Exhibit HH

The Rise of the Mesopredator

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Apex predators have experienced catastrophic declines throughout the world as a result of human persecution and habitat loss. These collapses in top predator populations are commonly associated with dramatic increases in the abundance of smaller predators. Known as "mesopredator release," this trophic interaction has been recorded across a range of communities and ecosystems. Mesopredator outbreaks often lead to declining prey populations, sometimes destabilizing communities and driving local extinctions. We present an overview of mesopredator release and illustrate how its underlying concepts can be used to improve predator management in an increasingly fragmented world. We also examine shifts in North American carnivore ranges during the past 200 years and show that 60% of mesopredator ranges have expanded, whereas all apex predator ranges have contracted. The need to understand how best to predict and manage mesopredator release is urgent—mesopredator outbreaks are causing high ecological, economic, and social costs around the world.

Keywords: indirect effects, intraguild predation, mesocarnivore, mesocarnivore release, trophic cascades

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Humans have persecuted apex predators for millennia. From wolves (*Canis lupus*) in Asia, North America, and Europe to jaguars (*Panthera onca*) in the Americas and lions (*Panthera leo*) and wild dogs (*Lycaon pictus*) in Africa, these efforts have resulted in the complete eradication or severe range reduction of large carnivores throughout the world (Gittleman et al. 2001). People try to eradicate apex predators for many reasons, but perhaps the most important motivator is simply that they compete with us for food. In North America, for example, predator control was widely practiced without restraint until the 1970s to increase the availability of wild game for human hunters and to reduce losses of domestic livestock (Sterner and Shumake 2001). In fact, government-sponsored predator control programs are still in place today (Brady 2007). The decimation of wolves and bears (*Ursus* spp.) in North America allowed populations of large game such as elk (*Cervus canadensis*) to flourish (Smith et al. 2003). However, populations of smaller game, such as pronghorn antelope (*Antilocapra americana*), did not always increase after the removal of top predators, and in fact they sometimes declined precipitously (Berger et al. 2008). Such counterintuitive observations have led ecologists to ask whether the persecution of apex predators actually causes some prey populations to decline. Research into these trophic mysteries during the past 20 years has revealed strong links between top predators and smaller "mesopredators" that offer an explanation for many of these unforeseen outcomes.

Traditional food-web ecology has focused on direct interactions among organisms representing three trophic levels. Predators, perched at the top of the food chain, eat prey animals situated one trophic level down, which in turn consume plants, the building blocks of the ecosystem (Hairston et al. 1960). However, real food webs are typically complicated by a network of direct and indirect interactions, by hierarchies among species within trophic levels, and by omnivorous species that simultaneously extend across multiple trophic levels. Such complexities often confound our best efforts to anticipate how wildlife populations and communities will respond to human intervention (Polis and Strong 1996). While mounting evidence suggests that apex predators can benefit prey populations indirectly by suppressing smaller predators, failure to consider this common interaction has caused some conservation efforts to backfire (Rayner et al. 2007) and has even triggered collapses of entire ecosystems (Terborgh et al. 2001, Myers et al. 2007). If we are to better predict the consequences of predator management, it is critical that we understand the dynamics of intraguild relationships among predators.

Here, we present an overview of "mesopredator release," the ecological phenomenon that frequently occurs when top-down control of predators is removed. We begin by defining mesopredator release—what is a mesopredator, exactly, and how do we know when it has been "released"? We discuss the global extent of mesopredator release, its consequences for people and ecosystems, and the trade-offs and limitations of current efforts to manage predators. We then illustrate the association between apex predator declines and mesopredator overabundance using North American terrestrial mam-

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malian carnivores as a case study. We end by identifying key factors and trophic theories that should help predict when mesopredator release will occur and the resulting strength of cascading effects on prey populations.

What is mesopredator release?

The ideas behind mesopredator release can be traced back several decades, when ecologists began observing that the removal of predators resulted in explosions of animal populations released from this control (e.g., Paine 1969, Pacala and Roughgarden 1984). The term "mesopredator release" was coined by Soulé and colleagues (1988) to describe a process whereby mammalian carnivores of intermediate body size were more prevalent in the absence of a larger carnivore, and bird populations were subsequently depressed. We define mesopredator release more broadly, as the expansion in density or distribution, or the change in behavior of a middle-rank predator, resulting from a decline in the density or distribution of an apex predator (Brashares et al. 2010). Although mesopredator release often leads to negative cascading effects on prey species, and is commonly reported in the context of trophic cascade theory (e.g., Berger et al. 2008, Brashares et al. 2010), it is essentially an intraguild interaction among predators.

Our definition addresses the ecological contexts associated with mesopredator release, but one portion of this term remains ambiguous: What exactly is a "meso," or middle-rank, predator? In the hypothetical food chain in figure 1, is the mesopredator a coyote, cat, rat, lizard, or spider? If the wolf is removed from the ecosystem, is the coyote (*Canis latrans*) promoted to apex predator? Some researchers have defined mesopredators as midranking mammalian predators within certain weight ranges (e.g., 1 to 15 kilograms; Buskirk 1999, Gehrt and Clark 2003), but such restrictions are somewhat arbitrary and unrelated to the ecological patterns central to the concept of mesopredator release. If the term is to be rooted in ecological theory, a mesopredator should be defined as any midranking predator in a food web, regardless of its size or taxonomy. Thus, a mesopredator in one ecosystem may be an apex predator in another, and one ecosystem may have several mesopredators (Roemer et al. 2009). Indeed, coyotes function as mesopredators in the Yellowstone ecosystem where wolves have been reintroduced (Berger et al. 2008), but they have ascended to the role of apex predator in other areas of the United States where larger predators have been extirpated (Crooks and Soulé 1999, Roemer et al. 2009). Likewise, feral cats (*Felis catus*) function as mesopredators in many continental ecosystems (Crooks and Soulé 1999) and as apex predators on many islands (Rayner et al. 2007, Bergstrom et al. 2009). Mesopredators are therefore best identified on the basis of characteristics of a given food web rather than on characteristics of an individual species. However, mesopredators promoted to the top of the food chain are not ecologically identical to the larger predators that have been extirpated; it is important to remember that these new apex predators are themselves the beneficiaries of mesopredator release.

Figure 1. What is a mesopredator? In this hypothetical ecosystem, wolves are the apex, or top, predator, followed by a chain of potential mesopredators (coyote, cat, rat, lizard, spider, dragonfly). Original artwork: Piper Smith.

