Urbanization and the Predation Paradox: The Role of Trophic Dynamics in Structuring Vertebrate Communities

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As the pace and extent of urbanization increase, an understanding of the mechanisms that shape wildlife communities in cities will be essential to their effective management. Predation could be an important determinant of the structure of these communities, but the research to date suggests a predation paradox: Vertebrate predator numbers increase with urbanization, whereas predation rates decline. We reviewed studies on predator abundance and the survival of terrestrial vertebrates in urban and nonurban contexts to evaluate whether the predation paradox is a widespread phenomenon. We conclude that there is substantial support for it. We discuss hypotheses to explain the paradox and suggest that urbanization has fundamentally altered trophic dynamics by reducing top-down control through multiple mechanisms and by increasing bottom-up forcing through the greater availability of anthropogenic foods. The hypotheses are summarized in a conceptual model that generates testable predictions designed to advance our understanding of trophic dynamics in metropolitan areas.

Keywords: urban ecology, animal behavior, community ecology, population ecology, vertebrate biology

Urbanization is radically and rapidly altering the Earth, leading to the formation of unique assemblages of vertebrate wildlife species in urban environments (Shochat et al. 2010). These assemblages differ greatly from those in adjacent undeveloped habitats but tend to be similar to communities in other cities, even those separated by wide geographic distances (McKinney 2006). This suggests that urban communities may be shaped by a set of forces that are unique to metropolitan areas (Shochat et al. 2006). Given the extent of urbanization and the predicted rate of urban expansion, an understanding of these forces is essential to designing and managing urban environments (Miller and Hobbs 2002).

Predation could be one of the primary forces shaping urban communities, because it is one of the fundamental mechanisms that structure natural communities (Shochat et al. 2006). Top-down control caused by predation can limit the population size of prey species below the level that available resources could otherwise support (Newton 1998). The effects of such regulation on community structure can be profound. Diversity may increase where predation limits the population size of organisms that might otherwise

exclude other species (i.e., *keystone predation*; Paine 1966). Conversely, prey populations may be extirpated where large numbers of one prey species support high densities of predators that also prey on other, less abundant species (i.e., *hyperpredation*; Smith and Quin 1996). Reduced prey populations might, in turn, release their food sources from top-down regulation (i.e., *trophic cascade*; Estes JA et al. 2011). Even the fear of predation can alter demographics and interspecies interactions through changes in behavior that minimize the risk of mortality (Bednekoff 2007).

Because of the myriad potential effects of predation, top-down control is a mechanism frequently invoked to explain the composition and structure of urban wildlife communities (Marzluff 2001). However, the research to date has been polarized along two lines of inquiry that have yielded seemingly contradictory conclusions (figure 1; Shochat 2004). In some behavioral and demographic studies, it has been reported that fearfulness and mortality are lower in urban settings—a phenomenon referred to as *predation relaxation* (also known as the *predator refuge* or *safe habitat hypothesis*)—the implication being that predation rates are also reduced in more developed areas (Gering

Potential trophic consequences

- Less predation
- Increased prey survival
- **Decreased top-down control**

- Greater predation
- Reduced prey survival
- **Increased top-down control**

Predation relaxation

Decreasing predation rates

Increasing predator abundance

Predator proliferation
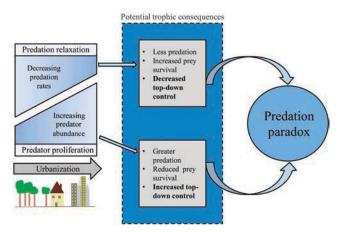
Urbanization

Predation paradox

*Figure 1. The predation paradox: Reductions in predation rates (*predation relaxation*) and increases in predator abundance (*predator proliferation*) lead to conflicting predictions regarding differences in top-down control between urban and nonurban environments.*

and Blair 1999, Shochat et al. 2006, Valcarcel and Fernández-Juricic 2009, Stracey 2011). Other research has shown that predator densities are frequently greater in cities than in rural or natural landscapes (Sorace 2002). This abundance of predators—here, termed *predator proliferation*—implies that predation pressure is actually greater in urban areas.

