The Ecological Role of the Mammalian Mesocarnivore

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Large mammalian carnivores are ecologically important because relatively few individuals can cause strong predation-driven direct effects or fear-driven indirect effects that can ripple through communities and, ultimately, influence ecosystem structure and function. Most mammalian carnivores are not large, however, but are small to midsized species collectively termed "mesocarnivores." Mesocarnivores are more numerous and more diverse than larger carnivores, and often reside in closer proximity to humans, yet we know little about how they influence communities and ecosystems. In this article we review the ecological role of the mesocarnivore and present examples where mesocarnivores drive community structure and function in roles similar to, or altogether different from, their larger brethren. Together, these examples substantiate the need for an assessment of the ecological role of mammalian carnivores beyond an examination of only the largest species. In particular, we emphasize the need to study the trophic penetrance of mesocarnivores and examine how ecological context modulates their functional role.

Keywords: mesocarnivore, apex predator, indirect effects, trophic cascades, carnivore community ecology

Large mammalian carnivores (species in the order Carnivora) are ecologically important because a few individuals can cause strong predation-driven direct effects or fear-driven indirect effects on communities and ecosystems (Ripple and Beschta 2004, Ray et al. 2005). Nevertheless, most carnivores are neither large nor at the apex of their ecological communities. Rather, they are small and midsized species (< 15 kilograms [kg]), often collectively termed "mesocarnivores." Mesocarnivores far outnumber large carnivores in species richness and are much more diverse in their behavior and ecology. These species can be solitary to highly social, frugivorous to hypercarnivorous, and habitat specialists of climax communities or generalists that live in close proximity to humans. Given their smaller size and ability to thrive in diverse habitats, mesocarnivores are usually more abundant than large carnivores, yet their impact within communities is generally assumed to be relatively minor.

The grace and strength of large carnivores, and the direct threat these animals sometimes pose to humans, may inspire or, alternatively, invoke fear; at the very least, they are charismatic species that warrant our respect. In contrast, mesocarnivores are often viewed as a resource to be harvested—as vermin or agricultural pests whose impacts on human activities are to be mitigated. Further, several elegant studies of the ecological role of large carnivores have been published (e.g., Estes et al. 1998, Berger et al. 2001, Ripple and Beschta 2007), but the ecological role of the mesocarnivore has received comparatively little attention. The irony here is that although we may revere large carnivores more than the "fox in the hen house," our collective actions are causing declines in large carnivores (Laliberte and Ripple 2004) that may often result in mesocarnivores becoming de facto apex predators (Crooks and Soulé 1999). Indeed, where large carnivores have been lost or where mesocarnivores have been introduced, there are important examples of mesocarnivores driving community structure. There are also instances in which mesocarnivores fill ecological roles, such as dispersers of seeds, that large, hypercarnivorous carnivores cannot.

Collectively, these observations suggest that there is a need to assess the ecological role of mammalian carnivores other than the largest species. To establish a baseline for comparison, we first review the known trophic effects of large carnivores and then, within the context of ecological theory, present case studies revealing similar roles played by mesocarnivores in distinct ecological contexts, such as when they are apex predators in insular communities or when they have been introduced. Finally, we speculate on the potentially important but understudied ecological effects of mesocarnivores on plant dispersal and disease dynamics.

Trophic cascades and the primacy of large carnivores as apex predators

Hairston and colleagues (1960) introduced the concept of a trophic cascade that involves direct and indirect interactions

among primary producers and both primary and secondary consumers. In this view, secondary consumers (predators) directly influence the abundance of primary consumers (herbivores), and thereby indirectly influence the abundance of primary producers by reducing the impacts of herbivory. This "green world hypothesis" assumes organisms can be aggregated into discrete trophic levels, and that the level of consumption by an upper tier influences the abundance of the lower tier: in odd-level trophic chains, plants flourish; in even-level trophic chains, they are suppressed (Polis and Strong 1996). Trophic cascades are manifested in two fundamental ways, as either species-level cascades or as community-level cascades (Polis et al. 2000). In species-level cascades, predation by an apex predator influences a particular component of the food chain; that is, one or only a few plant species. In community-level cascades, the composition and or biomass of the entire plant community is altered. Linear food-chain theory is perhaps too simple an abstract of community organization and dynamics, one that realistically represents very few communities because particular constraints are nearly always required for linear trophic relations to exist and precipitate cascades. These constraints include high edibility of the primary producers (e.g., algae), lack of spatial subsidies of alternative energy, and species-depauperate systems with strong recipient-controlled interactions; these conditions may occur in aquatic systems, but they rarely do in terrestrial communities (Polis and Strong 1996, Polis et al. 2000).