The extent of mesopredator release

Cases of mesopredator release have been reported on all continents except Antarctica, in a wide variety of systems, and at large spatial scales. In a recent review, Brashares and colleagues (2010) found 34 studies that examined mesopredator release in oceanic, freshwater, and terrestrial ecosystems. Cascading negative effects of mesopredator release have been documented for birds, sea turtles, lizards, rodents, marsupials, rabbits, fish, scallops, insects, and ungulates (Brashares et al. 2010). Although several studies found no evidence of mesopredator release following apex predator declines (e.g., Wright et al. 1994, Gehrt and Prange 2007), the weight of evidence suggests that mesopredator release is a common result of apex predator loss throughout the world.

Mesopredator release is often symptomatic of a fundamental ecosystem imbalance. For instance, several recent studies have described mesopredator release in systems where apex predators or mesopredators are exotic species. On many island systems worldwide, feral cats and rats (*Rattus* spp.) are exotic apex predators and mesopredators, respectively (Courchamp et al. 1999, Rayner et al. 2007). Similarly, the American mink (*Mustela vison*) invaded Finnish island archipelagoes when the native top predator, the white-tailed sea eagle (*Haliaeetus albicilla*), declined drastically in the

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1960s. The recent recovery of the sea eagle has reduced mink activity and may reduce mink populations (Salo et al. 2008). In other cases, imbalances occur when native apex predators such as dholes (*Cuon alpinus*) in Asia or wolves in North America are persecuted because they prey on domestic livestock. Numerous studies have highlighted the perverse consequences that can occur from such "nuisance control": the unleashing of even worse nuisances (i.e., mesopredators). For example, control of raccoons (*Procyon lotor*) in Florida to protect sea turtle eggs paradoxically resulted in increased predation on the eggs, because another egg predator, the ghost crab (*Ocypode quadrata*), was released from control by raccoons (Barton 2003).

Ominous accounts of widespread ecosystem collapses resulting from mesopredator release highlight the importance of this emerging problem. Among the first of these accounts was a classic study in the 4300-square-kilometer Lago Guri island system of Venezuela, where some of the islands created by a hydroelectric dam lacked predators. Monkeys exploded in abundance on the predator-free islands, denuding islands of vegetation and causing complete reproductive failure in birds by eating their eggs (Terborgh et al. 1997, 2001). Across sub-Saharan Africa, another primate mesopredator, the olive baboon (*Papio anubis*), has dramatically increased in abundance in areas where lion and leopard populations have been decimated (Brashares et al. 2010). Excessive predation by baboons is exacerbating declines in ungulate populations, and increasingly brazen troops of crop-raiding baboons force families to take children out of school to help guard fields (Brashares et al. 2010). A preliminary literature survey shows that the release of baboons has resulted in widespread conflict with humans and their livestock, pets, and crops. In the Atlantic Ocean, overharvesting of sharks led to population explosions of the cownose ray (*Rhinoptera bonasus*), which in turn reduced bay scallop (*Argopecten irradians*) populations to such low levels that a century-old scallop fishery was recently forced to close (figure 2; Myers et al. 2007). These examples demonstrate the kind of "ecological meltdown" that can occur in the absence of apex predators (Terborgh et al. 2001) and the direct economic and social harm that mesopredator release can cause.

Conservation efforts geared toward controlling exotic species can also be greatly hindered by mesopredator release. The potential for mesopredator release to complicate conservation efforts is particularly well illustrated in the case of islands that are infested by both rats and cats. Modeling efforts (Courchamp et al. 1999, Fan et al. 2005) and recent empirical research (Rayner et al. 2007) suggest that the control of cat populations can result in the release of rat populations and increased net predation on native prey. If control efforts unintentionally catalyze the release of an exotic mesopredator, even the best-intentioned conservation efforts may backfire and place ecosystems in greater jeopardy (Bergstrom et al. 2009).

Disentangling mesopredator release from land-use changes

Mesopredator outbreaks are commonly observed in fragmented habitats, an association that can be credited to three factors. First, apex predators tend to require more area than mesopredators and are therefore more likely to disappear when habitat is lost. Second, large predators are likely to encounter high levels of conflict with humans where fragmentation occurs, leading to higher levels of persecution. Last, fragmentation can add to the resources available to mesopredators, such as pet food, trash, crops, and crop pests, which often accompany development (Crooks and Soulé 1999, Wangchuk 2004). In scenarios in which this improved resource availability is primarily responsible for mesopredator outbreaks, the presence of large predators is even more critical because such top-down regulation is the only constraint on mesopredator abundance. When both top-down and bottom-up constraints on mesopredators' population growth are relaxed, as they most commonly are in fragmented landscapes, the setting is ideal for the explosive growth of mesopredator populations.

A fundamental challenge in demonstrating mesopredator release is ruling out alternative explanations for mesopredator overabundance, such as the habitat changes that often co-occur with the loss of apex predators. Uncertainty surrounding the causal mechanisms that underlie mesopredator outbreaks muddies prescriptions for management. If mesopredators in a given community are not in fact controlled by apex predators, then restoring the "top dogs" to that community may not reduce mesopredator abundance. Unfortunately, studies of mesopredator release often fail to demonstrate causal links between apex predator declines and mesopredator outbreaks. For example, Gehrt and Clark (2003) examined raccoon studies and cited low coyote-caused mortality (< 3%) as evidence that coyotes do not limit raccoon populations, and they concluded that negative spatial relationships between coyote and raccoon numbers more likely reflect differences in habitat selection. Gehrt and Prange (2007) also demonstrated that raccoons did not avoid coyotes in their Illinois study site. Litvaitis and Villafuerte (1996) similarly argued that the negative correlation between numbers of Egyptian mongoose (*Herpestes ichneumon*) and Iberian lynx (*Lynx pardinus*) in Spain resulted from differential habitat use rather than top-down control by lynx, but a subsequent path analysis supports the hypothesis that lynx do indeed control mongoose numbers (Palomares et al. 1998).