The apparent contradiction between predation relaxation and predator proliferation has been called the *predation paradox* (figure 1; Shochat 2004). Since the phrase was coined, much research has been conducted on predation in the context of urbanization for a wide variety of vertebrate species, but it remains unclear whether the predation paradox is a widespread phenomenon. Here, for the first time, we review this body of work to assess whether predation relaxation and predator proliferation are general features of terrestrial vertebrate communities in landscapes undergoing urbanization. We reassess the predation paradox in light of our conclusions and discuss mechanisms that could produce the observed patterns. Finally, we offer a new conceptual model of altered trophic dynamics in urban and nonurban environments as a means of stimulating and focusing future research. Throughout the article, we refer to *top-down control* in the context of predation. Although other interspecific interactions, such as disease and predation, can also limit population size, we do not discuss them here.

Literature search

Using topic searches in the Web of Knowledge (*http://thomson reuters.com/products_services/science/science_products/a-z/isi_web_of_knowledge*), we reviewed literature on predator numbers and prey survival for terrestrial vertebrates in urban landscapes. We focused on comparative studies of urban or suburban sites (hereafter, termed *urban*) with rural or undeveloped locations (*nonurban*) to avoid comparing investigations of urban and nonurban areas that were carried out

under different environmental conditions due to interannual variation. Studies in which multiple points were examined along gradients of urbanization were also included, although these were far less common. Nearly all studies were conducted in North America and Europe, so we restricted our review to these continents.

All searches for prey survival included the terms *urban** and *surviv** (the asterisk is a search wildcard), as well as a broad taxonomic descriptor such as *reptile*, *bird*, or *mammal*. Based on the findings from these articles, more specific searches were conducted in association with taxa common in urban environments, using terms such as *nest* and *rodent*. Queries regarding predators included *urban** and taxa-specific terms identified through the survival searches, such as *opossum*, *fox*, *coyote*, *cat*, and *raptor*. The references in relevant articles were searched for additional sources. Finally, we identified additional sources by searching the Web of Knowledge for studies in which articles included in our review were cited.

Predator proliferation

The first tenet of the predation paradox is that predators are more numerous in cities than in the surrounding landscape (Shochat 2004). The variety of vertebrate predators along the urbanization gradient is high and includes birds, mammals, and reptiles. Some of these are exclusively carnivores, but many are omnivorous, taking prey opportunistically (Iossa et al. 2010). Responses to urbanization vary by taxon (Haskell et al. 2001), with some avoiding developed areas and others reaching peak densities in cities (Rosenfield et al. 1995). Consequently, changes in the overall number of predators in metropolitan areas are an amalgamation of the different responses of species to urban development.

Apex predators found in wildlands are largely absent from metropolitan environments (Estes JA et al. 2011). These species, such as mountain lions and black bears, are sometimes seen in urban habitats—particularly at the interface of wildlands and cities—but the core of their home ranges is always in areas with minimal human disturbance (Iossa et al. 2010). Such top-level predators generally require extensive home ranges with adequate numbers of large prey where human interference is minimal (Beier et al. 2010)—attributes that do not characterize developed areas. In addition, human tolerance for predators generally declines with increases in the predators' body size, which leads to removals of large species from cities (Iossa et al. 2010). The loss of the top trophic level in urban environments could have profound indirect effects on other wildlife. The lack of top-down regulation on smaller predatory species could allow populations to increase greatly in abundance (i.e., *mesopredator release*; Prugh et al. 2009), resulting in a trophic downgrading by which middle-rank predators become the apex consumers of a system (Estes JA et al. 2011). Such species can reach much higher densities than large-bodied predators, which creates the potential for greater predation pressure on urban prey (Prugh et al. 2009).

