Ecological and Conservation Implications of Mesopredator Release

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Human knowledge of the ability of predators to regulate prey goes back at least 10,000 years, when cats were domesticated to control rodent pests in Syria and Turkey. However, our appreciation of the ability of predators to regulate other predators and the importance of these interactions for community structure is much more recent. Although ecological narratives (e.g., Leopold 1949) and studies of pest control in agricultural systems have long considered interactions between predators to be important to the dynamics of communities, the impact of top predator removal on intermediate predators was seldom considered empirically before the 1980s (see Terborgh and Winter 1980; Wilcove 1985). During this period, growing interest and concern about habitat fragmentation, the troubled status of large carnivores, and the apparent increase and spread of smaller predators led to a growth in studies examining the ecological consequences of top predator decline that continues today. A review of recent literature shows that the release of intermediate predators from top-down control is a critical component of many, though not all, trophic cascades (e.g., Polis et al. 2000; Table 13.1). In fact, over the last 15 years a multitude of studies from both terrestrial and aquatic systems around the world have examined the causes and consequences of what Hollywood might call *The Rise of the Mesopredator.*

Table 13.1. Characteristics of studies that have examined mesopredator release. Apex predator, mesopredator, and prey species of interest are shown, in parentheses if the species was not studied directly.

Reference	Location	Continent	Apex	Mesopredator	Prey	Method	Scale	Shape
l et al. (1995)	Montana	North America	Coyote	Red fox	Ducks	o	m	l
ton (2005)	Florida	North America	Raccoon	Crab	Sea turtle eggs	c	s	t
ger et al. (2008)	Wyoming	North America	Wolf	Coyote	Pronghorn	o	m	l
shares, this chapter	Africa	Africa	Lion	Baboon	Ungulates	o	l	t
rkepile and Hay (2007)	Florida Keys	Atlantic Ocean	Fish	Gastropod	Coral	c	s	l
tling and Burt (1995)★	Australia	Australia	Dingo	Red fox	(Unspecified)	o	l	l
ooks and Soulé (1999)	California	North America	Coyote	Cat	Birds and lizards	o	m	l
nhagen and Rushton (2007)	Sweden	Europe	Wolf, lynx	Red fox	(Hares, grouse)	o	l	t
es et al. (1998)	British Columbia and Alaska coast	Pacific Ocean	(Killer whale)	Sea otter	Sea urchin	o	l	l
ank et al. (2005)	Scotian Shelf	Atlantic Ocean	Cod	Shrimp, crab	Zooplankton	o	l	t
ehrt and Prange (2007)★	Illinois	North America	Coyote	Raccoon	(Unspecified)	o	s	l
elldin et al. (2006)	Sweden	Europe	Lynx	Red fox	(Unspecified but probably shared)	o	m	t
enke and Bryant (1999)	Texas	North America	Coyote	Badger, bobcat, gray fox	Rodents	o	m	t
hnson et al. (2007)	Australia	Australia	Dingo	Red fox	Marsupials	o	l	t
oyd (2007)★	South Africa	Africa	(Jackal, caracal)	(Cat, badger, fox, mongoose)	Birds	o	l	l
aezono et al. (2005)	Japan	Asia	Bass, bluegill	Crayfish	Invertebrates	c	s	l
laina and Jackson (2003)	Kenya	Africa	Dog, leopard, lion	(Mongoose, civet, others)	Songbirds	o	m	l
yers et al. (2007)	Eastern U.S. coast	Atlantic Ocean	Sharks	Cownose ray	Bay scallop	o	l	l

Study	Region	Location	Apex predator	Mesopredator	Focal prey	Method	Scale	Shape
Pacala and Roughgarden (1984)	North America	Caribbean island	Lizard	Spider	Insects	e	s	t
Palomares et al. (1995)	Europe	Spain	Lynx	Mongoose	Rabbit	o	m	t
Polis and McCormick (1986)	North America	California	Scorpions	Spiders and solpugids	Arthropods	e	s	t
Rayner et al. (2007)	Australia	New Zealand	(Cat)	(Rat)	Petrel	o	s	t
Rogers and Caro (1998)	North America	Michigan	Coyote	Raccoon	Song sparrow	o	s	l
Salo et al. (2008)	Europe	Finland	Sea eagle	American mink	(Birds, voles, amphibians)	o	m	l
Schmidt (2003)	North America	Illinois	(Coyote)	Raccoon	Birds	o	l	l
Schoener and Spiller (1987)	North America	Bahamas	Lizard	Spider	Insects	e	s	t
Sieving (1992)	North America	Panama	(Jaguar, eagle)	Monkeys, pigs, others	Birds	o	s	l
Soulé et al. (1988)	North America	California	Coyote	Gray fox	Birds	o	m	l
Sovada et al. (1995)	North America	North and South Dakota	Coyote	Red fox	Ducks	o	l	l
Stallings (2008)	North America	Bahamas	Nassau grouper	Smaller groupers	Other reef fish	e	s	l
Terborgh et al. (1997a)	South America	Venezuela	(Unspecified)	Monkeys	Birds	o	l	l
Wangchuk (2004)	Asia	Bhutan	Wild dog	Wild boar	(Unspecified)	o	l	l
Wilcove (1985)	North America	Eastern U.S.	(Mountain lion, bobcat)	(Cat, raccoon, opossum, others)	Birds	o	l	l
Wright et al. (1994)*	North America	Panama	Puma, jaguar	Mid-sized mammals	Small to mid-sized mammals	o	l	t

*Results from these studies are not interpreted by their authors as supporting the release hypothesis).

Method: e = experimental; o = observational. Studies were considered to be experimental if apex predators were reduced or excluded from replicated areas, and mesopredator and prey populations were monitored on experimental and control plots. Scale: s = small (0–100 km²), m = medium (100–1,000 km²), l = large (>1,000 km²). The shape of the apex–mesopredator–prey interaction is categorized as triangular (t) if the apex and mesopredator both rely on the focal prey and linear (l) if the apex predator relies on different prey than the mesopredator (listed focal prey are those eaten by the mesopredator in the study).

