Predators and Ecosystem Management

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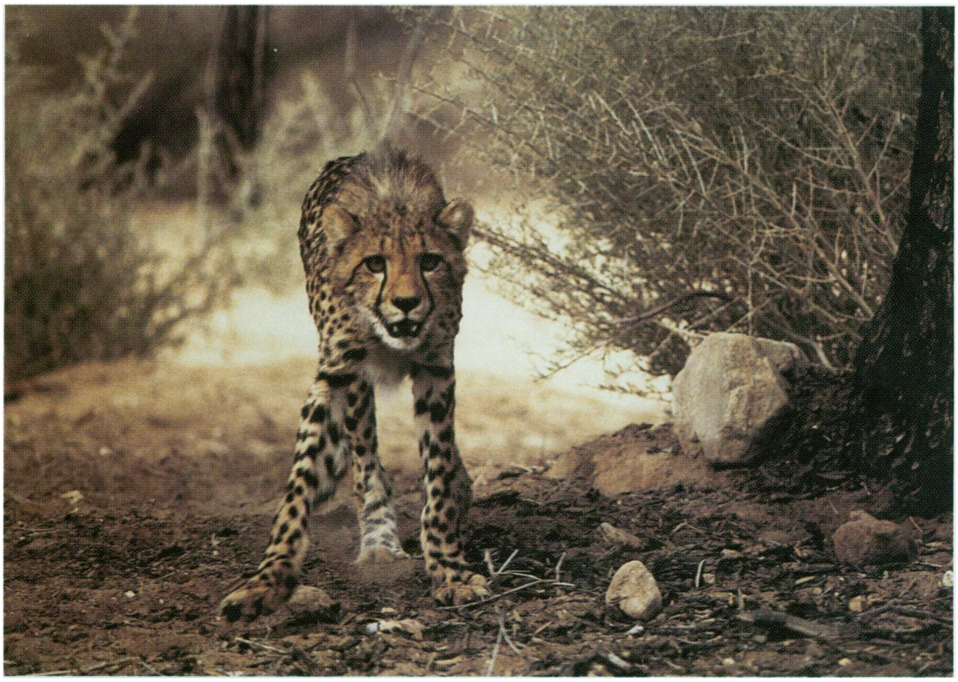

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Carnivores probably are of more interest to the general public than any other group of animals. Popularization of some of the most spectacular species in books and movies attest to their visceral appeal. While several aspects of carnivore biology are becoming well known to science (Gittleman 1989), others remain poorly understood. Perhaps the most poorly known and controversial dimension to carnivore ecology concerns their relationships with other species and the ecosystems in which they live. Predators have been promoted for maintaining "the balance of nature," maligned as our competitors, and the larger species often are feared as threats to human welfare. Here I will briefly review what is known or suspected about the roles played by predatory mammals in the workings of their ecosystems and discuss how we might achieve a better understanding of this issue.

Predators and ecosystems—2 perspectives

Food webs are an essential feature of every ecosystem and consumer-prey interactions are the fundamental linkage among species in every food web. Ecologists have dichotomized the nature of consumer-prey interactions into "bottom-up" and "top-down" processes (Hunter and Price 1992). In essence, the bottom-up view is one that concentrates attention on how resources (e.g., space, nutrients) influence higher trophic forms; the top-down view examines how the interactions between high level consumers (i.e., predators) and their prey influence lower trophic forms. This dichotomy provides a useful conceptual framework for discussing predators and their ecosystems because most of the pressing issues and current thinking relate to 2 analogous

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themes: (1) resources necessary to maintain viable predator populations, and (2) influences of predators on their ecosystems. Only the second of these will be discussed here. While the results from case studies indicate significant ecological roles for predators in a few species and ecosystems, the challenge is to determine if there are recurrent patterns elsewhere in nature and to understand when and why they occur.