Mammalian mesopredators (the term used here in reference to middle-rank predators in wildlands; Prugh et al. 2009)

are a common component of urban wildlife communities (Rodewald et al. 2011). These species are omnivorous, with the exception of the carnivorous bobcat (*Lynx rufus*), although the degree of omnivory varies by species (Iossa et al. 2010). All species will opportunistically consume small birds or mammals—particularly eggs, nestlings, and young (Iossa et al. 2010)—and so have the potential to increase predation pressure on prey species. Whether top-down forcing changes with urbanization depends in part on how predator numbers respond to urban development. These responses are species-specific and highly variable (table 1). Predators such as coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) frequently make use of urban environments, but they preferentially select habitats to minimize contact with humans (Riley 2006, Gehrt et al. 2009). There tends to be little difference in the density of such species between urban and nonurban environments (Iossa et al. 2010). Other mammalian predators, such as the raccoon (*Procyon lotor*), make use of a wide variety of natural and human-disturbed habitats and reach higher densities in cities (Prange et al. 2003). Mesopredators have also been introduced into urban environments in the form of domesticated species such as cats (*Felis catus*). These species are closely associated with human development and increase in abundance with human density (Sims et al. 2008).

Avian mesopredators are also present in cities and are represented by both carnivores and omnivores (Rodewald et al. 2011). Like mammalian mesopredators, omnivorous birds have the potential to affect predation pressure on other species by opportunistically taking vertebrate prey, particularly the young. Most of these species are members of the family Corvidae and generally respond positively to urbanization (table 1). For example, the black-billed magpie (*Pica pica*) routinely reaches its greatest recorded densities in cities (Jerzak 2001).

The number of carnivorous bird species generally declines with urbanization (Møller 2011), but species-specific changes in abundance are variable (table 1). Some species, such as the northern goshawk (*Accipiter gentilis*), have only recently colonized urbanized environments, and the relative sizes of urban and nonurban populations vary by city (Rutz 2008). Others, such as the red-tailed hawk (*Buteo jamaicensis*), are common inhabitants of urban areas, although their densities are lower than those in nonurban habitats (Stout et al. 1998). A few species, including the Cooper's hawk (*Accipiter cooperii*), reach their highest recorded densities in cities (Rosenfield et al. 1995).

Snakes are common predators of vertebrates in nonurban landscapes, but species richness and abundance generally decline with urbanization (Patten and Bolger 2003, Faeth et al. 2005). Some snakes use natural habitats and edges adjacent to urban areas (Zappalorti and Mitchell 2008), but the only terrestrial species that survive within developed habitats away from riparian corridors are small bodied and generally do not prey on vertebrates (e.g., Gaul 2008). Larger species with more extensive home ranges are typically killed by automotive traffic or people intolerant of their presence (Akani et al. 2002, Andrews and Gibbons 2008).

Overall, large-bodied carnivores and snakes appear to decline with increasing urbanization, omnivorous mammals and raptors exhibit highly variable responses, and introduced predators and avian omnivores increase in abundance. In few studies have changes in the overall assemblage of predators been enumerated across a gradient of urbanization, but the limited research on songbirds suggests that their predators increase with urban development (e.g., Haskell et al. 2001, Sorace 2002). Given that several avian carnivores and omnivores reach their highest densities in cities, that many other omnivores and raptors are present in both developed and undeveloped landscapes, that introduced predators such as cats exhibit high urban densities, and that large-bodied predators absent from urban settings naturally occur at low densities (Mattson 2007), we conclude that vertebrate predator numbers are likely greater in urban landscapes than in nonurban ones, as was purported in the predator proliferation hypothesis. However, more studies are needed in which the responses of the entire predator community to urbanization are examined in order to confirm that reductions in the numbers of snakes, large carnivores, and certain omnivorous mammals and raptors are compensated for by increases in the numbers of other predatory species.