MESOPREDATOR RELEASE DEFINED

The term *mesopredator release* first appeared in the scientific literature in 1988 (Soulé et al. 1988), but the concepts behind it can be traced back several decades (e.g., Paine 1969a; Terborgh and Winter 1980; Pacala and Roughgarden 1984; Wilcove 1985). Like many somewhat new and popular terms in the lexicon of science, *mesopredator release* has seen alterations and, perhaps, misapplications since it was coined 20 years ago. In the context of Soulé et al.'s (1988) article, the term was created to describe a process in which predators of intermediate body size (foxes and domestic cats) were more prevalent in the absence of a larger predator (coyote) and showed an increased effect on prey species (birds). The term is now often defined as any case in which a predator weighing approximately 3–20 kilograms plays an increasingly important role in regulating prey (Gehrt and Prange 2007). This common usage is problematic for two reasons: The somewhat arbitrary body size threshold has made the term unnecessarily restrictive and disjointed from ecological principles, and it places an emphasis on the impacts of mesopredators on prey rather than on the interactions of apex predators and mesopredators, where it belongs. In light of this confusion, we suggest the term *mesopredator release* be recast as a narrowing of Crowell's (1961) concept of ecological release (see also Terborgh and Faaborg 1973) to describe scenarios in which the absence or negative change in the density or distribution of an apex predator results in an expansion in density, distribution, or behavior of a middle-rank predator in a trophic web, irrespective of their relative or absolute body sizes. In most cases in which the term has been applied, mesopredator release is demonstrated or hypothesized to have a negative effect on the survival or productivity of predators and prey at lower trophic levels (popularly known as the mesopredator release hypothesis). However, such cascading effects should not be viewed as a required component of the term's definition.

CHAPTER OVERVIEW

In this chapter, we examine the history, significance, and practical implications of more than two decades of research on mesopredator release. We also briefly recount our own work on the causes and many consequences of the release of a primate mesopredator, the olive baboon (*Papio anubis*), in West Africa. An important manifestation of trophic cascades, the observation of mesopredator release provides ecologists with rare opportunities to illuminate and isolate com-

plex ecological relationships that otherwise are difficult to detect, much less measure. However, to the conservation biologist, the cascading effects or after-shocks that often accompany mesopredator release are cause for alarm and suggest that communities are easily pushed over thresholds to alternative ecosystem states. Such state changes may lead to dramatic shifts in community structure or, potentially, irreversible ecosystem meltdown (Chapter 4, this volume). In this chapter, we consider these and other aspects of mesopredator release as we set out to review the mesopredator release literature and, in the process, search for patterns among studies; discuss challenges, both conceptual and practical, that are faced in studies of mesopredator release; and examine the conservation implications of mesopredator release for management and policy.

REVIEWING THE LITERATURE

Likely cases of mesopredator release have been documented throughout the world in terrestrial, marine, and freshwater systems. Using Web of Science and Google Scholar searches with the terms *mesopredator**, *carnivore release*, and *meso-carnivore**, we identified thirty-four studies that investigated mesopredator release in thirty-two independent landscapes (Table 13.1). Because the term *mesopredator release* was not coined until 1988, our search probably missed earlier studies that used different terminology. Nonetheless, examination of more recent studies illuminates several interesting patterns. We begin by summarizing the systems, spatial scales, and methods that have been used to study mesopredator release. Based on results of these studies, we then highlight key factors that can affect the outcome of apex predator losses and mesopredator effects.

Mesopredator Studies

Studies of mesopredator release have been conducted most frequently in North America or in waters off the North American coast (twenty-one of thirty-four studies), commonly in systems where coyotes (*Canis latrans*) are the apex predator; cats, raccoons, skunks, or opossums are the mesopredators; and birds or rodents are the affected prey (eight studies, Table 13.1). However, studies focusing on mesopredator overabundance have been conducted in all continents except Antarctica, in a wide variety of systems, and at large spatial scales (n = nine state, country, or continent-wide studies). Studies often focus on ground-nesting birds as the prey of concern (fourteen studies). This is because nest depredation is the leading cause of reproductive failure for birds. Many bird populations are declining worldwide, and mesopredators are often important nest predators

(Chalfoun et al. 2002). Most of these studies used artificial nests to examine rates of nest depredation with respect to apex and mesopredator presence or abundance (e.g., Sieving 1992; Maina and Jackson 2003; Schmidt 2003). Other prey of concern include reptiles, amphibians, marsupials, rabbits, rodents, scallops, and ungulates. The weight of evidence suggests that mesopredator release is a common result of apex predator loss throughout the world.

Interestingly, the focal apex predators and mesopredators in published studies are often exotic or "undesirable" species. For example, on island systems cats are an exotic apex predator, and rats are an exotic mesopredator (Courchamp et al. 1999; Rayner et al. 2007). Similarly, in Japanese ponds, exotic bass and bluegill are apex predators and exotic crayfish are mesopredators (Maezono et al. 2005). Even when apex predators are native, such as wild dogs in Asia or coyotes in North America, they are usually considered to be undesirable because they prey on domestic livestock. Numerous studies have highlighted the perverse consequences that can result from such "nuisance control": the unleashing of even worse nuisances (i.e., mesopredators). For example, control of raccoons in Florida to protect sea turtle eggs paradoxically resulted in increased predation on the eggs because another egg predator, the ghost crab, was released from control by raccoons (Barton 2005). In contrast, one study has shown that suppression of beneficial mesopredators can damage ecological systems. In the Pacific Ocean, killer whales are an apex predator that have recently begun preying heavily on sea otters, a mesopredator that controls sea urchins. Without sea otters, urchin numbers explode, destroying kelp forests (Estes et al. 1998).

