The Importance of Large Carnivores to Healthy Ecosystems

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Abstract

*Land managers often are responsible for the maintenance of species diversity and resilience. This requires knowledge of ecosystem dynamics over decades and centuries. Resource-driven (*bottom-up*) models have guided early thought on managing species and ecosystems. Under this paradigm, carnivores have little ecological value, and throughout the 20th Century carnivore management strategies (often extirpation) have reflected that concept. An alternative hypothesis, however, states that herbivores reduce the biomass of plants, but in turn, the biomass of herbivores is checked by the presence of carnivores. As such, carnivores have great ecological value. Their predation activities create impacts that ripple downward through the trophic levels of an ecosystem. Here we discuss some potential pathways through which carnivores contribute to ecosystem processes and species diversity. The subtleties of these interactions have strong implications for management strategies of carnivores. Without considering these indirect impacts, short-sighted management strategies to reduce carnivores might cause extensive and long-term changes in ecosystem structure and function.*

Introduction

Aldo Leopold (1966: 197) wrote that, "One of the penalties of an ecological education is that one lives alone in a world of wounds." The wounds come in many types. In cities it is easy to experience congestion, traffic, noise, and fouled air. People accept that urban lights obliterate stellar pleasures. But our non-urban land has also been wounded by crop agriculture, mineral extraction, fire suppression, logging, pollution, and overgrazing (Terborgh and Soulé 1999). Despite Leopold's (1966) half-century old advice on "intelligent tinkering" we have not kept "every cog and wheel." Today, the scythe of extinction cuts 1000 times faster than historical background rates, and its pace is increasing (Wilson 1992).

That scythe has dire implications. Finely tuned interactions among species, physical environments, and ecological processes form the webs of life on our planet. Each web is not static, but continuously varies within certain bounds, and the species and systems have adapted over time to the range of variability in their particular region (Noss 1999). When "cogs or wheels" are lost, a system can fluctuate outside of the bounds to which it has adapted. Depending on which parts are lost, and the rate of loss, the pressure on a given system can ex-

ceed its ability to respond. Once such a vortex is entered, runaway positive feedback can make escape difficult, as altered structure and function can cause secondary waves of extinction that further heighten the instability.

We would like to discuss a specific category of such an event – the loss of carnivores and how that simplifies ecosystems over the long-term. Carnivores are not the only group whose decline has significantly impaired ecosystem processes. Pollinators, seed-dispersers, and even many small, often largely "invisible" organisms contribute enormously to the structure and function of biological communities (Buchmann and Nabhan 1996). We leave the task of reviewing the "sideways" effects of these organisms to others. Here we emphasize carnivores and their *top-down* effects.

How carnivores impact ecosystem health

When people discuss ecological interactions that determine abundance, distribution, and diversity across trophic levels, they often talk about *top-down* or *bottom-up* control. In the ecological sense, control means a qualitative or quantitative effect on ecosystem structure, function, and diversity (Menge 1992).

Simplified, if *bottom-up* control dominates, the system is regulated by energy moving upward from lower to higher trophic levels. Thus, increases in the biomass of consumers and their resources will parallel increases in productivity. Species richness and diversity are maintained by defenses of both plants and herbivores, or because competition forces species to specialize and use discreet niches (Pianka 1974; Hunter and Price 1992; Polis and Strong 1996). Because carnivores sit atop the food chain, *bottom-up* theories provide them with little ecological utility (Estes et al. 2001). They would receive more than they would contribute. Implicitly, this can justify politically-based management strategies that hold carnivore numbers artificially low or eliminate them altogether.

Alternatively, in a system with *top-down* regulation, herbivores can reduce the biomass of plants, but in turn, herbivore biomass is held in check by carnivores (Hairston et al. 1960; Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen and Oksanen 2000). This idea implies strong interactions among three general trophic levels: plants, herbivores, and carnivores.