Top-down effects

My perspective on predators and ecosystems has been colored by a single system—sea otters (*Enhydra lutris*) and kelp forests. Early accounts of this system identified food-web linkages through descriptions of the sea otter's diet, diets of their prey, etc. These studies demonstrated that sea otters feed on a variety of benthic marine invertebrates, some of which are herbivores; they revealed little however, about food-web dynamics or the functional role of sea otters in kelp-forest ecosystems. The opportunity to understand these relationships was provided by an accident of history—namely, overexploitation of sea otters in the Pacific maritime fur trade, which resulted in fragmentation of the otter's once continuous range. By comparing areas where sea otters were abundant with nearby areas where they no longer occurred, it was possible to gain insight into the sea otter's ecological role in kelp-forest ecosystems. Subsequently, it has been possible to observe the dynamics of particular kelp-forest ecosystems over time, as they were recolonized by expanding sea otter populations and changed from being otter-free to otter-dominated.

The view that has emerged is that of a "trophic cascade" (sensu Carpenter et al. 1985) with sea otter predation regulating herbivore populations and thereby protecting the autotrophs from destructive grazing (Estes and Palmisano 1974). Our subsequent research has focused on 3 related questions (Estes 1996): (1) how common are these relationships across the sea otter's historical range; (2) what are the consequences to other species in coastal ecosystems; and (3) how have sea otters and their immediate ancestors, by limiting populations of herbivorous invertebrates, influenced the evolution of plant-herbivore interactions? Surveys of coastal habitats in many areas of the North Pacific Ocean have revealed that kelp forests usually are extensively deforested where sea otters are absent whereas this condition is rare where otters occur (Estes and Duggins 1995). Documented indirect effects of the trophic cascade among otters, sea urchins (*Strongylocentrotus* spp.), and plants include facilitation of competitive interactions among kelp forest autotrophs (Dayton 1975, Duggins 1980, Reed and Foster 1984), increased production (Duggins et al. 1988), and behavioral and population-level effects on a variety of consumers such as glaucous-winged gulls (*Larus glaucescens*; Irons et al. 1985), sea stars (K. Vicknair and J. A. Estes, unpubl. data), sea ducks (D. B. Irons, G. V. Byrd, and J. A. Estes, unpubl. data), and kelp-forest fishes (Bodkin 1988, Ebeling and Laur 1988, Carr 1994). There is also evidence that these interactions have acted on evolutionary time scales to influence species-level characters. For example, the limiting influence of sea otters and their recent ancestors on populations of herbivorous invertebrates (particularly sea urchins) apparently freed the autotrophs from the need to evolve anti-herbivore defenses (Estes and Steinberg 1988, Steinberg et al. 1995). This could explain why the marine flora of temperate Australasia (where a predator of comparable influence to the sea otter is absent) contains comparatively high concentrations of secondary metabolites (Steinberg 1989) and why the North Pacific marine flora is so susceptible to destructive grazing (Harrold and Pearse 1987). In sum, there is mounting evidence that sea otter predation in kelp-forest communities, acting on ecological and evolutionary time scales, strongly influences a wide range of species- to ecosystem-level characteristics.

Ecological roles for other predatory mammals?

All animals and some plants are consumers. Broadly defined, all of these are predators and even the narrowest of definitions (i.e., excluding herbivores, parasites, and carnivores of low trophic status) includes thousands of species. Top-level predators, even narrowly defined, are or were features of every ecosystem. What we would like to know is whether most, some, or only a few of these species play comparable roles to that of the sea otter.

Power et al. (1996) define a keystone species as one whose abundance is relatively low but whose effect on its community or ecosystem is relatively large. Keystone functions exist for numerous species in many ecosystems (Mills et al. 1993, Power et al. 1996). Most of the published examples are of heterotrophs whose keystone roles are manifested through predation. There are remarkably few examples of mammals as keystone predators. The majority of purported keystones are fish and invertebrates, and most of the evidence for keystone species and trophic cascades comes from aquatic systems (Strong 1992). However, this may simply be the result of a lack of published information. It remains unclear whether keystone roles for predators are indeed most common in aquatic systems or simply yet to be discovered in terrestrial systems. The preponderance of examples of trophic cascades in aquatic systems may be explained by the amenability of lower trophic forms with short generation times to experimental study (Steele 1985).