Most mesopredator studies have been observational, in which existing patterns of apex predator, mesopredator, or prey abundance have been examined over time or space, sometimes long after the apex predator has been eradicated (Wilcove 1985). Many of these studies acknowledge that land use changes are intimately connected with the loss of top predators and that both factors can lead to increased mesopredator populations. Two studies have successfully used modeling techniques to separate the contributions of land use change and apex predator removal on mesopredator abundance (Crooks and Soulé 1999; Elmhagen and Rushton 2007). Seven experimental studies have also been conducted (Table 13.1), in which apex predator removals were replicated and the abundance of mesopredators and prey was monitored on control and removal plots. Six of the seven experiments resulted in significant cascades, wherein mesopredators increased and prey numbers decreased in the absence of apex predators. Cascading effects have also been shown by observational studies, but many of these studies monitored only two of the three levels relevant to mesopredator release, and cascading effects were therefore difficult to demonstrate. Only four studies failed to find evidence supporting the mesopredator release

hypothesis (Table 13.1), but this paucity of negative results could reflect publication bias. Because mesopredator release has been studied in so many different ways (e.g., behavioral changes, correlations in densities, presence or absence trends, artificial nest predation rates), a formal meta-analysis examining the hypothesis is not possible at this time.

Factors That Influence Mesopredator Release

The loss of apex predators may or may not cause mesopredator numbers to increase, and increased numbers of mesopredators may or may not cause prey populations to decline. Two factors should strongly influence mesopredator release: the productivity of the system and the strength of interactions between apex predators, mesopredators, and prey.

Theoretical ecology provides insights into the effect of productivity on mesopredator release. Theory predicts domination by mesopredators in low-productivity systems, domination by apex predators in high-productivity systems, and the greatest chances for coexistence in systems of intermediate productivity (Chapter 18, this volume; Oksanen et al. 1981; Holt and Polis 1997). This prediction has been supported by several empirical studies in laboratory and agricultural systems (e.g., Morin 1999; Borer et al. 2003). The recent study by Elmhagen and Rushton (2007) also demonstrates how the productivity of a system can moderate the strength of top-down effects such as mesopredator release. Using a spatially explicit, 90-year data set on wolf, lynx, and red fox numbers throughout Sweden, they show that top-down effects are strongest in the most productive regions. Put simply, mesopredators may be regulated by the limited abundance of prey rather than by predation in less productive areas. In productive areas, abundant food should allow mesopredator numbers to increase when control by apex predators is removed.

Regardless of system productivity, mesopredator release should be most dramatic when links between the species of interest are strong. Thus, high species diversity and wide diet niche breadths should weaken the strength of mesopredator release. Removal of an apex predator from a system with many apex predators, many mesopredators, and many prey species should not have a strong effect compared with a system dominated by a few species (Chapter 8, this volume). This was the case in one of the studies that failed to support mesopredator release (Lloyd 2007). The dramatic responses to predator loss on depauperate islands also support this idea (Terborgh et al. 1997a; Rayner et al. 2007). Likewise, if apex predators and mesopredators consume a variety of prey, the cascading impact of apex predator removal on a particular prey
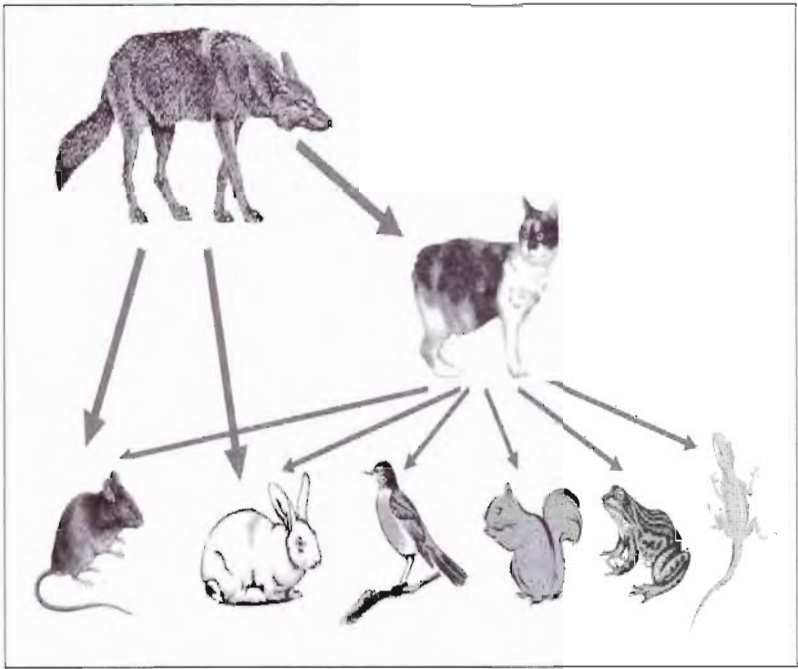
Figure 13.1. Example of a mesopredator interaction involving coyotes, domestic cats, and small vertebrates. Note the greater dietary breadth of cats compared with coyotes.

Differences in diet breadth and trophic position may explain why removal of apex predators often leads to increased predation pressure on lower trophic levels. Apex predators typically have a more restricted and carnivorous diet than mesopredators (Figure 13.1). Because mesopredators are positioned lower in the food web and tend to have a wider resource base than apex predators, they are poised to reach high densities and suppress a variety of prey species when released from top-down control (Roemer et al. 2001). Omnivorous meso-predators that switch easily between multiple food sources are demographically insulated from the rise and fall of individual prey species and thus maintain high densities where specialized predators could not. This is particularly evident in mesopredators that effectively use agricultural plants, livestock, or human refuse and reach and maintain strikingly high densities in modified environments (e.g., baboons, raccoons, and wild boars; Table 13.1).

