

## Plight of Predators

### *The Importance of Carnivores for Understanding Patterns of Biodiversity and Extinction Risk*

JOHN L. GITTLEMAN

MATTHEW E. GOMPPER

Predator species such as tigers and wolves are often symbols of conservation science, frequently serving as umbrella or flagship taxa for species-based conservation efforts. Predators also serve as important examples for how and why biodiversity is facing an unparalleled global extinction crisis. Here, we focus on the mammalian order Carnivora to assess arguments for the importance of a predator-based agenda in conservation, to observe global patterns of where mammalian predators are threatened, and to highlight factors influencing extinction risk, such as body size, life histories, and trophic level. On a local scale, evidence suggests that large predators may play a particularly important role in structuring ecological processes, and the loss of a few top predators may dramatically alter communities or even entire ecosystems. The role and relative importance of mid-sized or small predators, however, remains unclear, as does the role of predators in complex or highly biodiverse landscapes. Yet, given the potential importance of predators, it is essential to understand causes of their decline on a global framework. Toward this end, we show that there are particular global regions that are likely to suffer unusually high rates of extinction and describe the intricate interplay between anthropogenic effects and species' biology.

Predators receive considerable attention in the conservation sciences. Much of this attention is undoubtedly due to a charismatic image that draws attention from diverse segments of society. Nevertheless, there are good biological reasons for directing conservation resources to predators. Many of the biological and ecological characteristics of predators, such as rarity (Gaston 1994), reliance on scarce

and fluctuating resources (Fuller and Sievert 2001), and susceptibility to hunting pressures, raise the chances of extinction. Lessons learned from protecting predators also indicate that they sometimes legitimately serve as important models of conservation (Gittleman et al. 2002). For this reason, we do not ask in this chapter why predators often represent focal points for conservation agendas. Rather, we consider whether these species as a collective guild *deserve* such extensive attention. We do so by assessing the effects of the loss or gain of predators in natural systems. Because most predator-based conservation agendas focus on large, terrestrial mammalian carnivores, such as tigers, wolves, jaguars, and grizzly bears, we use examples mainly from the mammalian order Carnivora. Further, we ask if it is just these large predators that deserve special conservation emphasis because of their perceived ecological importance, or whether smaller or more omnivorous members of the order (e.g., weasels, jackals, foxes, small cats, and mongooses) also deserve such attention. How robust is the evidence that large and mid-sized Carnivora always play an especially important role where they are present? And, if this guild of species is indeed especially important, what and where are the threats to their continued persistence?

We begin by highlighting several cases showing the importance of top predators in structuring ecological communities. The top (or apex) predators in particular, rather than predators in general, are emphasized for two reasons. First, these animals exist at the very top of the food pyramid and are therefore relatively rare in terms of proportional biomass of the broader community and in terms of the absolute numbers of individuals found within any particular study site. As a result, where the influence of top predators is found to be important in structuring the ecological community, the per capita impact of each predator is especially great. Thus, although the population size of a top carnivore in any given region may be quite small, the behavior of any given individual can have tremendous importance for the rest of the community. This seems to be a point that even researchers actively involved in studies of large carnivores have failed to appreciate. It is in the study of apex carnivores that ethology interfaces with community and ecosystem ecology: the behavior of just a handful of individuals can fundamentally influence entire ecosystems.

Second, apex predators are themselves rarely the subjects of interspecific predation. Although this is not to say that predation on these animals never occurs, their populations are rarely limited by top-down effects, but rather are generally limited by bottom-up resource availability. This situation is in contrast to that of mid-sized carnivores, which are often limited by top-down effects and may therefore have their ecological impact on the broader community mediated by the presence of other predator species.

If indeed carnivores are deemed especially important biologically, then we need to conserve them. A first step toward this goal is to identify global patterns of carnivore distribution, diversity, and threat. By revealing these patterns, we attempt to apply lessons learned from local and regional studies to develop a more comprehensive and predictive science-based framework for identifying potentially vulnerable species before they decline.

### Wolves, Otters, and Orcas

Two “textbook” cases reveal the importance of apex predators as top-down controls of communities and even ecosystems: wolves (*Canis lupus*) in central North America, and sea otters (*Enhydra lutris*) in northern Pacific near-shore environments. Although wolves have been studied intensively in North America and Eurasia, most relevant here is the long-term work from Isle Royale, Michigan. This 544 sq. km national park lacked wolves until the late 1940s, when Lake Michigan froze over, allowing a pair of wolves to colonize the site (Mech 1966, Wayne et al. 1991). Over the past 40 years, wolf numbers have fluctuated between 10 and 50 individuals in two to three packs, and these individuals have had a significant effect on the island’s community. Wolves regulate moose (*Alces alces*) that in turn regulate the growth rates of balsam fir (*Abies balsamea*) in a tightly linked three-trophic-level system (Figure 17.1A; McLauren and Peterson 1994). Balsam fir is a dominant tree species on Isle Royale, and browsing on fir by moose determines its relative abundance in the overstory, seedling establishment, sapling recruitment, forest litter production and, on an ecosystem-level edaphic nutrient control (McInnes et al. 1992, Pastor et al. 1993,

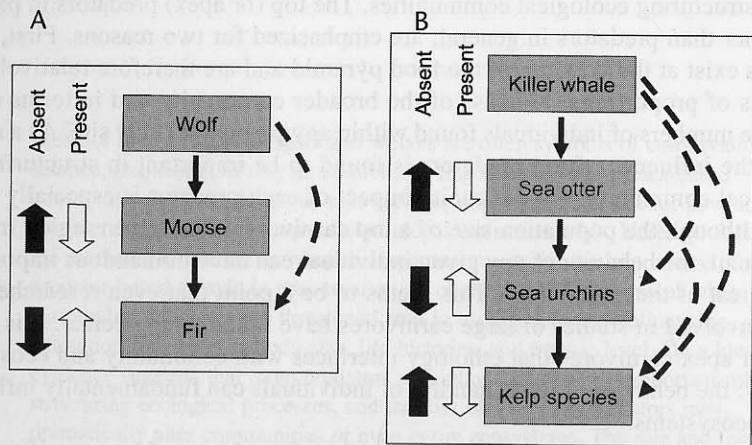


Figure 17.1. Conceptualized trophic interactions involving large top carnivores. (A) Three trophic-level systems in which wolves limit moose and beaver and thereby indirectly facilitate fir tree growth. Thin solid and thin dashed arrows represent direct and indirect trophic interactions, respectively. Thick arrows represent the relative influence of top predator presence (open arrow) or absence (filled arrow) on the relative biomass of lower trophic levels (upward arrows = increased biomass; downward arrows = decreased biomass). (B) Four-trophic-level interaction in which killer whales limit sea otters, thereby indirectly facilitating increased sea urchin biomass and decreased kelp biomass. (Adapted with permission from the following sources: Post, E., Peterson, R. O., Stenseth, N. C., and McLaren, B. E. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401:905–907. © 1999 Nature Publishing Group. Estes, J. A., Tinker, M. T., Williams, T. M., and Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476. © 1998 AAAS. McLaren, B. E., and Peterson, R. O. 1994. Wolves, moose, and tree rings on Isle Royale. *Science* 266:1555–1558. © 1994 AAAS.)

