturbances such as fire or large windstorms occur at times when moose density is already low (McLaren and Peterson 1994). This is strong evidence that wolves exert top-down control of a food chain.

Research in the Greater Yellowstone Ecosystem and elsewhere suggests elk populations not regulated by large predators negatively affect the growth of aspen (*Populus tremuloides*) (Kay 1990, Kay and Wagner 1994). Wolves, a significant predator of elk, may positively influence the aspen canopy through a trophic cascade caused by the wolf reducing elk numbers, modifying elk movement, and changing elk browsing patterns on young aspen (White et al. 1998; Ripple and Betscha 2003, 2004). Elk proliferated and aspen recruitment ceased when wolves disappeared from Yellowstone National Park (Ripple and Larson 2000).

Similarly, Berger et al. (2001a) showed that moose increased their numbers when wolves and grizzly bears (*Ursus arctos*) were absent. Because moose reduced the quality and quantity of willow, neotropical migrant birds fared better in areas where wolves and bears preyed on moose. These factors are being reversed with the reintroduction of wolves into Yellowstone in 1995 (Ripple and Betscha 2004). Today there are fewer moose and more willows, and birds are faring better.

RELATIONSHIPS BETWEEN LARGE CARNIVORES AND SMALLER PREDATORS

Large carnivores directly and indirectly affect smaller carnivores, or mesopredators, and therefore the community structure of small prey (Terborgh and Winter 1980; Soulé et al. 1988; Bolger et al. 1991; Vickery et al. 1994; Palomares et al. 1995; Sovada et al. 1995; Crooks and Soulé 1999; Henke and Bryant 1999; Schoener and Spiller 1999). Small prey distribution and abundance affect ecological factors such as seed dispersal, soil porosity, soil chemistry, plant biomass, plant nutrient content, and epizootics (Whicker and Detling 1988; Hoogland 1995; Detling 1998; Keesing 2000).

In California, Soulé et al. (1988) and Crooks and Soulé (1999) documented more species of scrub-dependent birds in canyons with coyotes than in canyons without coyotes. The absence of coyotes allowed opossums (*Didelphis virginianus*), foxes (*Vulpes* spp.), and house cats to proliferate. These species preyed heavily on songbirds and native rodents. Other researchers have observed the effects of mesopredator release in grasslands (Vickery et al. 1994; Henke and Bryant 1999), wetlands (Sovada et al. 1995), and Mediterranean forest (Palomares et al. 1995).

We think mesopredator release can manifest in at least three ways: population increases of smaller predators, modified niche exploitation, and altered community structure (largely because of the first two factors). An excellent example comes from Yellowstone. Wolves were extirpated from the park in the early part of the last century. In the absence of competition from wolves, coyotes assumed some of the ecological characteristics and functions of the larger canid, including forming packs and preying on large ungulates (R. L. Crabtree, pers. comm.). However, because they are smaller than wolves, coyotes could only partially fill the role of the apex predator. The dynamics of the predator/prey system were modified. Interspecific associations such as mutualistic relationships and coevolved food webs were disrupted. This in turn may have markedly altered the diversity and composition of the natural community, causing secondary extinctions or other unanticipated ripple effects, such as the loss of aspen, willow, beavers, and neotropical migrant bird species.

When wolves were reintroduced, they changed the distribution and abundance of coyotes, as they have done elsewhere (Paquet 1989, 1991, 1992; Crabtree and Sheldon 1999). In addition to these obvious competitive interactions, wolves also provide a regular supply of carrion, which is exploited by smaller carnivores.

MACROECOLOGICAL EVIDENCE FOR TOP-DOWN FORCES

The previous sections outlined some mechanisms through which the presence of carnivores can control ecosystems. How widespread are their impacts? Historically, many natural resources managers and biologists held the view that bottom-up forces drove ecosystem interactions (Polis and Strong 1996). Obviously, resource abundance and competition play important roles, but modern evidence shows that top-down effects function simultaneously (see Terborgh et al. 1999; Estes et al. 2001; Ray et al. 2005; Terborgh and Estes forthcoming). To ignore the indirect effects exerted by carnivores on diversity, structure, and function of an ecosystem could fatally flaw management strategies.