Differences in diet breadth and population density are two reasons why mesopredator populations that increase after apex predator removal should not be regarded as simply ecological replacements. In 60 percent (nineteen of thirty-two) of communities we surveyed (Table 13.1), mesopredators relied on a distinctly different suite of prey than sympatric apex predators. A second important difference lies in the foraging efficiency of apex predators and meso-

predators. Many mesopredators such as mongooses, snakes, civets, lizards, raccoons, and opossums can exploit their environment more thoroughly than the apex predators they replace because they are smaller and able to forage belowground and aboveground. This ability to scour the landscape for prey of various shapes and sizes, combined with the potential for occurring at high densities, explains how mesopredators can wreak havoc on a large portion of their community.

CHALLENGES IN DETECTING MESOPREDATOR RELEASE

Despite significant research interest, unambiguous demonstration of mesopredator release has often been difficult. The typical constraints of many ecological studies, such as short time scales and uncontrolled environmental variation, are exacerbated by the complexity of interactions at multiple trophic levels that must be examined in a test of mesopredator release. Terborgh et al. (1999) describe many of the fundamental challenges of this area of research, including the difficulty of studying apex predators that are rare or cryptic, the risk of inappropriate generalizations from studies relying solely on analysis of correlation, and the fact that mesopredator release is often invoked when the apex predator has already disappeared.

Each of the research approaches typically used has inherent limitations. For instance, meta-analyses of changes in apex predator, mesopredator, and prey populations (e.g., Gehrt and Clark 2003) may be limited by lack of correspondence in scale, habitat, and other factors in individual studies not necessarily designed to test for mesopredator release. Studies that do not track populations over time but merely examine the spatial distribution of predators, mesopredators, and prey may be confounded by uncontrolled variation in habitat (Gehrt and Clark 2003). Attempts to assess the spatial distribution of predators or prey may often reflect use rather than abundance (e.g., Crooks and Soulé 1999). Studies that track temporal changes in mesopredator or prey abundance may be unable to provide spatial replication because of the intensive monitoring needed, making it difficult to control for environmental variation or other outside influences (Rayner et al. 2007). Anecdotal accounts of population changes consistent with mesopredator release could result from natural population variability, particularly when results are not replicated in space or tracked for long periods of time (Wright et al. 1994). Finally, testing mesopredator release involves detecting a response in abundance or behavior (Ale and Whelan 2008) of the mesopredator when the apex predator is removed, but what magnitude of response really demonstrates release? Presumably, an increase in mesopredator

abundance that exceeds normal short-term variability should be detected. Ideally, studies would also demonstrate that predation by the apex predator is a limiting factor for the mesopredator population. A further complication is that the consequences of mesopredator release are realized only if an effect on the population of the prey species is also detected. In addition to changes in prey abundance, biologically significant changes in diversity, richness, or biomass of the prey species community could result from mesopredator release (Henke and Bryant 1999).

Despite these challenges, several studies have addressed problems inherent in teasing apart complex interactions between apex predators, mesopredators, and prey. For instance, Myers et al. (2007) compiled long-term data sets over a wide geographic extent to show that population trends for multiple species at all three trophic levels (apex predators, mesopredators, and selected prey species) have changed in a manner consistent with mesopredator release. The extensive anecdotal evidence for mesopredator release has been bolstered by controlled experimental approaches involving removal or reintroduction of apex predators with subsequent monitoring of mesopredator and prey communities (e.g., Henke and Bryant 1999). It is also increasingly recognized that variation in habitat quality must be controlled because mesopredator release may be weak in cases where trophic regulation is more bottom up than top down, as demonstrated by Elmhagen and Rushton (2007). The inconsistent evidence that apex predators control mesopredators (e.g., Gehrt and Prange 2007) could result from that variation or the weakening effect of increased food web complexity on mesopredator release. Techniques such as path analysis (e.g., Elmhagen and Rushton 2007) may be a particularly effective method for testing the strength of various trophic interactions and inferring mesopredator release. Although local variation in trophic control and food web complexity often confounds detailed predictions about the cascading impacts of removing or reintroducing apex predators, removal of top predators can be expected to have large and obvious consequences in most ecosystems.

An ideal study following experimental manipulation of a population of apex predators would examine both the mesopredator population or community and their prey through both time and space. In practice, that ideal will remain difficult to achieve. However, future studies should carefully consider the strength of interactions between apex and mesopredator in the context of the larger food web and the likelihood of bottom-up versus top-down control. More research is also needed on the often underestimated indirect effects of predation (such as changes in prey foraging behavior; Chapter 14, this volume) on mesopredators and their prey.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Mesopredator release was originally introduced in the context of highly fragmented landscapes (Diamond 1988; Crooks and Soulé 1999). Habitat fragmentation catalyzes mesopredator release in part because apex predators commonly have larger area needs than the mesopredators they control and thus are more sensitive to reductions in the size of remaining habitat. Wide-ranging species of large carnivores are particularly prone to population decline because they tend to spill out from small, isolated areas into regions of high conflict with humans (Woodroffe and Ginsberg 1998). Conversely, prey species driven to decline by mesopredator outbreaks may have small area needs and be tolerated, if not desired (e.g., game species; Palomares et al. 1995), by humans. Therefore, mesopredator release not only is intensified by habitat fragmentation but also extends fragmentation effects to species that might otherwise appear resilient to human-induced landscape changes. If fragmented landscapes that fail to retain apex predators are exceptionally vulnerable to the influences of mesopredators, as case studies from across the world indicate, then current rates of large carnivore declines and habitat loss are certain to set the stage for mesopredator outbreaks of increasing intensity.