Direct evidence for predatory mammals as keystone species

There is growing evidence that some predatory mammals play important roles in a number of terrestrial ecosystems. An interesting case is that of the gray wolf (*Canis lupus*)-moose (*Alces alces*)-balsam fir (*Abies balsamea*) system on Isle Royale (McLaren and Peterson 1994). Moose populations on Isle Royale purportedly are influenced by the number of wolves and thus the intensity of wolf predation. Growth rings in young fir trees show depressed plant growth rates for periods when wolves were rare and moose abundant, from which McLaren and Peterson (1994) inferred the existence of a wolf-induced trophic cascade. Wider-ranging effects on the forest ecosystem are suggested from known linkages among moose, microbes, and soil nutrients (Pastor et al. 1988). While Isle Royale may be atypical because of its faunal simplicity—other predators (e.g., bears [*Ursus* spp.]) and large ungulates (e.g., deer [*Odocoileus* spp.], caribou [*Rangifer tarandus*]) are absent, and wolf and moose densities are unusually high (Messier 1994, Van Ballenberghe and Ballard 1994)—this example suggests that trophic cascades do occur in terrestrial ecosystems in which large mammalian predators are the dominant high-level consumers and highlights the need for creative approaches in studying interactions of this sort.

Other examples suggest a variety of keystone roles for predatory mammals. Localized extinctions or near extinctions of coyotes (*Canis latrans*) in North America led to a phenomenon known as "mesopredator release;" the growth of populations of small to mid-sized predators (e.g., foxes [*Vulpes* spp.], skunks [*Mephitis* spp.], domestic cats [*Felis domesticus*]) that were otherwise limited by coyotes. The reduction or loss of coyotes thereby led to increased intensity of predation by the mesopredators and reduction or local extinction of their prey. Mesopredator release has been proposed for a number of systems, including chaparral (Soulé et al. 1988), grasslands (Vickery et al. 1992), and prairie wetlands (Ball et al. 1995, Sovada et al. 1995).

The evidence for keystone roles by large terrestrial carnivores, while often intriguing, is more circumstantial. Two potentially dominant and wide-ranging large carnivores in North America—grizzly bears (*Ursus arctos horribilis*) and gray wolves—now are absent from most of their historical range south of Canada. Gray wolves at one time may have limited coyotes (Sargeant et al. 1993), thus raising questions about the historical importance of mesopredator release. Other possible keystone roles for wolves are emerging with the recovery of wolf populations in North America. For instance, the reestablishment of wolves in the northern midwest has led to a restriction in the distance from aquatic habitats that beavers (*Castor canadensis*) can forage, limiting in turn, the effects of beavers on upland plant associations (Naiman et al. 1986, Pollock et al. 1995). Similarly, the reestablishment of wolves in other areas has been followed by declines in caribou, moose, elk (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*; Bergerud 1988, Messier and Crete 1985, Hatter and Janz 1994). Wolves also interact in complex ways with sympatric species of large predators. Grizzly bears in Yellowstone are relatively small and unproductive, qualities thought by Kay (1990) to have resulted from the limited availability of fruits caused, in turn, by elk overgrazing, as a result of the absence of wolves in the Yellowstone ecosystem. Conversely, there is some indication that increased wolf kills during winter create a seasonal food resource for grizzlies, thus precluding the bears' need to hibernate (Lime et al. 1993). Furthermore, wolves may affect cougars directly by running them off kills, thus forcing the cougars to kill more in order to survive (D. H. Pletscher, Univ. Montana, Missoula, pers. commun.). While some of these examples are anecdotal and speculative, collectively they suggest that terrestrial carnivores can have ecosystem-level effects, functioning in keystone roles and initiating trophic cascades.

The introduction of exotic predatory mammals on islands provides further evidence for important ecological impacts. Mongooses (*Herpestes* spp.) on islands of the tropical Pacific probably have contributed to the collapse of the native faunas (Fagerstone et al. 1995). Introduced domestic cats have had similar effects in Australia and on islands at temperate latitudes (King 1985) as have foxes in boreal to arctic regions (Bailey 1993). Conventional wisdom argues that exotic predators have stronger effects than their native counterparts because the prey are "evolutionary naive." Martin (1973) used this argument to explain why human colonization of the Americas caused such high rates of extinction during the Pleistocene in the New World megafauna. While that may be true, one could also argue that species often intermingle quickly following biotic interchanges (Vermeij 1993), and thus the introduction of exotic predators on islands is neither unusual nor unnatural when considered on the appropriate time scale.