Post et al. 1999). Although these top-down effects do not indicate that bottom-up or abiotic factors are unimportant (Vucetich and Peterson 2004), they do indicate that through indirect effects a small number of wolves can dramatically influence the structure of an entire community (see Schmitz, ch. 12 in this volume).

The role of wolves as top-down regulators of community structure is also observed in other areas. For instance wolves were reintroduced in the Greater Yellowstone Ecosystem (Idaho, Wyoming, and Montana) in 1995, and results of studies assessing the impacts of this restoration on other components of the ecosystem are now emerging (Smith et al. 2003). Most intriguing are the altered behavioral and foraging ecologies of prey species and mesocarnivores, and the direct and indirect impact of these changes. For instance, coyote numbers have declined by about 50%, but those that remain are using a novel resource, the carcasses of ungulates killed by wolves (Smith et al. 2003). Altered behavior of elk, moose, and other ungulates has resulted in changes to the vegetation community in Yellowstone and may be facilitating the return of beavers, despite this species’ also being a prey of wolves (Ripple et al. 2001, Ripple and Beschta 2003, Smith et al. 2003, Soulé et al. 2003). If the return of wolves truly facilitates the return of beaver to the landscape, the ecosystem-level effects are likely vast, because beavers themselves are ecosystem engineers (Wright et al. 2002). If these shifts in the foraging pressures of ungulates continue, one might expect broad changes to riparian vegetation structure and an associated increase in faunal richness, as already observed in cross-site comparisons that showed differences in moose browsing pressures (Berger et al. 2001).

Like wolves, sea otters also are the top predators in a three-trophic-level community (Paine 1966, Leibold 1996, Steiner 2003). Sea otters limit sea urchin size and densities. In the absence of otters, grazing pressures from urchins devastate kelp forests and result in increased habitat homogeneity and decreased faunal richness (Figure 17.1B). Conversely, colonization of an area by sea otters promotes the growth and maintenance of kelp forests and its associated communities. This top-down cause-and-effect relationship has been observed at multiple sites, from northern California to Alaska’s Aleutian Islands (Estes and Duggins 1995). How many otters are necessary to derive the interactive effects of the presence of a top predator? The question is difficult to assess. Recent work (Doroff et al. 2003, Soulé et al. 2003) has shown that the functional response relationships between otters, urchins, and kelp are non-linear and differ not only between sites, but also within sites. The key is whether the site starts as urchin dominated (without otters) or kelp dominated (with otters). Nonetheless, the proportional biomass of sea otters is likely minor relative to other components of the community.

An intriguing facet of the sea otter case study has been the impact of a new top carnivore, the killer whale (*Orcinus orca*), which has changed the three-trophic-level community to a four-trophic-level community, with relatively few otters, high urchin numbers, and low kelp density (Figure 17.1B; Estes et al. 1998). Recent evidence suggests that the arrival of orcas in this community is a function of prey switching. The traditional prey of killer whales are great whales, and the decline of the great whales may have resulted in orcas’ switching to progressively smaller prey before devastating sea otter populations (Springer et al. 2003). Nonetheless, the generality that a top predator is especially important because a few individuals can have



such a great effect is upheld. The decline in sea otters and kelp forests over 3300 km of Alaskan Aleutian Island near-shore environments may have been caused by changes in the foraging behavior of as few as *four* whales (Estes et al. 1998). The ability of non-Carnivora such as killer whales to determine community structure in systems that also include large Carnivora again emphasizes that it is not taxonomic membership per se that defines whether a species is an apex predator. Species such as large sharks, eagles, snakes, or crocodiles all represent likely candidate organisms that may drive the shape of communities and perhaps ecosystems. A similar phenomenon, called *keystone predators*, has been described among invertebrate communities.

### Mesocarnivores

These studies clearly indicate that some predators have the potential to strongly structure communities. However, these predators represent large top carnivores in relatively simple systems. Most carnivores are neither large nor at the apex of trophic pyramids. Especially relevant in the context of predator conservation is the ecological role of *mesocarnivores* (mid-sized carnivores) in structuring communities. Mesocarnivores make up the majority of species in the order Carnivora, but our understanding of their ecology is superficial. Indeed, although the term *mesocarnivore* itself has long been used in the ecological literature, we are not aware of a clear quantitative definition. Buskirk (1999) simply defines mesocarnivores as being 1–15 kg, but the term is often construed in a general sense to include all Carnivora that are not large top predators. Consequently, more than 90% of terrestrial Carnivora are mesocarnivores (Gittleman 1985).

The importance of small and mid-sized carnivores can be assessed at two levels: the role assumed by these predators when they are de facto top carnivores and the importance of these predators within communities that also contain large top carnivores. The former is a topic that has received a fair amount of attention under the heading of *mesocarnivore* (or *mesopredator*) *release* (Terborgh and Winter 1980, Soulé et al. 1988, Crooks and Soulé 1999). Because carnivore communities are strongly influenced by intraguild predation and competition, the loss of a top predator may result in a rise and fall of some secondary and tertiary carnivores, respectively. For instance, the loss of wolves from a community can result in an increase in coyotes that, in turn, can result in a decrease in foxes (Johnson et al. 1996). Conversely, a loss of coyotes can result in increases in foxes and other mesopredators (Sovada et al. 1995, Henke and Bryant 1999). The consequences of these interactions, which fundamentally involve a body-size-based shift in trophic status of mesocarnivores from formerly secondary or tertiary predator to apex predator, can be seen throughout the food web and in fundamental measures of biodiversity (Crooks and Soulé 1999).

Scenarios in which mesocarnivores are apex carnivores do not occur solely in disturbed systems where top carnivores have been lost. There are numerous regions without larger mammalian carnivores in which mesocarnivores such as procyonids, mustelids, and small canids (<8 kg) act as top carnivores (e.g., island systems; Roemer

et al. 2002, Cuarón et al. 2004). There also are habitats within areas that contain larger species that mesocarnivores species do not use. For example, otters (e.g., river otter, *Lutra canadensis*; range, 6–14 kg) dominate many freshwater habitats. Might river otters control aquatic systems in the same way sea otters and wolves may control marine near-shore and boreal forest communities?

In Missouri, river otters were virtually extirpated but were restored through intensive reintroduction efforts in the early 1980s and currently number about 10,000–18,000 (Missouri Department of Conservation, unpublished data). For this region, a stream system food web conceptualized from otter, fisheries, and macroinvertebrate studies suggests a four- or five-trophic-level system (Figure 17.2) in which river otters feed on centrarchids, carps, suckers, and the large crayfish that these fish, in turn, usually avoid (Rabeni 1992, Roberts 2003). Crayfish are known to strongly influence lower trophic levels (Whitledge and Rabeni 1997), so we expect that as an indirect effect of otter reintroduction, invertebrate and algal biomass should increase and decrease, respectively. A possible river-otter-driven trophic cascade, illustrates that even mid-sized carnivores can be important drivers (sensu Soulé et al. 2003) of communities and ecosystems. Indeed, such a finding would be in congruence with results of other aquatic community studies that have stressed the importance of top-down interactions (Wootton et al. 1996, Finlay et al. 2002). In freshwater systems where communities are often simple and there is a tight link between primary and secondary productivity, the top carnivores may greatly reduce prey populations, thereby causing trophic cascade (i.e., a series of strong indirect effects on populations two or more links down the food chain; Vanni et al. 1990, Strong 1992, Carpenter and Kitchell 1993, Polis and Strong 1996).