In addition to predator removal, other characteristics of fragmented landscapes probably increase mesopredator abundance. Mesopredators (e.g., feral cats; Soulé et al. 1988) may be subsidized by human food sources, for example, or otherwise directly benefit from habitat modifications (Litvaitis and Villafuerte 1996). Under such scenarios, mesopredators are likely to experience release from bottom-up constraints, and the strength of top-down effects can be expected to simultaneously increase (Elmhagen and Rushton 2007). Therefore, apex predation can be expected to play an increasingly important regulatory role as mesopredator resource availability improves. The loss of large carnivores in fragmented landscapes is of great ecological consequence not only where mesopredators are naturally heavily regulated by top predators but particularly where other fragmentation effects directly benefit mesopredators and remove resource constraints.

Population Control of Mesopredators

In the absence of apex predators, efforts to mediate the ecological consequences of mesopredators could be directed toward controlling overabundant populations, but several factors indicate that such management can be problematic. Overabundant mesopredators are likely to be characterized by high densities, high rates of recruitment, and high rates of dispersal, all of which may

make them resilient to control programs (Palomares et al. 1995). In addition, density-dependent responses to control efforts, public outrage, and unintended consequences for other species additionally can significantly complicate control efforts. Goodrich and Buskirk (1995) argue that to be effective, such control efforts must be intensive (and probably expensive) and therefore are less desirable management options than addressing the ecodisturbances generating overabundance. This contention is borne out by Henke and Bryant (1999), who observe that lowering coyote density by half in a 10-square-kilometer area of Texas entailed the lethal removal of 354 coyotes over a 2-year period.

Emerging studies of behavior-mediated interactions between predators and prey additionally hint that replicating the full ecosystem effects of apex predation is likely to be exceptionally difficult (Chapter 14, this volume). In a review of intraguild predation, for example, Palomares and Caro (1999) note that interactions between predators result not only in direct killing but also in avoidance in the form of shifts in space use, temporal segregation (activity pattern), and group formation. Although intensive management may be successful in controlling mesopredator densities, mimicking the behaviorally mediated ecosystem functions of apex predators is likely to be much more challenging.

Mesopredator release has also provided management lessons for eradication efforts that target both an invasive apex predator and an invasive mesopredator. Using multispecies models that accounted for the presence of two invasive predators (cats and rats) on native island birds, for example, Courchamp et al. (1999) conclude that the eradication of cats alone could result in a release in the rat population and ultimately intensified bird declines. More sophisticated models (Fan et al. 2005) similarly predict that as an apex predator, cats offer birds some degree of protection from rats. Recent field observations of island rat–petrel dynamics across systems that varied in elevation and presence of cats (Rayner et al. 2007) hint that the order of cat versus rat eradications dramatically influences the breeding success of native birds. Together, these studies and those showing the consequences of rat overabundance on nesting seabirds (Chapter 12, this volume) indicate that ignoring mesopredator release effects in control efforts could hasten rather than slow prey declines.

Perceived Costs of Large Carnivore Conservation

More than two decades of publications focusing on mesopredator release confirm that conserving apex predators is critical in preventing rippling waves of secondary extinctions (Terborgh and Winter 1980) that stretch across trophic levels (Terborgh 1988) and thus trigger widespread faunal collapse (Soulé et al. 1988). Nonetheless, the species most likely to prevent mesopredator outbreaks

are large carnivore species that are not only highly sensitive to habitat loss but often the focus of human–wildlife conflict. As noted by Palomares et al. (1995), large predators have particularly suffered from a public relations crisis where they are perceived to threaten prey species of value to humans.

Mesopredator release is of conservation significance not only because of its ecological and management implications but also because it highlights the need to revise long-standing perceptions of the social and economic costs of sustaining large carnivores. Whereas large carnivores have traditionally been viewed as clear competitors with humans for game species, for example, evidence of mesopredator release points to scenarios under which large carnivores can boost populations of desirable game species (Palomares et al. 1995; Rogers and Caro 1998) and thereby reduce conflict with game ranch objectives (Palomares and Caro 1999). As research on mesopredator release develops, suggestions that carnivore conservation can yield financial benefits (e.g., Rogers and Caro 1998) are being replaced by clear examples in which local extinctions of carnivores resulted in the collapse of prey populations that are economically valuable, such as fishery collapse in the absence of sharks (Myers et al. 2007) and waterfowl declines in the absence of coyotes (Sovada et al. 1995). Therefore, although mesopredator release has generated strong ecological arguments for ensuring carnivore persistence to best protect biodiversity (Soulé and Terborgh 1999), it also suggests that increased tolerance of carnivores may be beneficial in preventing large financial losses. Furthermore, the ecological consequences of recent carnivore reintroductions (e.g., wolves in Yellowstone; Berger and Gese 2007) imply that early state changes in ecosystems that result from the loss of apex predators can be reversed with their reintroduction, providing hope for the success of restoration efforts in remedying the progression of ecosystems to undesirable alternative states. Large carnivore conservation and reintroduction efforts might similarly provide a promising solution for reversing the social and economic costs of mesopredator release that are detailed in the following case study.

CASE STUDY: OLIVE BABOONS IN WEST AFRICA

Olive baboon outbreaks in Ghana, West Africa provide a striking example of mesopredator release and, more generally, illustrate the far-reaching effects of apex predator extinctions. In 1968, the Ghana Wildlife Division initiated a monitoring program in which staff at sixty-three posts spread throughout six protected areas (hereafter called parks) recorded the type and number of