An alternative view of food webs is the trophic spectrum, a primarily donor-controlled, species-rich conglomerate characterized by reticulate interactions, spatial subsidies, detrital shunts, temporal heterogeneity, and complex interactions that can include omnivory, cannibalism, interference competition, intraguild predation, apparent competition, and indirect behavioral responses (such as fear-driven foraging decisions) that together influence trophic interactions in extremely complex ways. This complexity would also tend to reduce trophic cascades to a trickle (Polis and Strong 1996, Polis et al. 2000). Although these complexities are more realistic in their characterization of natural communities, there are nonetheless some compelling examples of large mammalian carnivores acting as apex predators and precipitating community-level cascades.

For example, the presence of sea otters (*Enhydra lutris*) in nearshore communities of the North Pacific is critical to maintaining kelp forests. Loss of this 16 to 45 kg predator results in rapid growth of sea urchin (*Stongylocentrotus* spp.) populations, which then overgraze kelp and cause the decline of other kelp-dependent species (Estes et al. 1998). Sea otters are thus a highly interactive top predator in a tritrophic community, whose loss from the system has penetrating effects. Recent declines in northeast Pacific sea otter populations are associated with shifting foraging strategies by a much larger predator, the killer whale (*Orcinus orca*), and are accompanied by declines in kelp forests (Estes et al. 1998). This is a clear example of how a top predator (killer whale) preying on a keystone species (otters) can restructure a linear food chain by changing the number of trophic levels from odd to even, reshuffling a cascade.

The sea otter story is a classic example of a linear food chain in an aquatic system that is predicted by both recipient and more complex, donor-controlled models of food webs (Polis and Strong 1996). Trophic cascades in terrestrial systems are predicted to be less common, but again, in some instances, predation by large mammalian carnivores, including gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and pumas (*Puma concolor*), has altered the foraging behavior and reduced the abundance of large primary consumers. Subsequent reductions in browsing pressure on plant populations then caused large-scale changes in community structure (Berger et al. 2001, Ripple and Beschta 2006, 2007). Wolf predation has been shown to reduce the abundance of elk (*Cervus canadensis*) and other large ungulates and alter their use of habitats, which has caused regeneration of woody browse species (Ripple and Beschta 2005). In the absence of wolves, elk flourish and overgraze woody vegetation, reducing the forage base and the abundance of beaver (*Castor canadensis*), limiting nesting habitat for migratory songbirds, and even negatively affecting hydrological properties of riparian habitats by increasing erosion (Berger et al. 2001, Ripple and Beschta 2004, Beschta and Ripple 2008). The top-down pressure exerted by large mammalian carnivores ripples through the community, varying the quality of terrestrial and aquatic habitats.

An important aspect of the cascading effects of large carnivores is that only a few individuals or social groups can trigger large-scale changes. It was estimated that as few as four killer whales feeding exclusively on sea otters could have caused the observed changes in kelp forest communities (Estes et al. 1998). On the 544-square-kilometer Isle Royale, Michigan, the ecological effects of wolves were caused by just two or three packs (McLaren and Peterson 1994). Thus, it is clear that a relatively small number of large carnivores can directly or indirectly influence multiple trophic levels and precipitate community-level cascades that increase the abundance of primary producers, ultimately modifying habitats upon which other species depend.

Do mesocarnivores play a similar role? In most cases, mesocarnivores are not the top, or apex, predators in an ecosystem, but there are instances, such as on islands or where mesocarnivores have been introduced, where they can fill the role of apex predator and perhaps cause community-level cascades. In these unique circumstances, their collective ecological impact may be similar to and as profound as that of larger carnivores.

Native mesocarnivores in insular communities

In species-rich communities, complex interactions among predators and their prey may emerge (Sih et al. 1998). Predators can act in an additive fashion, such that the summation of their effects on their prey is greater than that of any single predator alone. Alternatively, nonadditive properties may

arise where predators act synergistically to have a cumulative impact on their prey that is greater than the sum of their individual predatory effects. Or in a divergent pattern, predators may interfere with one another, such as when one predator becomes the prey of another (intraguild predation), resulting in less cumulative predatory impact as predator diversity increases (Polis and Holt 1989). Complex interactions among predators and their prey make it difficult to predict what will happen when a single predator is added to or lost from the system.