The role of mesocarnivores is less clear in systems where opportunities exist to interact with larger carnivores, because few researchers have closely and explicitly studied trophic cascades involving the loss or gain of mammalian mesocarnivores in systems (a) that contain top mammalian predators and (b) in which the loss or gain of the mesocarnivore is not due to the presence or absence of a larger top carnivore. Instead, studies of mesocarnivores focus more on the direct interactions with one or a series of prey species, assessing to what extent prey numbers are a function of top-down or bottom-up processes (e.g., Krebs et al. 1995, Jedrzejewska and Jedrzejewski 1998). This is not to suggest that indirect effects are unimportant but rather that the trophic cascades associated with these events have not been well documented. In the rare system where mesocarnivore-prey dynamics have been well studied, in a two-trophic-level (or more) framework, results are complex. Long-term time series analyses and large-scale experimental studies of lynx (*Lynx canadensis*) and hare (*Lepus americanus*) interactions (Stenseth et al. 1997, Krebs, Boonstra, et al. 2001, Krebs, Boutin, et al. 2001) indicate that prey population dynamics are caused not by top-down or bottom-up factors acting alone or in the absence of other predators, but by the combination of all of these processes.

If indeed species such as river otter and lynx are fundamental drivers of community structure even in systems that have larger carnivores, are these examples typical of the importance of mesocarnivores? There is currently no clear answer, although several issues are certainly relevant. Most mesocarnivores are omnivores, feeding on multiple prey species and on multiple trophic levels. For example, the Procyonidae

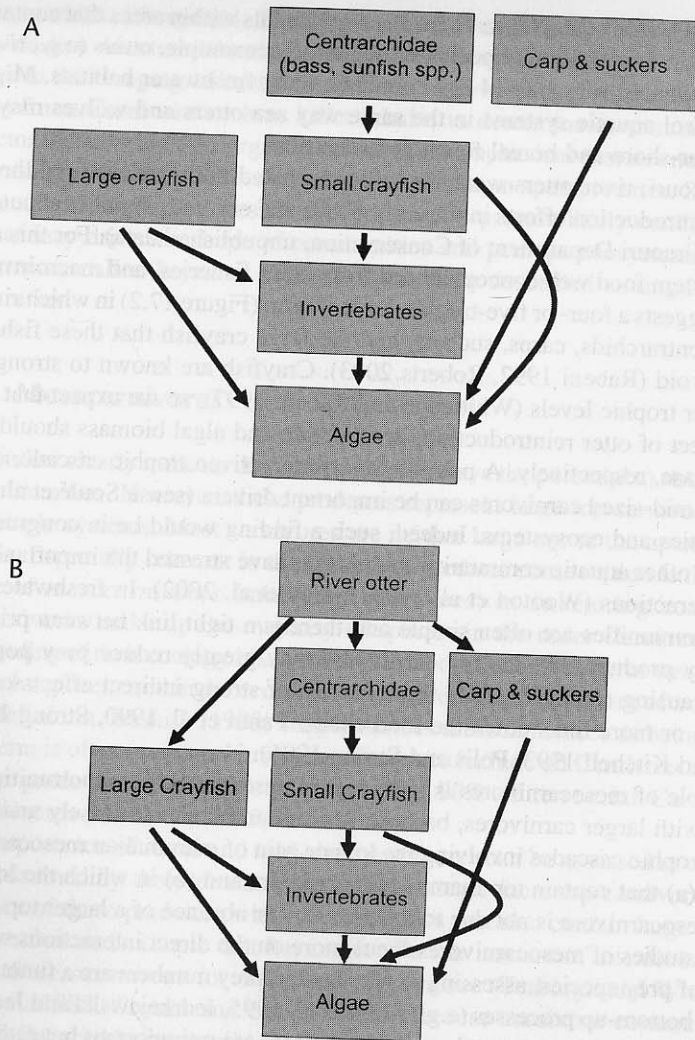


Figure 17.2. Hypothesized primary trophic interactions in a Missouri stream with and without river otters. (A) In systems without river otters, stream fish communities are dominated by Centrarchidae, carps, and suckers. Carps and suckers feed primarily on algae. Centrarchids feed primarily on small crayfish, which in turn feed on invertebrates. While crayfish and some fish also feed on algae, biomass of this trophic level is primarily limited by invertebrate biomass. (B) River otters feed primarily on large fish and on large crayfish (thereby also reducing small crayfish biomass). A decrease in fish and crayfish foraging pressures results in increased invertebrate biomass and an associated decrease in algal biomass. All arrows represent known, ecologically robust linkages (Rabeni 1992, Whitlege and Rabeni 1997, Roberts 2003).

(e.g., raccoons, coatis, and ringtails), Mephitidae (e.g., skunks), and small Canidae (e.g., foxes) all feed on plants, invertebrates, and vertebrates. Diverse feeding habits might act to buffer predator populations against fluctuations in nutrient availability of particular prey species (Eubanks and Denno 1999, and see Eubanks, ch. 1 in this volume). However, most vertebrate prey species of mesocarnivores are more strongly influenced by resource availability than by predation (Desy and Batzli 1989, Krebs et al. 1995, Jedrzejewska and Jedrzejewski 1998). In addition, invertebrates and plant material, principally fruit or nuts, dominate the diet of many mesocarnivore species. Yet, from the perspective of primary producers, mast or fruit output (and perhaps invertebrate population dynamics) is more a function of abiotic factors, and mesocarnivores rarely limit seed-to-seedling transition rates.

### Carnivores in Hyperdiverse Environments

Most of the world's biodiversity (including the Carnivora) exists in the tropics. Yet our knowledge about the role of carnivores is from simple, species-poor communities. In such communities, trophic cascades driven by the presence of top predators mimic theoretical expectations ( Hairston et al. 1960, Oksanen et al. 1981). In high-diversity tropical environments, however, food webs are far more complex, and have increased capacities for buffering and compensation among species (Strong 1992, Polis and Strong 1996). What is the empirical support for top vertebrate predators' controlling community structure in biodiverse terrestrial systems?

This issue has been studied mainly in Central and South America, where the apex predators are puma (*Felis concolor*) and jaguar (*Panthera onca*). If a single species of carnivore can drive community structure in biodiverse regions of the neotropics, evidence should be most apparent from studies of these species. Loss of these predators would result in increased population densities of the mesocarnivores, browsing mammals (e.g., deer), and seed predators (e.g., large rodent species) that are generally limited by large felids. In a scenario suggested by Terborgh and colleagues, outbreaks of these later species would form part of a trophic cascade that ultimately results in severely reduced seed and seedling survival, high rates of avian nest predation, and overall forest degradation (Terborgh and Winter 1980, Terborgh 1990, Terborgh 1992, Terborgh et al. 1997, Terborgh et al. 2001).