forty-one species of larger mammals encountered on monthly walking tran-
sects (Brashares et al. 2001). Transects were 10–15 kilometers in length, started
and finished at a ranger post, and were repeated monthly almost continuously
through 2004. The six parks in which monitoring occurred are characterized
by savanna habitat and, at 58–4,840 square kilometers in size, are the largest
members of a protected area system in Ghana that today includes 321 sites, 95
percent of which are smaller than 10 square kilometers (Figure 13.2). When
monitoring started in the late 1960s, wildlife communities in these parks were
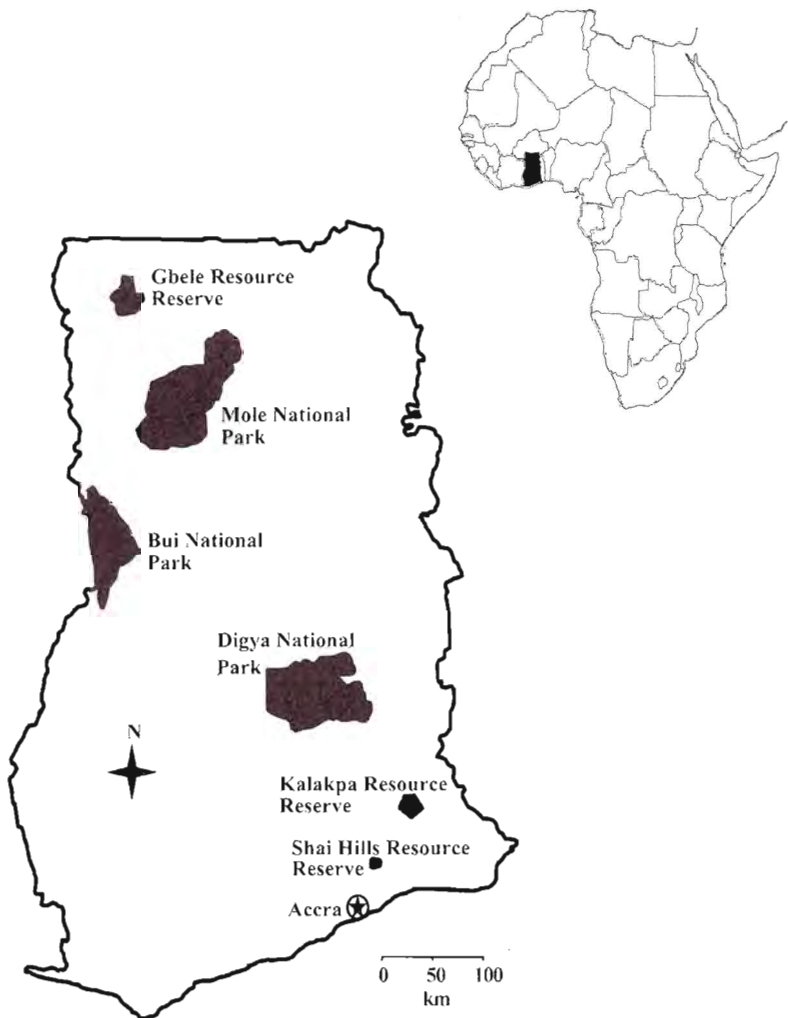largely intact, harboring a high diversity of ungulates and primates (thirty-three

Figure 13.2. Approximate location and size of six protected areas in Ghana, West Africa,
discussed in this chapter.

species) and eight species of large carnivores, including several that today are exceedingly rare (e.g., lion, *Panthera leo*) or regionally extinct (e.g., wild dog, *Lycaon pictus*) (Brashares et al. 2001; Brashares 2003). Thus, this 37-year data set provides unparalleled insight into the dynamics of wildlife populations and communities undergoing change (Brashares and Sam 2005), and, as relates to this chapter, a rare glimpse of the process of mesopredator release.

Large mammals in Ghana are actively hunted as bushmeat for human consumption, and count data from 1969–2004 show a 68 percent decline in wildlife biomass across the six monitored parks (Brashares et al. 2004). As elsewhere (see Woodroffe and Ginsberg 1998), Ghana's large carnivores are particularly hard hit by human activities (Brashares et al. 2001), in part because their low densities and slow rates of reproduction make them incapable of sustaining heavy harvest from bushmeat and pelt hunters but also because they are viewed as a threat to people and livestock and widely persecuted. Count data from the six parks show that the four largest carnivores in Ghana (lion, leopard, spotted hyena, and wild dog) declined from an average of 348 combined detections per month in 1969 (*SD* ±66) to 31 (±7) in 2004 (Figure 13.3). In fact, all large carnivores became extinct in three of the six parks by 1986. In the three parks where lion, leopard, and spotted hyena remained extant in 2004, they showed significant range contractions away from areas frequented by humans (Brashares, unpublished data). Nevertheless, wildlife declines were not evenly distributed across parks, and core areas within Ghana's three largest protected areas (Mole, Bui, and Digya national parks; Figures 13.3 and 13.4) show counts of predators and prey that resemble observations made almost 40 years ago.