Simple ecological communities represent systems in which the community effects of mesocarnivores may be more prominent because interactions in these communities may be linear, strong, and lacking compensation. That is, communities are more often simple rather than complex, resulting in linear food chains instead of reticulate webs; there are fewer players, so interspecific interactions are more tightly coupled; and there are few or no species available to fill a predatory role should one become vacant, thus the loss of a single predator has easily observable results. Islands often represent such communities. For example, the terrestrial community of the California Channel Islands contains just two native mammalian carnivores, the island fox (*Urocyon littoralis*; 1.5 to 2.5 kg in weight) and island spotted skunk (*Spilogale gracilis amphiala*; 0.5 to 0.7 kg), and only a few species of rodents. The island fox is endemic to six islands and the island skunk to two, Santa Cruz and Santa Rosa, where the two carnivores are sympatric. Recently, foxes underwent a precipitous decline on these two islands and on a third island, San Miguel, because of the arrival of a novel apex predator, the golden eagle (*Aquila chrysaetos*). Eagles were historically infrequent visitors to the islands, but recently have been able to colonize them by subsisting primarily on introduced pigs (*Sus scrofa*) and deer; these introduced prey formed an abundant resource that supported breeding eagles and allowed them to overexploit the fox (Roemer et al. 2002).

The decline in island foxes triggered a reorganization of the island food webs and revealed the dual ecological roles played by the fox as a superior competitor and midsized apex carnivore. Island foxes are competitively dominant to the island skunk, and on Santa Cruz and Santa Rosa, the declines of foxes led to 39- and 10-fold relative increases in skunks, respectively (Roemer et al. 2002, Jones et al. 2008). Furthermore, on San Miguel, where skunks are absent, the decline in foxes resulted in outbreaks of island deer mice, *Peromyscus maniculatus* (Coonan et al. 2000, Roemer et al. 2001). On a fourth island, San Clemente, a predator exclusion study showed that foxes and introduced feral cats (*Felis catus*) significantly influenced the population dynamics of introduced house mice (*Mus musculus*; Phillips 1999). Collectively, these studies from the Channel Islands show that mesocarnivores can play the role of apex predator by inhibiting competitors and controlling prey populations—especially in systems that lack high species diversity and large-bodied primary consumers. The question remains, however, whether these changes transcend to lower trophic tiers affecting plants. Perennial bushy

lupines (*Lupinus* spp.) are important nitrogen-fixing shrubs of coastal plant communities, and protecting seeds from rodent granivory and seedlings from herbivory significantly improves seedling emergence and recruitment, and increases population growth rates and abundance in mainland forms (Kauffman and Maron 2006). Because the abundance of *P. maniculatus* is higher in lupine-dominated habitats on the Channel Islands, a similar relationship may exist between silver lupine (*Lupinus albifrons*) and deer mice on the Channel Islands, with the plant-granivore interaction mediated by the island fox (figure 1).
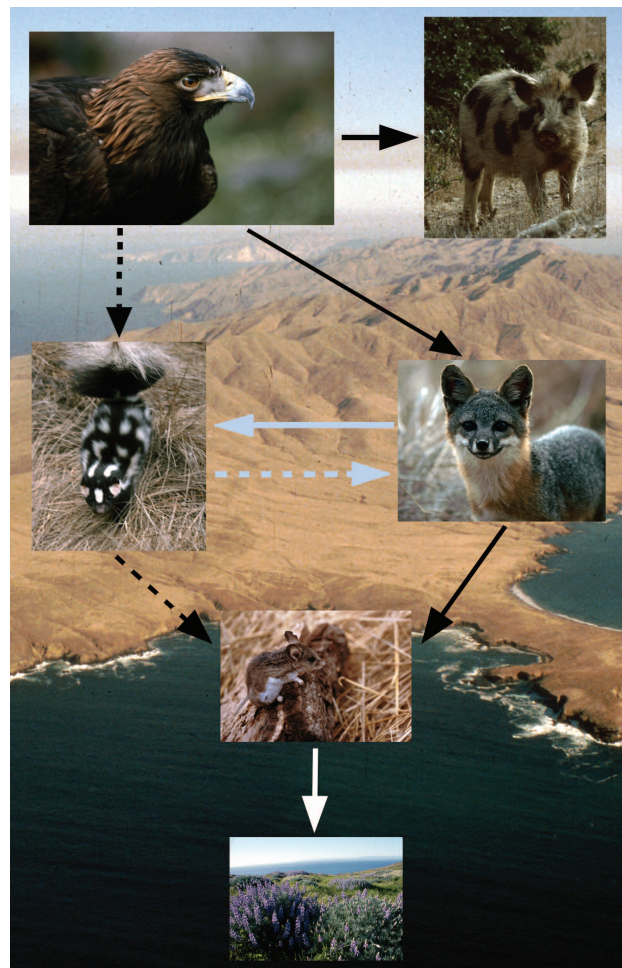
Figure 1. Golden eagles, diurnal birds of prey, were attracted to the California Channel Islands because of the abundance of pigs . Eagles also hunted the diurnal island fox but had minimal impact on the nocturnal skunk. Foxes are competitively superior to skunks, such that when foxes declined, skunk populations increased. Both carnivores feed on deer mice, which, in turn, have increased with the decline in foxes. Mice are significant seed predators of the silver lupine and could affect lupine population dynamics; lupine are important nitrogen-fixing plants that alter soil properties. Black arrows indicate predation, blue arrows indicate competition, and white arrows indicate herbivory. Dashed arrows indicate a reduced effect relative to solid arrows.