At very low levels of productivity, there is only one trophic level, plants (see Oksanen and Oksanen 2000). The only factors limiting plant biomass are available resources and competition with other plants for those resources. As productivity increases so does plant biomass, until there is enough productivity to support a second trophic level, the herbivorous consumers. With two trophic levels, herbivore biomass increases with increasing productivity, but their grazing activity limits plant biomass until productivity increases enough to support a third trophic level, the carnivores. Carnivores, in their role as keystone species, now limit the number of herbivores, and that reduces 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.

In short, with odd numbers of trophic levels, plants flourish, but even numbers of trophic levels limit plant growth. In contrast to *bottom-up* theory, when there is *top-down* regulation neither plant nor herbivore biomass increases linearly with increases in productivity. Instead, there is a stepwise accrual as the food chain lengthens (see Oksanen and Oksanen 2000).

Under *top-down* regulation, diversity can be maintained through the actions of keystone species (Paine 1966; Estes et al. 2001). Although a numerically dominant species may also serve that function, sometimes a species with low biomass can have an ecological effect that is disproportionate to its abundance. If a carnivore species checks a prey species that is competitively superior, or changes prey behavior in some way, then the carnivores are 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 ripple downward through a system affecting flora and fauna that seem ecologically distant from the carnivore (Terborgh 1988).

Of course, reducing trophic interactions to a dichotomous rubric 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). For example, while the number of trophic levels in a *top-down* cascade impacts plant biomass, the productivity from the *bottom-up* also affects the number of trophic levels (Fretwell 1987; Power 1992).

Scientists quickly recognized the qualitative and quantitative role a resource like food has for consumers. Until recently, however, knowledge about the impact of carnivores on a system remained more enigmatic. Large carnivores are difficult to research because of the necessary scale (temporal and geographical) and expense (Estes 1996). In many areas, they have already been eliminated or severely reduced in number (Weber and Rabinowitz 1996; Terborgh et al. 1999). Finally, social and political factors have militated against re-

search on the role of carnivores in ecological systems.

Impacts of carnivores on prey & plants

Carnivores control prey by direct and indirect methods. Through predatory activities, carnivores directly reduce numbers of prey (Terborgh 1988; Terborgh et al. 1997; Estes et al. 1998; Schoener and Spiller 1999). Indirectly, carnivores cause prey to alter their behavior so that they become less vulnerable (Kotler et al. 1993; Brown et al. 1994; FitzGibbon and Lazarus 1995; Palomares and Delibes 1997; Schmitz 1998; Brown 1999; Berger et al. 2001). They choose different habitats, different food sources, different group sizes, different time of activity, or they reduce the amount of time spent feeding.

By reducing the numerical abundance of a competitively dominant prey species (or by changing its behavior), carnivores erect and enforce ecological boundaries that allow weaker competitors to persist (Estes et al. 2001). If a predator selects from a wide-range of prey species, the presence of the predator may cause all prey species to reduce their respective niches and thus reduce competition among those species. Removing the predator will dissolve the ecological boundaries that check competition. As a result, prey species may compete for limited resources and superior competitors may displace weaker competitors leading to less diversity through competitive exclusion (see Paine 1966; Terborgh et al. 1997; Henke and Bryant 1999). The impact of carnivores thus extends past the objects of their predation. Because herbivores eat seeds and plants, predation on that group influences the structure of the plant community (Terborgh 1988; Terborgh et al. 1997; Estes et al. 1998). The plant community, in turn, influences distribution, abundance, and competitive interaction within groups of birds, mammals, and insects.

American Elk by Robert Savannah, USFWS.

At the beginning of this section, we briefly introduced the idea that plants suffer or thrive when there are even or odd numbers of trophic levels (Hairston et al. 1960; Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen and Oksanen 2000). Direct evidence for this idea came when sea otters (*Enhydra lutris*) were overexploited in the north Pacific (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, and kelp forest). Following sea otter decline because of the fur trade, marine invertebrate herbivores increased in number and devastated the kelp forest (creating a system with two trophic levels). This produced a cascade of indirect effects that reduced diversity in a host of fish, shorebirds, invertebrates, and raptors (see Estes 1996; Estes et al. 1978, 1989, 1998; Estes and Duggins 1995).