In recognition of this paucity of hard evidence for mesopredator release, several recent studies have used radiotelemetry to convincingly demonstrate apex predator control of mesopredators. For example, Crooks and Soulé (1999) showed that coyotes were a major source of mortality for cats in southern California, Berger and Gese (2007) found that wolf predation was a limiting factor for coyotes in the Greater Yellowstone Ecosystem, Helldin and colleagues (2006) showed that lynx (*Lynx lynx*) predation limited red fox (*Vulpes vulpes*) populations in Sweden, and Thompson and Gese (2007)

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determined that coyotes were the main predator and altered the behavior of swift foxes (*Vulpes velox*) in Colorado. Additionally, researchers conducted several experiments in which apex predator numbers were manipulated in replicated treatments and the responses by mesopredators and prey were documented (e.g., Pacala and Roughgarden 1984, Henke and Bryant 1999, Burkepile and Hay 2007, Stallings 2008). These studies show that mesopredator release can occur rapidly and dramatically when apex predators are removed, but an experimental approach is rarely possible at large scales and

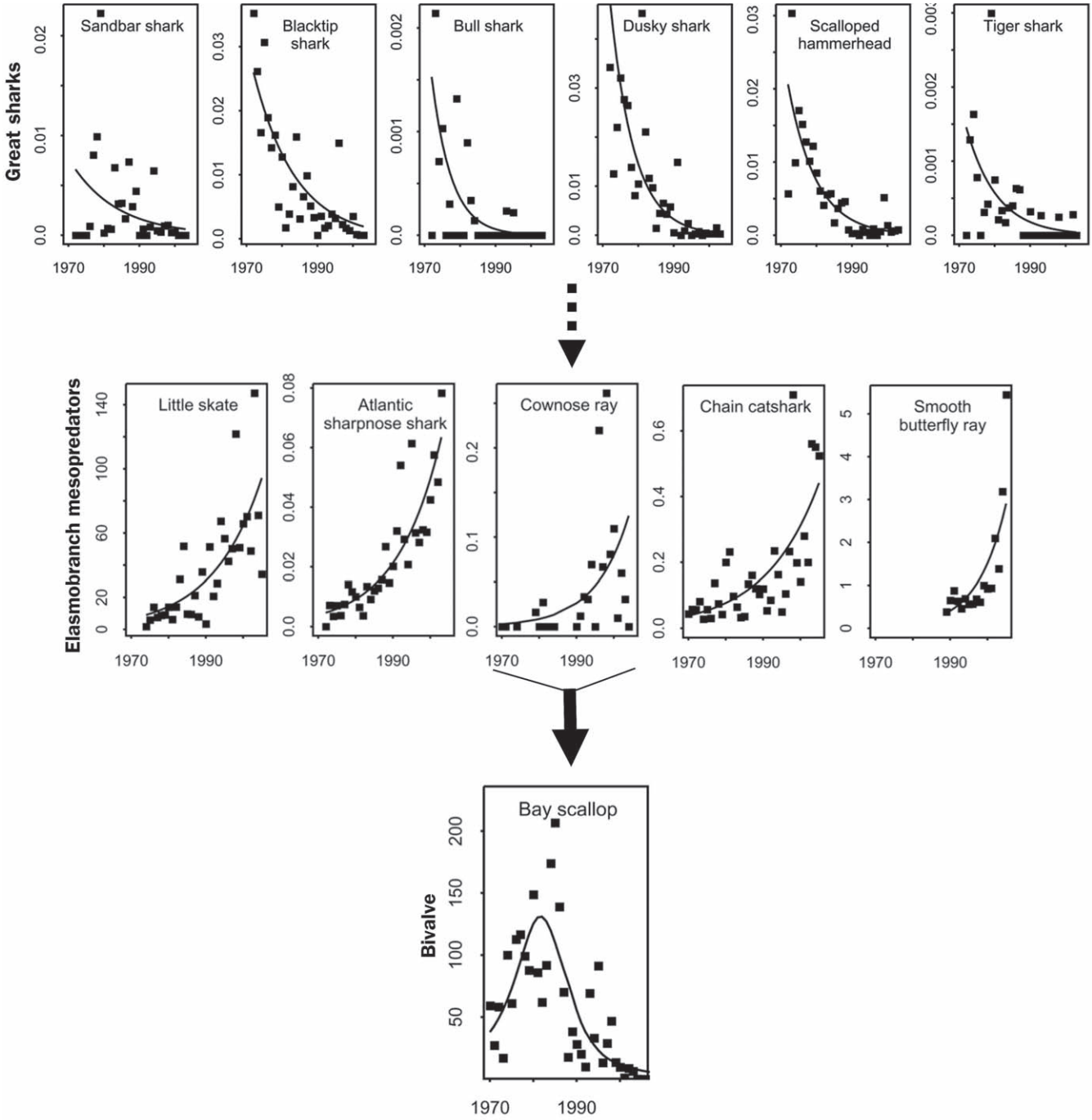

Figure 2. Yearly abundance estimates from surveys of great sharks (top level), elasmobranch (shark, ray, and skate) mesopredators (middle level), and bivalve prey, the bay scallop (bottom level). Adapted from Myers and colleagues (2007) and reprinted with permission from the American Association for the Advancement of Science. Abundance estimates were obtained from a variety of surveys conducted in the Atlantic Ocean from 1950 to 2005. See Myers and colleagues (2007) for survey details and scientific names. The dotted arrow between the top and middle trophic levels represents a loss of mesopredator control following shark declines; the solid arrow between the middle and bottom trophic levels represents increased control of bay scallops by the cownose ray mesopredator following release.

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with large carnivores. However, modeling approaches can be used to parse the relative contributions of bottom-up (habitat and resources) and top-down (apex predator) forces. This approach has been employed nicely in a large-scale study examining the relative influence of apex predators (wolves and lynx) and land-use changes on red fox populations in Sweden (Elmhagen and Rushton 2007).

Trade-offs inherent to predator management

Thus far, we have painted a rather bleak picture of ecosystems decimated by mesopredator outbreaks induced by large predator extirpations. However, predator management is characterized by complex ecological, economic, and social trade-offs. While large predators present many ecological benefits, they can also pose a serious threat to species of conservation concern. For instance, cougars (*Puma concolor*) contributed to the near extinction of endangered Sierra bighorn sheep in the 1990s (*Ovis canadensis sierrae*; Wehausen 1996). Any proposal to protect or reintroduce apex predators must acknowledge the full range of trade-offs involved in predator management.