Introduced mesocarnivores and their impacts on native communities

Numerous studies have shown that the introduction of a novel midsized carnivore into a naive community can have widespread direct ecological effects (Boitani 2001, Macdonald and Thom 2001, Salo et al. 2007). Introduced midsized carnivores can influence native carnivores through predation and competition, can be supported by introduced prey species, can dramatically limit or even eradicate native prey species, and can influence their geographical distribution. For example, on Baltic Sea islands, birds shifted their selection of breeding sites in the presence of introduced American mink (*Mustela vison*) because of predation risk. In the presence of mink, the islands with the most diverse breeding bird communities were those most isolated, and the removal of mink resulted in a redistribution of birds across the archipelago that was unrelated to distance between islands (Nordström and Korpimäki 2004). Mesocarnivores may also influence communities on much larger spatial scales. The decline of a significant portion of continental Australia's endangered species is linked to the introduction of cats and red foxes (*Vulpes vulpes*), with even larger macropods potentially limited by these carnivores (Banks et al. 2000). Examples of introduced mesocarnivores having important ecological impacts are available from virtually all families of terrestrial Carnivora that contain small to midsized species (Boitani 2001, Macdonald and Thom 2001).

Mesocarnivore response, facilitation, and disruption of nutrient and material subsidies

Although the direct effects of introduced or native mesocarnivores are important, more ecologically intriguing are the indirect effects that both influence and are influenced by mesocarnivores—effects that can occur over large areas, transcend ecosystems, and influence ecosystem process. Once again, coastal regions and islands are ripe areas for elucidation. Because of the land-sea interface, coastal regions are often subsidized by allochthonous inputs of organic materials and nutrients from the sea; in these instances, subsidies are predicted to increase mesocarnivore abundance (Rose and Polis 1998). Inputs averaging 27.9 kg per year per meter (m) of shoreline were documented along the Baja California coast, and caused an increased abundance of invertebrates and vertebrates, including higher densities of coyotes (*Canis latrans*), compared with inland locales (Rose and Polis 1998). Rose and Polis (1998) suggested that as many as 14 species of mammalian carnivores may occur at higher densities in coastal regions around the world, and that enhanced densities of mammalian carnivores in coastal regions may be globally common. Mesocarnivores in coastal regions occur at higher densities and exhibit more social flexibility, as evidenced by smaller home ranges and greater home range overlap in coastal areas of high prey density, compared with inland areas of low prey density (Eide et al. 2004). The direct and indirect ecological effects of heightened densities of coastal carnivores have received little attention.

Perhaps more fascinating is whether mesocarnivores can establish linkages among ecological communities by directly facilitating subsidy inputs. River otters (*Lontra canadensis*; 5 to 14 kg) may act as apex predators and precipitate trophic cascades among fishes and invertebrates in freshwater aquatic systems (Gittleman and Gompper 2005), but they may also import nutrients from marine to adjacent terrestrial ecosystems by depositing spraints along the shore (Ben-David et al. 2005, Crait and Ben-David 2007). Areas where otters formed latrines had higher levels of nitrogen and phosphorous than randomly selected sites, and apparently contributed to increasing habitat heterogeneity along the shoreline (Ben-David et al. 2005). Much as grizzly bears facilitate the movement of nitrogen and other nutrients from marine to terrestrial ecosystems (Gende et al. 2002), and killer whales link pelagic and nearshore marine communities (Estes et al. 1998), otters may have the potential to link aquatic and terrestrial communities.

Even more convincing evidence shows that mesocarnivores introduced to islands have the potential to thwart subsidy inputs, resulting in a complete reorganization of island communities. Arctic foxes (*Alopex lagopus*) introduced to the Aleutian Islands caused a dramatic shift in plant community structure and productivity, compared with islands not subject to fox predation (Croll et al. 2005, Maron et al. 2006). Foxes reduced seabird populations and concomitantly reduced average guano deposition by more than 60-fold; this altered nutrient input from oceanic (allochthonous) to terrestrial (autochthonous) and influenced soil fertility by reducing levels of both nitrogen and phosphorous. This change in soil fertility influenced plant abundance and productivity and transformed the floral community from grassland to maritime tundra (figure 2). Thus, mesocarnivores can respond to, facilitate, and thwart subsidy inputs.