Gradual recovery of the sea otter in recent years 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 in number, and that reduced the biomass of the kelp forest. Estes (personal communication) emphasized the importance of long-term studies; he stated that analyzing any five-year block of time from their 30 years of data would lead to different conclusions.

Similarly, Krebs et al. (2001) synthesized 40 years of studies on the snowshoe hare (*Lepus americanus*) cycle. This 10-year oscillation has been highlighted as a predator-prey cycle between lynx (*Lynx canadensis*) and hare in ecology textbooks. Krebs et al. (1995, 2001), however, revealed that we can only understand the process by analyzing all three trophic levels. To quote Krebs et al. (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 et al. (2001) stated that the dominant factor regulating the hare cycle was predation; the dynamics of the cycle were not changed by adding nutrients, and the immediate cause of death in 95% of the hares was predation. Furthermore, lynx were not the only predator for hares. Snowshoe hares, adult and juvenile, were killed by lynx, coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), great-horned owls (*Bubo virginianus*), small raptors, and small mammals, particularly red squirrels (*Tamiasciurus hudsonicus*) and ground squirrels (Krebs et al. 2001). When lynx were removed from the suite of predators, the hare cycle continued unchanged because of compensation (Stenseth et al. 1998). Both the sea otter study and snowshoe hare work demonstrated the importance of long-term studies, and accented the need to investigate predator-prey interactions over more than just two trophic levels, let alone only examining the interactions between one species of predator and one species of prey.

Long-term monitoring data from the boreal forest of Isle Royale indicate that predation by wolves (*Canis lupus*) affects the number and behavior of moose (*Alces alces*) (McLaren and Peterson 1994). This, in turn, affects the balsam fir 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 et al. 1999 and references within).

In the Neotropics, Terborgh et al. (1997) has taken advantage of a hydroelectric project that recently formed Lago Guri in Venezuela. The lake is 120 kilometers long and up to 70 kilometers wide with islands scattered throughout, and the experiment has both a temporal and spatial control. After seven years of isolation, nearly 75% of the vertebrate species have disappeared from the islands too small to hold jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Terborgh et al. 1997). The few species that remain are hyperabundant with gross effects on the plant community, and there is little regeneration of the canopy trees (Terborgh et al. 1997). This study continues.

As a final example, researchers working on grasslands in Texas found that nine months after coyote removal, rodent species richness and diversity declined compared to 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 treated grassland (Henke and Bryant 1999). The removal of coyotes allowed the Ord's kangeroo rat, a superior competitor, to increase in number and displace other species.

Impacts of predators on mesopredators

Large carnivores also directly and indirectly impact smaller predators, and therefore the community structure of small prey (Soulé et al. 1988; Bolger et al. 1991; Vickery et al. 1992; 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 affects ecological factors like seed dispersal, disease epizootics, soil porosity, soil chemistry, plant biomass, and plant nutrient content (Whicker and Detling 1988; Hoogland 1995; 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 behavioral release of opossums (*Didelphis virginianus*), foxes (*Vulpes* spp.), and house cats. These species preyed heavily on song birds and native rodents. The effects of mesopredator release have also been observed in grasslands (Vickery et al. 1992; Henke and Bryant 1999), wetlands (Sovada et al. 1995), and Mediterranean forest (Palomares et al. 1995).

Macroecological evidence for top-down forces

The previous section outlines some mechanisms through which carnivores can regulate ecosystems. But, how widespread are these impacts? There is a growing body of macroecological evidence to support the impact of carnivores on ecosystems. For example, Oksanen and Oksanen (2000) compare plant biomass and primary productivity in Arctic/Antarctic areas with and without herbivores. In areas with herbivores, the regression slope between plant biomass and increasing productivity is flat, whereas in areas without herbivores the regression slope between plant biomass and increasing productivity is positive and steep (Oksanen and Oksanen 2000). This mirrors their prediction from a perspective of *top-down* regulation (herbivores exert a controlling effect on plants).