Ideally, an evaluation of the full expense of mesopredator release would compare the costs of tolerating apex predators with the expense of managing mesopredator outbreaks in their absence. Although previous assessments of predator control programs provide some insight into such expenses, they also illustrate the difficulty in deriving the true economic cost of tolerating versus managing any given predator. For example, Berger (2006) examined a time-series data set of predators killed by federal agents in 17 US states over 60 years (1939–1998); she noted that coyotes, which colonized 11 of the states included in the data set after 1950, consistently constituted 75% to 95% of the animals killed each year. Although these statistics suggest that coyotes were particularly problematic (and indeed coyotes were perceived to be responsible for declines in the sheep industry over this time), the considerable amount of money ($1.6 billion) allocated to predator control efforts did not appear to have a significant impact on trends in sheep production (Berger 2006). These results indicate that such predator control programs probably do not make economic sense, because the benefits to the sheep industry and society as a whole are very likely lower than the costs to taxpayers.

In the face of costly mesopredator control programs, apex predators may offer an "ecosystem service" by providing cheaper and more effective mesopredator control. Rigorous cost-benefit analyses that take into account the ecosystem services of apex predators, as well as the costs associated with tolerating those predators, are sorely lacking. In the few cases in which data exist to compare economic losses from apex predators and the mesopredators they suppress, mesopredators appear to be equally damaging, if not more so. In their comprehensive review of carnivore management and human food production, Baker and colleagues (2008) reported annual monetary losses due to invasive red foxes in Australia as nearly 3.5 times higher than losses attributed to dingoes (*Canis lupus dingo*) and feral dogs (*Canis familiaris*), which suppress fox populations (Glen et al. 2007). Baker and colleagues (2008) also reported that losses of juvenile cattle to golden jackals (*Canis aureus*; 2.8% loss), a mesopredator, are similar to losses of cattle to wolves (< 3% loss) in Israel. The economic impacts of mesopredators should be expected to exceed those of apex predators in any scenario in which mesopredators contribute to the same or to new conflict with humans, but mesopredators occur at higher densities than apex predators and exhibit greater resiliency to control efforts.

Another reason the relative costs of top predator restoration versus mesopredator overabundance are not readily apparent is that economic impacts of mesopredator release often differ among stakeholders. For example, persecution of dholes in Bhutan was intended to protect livestock but led to greater numbers of wild boar (*Sus scrofa*) and to resultant crop devastation that in some cases caused abandonment of agricultural fields (Wangchuk 2004). Similarly, in North America, antelope hunters and sheep ranchers may appreciate the drop in coyote numbers that has accompanied the return of wolves to the intermountain west, whereas elk hunters and cattle ranchers may resent the resurgence of wolf depredation. Interestingly, the majority of financial compensation programs to mitigate human-wildlife conflict in North America are aimed at crop farmers to offset the costs of damage caused by deer (*Odocoileus* spp.; Wagner et al. 1997). This consequence of historic wolf control is not often acknowledged by opponents of predator reintroduction, or even by the farmers themselves. The relative financial losses caused by apex predators versus those caused by mesopredators and the ungulates they suppress often vary across time because of the delayed nature of release, thus making cost-benefit analyses more complex.

In cases where it may appear fiscally advantageous to extirpate apex predators and contend with mesopredator outbreaks, it is important to recognize that such disturbances can reduce the resiliency of ecosystems and lead to financial losses in the future. In the North Atlantic Ocean, for example, overfishing led to the collapse of a valuable cod fishery, but the cod collapse relaxed top-down control of shrimp and crab populations that are even more economically profitable than cod (Frank et al. 2005). Although in this instance decimation of the apex predator appears to have been economically advantageous, such "fishing down the food chain" is usually unsustainable and in time may lead to an ocean filled with little more than jellyfish and zooplankton (Pauly et al. 1998, Jackson 2008). Efforts to preserve or restore apex predators may be costly, but these financial costs may well be offset by the benefits of reduced mesopredator abundance and greater ecosystem resilience. Careful accounting of the full costs and benefits of apex predators and mesopredators will help clarify the impacts of predator management actions on ecosystems, economies, and societies.

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Can humans replace the role of apex predators?

Apex predators may be instrumental in preventing outbreaks of mesopredators and the consequent ecological, financial, and social problems, but significant roadblocks impede large carnivore conservation. Much of their habitat is gone. They sometimes kill people. They often kill animals that people like, such as pets, livestock, and ungulates. Direct lethal control of mesopredators by humans thus appears to be an attractive alternative to apex predator conservation. By controlling mesopredator populations ourselves, could we avoid the costs of mesopredator overabundance, while also avoiding the costs of living with lions, wolves, tigers, bears, and sharks?

Several factors indicate that such management can be problematic. Overabundant mesopredators are often resilient to control programs because they are characterized by high densities, high rates of recruitment, and high rates of dispersal (Palomares et al. 1995). Lethal control can thus be likened to mowing a lawn, in that persecution induces vigorous growth in the mesopredator population. Critics have argued that such control efforts must be intensive (and most likely expensive) to be effective, and that management options that address the disturbances underlying mesopredator overabundance would be more effective (Goodrich and Buskirk 1995).

Why are apex predators more effective than humans at controlling mesopredators? Emerging studies of behavior-mediated interactions indicate that it is exceptionally difficult to replicate the full ecosystem effects of apex predation (Peckarsky et al. 2008). In a review of intraguild predation, Palomares and Caro (1999) noted that interactions between predators result not only in direct killing but also in avoidance behavior and defensive group formation. Fear of predation can therefore have an even stronger impact on food webs than the killing itself (Brown and Kotler 2007). The reintroduction of wolves to the Greater Yellowstone Ecosystem is a particularly compelling example of such behaviorally mediated interactions. Reintroduced wolves reduced elk populations through direct killing, but the extent of the wolves' influence in the ecosystem was greatly increased because of the fear-induced shift in elk behavior. Elk began to avoid the riparian areas they had favored in the absence of wolves and moved to safer areas. As a result, the vegetation recovered along stream banks, sparking the recovery of beaver (*Castor canadensis*) populations (Ripple and Beschta 2004). Likewise, a recent experiment in the coral reefs of the Bahamas showed that large groupers (*Epinephelus striatus*) benefit small reef fish by changing the behavior of smaller groupers (*Cephalopholis* spp.; Stallings 2008). The smaller, fish-eating groupers spent less time foraging and more time hiding in the presence of the larger, invertebrate-eating groupers; reef fish abundance was thus higher in the presence of large groupers solely as a result of the behavioral response of smaller groupers. These examples suggest that replicating the full suite of influences that apex predators exert on mesopredators is likely to be exceptionally challenging, if not impossible.