The extirpation of large carnivores in three of Ghana's six savanna parks provides a somewhat replicated natural experiment for examining the effect of apex predator removal on mesopredators. Moreover, the three parks currently without apex predators lost them at distinctly different times (approximately 1976, 1983, and 1986, respectively); thus, community responses to predator removal are expected to be staggered in time. A visual examination of counts for all forty-one species in the six parks shows only one species, olive baboon, was consistently observed more frequently and along more transects in 2004 than in 1969 (Figure 13.3). Specifically, olive baboons showed a 365 percent increase in observations over this period, and as quantified from an analysis of sightings over time at the sixty-three sampling sites, the species expanded its range within parks by more than 500 percent (Brashares, unpublished data). However, these increases in baboon abundance and distribution did not occur evenly across parks. Consistent with a hypothesis of mesopredator release, baboons showed the greatest increases in the three parks where apex predators became
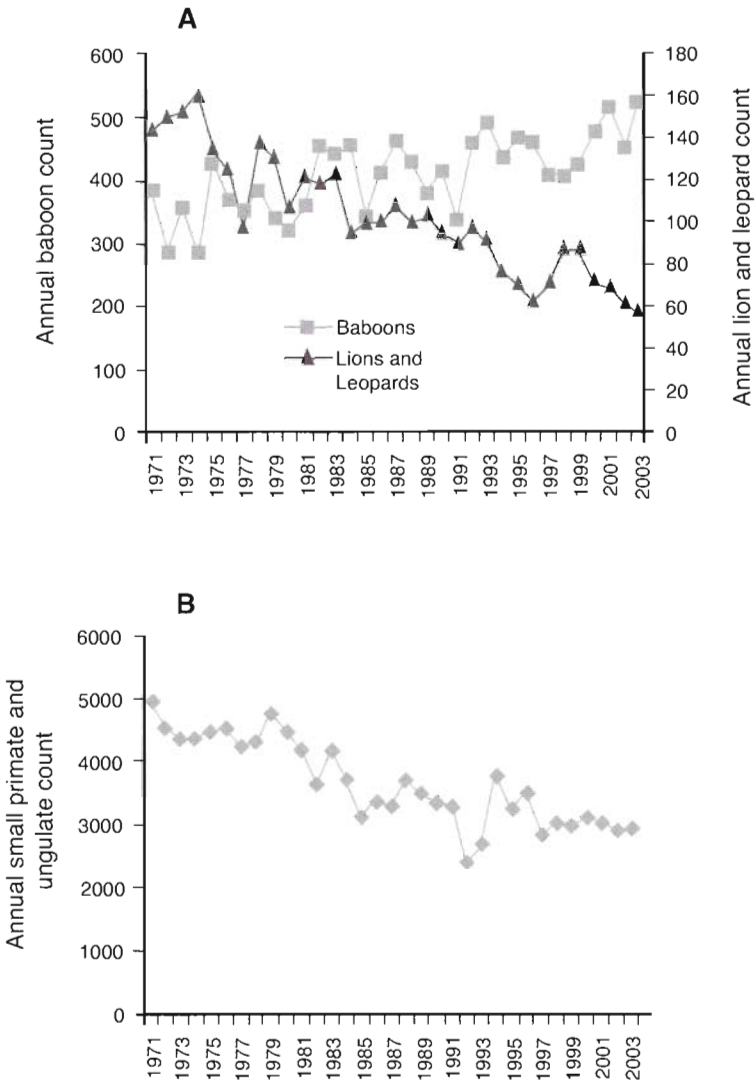
A

B

Figure 13.3. Average annual counts from 1971 to 2003 of **(a)** lions and leopards (triangles) and baboons (squares) and **(b)** 11 species of smaller (less than 10 kilograms) primates and ungulates at 20 largely intact sites within parks in Ghana where apex predators remain common.

extinct. The rate of baboon increases was correlated closely with apex predator declines ($r = 0.72–0.88$, using a 3-year lag). Even in parks that maintained apex predators, baboons were observed to spread and increase in density in areas where large predators were absent. These broad- and fine-scale temporal and spatial responses of this mesopredator to the removal of apex predators were quantified both through time series analyses and multiple regression models
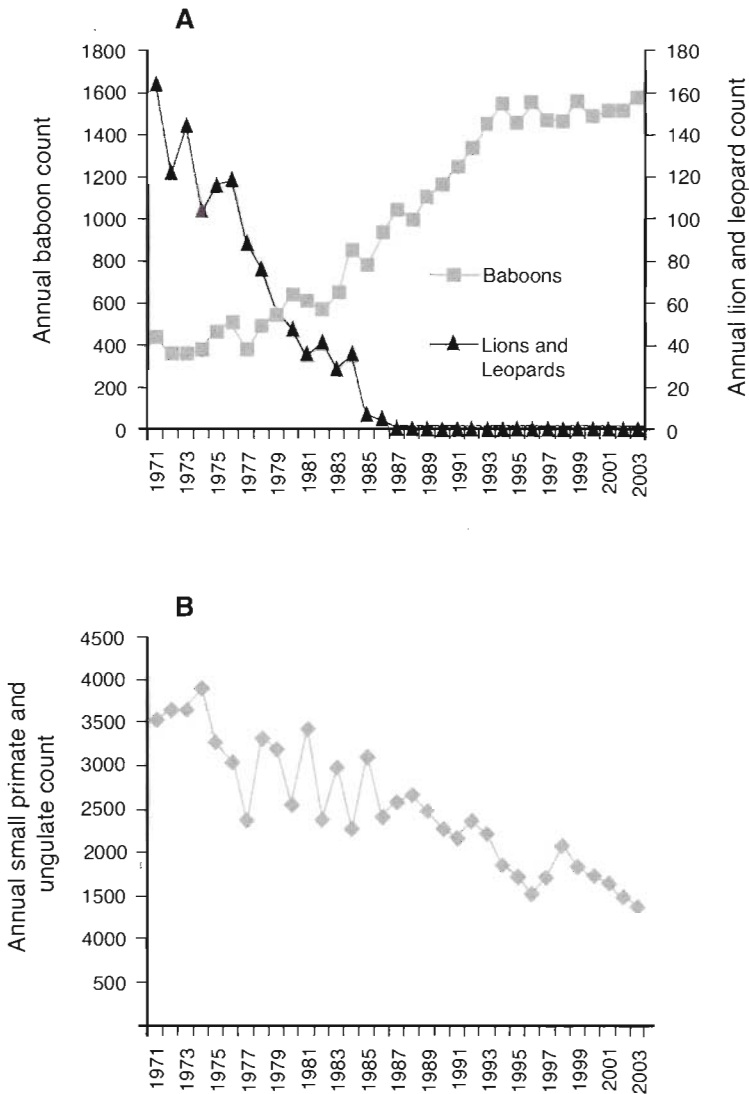
Figure 13.4. Average annual counts from 1971 to 2003 of **(a)** lions and leopards (triangles) and baboons (squares) and **(b)** 11 species of smaller (<10 kilograms) primates and ungulates at 20 altered sites within parks in Ghana where apex predators were extirpated before 1987.

that selected lion and leopard density, above seven other biotic and abiotic variables, as the single best predictor of baboon occupancy and growth rates within parks (Brashares, unpublished data). Finally, although apex predator extinctions occurred at different times in the six parks, increases in baboon density and range after predator extinctions followed similar trajectories and, amazingly, a consistent 3-year time lag (Brashares, unpublished data).