Outside the Arctic/Antarctic, most macroecological evidence for impact of carnivores on ecosystems must be viewed with caution because humans have already altered such a large percentage of temperate and tropical systems. This complicates our ability to tease out effects of carnivores from those of humans. Nevertheless, we believe it is important to conduct such analyses, and the evidence that does exist suggests that carnivores are important.

For example, Crête and Manseau (1996) and Crête (1999) compared the biomass of ungulates to primary productivity along latitudinal gradients. For the same latitude, ungulate biomass was five to seven times higher in areas where wolves were absent compared to where wolves were present. In areas of former wolf range, but

where currently no wolves exist, a regression of ungulate biomass to primary productivity produced a positive slope (Crête 1999).

Four recent reviews also support the importance of carnivores to systems. Considering the qualitative and quantitative evidence as a whole, Terborgh et al. (1999) concluded that top-down control was stronger and more common than previously thought. In addition, Schmitz et al. (2000) conducted a quantitative meta-analysis of trophic cascades in terrestrial systems. Their definitions limited data to invertebrates and small vertebrates, but they detected trophic cascades in 45 of the 60 tests (Schmitz et al. 2000). In other words, in 75% of the studies, predator removal had a significant direct impact on herbivore numbers (positive), and that had a significant impact on plant damage (positive), plant biomass (negative), and plant-reproductive output (negative). They concluded that trophic cascades were present under different conditions, with different types of predators, and occurred more frequently than currently believed (Schmitz et al. 2000).

Another quantitative meta-analysis examined terrestrial trophic cascades in arthropod-dominated food webs (Halaj and Wise 2001). The investigators reported that 77% of the 299 experiments showed a positive response of herbivores when predators were removed (Halaj and Wise 2001). Whereas Schmitz et al. (2001) suggested that the strength and pattern of terrestrial cascades were equal to aquatic cascades, Halaj and Wise (2001) suggested that terrestrial trophic cascades were weaker than aquatic cascades.

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

Drastic changes in ecosystems have been linked to carnivore extirpation or control. For example, managers have reduced carnivore numbers to keep ungulates at artificially high levels for recreational hunting. Yet, overabundance of white-tailed deer (*Odocoileus virginianus*) has been shown to reduce numbers of native rodent species, cause declines in understory nesting birds, obliterate understory vegetation in some forests, and even eliminate regeneration of the oak (*Quercus* spp.) canopy (Alverson 1988, 1994; McShea and Rappole 1992; McShea et al. 1997). Similarly, hyperabundance of moose in areas of the Greater Yellowstone Ecosystem without wolves and grizzly bears (*Ursus arctos*) has reduced neotropical migrant bird populations (Berger et al. 2001). Ripple and Larson (2000) have reported that aspen (*Populus tremuloides*) overstory recruitment ceased when wolves disappeared from Yellowstone National Park. Wolves are a significant predator of elk (*Cervus elaphus*), and wolves may positively influence aspen overstory through a trophic cascade caused by reducing elk numbers, modifying elk movement, and changing elk browsing patterns on aspen (Ripple and Larson 2000).

If we continue to manage carnivores without considering the indirect effects on habitat quality and species diversity, we will undoubtedly continue to alter the structure and function of an area in ways that we may later regret. We contend 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 different conditions

We stress that the subtleties of interactions can vary significantly under different environmental conditions. Abiotic factors, such as type, frequency, and scale of natural disturbance (see Connell 1978) can influence the relative importance of *top-down* or *bottom-up* forces. Disturbance over large geographic scales shortens food chains (at least temporarily) and thus changes interaction dynamics among trophic levels (Menge and Sutherland 1976).