Indirect evidence for predatory mammals as keystone species

Although there are few striking examples of trophic cascades involving predatory mammals (the wolf-moose-balsam fir example from Isle Royale is an exception), there are many reports in which one half (carnivore-herbivore) or the other (herbivore-plant) of this 3-trophic-level interaction have been documented or inferred.

Herbivore–plant interactions. Evidence of strong interactions between herbivorous mammals and plants frequently is expressed through the limiting effects of herbivores on plant populations or through the limiting influences of plant forage on herbivores. In either case, control of herbivores by predators would be expected to disrupt these plant-herbivore interactions. Some of the best examples of strong herbivore-plant interactions are from Africa where large ungulate populations exert a variety of impacts on forest, savanna, and grassland habitats (McNaughton 1985, Owen-Smith 1988, Sinclair and Norton-Griffiths 1979, Laws et al. 1975). Significant ungulate-plant interactions have been demonstrated for deer and caribou on Alaskan islands (Klein 1965, 1968), elk in Yellowstone (Servheen and Knight 1993), large herbivores in North American grasslands (Mack and Thompson 1882), and introduced ungulates in New Zealand (Caughley 1983). Populations of numerous rodent and lagomorph species undergo extreme fluctuations in abundance and at the peaks of these cycles often have strong effects on plants (Ostfeld and Canham 1993). In some cases these cycles probably are driven by predation (Krebs 1996).

Carnivore–herbivore interactions. Terrestrial carnivores can limit populations of herbivorous mammals. Ungulates have declined following range increases or reintroductions of predators. For instance, the growing gray wolf population in northern Montana has seen a concurrent decline in elk and white-tailed deer density and most known ungulate mortality that occurred during this period was caused by predation (D. Pletscher, Univ. Montana, Missoula, pers. commun.). Deer populations have declined after the reintroduction of lynx (*Lynx lynx*) in the Swiss Alps (Breitenmoser and Hatter 1993) and bobcats (*Lynx rufus*) onto a barrier island of the southeastern United States (Diefenbach et al. 1993). Furthermore, the steady increase of deer populations in North America may be a response to the extirpation of large predators, especially wolves, although it is difficult to disentangle this influence from the confounding influence of habitat changes, especially those associated with agricultural development. Finally, the ubiquitous nature of predator control programs reflects a perception that these animals limit their prey. Although predator control is usually undertaken to protect domestic livestock, it is also used to reduce mortality and enhance population abundance of native species (e.g., wolf control in Alaska). Many terrestrial predators appear capable of limiting prey populations. Unfortunately, there are few instances where scientists have looked simultaneously at mammalian predators, herbivores, and plants in terrestrial ecosystems, and virtually none where they have evaluated the radiating consequences of trophic cascades in distantly connected parts of the food web.

Approaches to understanding the role of predators in nature

The evidence that predatory mammals play important roles in a variety of natural ecosystems ranges in quality from fairly compelling to highly conjectural. Most species and systems have not been studied and many may never be. Thus, can we reasonably hope to develop predictive theories for the ways in which predators influence ecosystems? There are 2 philosophical approaches to problems of this nature. One (the inductive approach) is to assemble a list of case studies and search for patterns among them. For instance, of the studies that demonstrate important roles for predators versus those that do not, are there differences in such features as the demographic patterns of lower trophic forms, the vulnerability of lower trophic forms to population regulation by predation, or ecosystem-level characteristics (e.g., production, nutrient regimes, trophic complexity)? A second (deductive) approach is to formulate *a priori* hypotheses about characters of a species or ecosystem that are responsible for some particular function of predation (e.g., a trophic cascade, increase in species diversity, change in production, etc.) and then test this by conducting studies with species or systems in which the character is absent or present.