Problematically, much of the evidence for the importance of predators in neotropical forests is based on observations from extremely degraded environments or very small habitat remnants that have lost not one or two species, but rather about 75% of their vertebrate fauna (Terborgh et al. 1997, Terborgh et al. 2001, Lambert et al. 2003). Studies of more intact systems, or systems that have lost only a single predator, are rare. Such studies that have implicated the importance of large cats have often focused on Barro Colorado Island (BCI), Panama, a site where large felids sometimes visit but are not resident, so predation pressures from large felids is considered weak. For instance, comparisons of BCI and Manu, Peru, where large felids are common and predation risk is probably high, suggest that densities of many mid-sized mammals on BCI are inordinately intense because of loss of large predators (Terborgh and Winter 1980, Terborgh 1990). Yet some (Wright et al. 1994) ques-



tion both the notion that mammalian densities on BCI are extreme and the conclusions taken from the BCI-Manu comparison regarding the importance of top-down processes in structuring neotropical communities. Studies of seed and seedling herbivory by mid-sized mammals at both sites also identified no differences in herbivore pressures (Terborgh and Wright 1994), although comparisons between BCI and an adjacent mainland site where large felids persist did identify greater levels of seed loss (Asquith et al. 1997). These equivocal results indicate the need for additional research to buttress any suggestion for the importance of large predators as community or ecosystem drivers in regions with high biodiversity.

### Synopsis: Are Carnivora Important?

From the evidence discussed we conclude that in some systems mammalian carnivores do play a fundamental role in structuring faunal and floral communities, and it is likely that this influence is of such magnitude as to drive ecosystem-level changes. We also observe that the influence of carnivores derives not from the size of the animal per se, but rather from its ability to limit the biomass or resource use of an entire lower trophic level or functional guild. Given relatively few long-term studies of the indirect effects of Carnivora outside temperate systems, it is too early to determine whether the disproportional importance of individual predators is a general rule of thumb for more biodiverse regions. There has also been little study of the importance of the presence or absence of Carnivora that are true omnivores.

If carnivores are potentially very important in structuring communities, it follows that we should be especially mindful of the persistence of these species. Carnivores not only may be disproportionately important, but also may suffer disproportionately high risks of local extirpation and global extinction (Gittleman et al. 2002). We therefore now address where and why there is an interesting disparity between some carnivores that are at a high risk of extinction, such as the giant otter and black-footed ferret, and others, like the small Indian mongoose and red fox, whose populations are thriving.

### Global Range and Species Richness Patterns

Where species live and what factors influence the processes of distributional decline are paramount for understanding changes in global biodiversity (Gaston and Spicer 1998). Thus, for our discussion of how mammalian carnivores can be used as models for understanding predators, it is important to know where carnivores live around the planet as a first step toward global conservation. Admittedly, worldwide distributions of species biodiversity are poorly described; most species have not been mapped even in the most rudimentary fashion (Gaston 2003). This situation is frustrating, because, of all the rubrics of conservation, we know that small geographic range size is the single greatest biological factor contributing to extinction. Thus, the fact that over half of all mammal species live in a land area smaller than the country of Spain, or that, among single species, the black-footed ferret has an extremely small

range compared to the tens of millions of sq. km of the red fox, the widest of all globally distributed mammals, is both biologically meaningful and importantly symbolic for conservation science. Our lack of geographic knowledge is perhaps not surprising, given that the alpha taxonomy for most species is not known (Wilson 2002). For mammals, a complete geographic range database has only recently been placed in any sort of geographic information system (GIS) platform so that global distributions of species richness and extinction risk can be assessed (Brown et al. 1996). Here, we summarize results from Sechrest's (2003) new geographic range database for all mammals, results based on the digitizing of more than 1,700 source maps and on using them in a GIS to assess general patterns of carnivore extinction risk.

In terms of global mammal distributions, most mammal species have fairly small geographic ranges (Figure 17.3), the extent of occurrences being less than 250,000 sq. km (Sechrest 2003). Across all organisms studied so far and across different ecological scales, species range size distributions show that the smallest range size class is the most common (Gaston 2003). That is, there are many more species with narrow global ranges and few with large ranges, suggesting that most species are relatively rare, at least spatially. For mammals, this skew is observed in both predatory carnivores (including canids, felids, and mustelids) and clades that usually comprise their prey (artiodactyls, lagomorphs, and rodents).

The geographic range size of terrestrial carnivores is generally large and statistically greater than species in other mammalian orders, with an average of 6 373 986 sq. km for Carnivora, compared to an average for all mammals of over 1.5 million sq. km, areas roughly comparable to Australia and Alaska, respectively. Carnivores characteristically are able to move over large areas because of their relatively large body size, extensive home ranges, flexibility in diet and physiology, habitat breadth, and overall need to move in response to fluctuations in prey. Simultaneously, some carnivores are also relatively immune to anthropogenic effects, and, as their habitats are shrinking, the range declines are not as great. For example, across a select group of mammals, the spotted hyaena has lost only 14% of its global range (Ceballos and Ehrlich 2002). Of the 28 orders of mammals (Wilson and Reeder 1993), only the Carnivora, Artiodactyla, and Didelphimorphia have a small proportion (<20%) that are endemic with restricted ranges of less than 50 000 sq. km, a threshold for generally defining endemism (Terborgh and Winter 1983). The only truly endemic carnivores are island forms such as the Malagasy clade of herpestids and viverrids and the California Channel island fox (*Urocyon littoralis*). Overlaying all range distributions across mammals reveals that the greatest species richness is around the equator, with 34% (1,621 of 4,740 terrestrial mammals) ranging in and around the tropics (Figure 17.4A). A similar pattern is observed across genera and families, indicating that geographic ranges are to some extent phylogenetically correlated (Jones et al. 2004).

Do most carnivore global distributions coincide with the distributions of their prey? Surprisingly, this question has never been addressed quantitatively on a global scale. The reason is a combination of lack of accurate maps for most individual species, lack of a complete database of maps across large taxa, and lack of analytical tools for overlaying hundreds of the maps onto one another and simultaneously assessing