Like other savanna baboons, olive baboons are opportunistic omnivores that augment their primarily vegetarian diet with insects, eggs, birds, reptiles, mammals, and fish (Hamilton and Busse 1978; Norton et al. 1987; Barton and Whiten 1994). Olive baboons are extremely efficient foragers and capable of organized hunting (Strum 1975) and, like other dominant mesopredators, show greater dietary breadth than apex predators in their community. These features and the fact that in the absence of large carnivores baboons can sustain local densities orders of magnitude higher than apex predators (Brashares, unpublished data) suggest that these mesopredators, once released, can have greatly amplified impacts on their prey. Strum (1975) observed the development of a "tradition" of carnivory in olive baboon troops in Kenya, and many other authors comment on high rates of predation by savanna baboons on young antelope, large rodents, and small primates (e.g., Hamilton and Busse 1978). Observations in the field and analysis of count data suggest that olive baboons in Ghana have assumed the role of top predator where apex predators are removed. The impact of baboons on their prey is most easily quantified by comparing population trends of potential prey species in areas where baboons have become superabundant with those in areas where they have not (i.e., where apex predators remain extant). Such an analysis reveals that increases in baboon density and range are correlated closely ($r = 0.65$–0.92 with a 2-year lag) with accelerated declines of five species of smaller primates and nine species of antelope (Figure 13.4). In the most extreme cases, estimates of annual growth rates in populations of smaller monkeys (e.g., *Cercopithecus petaurista* and *Chlorocebus sabaeus*) and ungulates (e.g., *Ourebia ourebi*) shift from values above 1.1 to below 0.7 within 2 years of baboon outbreaks, with local extinction of these prey occurring within 5 years of outbreaks. In sum, although higher concentrations of prey in the presence of apex predators may seem counterintuitive, spatial patterns of wildlife communities in Ghana mirror other cases of mesopredator release in that primates and smaller ungulates persist in highest densities where apex predators remain most abundant.

One obvious alternative explanation for this pattern posits that apex carnivores, primates, and ungulates, but not baboons, are negatively affected by bushmeat hunting, and this pressure, rather than trophic cascades or mesopredator release, has created a community in which one species is hyperabundant and others rare. However, this hypothesis ignores several key details of the long-term data: Identical cascades are observed in areas of Ghana's parks where apex predators are absent but hunting does not occur or occurs at low rates; the staggered timing of apex predator extirpation, baboon release, and prey declines, replicated in three different parks, suggests causation more than correlation; and

ungulate species too large to experience predation by baboons (e.g., buffalo, *Syncerus caffer*, roan antelope, *Hippotragus equinus*) but prized by bushmeat hunters do not show accelerated declines where apex predators are extirpated. Furthermore, baboons are hunted as intensively or more so than other species in their community, particularly when they occur near human settlements, a fact that stands in contrast to the alternative hypothesis outlined earlier. Preliminary results of stable isotope analysis of baboons in Ghana's parks also support the hypothesis that baboons released from predation increase their reliance on animal prey. Tissue samples from baboons living in high density (without apex predators) showed significantly higher nitrogen-15 isotope ratios (an indication of a more carnivorous diet) than those living in intact wildlife communities (8.6 $\pm$ 0.8 per mil vs. 5.5 $\pm$ 0.6 per mil; n = 7 and 5, respectively). However, broader sampling is needed before this result can be confirmed because current sample sizes are prohibitively small and the observed differences in nitrogen-15 isotope ratios could reflect only a transient shift in diet.

The impact of baboon release is observed not only in declines of primates and ungulates but also in reduced rates of nest success among ground- and tree-nesting birds. A 4-year study of nest success in areas of high and low baboon density showed that nests subject to heavy predation by baboons had average fledging rates of 19 percent ($\pm$6 percent; n = 132 nests), as compared to average rates of 52 percent ($\pm$11 percent; n = 169). It is likely that reptiles, insects, parasites, and perhaps vegetation structure will also show a response to high baboon densities in Ghana's parks, but data necessary to test the impact of this mesopredator release on these groups are yet to be collected.

CONCLUSIONS

Surprisingly few studies have attempted to quantify or have even considered the short- and long-term costs of mesopredator release for people (Chapter 20, this volume). Efforts to identify the economic, social, or public health implications of hyperabundant raccoons, rampaging red foxes, and egg-hungry rats may have no place in formal community ecology, but such pursuits may go far toward enlisting the help of the public in conserving apex predators. The case of baboon release in Ghana lends itself to such outreach for several reasons. First, savanna baboons become voracious predators of crops and livestock where they are released from predation (Butler 2000; Hill 2000). This conflict goes far beyond Ghana, and among large mammals baboons are the greatest threat to crops and livestock in twenty-seven countries in sub-Saharan Africa

(Brashares, unpublished data). Villages suffering loss of crops and livestock to baboons must enlist the services of school-age children as crop guards, and this reduces school attendance rates and exposes children to physical harm. Second, baboons compete directly with rural people in Ghana and elsewhere for wild sources of animal protein. Terrestrial wildlife, most often antelope and rodent species, is the primary source of animal protein and a major source of livelihoods for tens of millions of Africans (Brashares et al. 2004), and populations of these harvested species do not persist in areas of high baboon density. Last, baboons and humans share many parasites and pathogens, and baboon outbreaks, particularly near human settlements, create hotspots of infectious disease for wildlife, people, and livestock (Brashares, unpublished data). Taken together, the economic, social, and health costs of this mesopredator release dwarf the investment that would be necessary to restore, protect, and manage Africa's apex predators.