Bottom-up and top-down control in complex communities with mesocarnivores

Islands represent relatively simple communities, and when predators are introduced, perturbations to the system may be pronounced and easily observed. Studies of more complex communities show that mesocarnivores have strong effects on their prey species, but their impact on other aspects of the community is less obvious, and bottom-up control of prey abundance may limit the potential for strong top-down indirect effects (e.g., Jedrzejewska and Jedrzejewski 1998). In at least one example, the exclusion of mesocarnivores (primarily lynx, *Lynx canadensis*) resulted in higher numbers of their prey (snowshoe hare, *Lepus americanus*), but little or no change in plant biomass or community structure (Sinclair et al. 2000). Those few studies that have examined the broader ecological role of mesocarnivores have shown that the important question is not whether trophic cascades occur, but how strong these indirect effects are, how temporally variable they are, and how important they are relative to bottom-up effects.
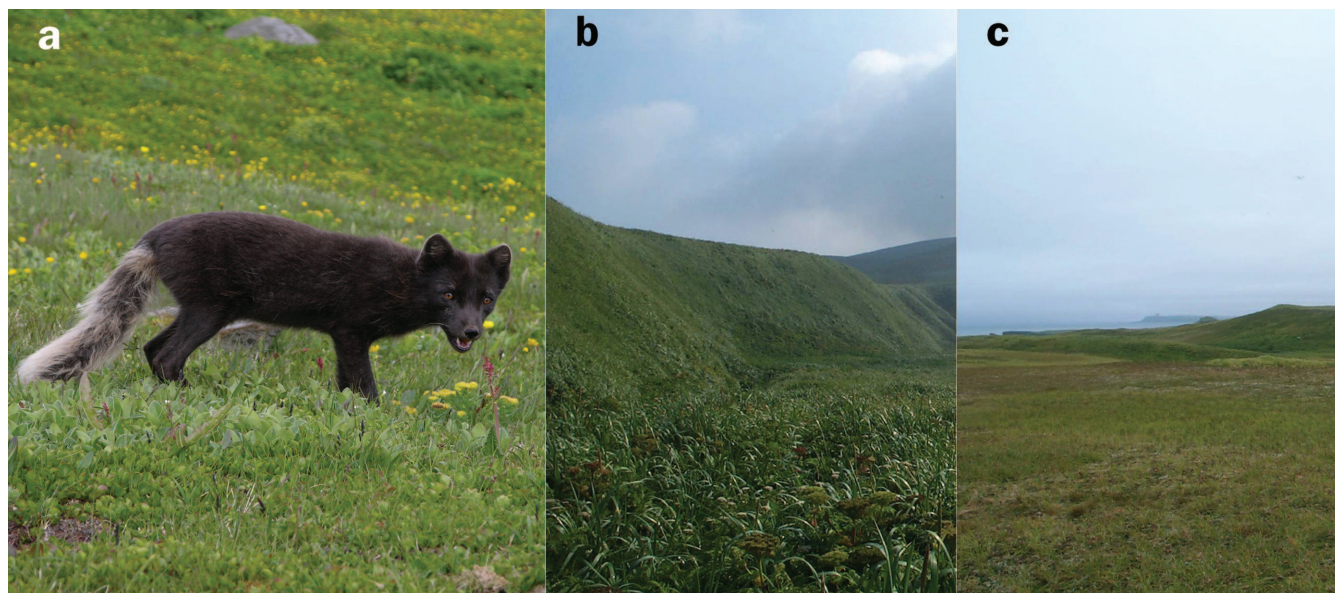
Figure 2. Arctic foxes (a) introduced to islands in the Aleutian archipelago decimated seabird populations and altered nutrient cycles. On fox-free islands, nutrient input was allochthonous and a result of seabird-derived guano that produced lush grasslands (b). Once foxes were introduced and seabird colonies became reduced or eradicated, nutrient input became autochthonous, soil nitrogen and phosphorous levels declined, and habitat shifted to maritime tundra (c). Thus, the presence of Arctic foxes directly influenced seabird populations and indirectly influenced island vegetation by altering the origin of nutrient inputs. Photographs: Courtesy of Michael Kam (a) and John Maron (b and c).