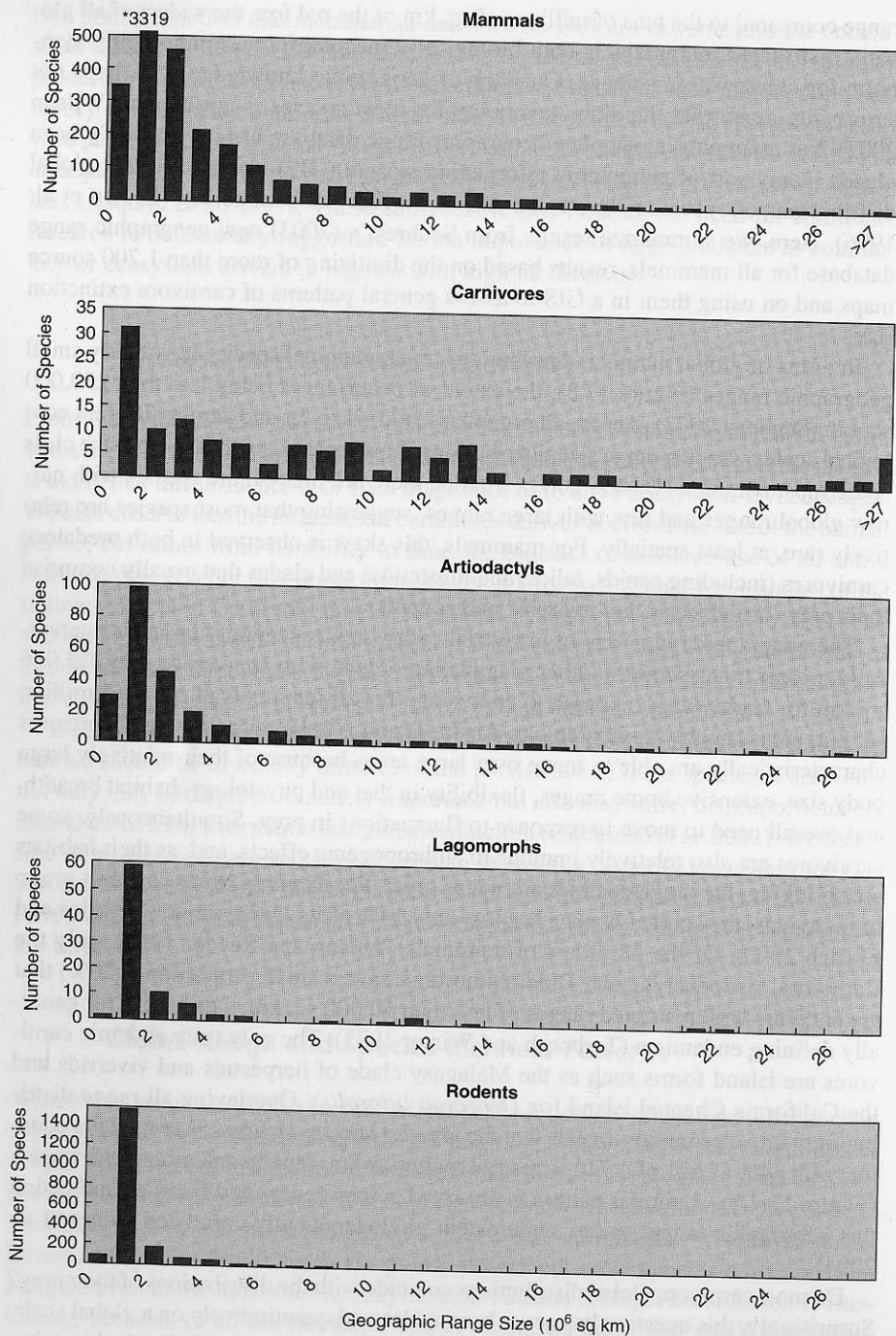


Figure 17.3. Global species range size distributions for mammals, carnivores, and associated taxa (artiodactyls, lagomorphs, rodents) representing prey. Range size  $\times$  one million sq. km. Based on data compiled from Sechrest (2003).

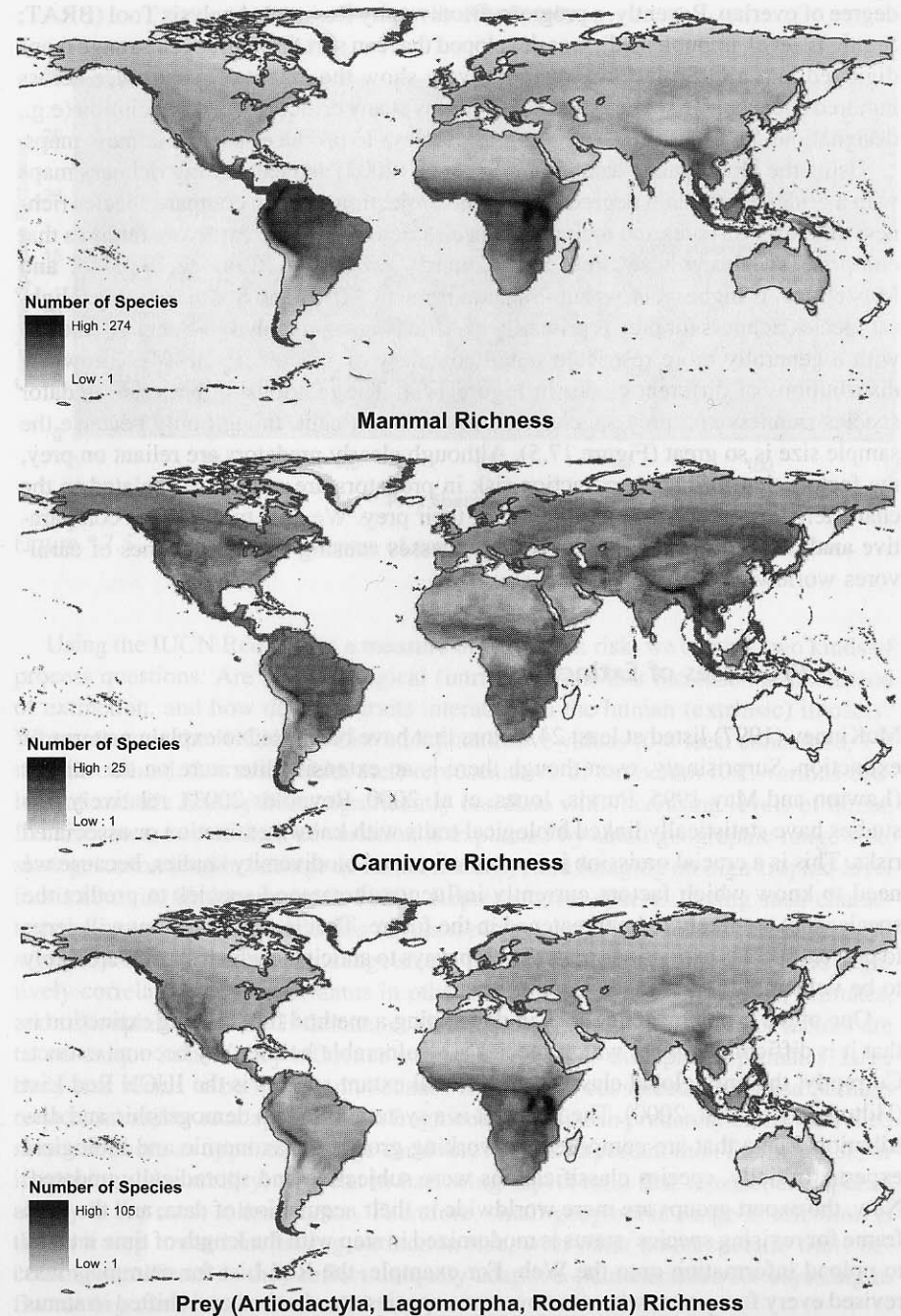


Figure 17.4. Global species richness of (A) mammals, (B) predatory carnivores (canids, felids, mustelids), and (C) associated prey (artiodactyls, lagomorphs, rodents). Equal area map projection, divided into grid cells of equal area ( $\sim 111$  sq. km). Levels of species richness are represented by color-scale intensities (see scale). Based on data compiled from Sechrest (2003).



degree of overlap. Recently, a program, Biodiversity Research Analysis Tool (BRAT; Smith, E., et al. unpublished), was developed that can sort through species range maps digitized into a GIS platform, quantitatively show the extent of occurrence across hundreds of species, isolate range distributions at any critical level of resolution (e.g., designations for endemics), and use grid overlays to produce species richness maps.