Climatic patterns, such as *El Niño* or *La Niña* affect the ability of keystone predators to regulate prey in aquatic (Sanford 1999) and terrestrial systems (Ballard and Van Ballenberghe 1997; Post et al. 1999). In years that the North Atlantic Oscillation produces deep snow-cover, moose (*Alces alces*) are more vulnerable to wolf predation (Ballard and Van Ballenberghe 1997; Post et al. 1999). Thus, the fir forest of Isle Royale is released from heavy browsing, more seedlings are established, more saplings survive, and litter production and nutrient dynamics are affected (Pastor et al. 1988; Post et al. 1999). Similarly, seasonality can alter rates of compensatory mortality and natality, and thus change population density of prey (Boyce et al. 1999).

Behaviors like migration allow animals to make use of food over a larger area (Fryxell et al. 1988). If terrestrial predators are unable to follow migrating ungulates over a long distance movement, 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 both 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).

We have already discussed the link between level of productivity and number of trophic levels. Behavior of predator and prey, however, also changes as habitats progress along a cline from open (e.g., steppe grassland) to closed (e.g., tropical forests or kelp beds). The physical habitat in which an animal lives imposes adaptive pressures that mold behaviors and population structures, which in turn affect the role of predation.

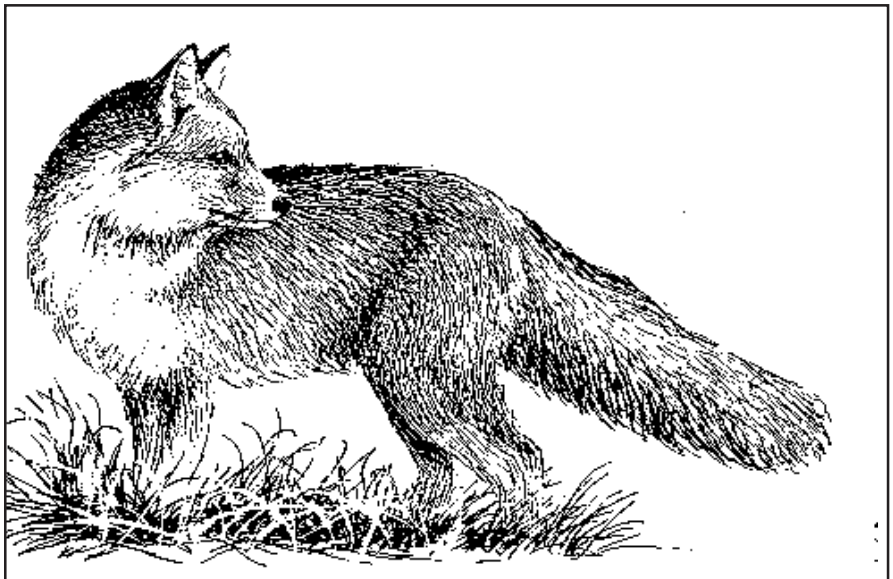
In open habitats, prey species can detect predators at a distance and flee or enter burrows. Sociality enhances avoidance capabilities, as does large body size. Such traits may reduce the number of prey species that are available to a given predator. In response, grassland predators may become more specialized on one or a few prey species to increase the probability of capture (MacArthur and Pianka 1966; Hornocker 1970; Schaller 1972; Emmons 1987). When the number of prey species available to a predator is reduced, the interactive links between prey species and the predator should be fewer and stronger (McCann et al. 1998). Such a system should undergo stronger oscillations, and therefore be less stable, than a system characterized by many links (McCann et al. 1998; for examples see Erlinge et al. 1991; Hanski et al. 1991; McKelvey et al. 1999).

Specialist predators play a *top-down* role as part of the entire suite of predator species. Models of *top-down* interactions between specialized carnivores and prey function because of self-limitation factors in the prey (Turchin et al. 2000). For example, both predator and prey start at low numbers. Prey numbers build to the point where further growth is inhibited by social interactions, and prey numbers then stabilize at a peak density. Thus they now supply a positive energy balance to carnivores, which increase rapidly in number. When carnivore numbers rise quickly, heavy predation causes prey to decline, or hastens a decline caused by other factors. Thus, specialized carnivores, as part of a suite, exert control on a system, and that control is strongest when the given prey cycle is past its peak or in decline.