Perhaps the most insightful work to date comes from comparisons of sites with and without mesocarnivores. In Finland, exclosures in boreal grasslands that reduced predation by foxes, mustelids, and birds of prey resulted in major increases in vole (*Microtus agrestis* and *Microtus rossiaemeridionalis*) densities, which in turn increased the cover of annuals and biennials and decreased the cover of short grasses (Norrdahl et al. 2002). Similarly, in Norway, predator-intact (primarily mustelids) habitats had gray-sided vole (*Clethrionomys rufocanus*) densities and plant damage up to five times lower than predator-free habitats (Hambäck et al. 2004). However, both studies found that the impact of these indirect effects depended on plant community composition as well as on season. In winter, the exclusion of mesopredators and the resulting high numbers of voles caused major reductions in plant biomass. Nevertheless, in the boreal grasslands, the long-term impact of this biomass decline was minimal because abiotic factors such as ice and frozen ground protected most herbaceous plants from herbivores, and voles starved before these unavailable plant species were affected (Norrdahl et al. 2002). In the more woody, scrubland community, winter did not provide a temporal refugium for woody species, and so stronger indirect effects persisted; the cover of shrubs was reduced up to 50% in mesocarnivore-free habitats compared with predator-intact sites (Hambäck et al. 2004).

Studies in northern Chile also show the need for considering a temporal component when assessing the ecological role of mesocarnivores. In Parque Nacional Bosque Fray Jorge, the top mammalian predator is the culpeo fox (*Lycalopex culpaeus*; 4 to 11 kg). Long-term examinations of predators, their small mammal prey, and the plant community have shown that temporal variability in abiotic factors strongly influences the driving role of predators (Jaksic et al. 1997, Meserve et al. 2003). Exclusion of predators from study plots of semiarid thorn scrub resulted in greater densities of some important rodent species, with associated effects on some plant species. These effects, however, played out against a backdrop of community dynamics that was primarily resource driven. Top-down effects were lost during dry years when predator abundance was too low to have an impact on the rodent populations. Moreover, rodent numbers were more profoundly affected by El Niño–driven years of high rainfall than by predation (Gutiérrez et al. 1997, Jaksic et al. 1997, Meserve et al. 2003), as appears to be true of rodent populations in many arid and semiarid systems (Holmgren et al. 2006). Thus, the important insight of these Chilean studies is that the potential for midsized carnivores to cause trophic cascades is mediated by stronger abiotic factors that vary resource abundance over time (Meserve et al. 2003).

Intraguild predation and the influence of carnivore body size on ecological role

In much of the world, mesocarnivores are now apex predators in their communities. This widespread ascendancy of mesocarnivores to the role of apex predator is a relatively recent phenomenon engendered by anthropogenically driven extinctions and range contractions of large carnivores (Laliberte and Ripple 2004). It might be expected that these more generalized species would have a lesser, or at least a more diffuse, impact within a trophic web than do larger species.

However, mesocarnivore numbers are likely to increase substantially in the absence of larger carnivores, owing to a reduction in both exploitative and interference competition, including its most extreme form, intraguild predation (IGP).

IGP occurs when at least two predators compete for shared prey and one predator, usually the larger, kills its smaller competitor (Polis et al. 1989, Donadio and Buskirk 2006, Vance-Chalcraft et al. 2007). The effects of IGP on prey populations are varied. In communities in which IGP can be mutual (i.e., with both predators reciprocally practicing IGP), an increase in predator diversity will result in prey release. However, if IGP is unidirectional, as is generally the case among mammalian carnivores, and the smaller predator is a better exploitative competitor, prey populations will typically be enhanced with the addition of a top predator, and suppressed with the addition of a smaller or intermediate-sized predator (Vance-Chalcraft et al. 2007). For example, in the Yellowstone ecosystem, wolves kill coyotes and influence their distribution across the landscape; where wolf abundance is low and coyote abundance is high, pronghorn fawn (*Antilocapra americana*) survival is drastically reduced (Berger et al. 2008).