There is a growing body of macroecological (i.e., ecology at large geographic and spatial scales) evidence to support the impact of carnivores on ecosystems. For example, Oksanen and Oksanen (2000) compared areas with herbivores to areas without herbivores to determine differences in plant biomass and primary productivity. They studied fifty-one locations in Arctic or Antarctic regions. In areas with herbivores, as plant biomass increased, productivity remained about the same, whereas in areas without herbivores, as plant biomass increased, productivity increased rapidly (Oksanen and Oksanen 2000). These observations support their hypothesis of top-down regulation.

Beyond the Arctic and Antarctic, most macroecological evidence for impacts of carnivores on ecosystems must be viewed with caution because humans have altered a large percentage of temperate and tropical biomes. This complicates our ability to separate the effects of carnivores from those of humans. Nevertheless, evidence suggests that carnivores are important.

Crête and Manseau (1996) compared the biomass of ungulates to primary productivity along a 1,000 km (620 mi.) north–south latitudinal gradient on the Québec-Labrador peninsula, and Crête (1999) did the same over North America. At the same latitude, there were five to seven times more ungulates in areas where there were no wolves compared to where wolves were present. In areas of former wolf range but where no wolves currently exist, the ungulate biomass regressed to primary productivity, producing a positive slope (Crête 1999).

In Poland, red deer (elk) irrupted after persecution eliminated wolves, and roe deer (*Capreolus capreolus*) irrupted when humans extirpated European lynx (*Lynx lynx*) (Jedrzejewska and Jedrzejewski 1998 in Jedrzejewski et al. 2002). Eliminating carnivores from an area that evolved with strong predator-prey interactions may have a severe impact through a trophic cascade.

Having reviewed both qualitative and quantitative evidence across a number of different ecological systems, Terborgh et al. (1999) concluded that top-down control was stronger and more common than previously thought. Schmitz et al. (2000) conducted a quantitative meta-analysis of trophic cascades in terrestrial systems using data from sixty independent tests in forty-one studies. Their analysis, limited to invertebrates and small vertebrates, detected trophic cascades in forty-five of the sixty tests. They showed that predator removal had a significant, direct impact on herbivore numbers and on plant damage (positive) and reduced plant biomass and plant-reproductive output (negative). Schmitz et al. concluded that trophic cascades were present under a variety of conditions with different types of predators and occurred more frequently than is currently believed.

Another quantitative meta-analysis examined forty scientific papers on terrestrial trophic cascades in arthropod-dominated food webs (Halaj and Wise 2001). They reported extensive evidence supporting terrestrial trophic cascades. Indeed, 77 percent of the 299 experiments showed a positive response on the part of herbivores when predators were removed (Halaj and Wise 2001).

Finally, Estes et al. (2001) reviewed the impacts of predation in a variety of ecosystems, including rocky shores, kelp forests, lakes, rivers and streams, oceanic systems, boreal and temperate forests, coastal scrub, tropical forests, and on islands with exotic predators. They concluded that predation has dramatic impacts at organizational levels ranging from individual behavior to system dynamics and on time scales ranging from ecological to evolutionary (Estes et al. 2001).

Failing to recognize the role of carnivores can produce drastic changes in ecosystems (Terborgh and Estes forthcoming). For example, wildlife managers have reduced carnivore numbers to keep ungulates at artificially high levels for recreational hunting. Yet, an overabundance of white-tailed deer has been shown to reduce numbers of native rodent species, produce declines in understory nesting birds, obliterate understory vegetation in some forests, and even eliminate regeneration of the oak (*Quercus* spp.) canopy (Alverson et al. 1988, 1994; McShea and Rappole 1992; McShea et al. 1997).

If we continue to manage carnivores by reducing their numbers without considering the indirect effects that will cascade through a system, we will undoubtedly continue to alter the structure and function of native ecosystems in ways that we may later regret. We believe that it is not a question of whether or not carnivores play an important role; it is a question of how they play their role in trophic interactions.