Predation relaxation

The second tenet of the predation paradox is that predation pressure decreases as urbanization increases (Tomialojc 1982, Gering and Blair 1999, Shochat 2004). In other words, a smaller proportion of a given population succumbs to predation in more urbanized habitats than in less developed areas (Shochat 2004). Urban predation has typically been studied indirectly through changes in survival rates, presumably because of the difficulty in observing actual depredations. Changes in survival rates reflect the collective responses to the various sources of mortality that organisms face, including

*Table 1. Relative abundance for predators in urban and nonurban habitats (*n = 60*).*

	Higher in urban	Equivalent	Lower in urban
Mammals	20	11	9
Birds of prey	6	2	11
Corvids[a]	27	6	13

Note: Investigations in which results were reported for more than one species were included multiple times. Studies of urban gradients in which results were reported for more than one habitat type within the categories of *urban* or *nonurban* were included if the density or abundance response to urbanization was linear or if the two response types did not differ between habitat types within a category. In four studies not included in the table, the abundance of the burrowing owl (*Athene cunicularia*), jackdaw (*Corvus monedula*), and black-billed magpie (two studies) exhibited a hump-shaped curve in response to increasing urbanization. Taxa that were represented by only a single study were not included in this table (e.g., snakes).
[a]Avian species in the family Corvidae.

disease, starvation, severe weather, toxins, hunting, collisions with structures or vehicles, electrocution, and predation (Newton 1998). Each factor may change with urban development but not necessarily in similar ways (e.g., Gosselink et al. 2007). Nevertheless, predation is often a principal determinant of overall survival, and in the absence of detailed information on the cause of death of individuals, changes in survival rates can serve as a useful proxy for the relationship between predation pressure and development (Stevens et al. 2007).

Most studies of urban survival have been focused on the various life stages of birds (i.e., in the nest, juveniles, and adults), particularly of songbirds (table 2). Investigations in which artificial nests were used have been particularly popular, but such studies are not included here because the utility of this method is questionable in many cases (Faaborg 2010). Research on other taxa has been less common and is reviewed here in the context of supporting or refuting the trends observed for songbirds. We also discuss behavioral experiments that have been used to assess predation pressure at different levels of urban development.

The survival rates of songbirds typically increase or do not respond to urbanization (table 2). We found twice as many

studies documenting reduced adult mortality in urban versus nonurban areas as we did those that showed no change, and in only a single investigation was it concluded that adult survivorship was greater in nonurban settings. The survival rates for first-year songbirds did not differ, regardless of the degree of urbanization, with few exceptions. Regarding the nesting stage, the majority of studies showed no difference in urban and nonurban settings—a trend confirmed by a recent review of avian demography and urbanization (Chamberlain et al. 2009). However, nearly half of these investigations were conducted in natural habitat fragments in which *urbanization* was defined on the basis of changes in the landscape surrounding the study sites. When considering only those projects in which changes in urban development within study sites were compared, almost twice as many showed greater survival of nests in more urban environments as those that reported no response to urbanization. Similar investigations have been conducted for birds of prey, but no clear patterns have emerged, because of the small number of studies (table 2).

A number of researchers have gone beyond using survival as a proxy measure for predation by quantifying sources of mortality or by experimentally manipulating predator numbers. Predation rates were not reported in any investigations of songbird survival at the adult or juvenile stage, but predation was measured in a number of nest survival studies (table 2). With few exceptions, predation rates were lower in urban habitats than in nonurban ones. Stoate and Szczur (2006) experimentally assessed the importance of predation by manipulating predator numbers along an urbanization gradient. In this study, nest survival for the spotted flycatcher (*Muscicapa striata*) was initially higher in residential gardens than in woodlands, but several years of predator control led to similar rates of nest failure in urban and nonurban sites (Stoate and Szczur 2006). This result suggests that, at least for this species, predation is the cause of lower nest survival in nonurban areas. Another study in which the abundance of a particular predator (the black-billed magpie) was manipulated showed that productivity in city parks was unaffected by magpie numbers for 10 different songbird species (Chiron and Julliard

Table 2. Changes in survival and predation rates in nonurban and urban habitats (n = 72).