Although IGP in carnivores has received considerable attention (Palomares and Caro 1999, Donadio and Buskirk 2006), how it mediates mescarnivore competition and the relative abundance of competing mesocarnivores, as well as how its effect is manifested at lower trophic levels, has been less well studied. Because IGP within the Carnivora typically involves a larger apex predator preying upon smaller mesocarnivores, the removal of apex predators is likely to result in a release of one or more mesocarnivores. This can produce a variety of outcomes, depending on the ecological role of the released species. If the released species is largely carnivorous, its impact will most likely be felt directly by its prey and other competing mesocarnivores that may succumb to IGP. For example, the coyote is a relatively large mesocarnivore with a mostly carnivorous diet. In southern California, the loss of wolves allowed coyotes to assume the role of apex predator, but only in habitat patches large enough to support them (Crooks and Soulé 1999). The presence of coyotes inhibits the use of these larger habitat patches by the smaller predators that they kill (e.g., domestic cats; Virginia opossum, *Didelphis virginia;* raccoon, *Procyon lotor*); where coyotes are absent, these other mesocarnivores become important nest predators causing declines in songbird populations (Crooks and Soulé 1999). Thus, coyotes, either directly, through IGP, or indirectly, through the fear of IGP, influence the abundance and distribution of mesocarnivores, which can enhance songbird populations in southern California, much as the presence of wolves and grizzly bears reduces herbivory by ungulates on riparian plants, enhancing nesting habitat for migrant songbirds in Wyoming (Berger et al. 2001).

Alternatively, if the released mesocarnivore is more frugivorous, its impact may be felt directly by the plant community. For instance, in Spain, frugivorous passerines, corvids, and medium-sized carnivorous mammals (red foxes; Eurasian badgers, *Meles meles*; and stone martens, *Martes foina*) are known to be seed dispersers of a common fleshy-fruited tree, *Prunus mahaleb.* Birds tended to disperse seeds short distances (< 250 m), whereas mesocarnivores moved seeds as far as 1 kilometer, with most seeds dispersed between 650 and 700 m (Jordano et al. 2007). Mesocarnivores deposited more of their seeds in open habitats, where seed germination rates are predicted to be higher, and were responsible for the greatest proportion of immigrants into adjacent tree populations, based on estimates of gene flow among trees (Jordano et al. 2007). Because most large carnivores are hypercarnivorous, their role in influencing plant recruitment would be indirect, in the taking of seed predators, rather than direct, in the case of these European mesocarnivores. Loss of mesocarnivores from such a system could seriously affect gene flow and tree recruitment rates (Guimaräes et al. 2008).

Even relatively carnivorous mesocarnivores may shape plant communities indirectly through predation on seed predators. Many seed predators are granivorous rodents that hoard cached seeds (larder hoard) or disperse seeds in numerous caches (scatter hoard). For example, in Neotropical forests, the Central American agouti (*Dasyprocta punctata*) and other rodents in the family Dasyproctidae are primary predators of large-bodied seeds, removing seeds from under the parent tree and burying them elsewhere for later harvest. These rodents are seed predators whose abundance influences seed recruitment and seedling regeneration (Asquith et al. 1997, DeMattia et al. 2004). Yet the seed predator can become a seed disperser when the memory of a seed burial site is lost, as happens when the rodent responsible for the burial dies, which increases both seed and seedling survival. Mesocarnivores such as ocelots (*Leopardus pardalis*) are major predators of dasyproctids and may be a primary driver of the abundance of large-bodied seed predators (Moreno et al. 2006). Mesocarnivores may therefore indirectly influence forest plant regeneration by directly influencing the population dynamics of mammalian seed predators and thus the fate of their cached seeds. Such a mechanism could be widespread, occurring wherever there are important seed predators that are themselves the prey of mammalian carnivores.

Importantly, large apex carnivores are unlikely to play either the role of seed disperser or hunter of seed predators simply because of their size. The diets of mammalian carnivores are a result of two primary processes: net energy gain and the energy expended to capture and subdue prey (Carbone et al. 1999, 2007). These two forces constrain food choice in carnivores. In the case of smaller carnivores, those less than 15 to 20 kg, an omnivorous diet of small vertebrate prey, invertebrate prey, and plant material can meet their relatively low absolute energetic demands. When carnivores reach body sizes above this threshold (> 15 to 20 kg), the energy expended to catch sufficient small prey to sustain their larger body mass exceeds the caloric return, so carnivores must switch to large vertebrate prey (Carbone et al. 1999). To do so, their skulls, jaws, and teeth are modified to handle greater stresses incurred in killing prey their own size or larger (Van Valkenburgh 2007). Because large carnivores

cannot meet their energetic needs with the diet of a meso-carnivore, they are also unable to fill the unique ecological roles of some smaller carnivores.

Revenge of the mesocarnivores?