RELATIVE STRENGTH OF INTERACTIONS UNDER VARIOUS CONDITIONS

While carnivores such as wolves exert top-down influences on communities, those influences vary significantly under different environmental conditions. The level of influence is a complex and situational event. Abiotic, or nonbiologic, factors such as type, frequency, and scale of natural disturbance (e.g., fire, flood, windthrow) can influence the relative importance of top-down or bottom-up forces (see Connell 1978). Disturbance over large geographic areas shortens food chains (at least temporarily) and thus changes interaction dynamics among trophic levels (Menge and Sutherland 1976). As Sanford (1999) found, climatic patterns such as El Niño or La Niña affect the ability of highly interactive predators to regulate prey in aquatic systems. Ballard and Van Ballenberghe (1997) and Post et al. (1999) found the same for terrestrial systems. Seasonally driven mechanisms can alter rates of compensatory mortality and natality, or birthrates, and thus adjust the impact of predation on the population size of prey (Boyce et al. 1999b). A region's productivity level can influence what threshold of distribution and abundance for the predator allows that predator to exert its role in an ecosystem.

Behaviors such as migration enable animals to make use of food over a larger area (Fryxell et al. 1988). If terrestrial predators such as wolves are unable to follow migrating ungulates such as caribou (*Rangifer tarandus*) over a long distance, then they will have less relative impact on population numbers of the migrants (Fryxell et al. 1988; Fryxell 1995). Migratory wildebeests (*Connochaetes taurinus*) fit the hypothesis of predation-sensitive foraging, where food supplies and predation interact to regulate populations (Sinclair and Arcese 1995). Like the earlier example of snowshoe hares, predation is the final agent of mortality. Unlike the case of the hares, however, food supply plays a driving role in mortality of wildebeests by predation: as food supply decreases, wildebeests increase their risk to find food (Sinclair and Arcese 1995).

The physical habitat in which an animal lives imposes adaptive pressures that mold behaviors and population structures, in turn affecting the role of predation. Behavior of a predator is important: Is it social or solitary? Is it a cursorial hunter or a sit-and-wait hunter? Is it a generalist or a specialist? Among prey species, sociality and large body size enhance predation-avoidance capabilities.

The strength of interaction between species is complex and situational. Even within the same species, it can be difficult to extrapolate results from one part of the range to another (Soulé et al. 2003a, 2005).

CARNIVORES AND MANAGEMENT

Scientific data increasingly indicate that carnivores play an important controlling role in an ecological system (see Terborgh et al. 1999; Ray et al. 2005; Terborgh and Estes forthcoming). Yet, carnivore control as institutionalized by several government agencies has historically been the center of management solutions. Intensive management regimes often do not fully consider the circumstance, season, behavior, or other conditions that affect the complex role of carnivores in the system.

Short-term control and hunting restrictions may be necessary when a system is highly perturbed, or fluctuating outside its normal bounds of variability. Just as heavy human harvest can influence prey numbers, so too can predators, particularly when prey densities are low (Boyce et al. 1999b). However, rather than focusing solely on symptoms, we need to ask deeper questions about why our systems are perturbed.

What indirect effects ripple through a system if managers or hunters reduce carnivore numbers below the bounds of their natural variation? What will happen to vegetation and nongame species diversity if we try to hold ungulate numbers at unnaturally constant and high numbers for recreational hunting? Can we manage populations of predator and prey in ways that more closely resemble natural patterns? (Indeed, managing ungulate production for hunter success philosophically differs little from managing livestock for meat production.) A quote in W. B. Ballard et al. (2001, 107) is telling:

> Biologists continue to debate whether predation is a regulatory or a limiting factor, but to wildlife managers who are responsible for managing deer populations to provide hunting and viewing opportunities, the distinction between these terms may not matter.

It should. Evidence indicates that our lack of understanding (or lack of caring) about the role of carnivores in ecosystem processes has damaged the systems we try to manage. Eradicating and reducing carnivores such as wolves and pumas has, by removing a critical element, simplified systems by reducing biodiversity, largely by eliminating the carnivores' keystone role of ungulate predation.