Using the global range database of Sechrest (2003) and calculating richness maps with a gridded one-tenth degree geographic projection, we can compare species richness among carnivores and their prey. Species richness for the carnivore families that comprise species whose diets are primarily predatory (Canidae, Felidae, and Mustelidae) is highest across sub-Saharan tropical Africa and Southeast Asia. Highest species richness for prey is primarily in Africa (again, mainly sub-Saharan), though with a generally more restricted range boundary of species richness, as shown in distributions of different clades in Figure 17.4. The relationship between predator species richness and prey species richness is significant, though only because the sample size is so great (Figure 17.5). Although clearly predators are reliant on prey, the factors that influence extinction risk in predators are only partly related to the characteristics, or at least distribution, of their prey. We now turn to what comparative analyses tell us about the general processes causing species declines of carnivores worldwide.

### Processes of Extinction

McKinney (1997) listed at least 24 factors that have been used to explain patterns of extinction. Surprisingly, even though there is an extensive literature on the subject (Lawton and May 1995, Purvis, Jones, et al. 2000, Reynolds 2003), relatively few studies have statistically linked biological traits with known extinction or associated risks. This is a crucial omission in conservation and biodiversity studies, because we need to know which factors currently influence threatened species to predict the species that are likely to be threatened in the future. That is, a science that will serve to prevent species extinctions must develop ways to anticipate which species are likely to be vulnerable.

One of the problems, of course, in developing a method for studying extinction is that it is difficult to assess which species are vulnerable before they become extinct. Currently, the only global classification for all extant species is the IUCN Red List (Hilton-Taylor et al. 2000). The Red List is a system based on demographic and distributional data that are composed by working groups of taxonomic and biological experts. Initially, species classifications were subjective and sporadically updated. Now, the expert groups are more worldwide in their acquisition of data, and the time frame for revising species' status is modernized in step with the length of time it takes to upload information onto the Web. For example, the Red List for mammals was revised every few years, whereas now some species are checked and shifted in status on monthly intervals, with the entire class reevaluated approximately every year. Although Red List classification is not perfect, the database is useful for assessing biological reasons underlying the variance in species extinction risk (Mace 1995, Mace and Balmford 2000).

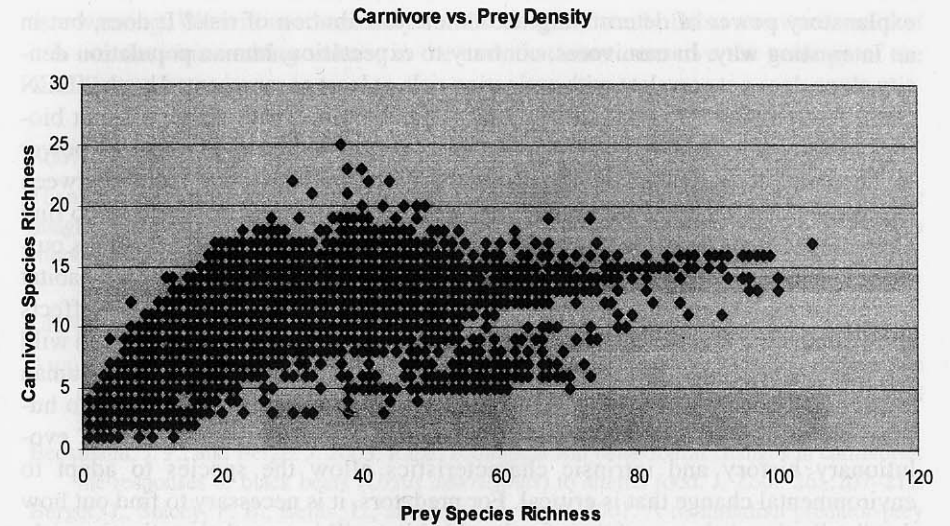


Figure 17.5. Global species richness of predatory carnivores and associated prey taxa.

Using the IUCN Red List as a measure of extinction risk, we can ask two kinds of process questions: Are there biological (intrinsic) traits that increase the likelihood of extinction, and how do these traits interact with the human (extrinsic) impacts? When we code the IUCN Red List into quantitative values (0 = least concerned, 1 = near threatened, 2 = vulnerable, etc.) representative of extinction risk, various ecological and life history traits significantly correlate with increasing levels of threat. In carnivores, over a third of variation is explained by small geographic range size, slow gestation length, late age at sexual maturity, and foraging on high-trophic-level foods (Purvis, Gittleman, et al. 2000). Representative species having such characteristics are many felids, wild dog (*Lycaon pictus*), and black-footed ferret (*Mustela nigripes*). To date, geographic range size is the sole factor that consistently and negatively correlates with threat status in other mammal groups, such as bats, primates, and marsupials (Purvis, Gittleman, et al. 2000, Jones et al. 2003). Other factors are taxon-unique in how they influence extinction risk. For example, in primates, large body size seems to be important, because it enhances conspicuousness and perhaps reduces an ability to adapt to habitat fragmentation. Size in predatory carnivores (i.e., mesocarnivore as opposed to large carnivore) is less important than life histories for increasing vulnerability, whereas in bats wing aspect ratio that represents dispersal ability is the most salient factor. Therefore, small geographic range distribution is the first step toward increasing extinction risk, with other taxon-specific traits becoming significant as they reflect uniquely adaptive characteristics for adjusting to fluctuating environmental conditions.

Biological correlates of extinction thus help in developing a model that may predict why some species are more vulnerable to extinction while others are seemingly immune. We can now address the second part of our question: Do we find that a coupling of anthropogenic factors with these biological correlates increases

explanatory power of determining taxonomic distribution of risk? It does, but in an interesting way. In carnivores, contrary to expectation, human population density alone does not correlate with extinction risk, at least as represented by the IUCN classification (Cardillo et al. 2004). But when combined with the significant biological traits just discussed, human population density increases explanatory power in the model up to 80%, revealing that there are strong interactive effects between exposure to human populations and a species' biology. It will be insightful to find out whether other taxonomic groups, as well as other anthropogenic qualities outside human density (e.g., global climate change, exotic species introductions, habitat fragmentation), show similar comparative patterns. Perhaps the interactive effects show something that we have intuitively known. The observation that African wild dogs are going extinct while black bears are proliferating in regions with high human impact (Beckmann and Berger 2003) is clearly not the result of exposure to humans per se. Rather, it is the biological differences and the way each species' evolutionary history and intrinsic characteristics allow the species to adapt to environmental change that is critical. For predators, it is necessary to find out how the distributional change of their food and habitat will impact their extinction risk. As we previously noted, many carnivore populations are influenced by relatively few variables. Identifying these critical variables must increasingly demand our attention.