	Survival			Predation			
	Higher in urban	Equivalent	Lower in urban	Higher in urban	Lower in urban	Unimportant or equivalent	Unreported
Songbirds							
Nest	14	20	5	2	10	3	24
First year	1	5	2	0	0	0	8
Adult	6	3	1	0	0	0	10
Birds of prey							
Nest success	3	3	4	0	1	1	8
First year	2	1	1	0	1	1	2
Adult	1	3	0	0	0	1	3
Mammals[a]							
Adult rodents	3	2	0	0	2	0	3
Adult mesopredators	3	4	0	0	4	2	1
First-year mesopredators	2	0	0	0	2	0	0

Note: Studies in which low or equivalent predation rates were documented in urban and nonurban habitats (*unimportant or equivalent*) or in which predation rates were not reported relative to changes in urbanization (*unreported*) are also summarized here. Investigations in which results were reported for more than one species or life stage (i.e., *nest*, *first year*, *adult*) were included multiple times. Studies of urban gradients in which results were reported for more than one habitat type within the categories of *urban* or *nonurban* were included if the survival or predation response to urbanization was linear or if the two response types did not differ between habitat types within a category. In two studies not included in the table, burrowing owl and American crow (*Corvus brachyrhynchos*) survival exhibited a hump-shaped curve in response to increasing urbanization.

[a]Three comparative studies of survival were found for two large mammal species—two for the black bear (*Ursus americanus*) and one on the white-tailed deer (*Odocoileus virginianus*). These were not included in the table because of a lack of additional studies on these taxa.

2007), which suggests that this predator may have little impact on nest survival in urban settings.

Like the songbird studies, comparative investigations of mammalian mortality generally showed little response or greater survival with increasing urbanization (table 2). Small mammals such as the fox squirrel (*Sciurus niger*) exhibited lower mortality rates in more urbanized habitats (McCleery et al. 2008), whereas the survival of other species, such as the Norway rat, was unaffected by urbanization (Glass et al. 1989). A recent review on the order Carnivora concluded that urban and rural carnivores generally do not differ in mortality rates (Iossa et al. 2010). However, some species, such as the domestic cat and raccoon, have elevated survival rates in cities (Prange et al. 2003, Schmidt et al. 2007). Where sources of mortality were reported, predation rates were routinely lower in urban environments (table 2). For some species, depredation strongly affected rural population dynamics (e.g., McCleery et al. 2008), whereas other mammals appeared to be more affected by disease and collisions with automobiles, regardless of the degree of urbanization (e.g., raccoons; Prange et al. 2003).

An alternative to measuring survival rates is to assess the changes in predation pressure by documenting antipredator behavior. Organisms respond to the threat of predation with a wide variety of behaviors, including flocking or schooling, altered habitat selection, and increased vigilance (Caro 2005). These responses represent a trade-off between avoiding depredation and engaging in other activities, such as foraging, social interactions, or care for offspring (Brown 1988). Consequently, if all other factors are equal (e.g., food availability, social standing, reproductive potential), an organism should display increased antipredator behavior where predation pressure is greater (Caro 2005).

Antipredator behavior has been studied experimentally by quantifying giving-up densities and flight-initiation distances. The former measures the risk of predation by focusing on foraging efficiency with the assumption that organisms will consume less food where the chance of being depredated is greater (Brown 1988). Giving-up density experiments on songbirds (Shochat et al. 2004) and squirrels (Bowers and Breland 1996) have shown that urban animals routinely consume more food than their nonurban counterparts. These results support the notion that the risk of predation is lower in more developed areas. Flight-initiation distances measure how close an organism is willing to allow a potential predator to approach before it flees. These distances are generally shorter in more urban areas for songbirds and squirrels (e.g., McCleery 2009, Møller 2009; but cf. Valcarcel and Fernández-Juricic 2009), which again suggests that the perception of predation risk is lower in more urbanized settings.