Not only have we reduced carnivore numbers, but we have also managed for unnaturally high numbers of ungulates. The elk population in Colorado currently exceeds the carrying capacity of the range. In 2001, the Colorado Division of Wildlife wanted to reduce elk numbers from about 260,000 to 190,000 (Meyers 2002). After an elk count showed that numbers had swelled to 305,000 in the spring of 2002, the Division of Wildlife raised its target population to 230,000. Adjusting target goals after the fact does not change the land's productivity, and the winter of 2001–2002 was very dry. We would do well to remember the experience of the Kaibab Plateau, where the mule deer (*Odocoileus hemionus*) population grew so large in the absence of predation that the animals depleted their food base, eventually leading to mass starvation.

None of these questions is new. Aldo Leopold asked many of them a half century ago. Yet, as long as we think mainly from paradigms of hunter harvest—or silviculture, or livestock production—and fail to think in terms of ecosystem function, we will continue to lose diversity despite good intentions, higher budgets, and increasing human effort.

In short, wildlife management policies based on reducing carnivore numbers have caused, and will continue to cause, severe harm to many other organisms that seem distantly removed from the apex trophic layer (see Terborgh 1988; Terborgh et al. 1999; Terborgh and Estes forthcoming). For these reasons, we believe that carnivore policy and ungulate management must be driven by sound ecological science at the ecoregion, or landscape, scale.

IMPORTANCE TO PEOPLE

Nature and the wildlife it contains provide physical, emotional, and intellectual benefits to people (Kellert 1996; Decker et al. 2001). Large carnivores epitomize the so-called charismatic megafauna; that is, large, charismatic species such as wolves and polar bears (*Ursus maritimus*) that tend to enjoy greater support among most people (Kellert 1996). People appreciate large carnivores for the cultural, aesthetic, existence, economic, and other values they represent (Kellert 1993, 1996). Other people disdain large carnivores based on fears for human, livestock, or pet safety; the negative economic impact they sometimes cause; and issues of private property rights and government actions that they believe large carnivores represent (Kellert 1996; Kellert et al. 1996; Meadow et al. 2005; see chap. 6).

The significance of some species from a historical or other human-centered perspective leads to strong personal and symbolic values (Shepard 1978; Kellert 1986b, 1996; Reading 1993). Large carnivores such as wolves and bears provide symbolic, religious, and historical values to many people (Rolston 1985; Hardy-Short and Short 2000). These animals often invoke a feeling of awe and enlivened senses among humans (Kellert 1996; Hardy-Short and Short 2000). As a result, in many cultures people revere or revered large carnivores (Luckert 1975; Campbell 1988; Nelson 1993). Hoping to tap into the admired attributes of large carnivores, such as hunting prowess, stealth, strength, and speed, people created religious and social societies centered on these among other animals (Levi-Strauss 1963, 1966; Campbell 1988). Large carnivores continue to symbolize such traits today, as any list of sports teams' and luxury products' names attest.

The beauty and symbolic nature of large carnivores inspires many people (Kellert 1993, 1996; Kellert et al. 1996). That inspiration often stimulates the mind and results in an artistic outpouring (van Diern and Hummelinck 1979; Rolston 1981; Reading 1993). As a result, animals like bears, tigers (*Panthera tigris*), and wolves often form the foci of literature, poems, paintings, sculptures, and dance. These animals and the art they inspire provide a source of satisfaction, well-being, and contentment to many people who view them (Kellert 1996).

People also develop strong emotional attachments to large carnivores based on moral and ethical considerations (Kellert 1980, 1996; Reading 1993). Many of these people will never see a polar bear or grizzly bear in the wild, but they want these animals to exist. To these people, such intrinsic "existence values" are important and influential (Rolston 1981; Brown et al. 2001). People donate substantial sums of money to ensure the conservation of large carnivores and often vote to further their protection. For some, the animals are not only important to themselves, but they also want to ensure that their children or grandchildren have the opportunity to see them in the wild. Social scientists dub these "bequest values" (Brown et al. 2001). Other people embrace altruistic values toward carnivores—they simply recognize that other people want to see them, whether or not they relate to them.