Structurally complex systems, such as tropical forests, can be populated by prey species that do not generally migrate over long distances, have the large size, or have highly socialized anti-predator behaviors. Predators typically hunt by ambush and might have access to more species of prey than predators hunting by pursuit in structurally open systems. They tend to take available prey in relation to abundance and vulnerability (Emmons 1987; Terborgh 1988). If relative abundance of prey species changes, then the predators can switch to another prey that is commonly encountered and meets energetic demands (MacArthur and Pianka 1966).

Through opportunistic predation, carnivores can maintain prey assemblages, which in turn maintains the structure of the plant community (Terborgh 1988; Estes 1996; Terborgh et al. 1997, 1999). When a top carnivore is opportunistic, the links between that carnivore and the diverse prey community should be numerous. Because such predators switch among prey species, fluctuations in numbers of a given prey species have less effect on the predator (and system) than fluctuations in systems with fewer and stronger links (McCann et al. 1998; see also Erlinge et al. 1984, 1988, 1991; Hanski et al. 1991).

Because the diet of an opportunistic predator is broad, it can be expected to exert broader top-down community effects than a species of specialist predator. For carnivores to have top-down influence, they must maintain a certain population density, yet the rate of increase generally is lower for predators than for prey. An opportunistic carnivore can maintain its population numbers at an influential level, however, by switching among alternative prey as the relative numbers of the prey species change (Erlinge et al. 1984). Thus an opportunistic predator can exert constant top-down influence throughout the population cycle of prey, whereas a specialist predator exerts its strongest influence on prey numbers when the prey are in the declining phase of their cycle. Thus, unlike the strongly



Fox by Robert Savannah, USFWS.

fluctuating time-series signatures of specialized predators and prey, we expect the time-series signature of opportunistic predators and their suite of prey to be more stable.

Carnivores and management

Scientific data increasingly indicate that carnivores play an important role in ecological health. Yet, carnivore control has been the center of our management solutions, and it even has been institutionalized by several government agencies. When control is used, there typically is little consideration of the circumstances, season, behavior, or other conditions that affect a carnivore's role in its system.

Short-term control and hunting restrictions sometimes are necessary when a system is highly perturbed. As with heavy human harvest, predators can influence prey numbers, particularly when prey densities are low (Boyce et al. 1999). But such tactics only address a symptom. We need to ask deeper questions about why our systems are perturbed. What indirect effects could ripple through a system if carnivores are reduced below the bounds of their natural variation? What will happen to vegetation and non-game species diversity if we try to hold ungulate numbers at unnaturally constant and high numbers for recreational hunting? Can we manage populations of predators and prey in ways that more closely resemble natural patterns? We emphasize that predators impact prey populations in more than a demographic fashion. They change movement and activity patterns, and these behavioral effects can have ecological significance.

These are not new questions (see Leopold 1966). Yet, as long as we fail to think in terms of an ecosystem, we will continue to lose diversity despite good intentions, higher budgets, and increasing human effort. In short, management policies based on reducing carnivore numbers have caused, and will continue to cause, severe harm to many other organisms (see examples in Section 2).

For these reasons, we contend that science is increasingly relevant to decision-making. But typically, when faced with political and economic resistance, conservation strategies for large carnivores have been compromised by trying to move incrementally—perhaps trying to protect small numbers of a top carnivore in a few locations. While this might prevent taxonomic extinction (at least in the short-term) it does little to mend ecosystems. In short, past policies, driven by paradigms that view carnivores as pests to agriculture, sport hunting, and development, continue to play a stronger role than new scientific information. As a result, ecosystems continue to decline. While incremental approaches may work with species that still have some biological resilience, too many large carnivore species have declined drastically (see Weber and Rabinowitz 1996) and are too close to extinction for such tactics.

Leopold (1966) once said that if we are content relegating grizzlies to Alaska it would be like relegating happiness to heaven. The problem is, we might never get to either place. The politics of carnivore management will continue to take precedent over biology as long as we let it. Unless we put biological sideboards on carnivore management, we will continue relegating happiness to heaven. And we won't get there.

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