Midsized mesocarnivores and large carnivores may compete for resources, and this is the primary explanation for the extensive IGP observed among the Carnivora (Palomares and Caro 1999, Donadio and Buskirk 2006). However, the negative top-down effects of large carnivores on mesocarnivores could be mediated by the role mesocarnivores may play as reservoirs of pathogens that harm large carnivores. The most important diseases of carnivores are caused by generalist pathogens (in particular, parvo-, rabies, and distemper viruses; PRD); numerous carnivore taxa are highly susceptible to these microparasites, and the potential for cross-species transmission, or spillover, is high (e.g., Nel et al. 1997, Kauhala and Holmala 2006). While viral transmission can potentially spill between carnivore species irrespective of body size, the high densities of mesocarnivore species mean that these smaller species are more likely to act as reservoirs for pathogens that occasionally spill over into populations of larger carnivores, rather than vice versa. Depending on viral strain and host competency, as well as intra- and interspecific contact rates, the impact of these spillover events can be limited to just a few individuals, or may lead to large-scale epidemics. For instance, spillover of PRD has been implicated as a causal agent in the population declines of African lions (*Panthera leo*), gray wolves, African hunting dogs (*Lycaon pictus*), and Ethiopian wolves (*Canis simiensis*) (Funk et al. 2001, Woodroffe et al. 2004). In most cases, such spillover derives from viruses enzootic in domestic dog (*Canis familiaris*) populations. However, PRD and several other important parasites of carnivores may be maintained in native mesocarnivores independent of maintenance in domestic carnivores (e.g., Guerra et al. 2003, Sabeta et al. 2007). Presumably, sylvatic maintenance, spread, and spillover risk associated with these pathogens are driven in part by the high population densities attained by mesocarnivores (Smith et al. 2002, Gordon et al. 2004).

The extent to which the spillover of pathogens from mesocarnivores may result in declines in large carnivores, which, in turn, precipitate community-level changes is relatively unstudied. However, two studies are suggestive of the need for additional attention. First, following the introduction of canine parvovirus from dogs into the Isle Royale wolf population, wolf numbers plummeted, precipitating a switch from top-down to bottom-up regulation of the moose (*Alces alces*) population (Wilmers et al. 2006). Similarly, some lion populations may be regulated by disease, including canine distemper transmitted from dogs (Kissui and Packer 2004). This may result in changes in populations of the prey of lions (Sinclair et al. 2007), which could possibly induce changes at lower trophic levels. Where native mesocarnivores act as reservoir populations for pathogens that limit large carnivore populations, mesocarnivores may indirectly influence some of the top-down processes attributed solely to apex carnivores.

Conclusions

Earlier important work identified the interactions between large and midsize carnivores and the potential ecological ramifications of processes like "mesopredator release" (e.g., Crooks and Soulé 1999, Berger et al. 2008), yet the role of the mammalian mesocarnivore may be far richer than previously considered. The available theoretical and empirical data suggest that in many cases, mesocarnivores may be fundamentally important drivers of ecosystem function, structure, or dynamics. Their impact can be especially profound in three scenarios: (1) when larger carnivores are absent, (2) on island ecosystems or mainland localities where community composition is relatively simple, and (3) where they represent nonnative introductions. Further, mesocarnivores may thwart nutrient subsidies, completely altering floral communities, or potentially facilitate nutrient flows linking adjacent ecosystems; they can drive native species to extinction and cause significant redistributions of their prey; and they may occupy unique roles that cannot be filled by larger-bodied carnivores, such as when they are direct dispersers of seeds or predators of important seed dispersers. They also may mediate the effects of large carnivores when they are reservoirs for pathogens that limit large carnivore populations. In different ecological contexts, their role may transcend trophic levels to influence primary producers, or it may not—it is clear that like any other organism, their particular role and its ecological effect are the result of complex interactions with both biotic and abiotic components of their communities.

Most trophic studies involving mesocarnivores have been carried out within simplified carnivore communities (i.e., on islands or where large carnivores are absent) in which predator diversity is low and there is reduced or no redundancy. Unlike the modern East African Serengeti or the North American Pleistocene, where there are or were multiple apex predators as well as mesocarnivores, most modern temperate ecosystems include only one or two apex predators (Van Valkenburgh 1989, Van Valkenburgh and Hertel 1998, Sinclair et al. 2003). Diverse apex predator guilds are characterized by strong interactions (competition, kleptoparasitism, IGP) among species that very likely limit the dominance of any single species, resulting in more diffuse effects on mesocarnivores, and overall resilience and stability within the predator community (e.g., see Worm et al. 2006). The simplification of many of our continental carnivore faunas has rendered them more similar to those of islands in which there are very few players and the elimination or expansion of one can have strong ecosystem-level effects. Because mesocarnivores are less vulnerable to extinction than larger carnivores (Purvis et al. 2000), their ascension to apex predator status in various communities is likely to become more common, and thus a renewed effort is needed to understand the dynamics and community-level interactions of these species.

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