Can mesopredators replace the role of apex predators?

Since large carnivores are difficult to conserve, and humans are likely to be poor ecological replacements, perhaps mesopredators themselves could fill the role of apex predator. This scenario commonly occurs when an apex predator is fully eradicated and the mesopredator directly below the former apex predator in the trophic hierarchy becomes a replacement (figure 1). Indeed, in a few cases, mesopredator behavior has shifted to more closely resemble the behavior of the former apex predator. For example, coyotes can form larger packs and hunt larger game in the absence of wolves (Gese and Grothe 1995).

If mesopredators can replace the role of apex predators, it is tempting to conclude that their ascendancy is not so problematic after all, from an ecological perspective. However, this line of reasoning is dangerous for two reasons. First, the upgrading of former mesopredators to apex predator status epitomizes the problem of "shifting baselines" (Baum and Myers 2004). When we become accustomed to successive stages of environmental degradation, an intact ecosystem can easily transform into a weedy landscape that harbors few desirable native species. Second, mesopredator populations that increase following the removal of apex predators tend to have fundamentally different relationships with people and ecosystems. While large carnivores generally avoid human-dominated regions, mesopredators can reach high densities in developed areas, increasing the likelihood of disease outbreaks and other conflicts between humans and wildlife. Additionally, large predators tend to have a more restricted and carnivorous diet than mesopredators. Omnivorous mesopredators that consume agricultural plants can reach particularly high densities in modified environments, as baboons and wild boars have. Furthermore, mesopredators should be more efficient than top predators at exploiting a shared resource, or they would not be able to successfully compete for the resource while being persecuted by the larger species (Holt and Polis 1997, Vance-Chalcraft et al. 2007). Thus, mesopredators have the potential to exploit prey resources more thoroughly than top predators do.

The ascendancy of the coyote in North America is an excellent example of the pitfalls mentioned above. The fact that coyotes are now considered top predators throughout much of the United States illustrates the problem of shifting baselines and the promotion of mesopredators to apex status. While coyotes may suppress some mesopredators, they display several classic mesopredator traits themselves: They have an omnivorous, opportunistic diet; tolerate close contact with humans; and flourish despite intense persecution. Because of these traits, coyotes will never fully replace the role of the top predators that once controlled their numbers. The dominance of coyotes across several habitats and the high cost of efforts to control them illustrate that the serial promotion of mesopredators to apex status may be a less effective means of maintaining ecosystem integrity than learning to live with true apex predators and protecting their habitat.

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The question remains, however: How do we learn to live with the original apex predators? Coexistence with predators requires humans to be willing and able to modify their own behavior. For example, in suburban areas of the United States, proper trash management and prohibition of wildlife feeding (whether predators or prey) reduces the likelihood of conflict with scavenging predators such as bears and coyotes (Beckmann and Berger 2003). In rural areas around the world, compensating livestock owners for losses to predation is a commonly used tactic to encourage tolerance of predators. However, these programs can be subject to fraud and provide no incentive for ranchers to take steps that reduce conflict, such as using guard animals or improving pens (Baker et al. 2008). A promising alternative program, community-run insurance, has been pioneered in Bhutan to improve coexistence among livestock owners and snow leopards (Wang and Macdonald 2006). Through self-policing, this program has reduced fraud, and it uses discounted premiums and bonuses as incentives to improve animal husbandry practices (Snow Leopard Trust 2009). A combination of tactics such as educational programs in urban and suburban areas, programs to reduce financial losses in rural areas, and improved habitat management will all be necessary to successfully coexist with large predators in human-modified landscapes.

Case study: North American carnivores

To illustrate changes in the distributions of apex predators and mesopredators over time, we examined historic (from the 18th and 19th centuries) and current range maps for 36 species of terrestrial mammalian carnivores that occur in North America (table 1). Seven of these species can be considered apex predators—the three bear species, two large cats (cougar and jaguar), the largest canid (wolf), and the largest mustelid (wolverine, *Gulo gulo*). Although coyotes and some other carnivores now function as apex predators in many areas, for the analyses presented here, we categorized species on the basis of their historic rather than their current ecological roles. We excluded the red wolf (*Canis rufus*) from our analysis because of the uncertainty regarding its historical distribution and taxonomic status. Shapefiles for most range maps were the same as those used by Laliberte and Ripple (2004) in their analysis of carnivore and ungulate range contractions. While Laliberte and Ripple (2004) focused on predators and prey that had lost more than 20% of their range, here we compare distributional changes of apex predators and mesopredators. Because of the various inaccuracies associated with mapping changes in geographic ranges (Laliberte and Ripple 2004), we use these maps to examine broadscale patterns of change and caution readers against using the maps to infer fine-scale patterns. We conducted our analyses using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California) and calculated percentage changes in species distributions as

$$-100\left(1-\frac{\textit{current range}}{\textit{historic range}}\right).$$

Our analysis of distributional changes indicates that the ranges of apex predators in North America have contracted by 2% to 76%, whereas changes in mesopredator ranges have been far more variable, with expansions of 40% (coyotes) and contractions of nearly 100% (black-footed ferrets; table 1). Overall, 60% of mesopredator ranges have expanded, whereas all apex predator ranges have contracted (table 1). Historically, two to five apex predators occurred in any given location throughout North America, but today they are completely absent from most of the east-central United States and have declined in all areas except British Columbia and Alaska (figure 3a–3c). In fact, some parts of the northern prairies once harbored five apex predator species, but now there are none. In contrast, mesopredator species richness has increased in areas scattered throughout North America (figure 3f). While mesopredator richness has declined in many areas where apex predators have also been extirpated (figure 3i), the ranges of apex predators have on average contracted more than the ranges of mesopredators (42% vs. 3%, respectively).

Taken together, the number of mesopredators per apex predator in North America today is far higher and more spatially variable than it used to be. Historically, the number of mesopredators per top predator never exceeded nine, aside from a mesopredator "hot spot" in central California (figure 3g). Today, there are as many as 17 mesopredators per top predator in some areas (figure 3h). This dramatic change in North America's predator landscape is very likely mirrored around the world, with consequences that we are just beginning to fully understand (Roemer et al. 2009).

Can we predict mesopredator outbreaks?