The challenges

The former (inductive) approach assumes that scientists have adequately explored the roles of predatory mammals for a range of representative species and ecosystems, and that negative findings have been reported as consistently in the literature as those that were positive. Neither of these assumptions is true. Syntheses from the published literature are problematic because ecologists tend to work in systems they think will yield conclusive results quickly and negative results often are not published. These are the same problems that plagued Connell (1983), Schoener (1983) and others in their efforts to assess the importance of competition in natural communities, a subject for which there were many more definitive studies. The latter (deductive) approach, while powerful conceptually, presumes that a predator's function in a particular system can be determined with reasonable ease and certainty, usually a false assumption. Manipulative experiments in which predators are removed or added and results contrasted with unmanipulated controls provide the most compelling evidence, and this approach has been used in a number of past studies to demonstrate keystone predatory roles and trophic cascades (reviewed in Carpenter and Kitchell 1993, Mills et al. 1993, and Power et al., 1996). However, the majority of examples are of species and systems that are amenable to experimentation because of the short generation times and limited mobility of key players. Not surprisingly, many of the best examples of keystone roles of predators come from lakes, streams, and rocky shores, whereas similar examples for predatory mammals are so few. When legal and ethical problems of conducting research on politically sensitive species are added to the logistical difficulties, it is hardly surprising that so little is known about the roles played by predatory mammals in their ecosystems.

If there are recurrent patterns in the functioning of predators across species and ecosystems, the only clear conclusion at this point is that they will be difficult to unravel. My own view of the most basic research needs are for (1) a blend of inductive and deductive logic in future attempts to synthesize results across systems, and (2) more creative approaches to the study of specific systems. Replicated manipulations of predator abundance, while appealing, are unrealistic for most species, and inferences made solely from static food webs (i.e., from descriptions of who eats whom), while relatively easy, are not very informative. For most predatory mammals it may be necessary to use opportunities as they arise to compare functioning ecosystems. This can be accomplished by examining:

1. changes in ecosystem structure with natural variation in predator abundance (as McLaren and Peterson did for wolves on Isle Royale),
2. change between habitat fragments containing or lacking the predator within a once-continuous distribution (as my colleagues and I have done with the sea otter),
3. changes through time as over-exploited species recover or continue toward extinction (as Laws [1977] has done with baleen whales in Antarctica).

Opportunities like these, while fortuitous, uncontrolled, and usually unreplicated, occur often and should be exploited by researchers. Reintroductions and removals are common practices in wildlife management and offer important opportunities for scientists and managers to work together in seeking knowledge about the role of predators in ecosystems (Mech 1995).

Conclusions

Ecosystem management has recently emerged as the rubric of conservation and wildlife biology and as an alternative to the traditional approach of species-level management. This approach, while still loosely defined, is now embraced by some resource-management agencies because of the growing realizations that: (1) species persist or disappear and populations grow or decline primarily in response to changes in their habitats, and (2) the number of species is too great and time is too short to conserve biodiversity in any other way. While few would question the logic of this strategy, there are many who question its wisdom and practical application. The reality is that species are the units of extinction whereas the linkages between species and ecosystems remain obscure (Jones and Lawton 1995). Therefore, the keystone species concept may offer a valuable approach to conservation issues because keystone species and ecosystems are linked in ways that are both understandable and well documented. Given that keystone species are comprised disproportionately of predators (as suggested by Power et al. 1996) and the apparently wide occurrence of trophic cascades, predatory mammals are probably vital to the integrity of many ecosystems. Thus, the requirements of predators may well define practical guidelines for ecosystem management.

Populations and species are being lost in our rapidly changing world at ever-increasing rates, and the loss of predatory mammals may be disproportionately high. If we are to realize our professed ethic of responsible stewardship for an inevitably changing world, we must learn how to conserve predators and understand what the consequences will be if we fail.

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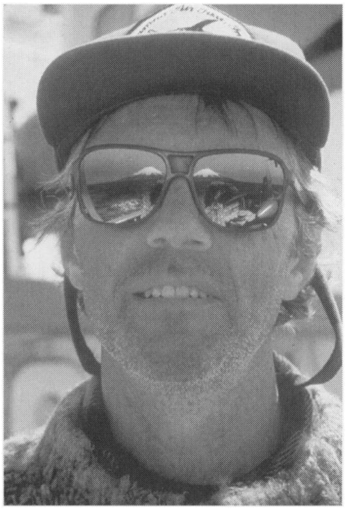

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