### Saving Predators: A Cruel Bind

In this chapter, we have summarized many factors that are relevant to understanding problems of predator conservation. This is not a thorough list, yet it reveals the complexity of what is involved in making decisions at various scales, from local to regional to global issues, all confronting which predator species are threatened, where the threat is happening, and why the threat is occurring in some species and not in others. Clearly, from the body of evidence reviewed here and described throughout this book, we are amassing effective data to adequately answer many scientific questions of conservation, and developing the means for establishing a predictive science in which we can anticipate what species and geographic areas require close vigilance to prevent extinction.

But, in the end, this is only part of the problem. There remain exceptionally hard decisions that will force us to select which predators to save when we know that the scientific answer is a stalemate. An example is provided by the island fox (*Urocyon littoralis*) endemic to the California Channel islands. Colonization of the islands by golden eagles (*Aquila chrysaetos*) has all but eliminated foxes on three of seven islands (Roemer et al. 2002). What happens when the primary food source (feral pigs), the culprit that initially attracted eagles to cause declines in the foxes, is eradicated? Simulation studies show that the problem will not be solved: eagles will simply shift their attention to foxes, thus increasing the foxes' chances of extinction. The real solution will rest with our decision about whether to protect an endangered predator (the island fox) or a protected predator (the golden eagle). This example should serve

as a warning. We will need not only solid scientific data, but also an awareness that it is our decision-making values, in the end, that must conserve the ecology of the world's predators.

### Acknowledgments

Thanks to J. Estes for insights on sea otters and near-shore communities and to C. Rabini for insights on river-otter-dominated communities. The work on global geographic ranges was supported by a grant from the National Science Foundation (DEB/0129009).

### Literature Cited

- Asquith, N. M., Wright, S. J., and Claus, M. J. 1997. Does mammal community composition control seedling recruitment in neotropical forests? Evidence from islands in central Panama. *Ecology* 78:941–946.
- Beckmann, J. P., and Berger J. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J. Zool.* 261:207–212.
- Berger, J., Stacey, P. B., Bellis, L., and Johnson, M. P. 2001. A mammalian predator-prey imbalance: grizzly bears and wolf extinction affect avian neotropical migrants. *Ecol. Applic.* 11:947–960.
- Brown, J. H., Stevens, G. C., and Kaufmann, D. M. 1996. The geographic range: size, shape, boundaries and internal structure. *Annu. Rev. Ecol. Syst.* 27:597–623.
- Buskirk, S. W. 1999. Mesocarnivores of Yellowstone. In: *Carnivores in Ecosystems: The Yellowstone Experience* (Clark, T. W., Curlee, P. M., Minta, S. C., and Kareiva, P. M., eds.). New Haven, Conn.: Yale University Press; 165–187.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., and Mace, G. M. 2004. Human Population Density and Extinction Risk in the World's Carnivores. Public Library of Science.
- Carpenter, S. R., and Kitchell, J. F. 1993. *The Trophic Cascade in Lakes*. Cambridge: Cambridge University Press.
- Ceballos, G., and Ehrlich, P. R. 2002. Mammal population losses and the extinction crisis. *Science* 296:904–907.
- Crooks K. R., and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- Cuarón, A., Morales-Martinez, M., McFadden, K. W., Valenzuela, D., and Gompper, M. E. 2004. The status of dwarf carnivores on Cozumel Island, Mexico. *Biodiver. Conserv.* 13:317–331.
- Desy, E. A., and Batzli, G. O. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology* 70:411–421.
- Doroff, A. M., Estes, J. A., Tinker, M. T., Burn, D. M., and Evans, J. A. 2003. Sea otter population declines in the Aleutian archipelago. *J. Mammal.* 84:55–64.
- Estes, J. A., and Duggins, D. O. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.* 65:75–100.
- Estes, J. A., Tinker, M. T., Williams, T. M., and Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Eubanks, M. D., and Denno, R. F. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* 80:1253–1266.
- Finlay, J. C., Khandwala, S., and Power, M. E. 2002. Spatial scales of energy flow in food webs of the South Fork Eel River. *Ecology* 83:1845–1859.