Because the loss of apex predators may or may not cause mesopredator numbers to increase, the ability to better predict mesopredator responses to the reintroduction or removal of apex predators would greatly enhance the effectiveness of conservation and management efforts. The suppression of mesopredators by apex predators is often (but not always) due to intraguild predation, which is "the killing and eating of species that use similar, often limiting, resources and are thus potential competitors" (Polis et al. 1989). The occurrence of intraguild predation in food webs is the norm rather than the exception (Arim and Marquet 2004), and the unique dynamics that result from the interplay between competition and predation have sparked a rich body of theory over the past decade (e.g., Holt and Polis 1997, Holt and Huxel 2007, Amarasekare 2008). On the basis of these theories, Brashares and colleages (2010) identified two ecosystem characteristics that should strongly influence the probability and severity of mesopredator release: ecosystem productivity and species diversity.

The impact of ecosystem productivity on relationships among predators has been well explored in theoretical studies of intraguild predation (e.g., Holt and Polis 1997, Amarasekare 2008). In low-productivity systems, theory predicts that apex predators should often become extinct even in the absence of human influence, and mesopredators should

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then be regulated by the limited supply of food rather than by predation (Holt and Polis 1997). In high-productivity systems, on the other hand, apex predators should have enough resources to effectively dominate and suppress the mesopredators. These predictions have been supported by several empirical studies. For example, Borer and colleagues (2003) showed that an apex parasitoid dominated citrus fields that produced large numbers of prey, whereas a

Table 1. Distributional changes of extant terrestrial mammalian carnivores in North America.

Type	Family	Species	Common name	Historic range (square kilometers)	Current range (square kilometers)	Range change (percentage)	Mass (kilograms)
Apex predator							
	Canidae	*Canis lupus*	Gray wolf	18,500,519	10,683,329	–42.3	34.9
	Felidae	*Puma concolor*	Cougar	10,964,140	6,954,511	–36.6	48.0
	Felidae	*Panthera onca*	Jaguar	2,410,251	580,713	–75.9	81.2
	Mustelidae	*Gulo gulo*	Wolverine	13,041,287	8,249,518	–36.7	16.3
	Ursidae	*Ursus maritimus*	Polar bear	2,710,851	2,648,163	–2.3	286
	Ursidae	*Ursus americanus*	Black bear	15,929,861	9,630,070	–39.5	111
	Ursidae	*Ursus arctos*	Grizzly bear	11,324,188	5,045,751	–55.4	204
Mesopredator							
	Canidae	*Canis latrans*	Coyote	12,113,121	16,983,670	40.2	11.8
	Canidae	*Vulpes macrotis*	Kit fox	1,535,361	1,773,415	15.5	2.7
	Canidae	*Vulpes vulpes*	Red fox	13,900,681	15,596,352	12.2	5.7
	Canidae	*Urocyon cinereoargenteus*	Gray fox	7,774,945	8,187,349	5.3	4.2
	Canidae	*Urocyon littoralis*	Channel Island fox	824	824	0.0	1.9
	Canidae	*Alopex lagopus*	Arctic fox	5,842,376	5,549,225	–5.0	4.5
	Canidae	*Vulpes velox*	Swift fox	1,777,144	711,213	–60.0	2.8
	Felidae	*Leopardus pardalis*	Ocelot	—	1,195,677	—	8.8
	Felidae	*Puma yagouaroundi*	Jaguarundi	—	757,036	—	8.1
	Felidae	*Leopardus wiedii*	Margay	—	683,843	—	3.7
	Felidae	*Lynx rufus*	Bobcat	10,133,689	9,649,937	–4.8	8.6
	Felidae	*Lynx canadensis*	Lynx	11,123,933	8,097,953	–27.2	8.9
	Mephitidae	*Spilogale gracilis*	Western spotted skunk	3,701,352	3,939,544	6.4	0.6
	Mephitidae	*Spilogale putorius*	Eastern spotted skunk	2,849,469	2,908,993	2.1	0.5
	Mephitidae	*Mephitis mephitis*	Striped skunk	12,034,379	12,133,985	0.8	1.8
	Mephitidae	*Conepatus leuconotus*	American hog-nosed skunk	2,275,234	2,289,963	0.6	3.5
	Mephitidae	*Mephitis macroura*	Hooded skunk	8,224,105	8,187,388	-0.4	1.0
	Mustelidae	*Taxidea taxus*	Badger	7,618,124	8,922,205	17.1	6.1
	Mustelidae	*Mustela nivalis*	Least weasel	10,273,765	11,101,721	8.1	0.05
	Mustelidae	*Mustela erminea*	Ermine	13,665,925	13,844,535	1.3	0.1
	Mustelidae	*Mustela frenata*	Long-tailed weasel	10,397,899	10,376,157	–0.2	0.2
	Mustelidae	*Mustela vison*	American mink	15,021,777	13,197,127	–12.1	0.9
	Mustelidae	*Martes americana*	Marten	9,407,025	7,602,942	–19.2	0.6
	Mustelidae	*Lontra canadensis*	River otter	15,595,641	11,774,876	–24.5	6.2
	Mustelidae	*Martes pennanti*	Fisher	6,493,895	3,475,252	–46.5	2.6
	Mustelidae	*Mustela nigripes*	Black-footed ferret	2,513,508	1,595	–99.9	0.8
	Procyonidae	*Procyon lotor*	Raccoon	9,640,232	11,371,576	18.0	4.4
	Procyonidae	*Nasua narica*	White-nosed coati	1,686,002	1,725,147	2.3	3.8
	Procyonidae	*Bassariscus astutus*	Ringtail	11,188,536	11,417,378	2.0	1.0

Note: Historic range maps were unavailable for the ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), and jaguarundi (*Puma yagouaroundi*). The mass given is for adult individuals (Ernest 2003).