Large carnivores head the list of species people want to see when they engage in wildlife-based recreation, and people often expend great effort in trying to catch a glimpse of them in natural settings (van Dieren and Hummelinck 1979; Rolston 1981; Reading 1993). As a result of the satisfaction many people obtain from direct experiences with large carnivores, they spend money traveling to view them and purchase products featuring these animals (Kellert 1996).

Large carnivores also add value to outdoor recreation that is not wildlife-based, because people often place additional value on seeing these animals or simply knowing they are around (Rolston 1981; Shaw 1987; Brown et al. 2001). The economic impact of wolf restoration to Yellowstone National Park, for example, generates an additional $35 million per year in revenue for the region surrounding the park, and, because those dollars turn over in the local communities, the wolves have created an overall impact of $70 million per year to the local economy (Duffield et al. 2006; Stark 2006; Anonymous 2007). Indirect recreational values accrue from books, television shows, and magazines devoted to these animals (Bryan 1980; Kellert 1996). Product branding (Tony the Tiger, Mercury Cougar, Chicago Bears) helps companies sell products from cars to sports teams to corn flakes to camping gear to sporting event tickets.

Not all values ascribed to large carnivores are positive, however. Some people dislike large carnivores because they represent a threat to the safety of humans, pets, or livestock (Kellert 1980, 1995; Reading 1993; Hardy-Short and Short 2000). That dislike often extends well beyond concerns for safety. As Kellert (1996, 105) stated with respect to wolves:

> As the extent and viciousness of the killing often reached irrational proportions, one suspects the wolf may have performed roles beyond the merely utilitarian. Destroying the wolf may have also reflected the urge to rid the world of an unwanted and feared element in nature, perhaps even the settler's atavistic potential to succumb to the allure of wildness and the absence of civilizing control.

Kellert (1996, 110) goes on to suggest that for some people, "the wolf, grizzly bear, puma, and other large predators remain a vivid reminder of the necessity to combat and repress wild nature in the never ending struggle to render the land safe and productive." To other people, large carnivores have come to symbolize governmental interference in how they manage private property or interact with wildlife (Kellert 1996; Meadow et al. 2005). For centuries, governments helped people to control or eradicate large carnivores (Lopez 1978; Dunlap 1988; Kellert 1996), so it is not surprising that the recent shift by many government agencies from control to conservation has been met with bewilderment and anger by some sectors of society.

Despite some of the negative values they engender, overall, large carnivores stimulate the imagination and inspire a sense of awe and wonder for many people, making them among the most highly valued of all species. It is difficult to place a monetary figure on many of the values ascribed to large carnivores (Brown et al. 2001). The result is that they often go underappreciated in traditional economic analyses and therefore governmental policies. Yet, that is slowly changing as decision makers increasingly recognize that not all parts of a cost-benefit analysis are easily captured using traditional methods (Brown et al. 2001; Loomis 2004).

CONCLUSIONS

Large carnivores are ecologically important, often disproportionately important, to the ecological systems they inhabit. Yet they are also important to people for a variety of other reasons, including cultural reasons, aesthetics, their right to exist, and the economic benefits they sometimes accrue. These animals often exert strong influence on ecological systems through top-down regulation, in which they affect herbivores that in turn affect vegetation. The mechanisms of top-down regulation include direct effects, through predation, and indirect effects, in which large carnivores influence the behavior of their prey. By controlling populations of smaller predators, large carnivores also reduce pressure on the prey of these mesopredators.

Evidence for the importance of large carnivores to the ecological systems they inhabit continues to mount. Many people value the role that these charismatic animals play in the systems they inhabit, but people value large carnivores for a variety of other reasons as well, including symbolic, existence, aesthetic, recreational, and other values. Of course, many people also hold negative values and attitudes toward large carnivores. Thus, the human dimensions of large carnivore management may rival or surpass the ecological challenges of their management.