- Fuller, T. K., and Sievert, P. R. 2001. Carnivore demography and the consequences of changes in prey availability. In: *Carnivore Conservation* (Gittleman, J. L., Funk, S., Macdonald, D., and Wayne, R. K., eds.). Cambridge: Cambridge University Press; 163–178.
- Gaston, K. J. 1994. *Rarity*. London: Chapman & Hall.
- Gaston, K. J. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford: Oxford University Press.
- Gaston, K. H., and Spicer, J. I. 1998. *Biodiversity: An Introduction*. Oxford: Blackwell.
- Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* 67:540–554.
- Gittleman, J. L., Funk, S. M., Macdonald, D., and Wayne, R. K. 2002. *Carnivore Conservation*. Cambridge: Cambridge University Press.
- Hairston, N. G., Smith, F. E., and Slobodkin, L. B. 1960. Community structure, population control, and competition. *Am. Nat.* 94:421–425.
- Henke, S. E., and Bryant, F. C. 1999. Effect of coyote removal on the faunal community in western Texas. *J. Wildlife Manag.* 63:1066–1081.
- Hilton-Taylor, C. 2000. 2000 IUCN Red List of Threatened Species. Gland, Switzerland: IUCN.
- Jedrzejewska, B., and Jedrzejewski, W. 1998. *Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study*. New York: Springer-Verlag.
- Johnson, W. E., Fuller, T. K., and Franklin, W. L. 1996. Sympatry in canids: a review and assessment. In: *Carnivore Behavior, Ecology, and Evolution* (Gittleman, J. L., ed.). Ithaca, N.Y.: Cornell University Press; 189–218.
- Jones, K. E., Purvis, A., and Gittleman, J. L. 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161:601–614.
- Jones, K. E., Sechrest, W., and Gittleman, J. L. 2004. Age and area revisited: identifying global patterns and implications for conservation. In: *Phylogeny and Conservation* (Purvis, A., Gittleman, J. L., and Brooks, T. M., eds.). Cambridge: Cambridge University Press.
- Krebs, C. J., Boonstra, R., Boutin, S., and Sinclair, A. R. E. 2001. What drives the 10-year cycle of snowshoe hares? *Bioscience* 51:25–35.
- Krebs, C. J., Boutin, S., and Boonstra, R. 2001. *Ecosystem Dynamics of The Boreal Forest: The Klauane Project*. New York: Oxford University Press.
- Krebs, C. J., Boutin, S., Boonstra, R., Sinclair, A. R. E., Smith, J. N. M., Dale, M. R. T., Martin, K., and Turkington, R. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- Lambert, T. D., Adler, G. H., Riveros, C. M., Lopez, L., Ascanio, R., and Terborgh, J. 2003. Rodents on tropical land-bridge islands. *J. Zool.* 260:179–187.
- Lawton, J., and May, R. M. 1995. *Extinction Rates*. Oxford: Oxford University Press.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.* 147:784–812.
- Mace, G. M. 1995. Classification of threatened species and its role in conservation planning. In: *Extinction Rates* (Lawton, J. H., and May, R. M., eds.). Oxford: Oxford University Press; 197–213.
- Mace, G. M., and Balmford, A. 2000. Patterns and processes in contemporary mammalian extinction. In: *Priorities for the Conservation of Mammalian Diversity* (Entwhistle, A., and Dunstone, N., eds.). Cambridge: Cambridge University Press; 27–52.
- McInnes, P. F., Naiman, R. J., Pastor, J., and Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73:2059–2075.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* 28:495–516.
- McLaren, B. E., and Peterson, R. O. 1994. Wolves, moose, and tree rings on Isle Royale. *Science* 266:1555–1558.
- Mech, L. D. 1966. *The wolves of Isle Royale*. Fauna Series no. 7. Washington, D.C.: U.S. National Park Service.
- Oksanen, L., Fretwell, S. D., Arruda, J., and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240–261.
- Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65–75.
- Pastor, J., Dewey, B., Naiman, R. J., MacInnes, P. F., and Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467–480.
- Polis, G. A., and Strong, D. R. 1996. Food web complexity and community dynamics. *Am. Nat.* 147:813–846.
- Post, E., Peterson, R. O., Stenseth, N. C., and McLaren, B. E. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401:905–907.
- Purvis, A., Gittleman, J. L., Cowlshaw, G., and Mace, G. M. 2000. Predicting extinction risk in declining species. *Proc. R. Soc. Lond.* 267:1947–1952.
- Purvis, A., Jones, K. E., and Mace, G. M. 2000. Extinction. *BioEssays* 22:1123–1133.
- Rabeni, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. *Can. J. Fish. Aquat. Sci.* 49:1714–1721.
- Reynolds, J. D. 2003. Life histories and extinction risk. In: *Macroecology* (Blackburn, T. M., and Gaston, K. J., eds.). Oxford: Blackwell; 195–217.
- Ripple, W. J., and Beschta, R. J. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *For. Ecol. Manag.* 184:299–313.
- Ripple, W. J., Larsen, E. J., Renkin, R. A., and Smith, D. W. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biol. Conser.* 102:227–234.
- Roberts, N. 2003. River otter food habits in Missouri (M.S. thesis, University of Missouri, Columbia, Mo.).
- Roemer, G. W., Donlan, C. J., and Courchamp, F. 2002. Golden eagles, feral pigs and insular carnivores: how exotic species turn native predators into prey. *Proc. Nat. Acad. Sci. U.S.A.* 99:791–796.
- Sechrest, W. W. 2003. *Global diversity, endemism, and the conservation of mammals* (Ph.D. dissertation, University of Virginia, Charlottesville, Va.).
- Smith, D. W., Peterson, R. O., and Houston, D. B. 2003. Yellowstone after wolves. *Bioscience* 53:330–340.
- Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M., and Hill, S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conser. Biol.* 2:75–92.
- Soulé, M. E., Estes, J. A., Berger, J., and Martinez del Rio, C. 2003. Ecological effectiveness: conservation goals for interactive species. *Conser. Biol.* 17:1238–1250.
- Sovada, M. A., Sargeant, A. B., and Grier, J. W. 1995. Differential effects of coyotes and red foxes on duck nest success. *J. Wild. Manag.* 59:1–9.
- Springer, A. M., Estes, J. A., van Vliet, G. B., Williams, T. M., Doak, D. F., Danner, E. M., Forney, K. A., and Pfister, B. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proc. Nat. Acad. Sci. U.S.A.* 100:12223–12228.
- Steiner, C. F. 2003. Keystone predator effects and grazer control of planktonic primary production. *Oikos* 101:569–577.
- Stenseth, N. C., Falck, W., Bjørnstad, O. N., and Krebs, C. J. 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between lynx and hare. *Proc. Natl. Acad. Sci. U.S.A.* 94:5147–5152.

- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747-754.
- Terborgh, J. 1990. The role of felid predators in neotropical forests. *Vida Silvest. Neotrop.* 2:3-5.
- Terborgh, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24:283-292.
- Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D., et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923-1926.
- Terborgh, J., Lopez, L., and Tellos, J. S. 1997. Bird communities in transition: the Lago Guri Islands. *Ecology* 78:1494-1501.
- Terborgh, J., and Winter, B. 1980. Some causes of extinction. In: *Conservation Biology: An Evolutionary Ecological Perspective* (Soule, M. E., and Wilcox, B. A., eds.). Sunderland, Mass.: Sinauer; 119-133.
- Terborgh, J., and Winter, B. 1983. A method for siting parks and reserves with special reference to Columbia and Ecuador. *Biol. Conser.* 27:45-58.
- Terborgh, J., and Wright, S. J. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75:1829-1833.
- Vanni, M. J., Luecke, C., Kitchell, J. F., Allen, Y., Temte, J., and Magnuson, J. J. 1990. Effects on lower trophic levels of massive fish mortality. *Nature* 344:333-335.
- Vucetich, J. A., and Peterson, R. O. 2004. The influence of top-down, bottom-up, and abiotic factors of the moose (*Alces alces*) population of Isle Royale. *Proc. R. Soc. Lond. B* 271:183-189.
- Wayne, R. K., Gilbert, D. A., Lehman, N., Hansen, K., Eisenhawer, A., Girman, D., Peterson, R. O., Mech, L. D., Gogan, P. J. P., Seal, U. S., and Krumenaker, R. J. 1991. Conservation genetics of the endangered Isle Royale gray wolf. *Conser. Biol.* 5:41-51.
- Whitledge, G. W., and Rabeni, C. F. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analyses. *Can. J. Fish. Aquat. Sci.* 54:2555-2563.
- Wilson, D. S., and Reeder, D.-A. 1993. *Mammals Species of the World*. Washington, D.C.: Smithsonian Institution Press.
- Wilson, E. O. 2002. *The Future of Life*. New York: Knopf.
- Wootton, J. T., Parker, M. S., and Power, M. E. 1996. The effect of disturbance on river food webs. *Science* 273:1558-1560.
- Wright, J. P., Jones, C. G., and Flecker, A. S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96-101.
- Wright, S. J., Gompper, M. E., and DeLeon, B. 1994. Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71:279-294.

## Index

- aggregative response, 241, 244
- allelochemicals
- allomone, 140
  - kairomone, 140
  - synomone, 140
- amygdala, 180-181
- antipredator defenses
- alarm pheromones, 145
  - aposematism, 91, 127-129
  - behavioral, 91, 94-96, 97, 106
    - subterfuge behaviors, 126-127
  - camouflage, 124-126
  - contrast enhancement, 117-119
  - ecological defenses, 84, 264
  - evasion, 91-92
  - fleeing, 269
  - lack of response (immobility) in prey, 170, 268-269
  - predator-induced phenotypic variation, 191
    - ontogenetic constraints, 194-198
    - phylogenetic constraints, 198-201
  - role of learning (*see learning*)
- subterfuge behaviors, 126-127
- trade-offs, 91, 193, 264
- visual ploys, 124-129
- apex predators. *See predator: apex predator*
- assemblage
- comparing assemblages, 346-347
    - Robbins's curves, 348-352
  - definition, 346
  - nature of assemblages, 351
- assemblage control hypothesis, 347.
- See also species assemblage control hypothesis*
  - importance of single versus multiple predators, 357
  - and intraguild predation, 358
  - and species abundance distribution, 357-359
- associative learning. *See also learning*
- role of herbivore-induced plant volatiles, 143
- auditory scene analysis, 87. *See also visual natural scenes*