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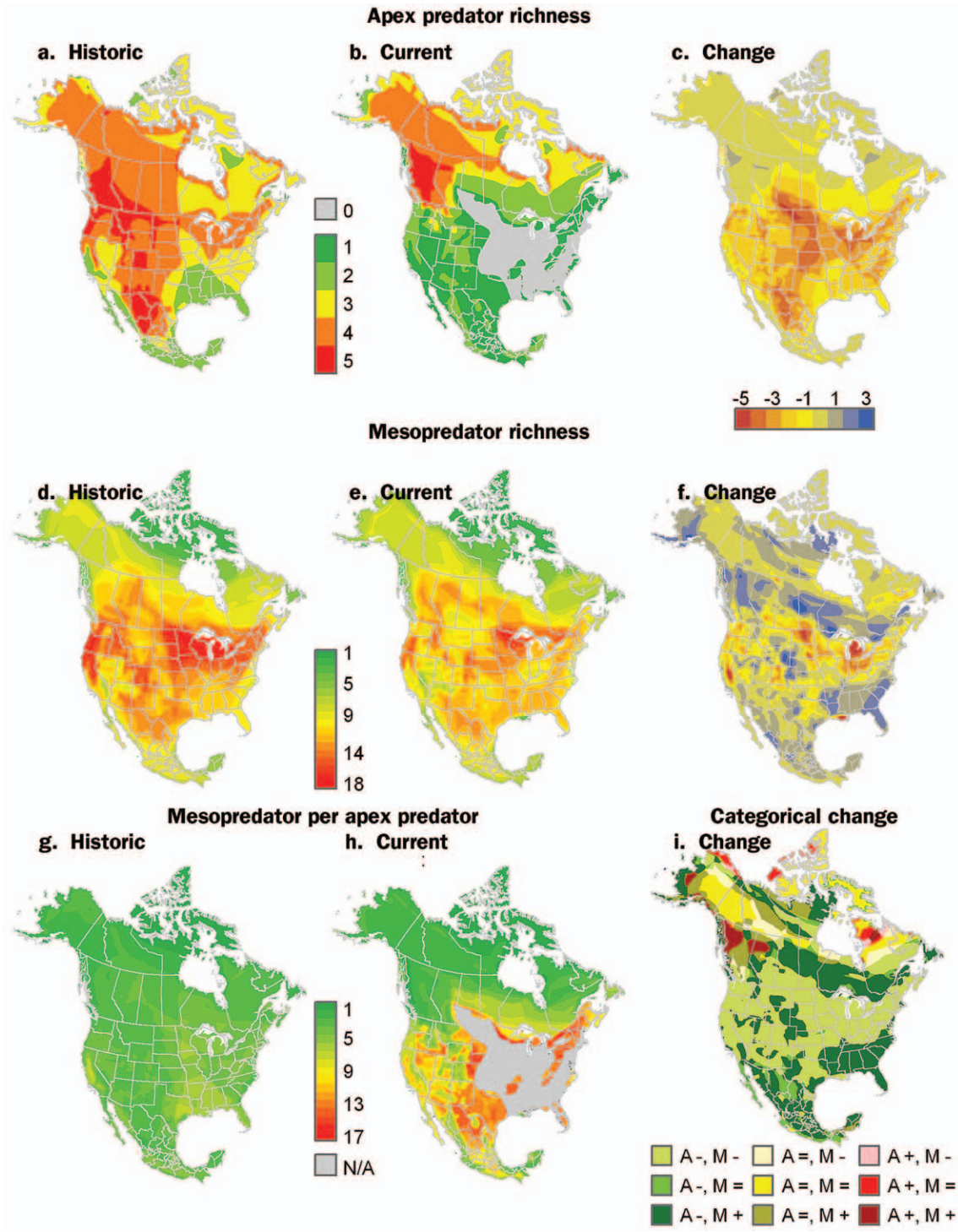

Figure 3. Distributional changes of mammalian carnivores in North America. The 7 apex predator species and 26 mesopredator species used to create the maps are listed in table 1. (Historic maps for three small tropical cats [jaguarundi, ocelot, and margay] were unavailable and these species were excluded from our analyses.) Changes in species richness for apex predators (c) and mesopredators (f) were calculated by subtracting current ranges (a, d) from historic ranges (b, e). Historic (g) and current (h) numbers of mesopredators per apex predator were calculated by dividing historic (d) and current (e) mesopredator richness by historic (a) and current (b) apex predator richness. The map of categorical change (i) shows regions characterized by an increase (+), decrease (–), or no change (=) in apex predator (A) and mesopredator (M) richness. Areas of complete apex predator extirpation are shown in gray (b, h). Historic ranges were digitized from maps based on field sightings from the 18th and 19th centuries (see Laliberte and Ripple [2004] for details). We smoothed the range boundaries using a 5-kilometer mean moving-window analysis to account for uncertainty in the historic distributions.

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"mesoparasitoid" dominated relatively unproductive fields. Similarly, Elmhagen and Rushton (2007) found that wolves and lynx were more effective at suppressing red fox numbers in the more productive regions of Sweden over a 90-year period. Because regions with high productivity are often converted to agriculture, one of the most effective ways to reduce the risk of mesopredator outbreaks should be to increase the suitability of agricultural areas for large carnivores (e.g., through increased connectivity; Kramer-Schadt et al. 2004).

While high productivity should make mesopredator release more likely if the apex predator is removed, high species diversity should have the opposite effect (Brashares et al. 2010). Removal of one apex predator from a system with many apex predators, many mesopredators, and many prey species should not have a strong effect compared with removal from a system dominated by a few species. The dramatic changes due to predator loss that have been observed on relatively depauperate islands support this idea (Terborgh et al. 1997, Rayner et al. 2007). Maintaining the overall diversity of an ecosystem should therefore act to buffer against severe mesopredator outbreaks.

Can we predict the strength of cascading effects?

Global declines in populations of birds, fish, reptiles, rodents, and ungulates have catalyzed concerns about mesopredator release. In fact, the primary goal of mesopredator release studies is usually the detection of these cascading effects (e.g., Wallach et al. 2009). In order to predict the cascading effects of apex predator removal or reintroduction on prey species, the strength and structure of the interactions among apex predators, mesopredators, and prey species must be identified.

Interactions among apex predators, mesopredators, and prey species fall into two basic structural categories: linear and triangular (figure 4). The key distinction between linear and triangular interactions is shared predation: The apex predators and mesopredators rely primarily on a shared prey item in a triangular interaction, whereas the apex predator relies on different prey in a linear interaction. In figure 4, the coyote-fox-bird interaction is linear: Coyotes rarely prey on birds, so there is no direct connection between these species. In contrast, the cat-rat-bird interaction is triangular, because cats prey heavily on both rats and birds.

Because a linear interaction is basically a classic trilevel trophic cascade, predicting the effect of apex predator removal on prey appears to be straightforward: A decline in the apex predator should cause an increase in the mesopredator and a decrease in the prey. However, placing the linear interaction within the context of the greater food web reveals much more complexity. In figure 4a, the coyote-fox-bird interaction is expanded to include other prey items eaten by coyotes and foxes. Coyotes rely primarily on lagomorphs and rodents as prey, and foxes also eat these species. Thus, the food web contains two triangular interactions (coyote-fox-rodent, coyote-fox-lagomorph) in addition to the linear coyote-fox-bird focal interaction. In a controlled experiment in Texas,

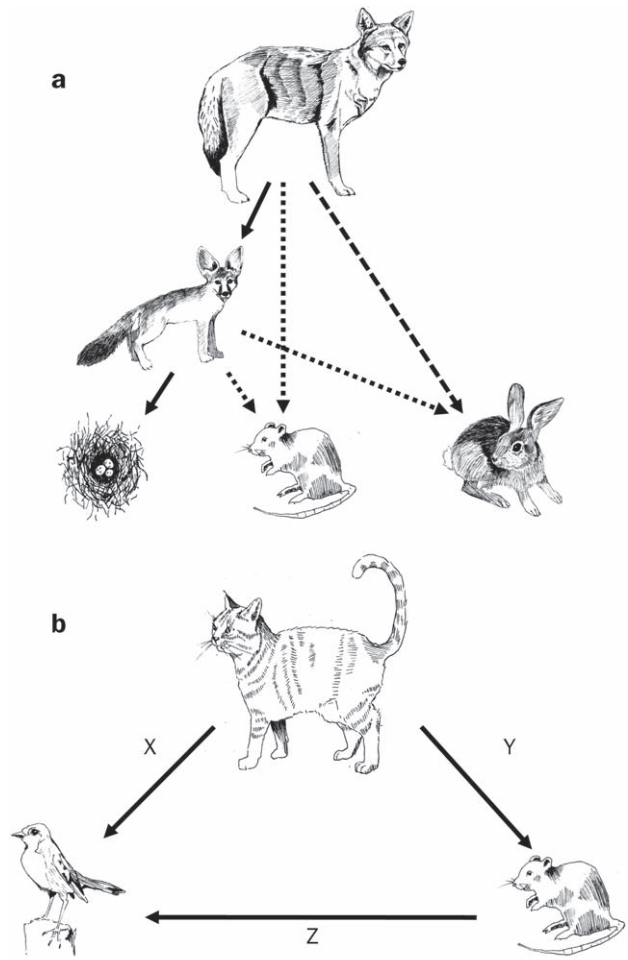

Figure 4. Example of (a) a linear mesopredator interaction (coyote-fox-bird) and (b) a triangular mesopredator interaction (cat-rat-bird). Dotted lines in (a) represent the expanded food web that the linear interaction is part of. In (b), X, Y, and Z represent the strengths of the interactions between species. Original artwork: Piper Smith.

removal of coyotes resulted in much higher mesopredator abundance (bobcats, *Lynx rufus*; skunks; gray foxes, *Urocyon cinereoargenteus*; and badgers, *Taxidea taxus*), but the increase in mesopredators did not lead to the decreased rodent numbers that classic trophic cascade theory would predict (Henke and Bryant 1999). In fact, Ord's kangaroo rat (*Dipodomys ordii*) populations increased and competitively excluded other rodents, leading to higher rodent density in areas from which coyotes were removed. This result suggests that coyotes were more effective predators of kangaroo rats than were the mesopredators that replaced them. Because these mesopredators tend to target other prey species such as birds, insects, and reptiles, it is possible that cascading mesopredator effects would have been detected if other prey had been monitored. This example illustrates that the effects of apex predators and mesopredators will be best understood when placed within the larger food web (Holt and Huxel 2007).

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All other things being equal, shared predation (a triangular interaction) should reduce the cascading effects of mesopredator release. This is because the apex predator limits prey directly in a triangular interaction, and the mesopredator must therefore replace and exceed predation by the apex predator for the cascading effects of apex predator removal to become apparent. Because mesopredators tend to be more efficient than apex predators, they may often be able to achieve these higher predation rates (Vance-Chalcraft et al. 2007). If an apex predator instead obtains its food primarily from other prey (as in the case of a linear interaction), then even small increases in predation by the mesopredator following removal of the apex could be sufficient to enable detection of cascading effects. Brashares and colleagues (2010) found that 60% of documented apex-mesopredator-prey interactions were linear and 40% were triangular (out of 32 studies).

In addition to the structure of the relationships between predators, the strengths of these relationships can aid specific predictions about the influence of apex predators on other trophic levels. In the case of a triangular interaction, the strengths of the three paths that make up the triangle dictate the consequences of losing an apex predator. Consider the cat-rat-bird triangular interaction in figure 4b, where X is the strength of cat control of birds, Y is the strength of cat control of rats, and Z is the strength of rat control of birds. Assume the current populations are stable (i.e., growth rates are 0), and that interaction strengths are measured in terms of the increase in the suppressed species' population growth that would occur if predation were removed. If a cat eradication program is to successfully increase bird numbers, the following condition must be met: $X > Y \times Z$. That is, for the bird population to increase after cats are removed, the direct suppression of birds by cats (X) must be greater than the combined effect of the release of rats (Y) and the suppression of birds by rats (Z). This model can be expanded to include bottom-up forces such as productivity, and these predictions can be tested in real systems using path analysis (cf. Elmhagen and Rushton 2007). Wildlife managers seeking to restore ecosystems would do well to determine the nature and strength of links between apex predators, mesopredators, and prey before attempting costly eradication or reintroduction programs.

Conclusions

The loss of apex predators as a result of persecution and habitat conversion has created outbreaks of mesopredator populations throughout the world. The ecological release of mesopredators has negatively affected our oceans, rivers, forests, and grasslands, placing added strains on prey species that in many cases are already struggling. As songbird populations precipitously decline and other prey populations collapse as a result of, in part, elevated predation rates, the full ecological, social, and economic implications of mesopredator release are beginning to emerge. Restoration of apex predators to areas where they have been extirpated could do much to stem the tide of undesirable consequences of mesopredator release. However, the daunting task of apex predator conservation will require substantial habitat restoration, greater public acceptance of large carnivores, and compromises among the people most directly affected by these predators. Careful application of trophic theory and strategies to balance the trade-offs inherent to the management of apex and mesopredators are urgently needed; reversing and preventing mesopredator release is becoming increasingly difficult and costly as the world's top predators continue to edge toward obliteration.

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