The collective evidence supports the idea that predation pressure on vertebrate prey is lower for urban populations than for nonurban ones—or, at the very least, they are similar. In very few studies were lower survival rates documented in urban habitats. Studies of adult songbird survival and giving-up density experiments offer strong support for predation relaxation, as does the majority of the literature on flight-initiation distances. The nest survival rates of songbirds are dependent on the scale of urbanization considered; urban development of the landscape surrounding habitat fragments does not affect nest failure within the fragments, whereas development of the habitat itself generally improves nest survival. Survival of first-year birds appears to be unaffected by urbanization. Studies of mammals have produced more equivocal results. The population dynamics of some species may not be strongly influenced by predation, regardless of the degree of urbanization; this is particularly true for larger mammals. However, where depredations have been directly documented, the predation rates on bird nests and mammals are consistently lower in more urban contexts. Although more research may further clarify how predation pressure on various taxa changes with urbanization, the evidence to date suggests that predation relaxation may be occurring in urban landscapes.

The predation paradox revisited

The weight of evidence to date indicates that overall predator numbers tend to increase with urbanization, whereas the predation pressure on urban populations may be lower than that in nonurban areas, which gives credence to the predation paradox. Trophic linkages between predators and prey appear to be decoupled such that predator abundance does not reflect the predation levels experienced by urban prey (Rodewald et al. 2011). This decoupling underscores a profound difference between urban and natural environments, not only in terms of habitat structure but also in terms of the mechanisms shaping vertebrate communities (Shochat et al. 2006). What are the potential mechanisms that could explain low predation rates in urban areas in which predator densities are high?

The predation rate of a population is the proportion of that population killed by predators per unit of time. This rate is a function of the population sizes of the predators and prey and the average consumption of prey per predator (Mills 2007). Reductions in predator numbers or in per capita prey consumption or an increase in prey abundance can depress predation pressure. Because predator numbers appear to be relatively high in urban habitats, prey must be hyperabundant or the per capita prey consumption must be drastically lowered in order to account for reductions in predation pressure. A number of mechanisms, which are not mutually exclusive, could increase prey abundance or reduce the proportion of vertebrate prey in predator diets (Stracey 2011). Below, we describe each potential mechanism as a hypothesis explaining the predation paradox.

Predator subsidy consumption. Humans import massive amounts of resources to sustain our urban and suburban lifestyles (Faeth et al. 2005, Shochat et al. 2006). Fertilizer and water subsidies sustain plants for a longer period of the

year, which in turn produces more abundant and predictable crops of seeds and fruits compared with native vegetation (Shochat et al. 2006). Many people provide wildlife with food either directly (e.g., bird feeding; Robb et al. 2008) or indirectly (e.g., pet food or garbage; Chace and Walsh 2006). The net effect is a subsidization of natural food resources that is likely to increase the carrying capacity of urban environments for many species. Nearly all omnivorous predators (including mammals and birds) consume anthropogenic food in cities, although the dietary proportion varies by species (Iossa et al. 2010). Domestic cats take fewer prey as urbanization increases (Churcher and Lawton 1987), and a greater availability of anthropogenic food has been associated with higher survival rates for urban raccoons (Prange et al. 2003). The combination of abundant food resources and diet shifts could result in much larger populations of omnivorous predators that consume fewer vertebrate prey per capita (Chace and Walsh 2006, Rodewald et al. 2011). The predator subsidy consumption hypothesis proposes that the change in diet composition is sufficient to reduce predation pressure on prey species, regardless of increases in the number of omnivorous predators.

Prey hyperabundance. One of the general trends to emerge from the many studies of urban community ecology is that certain prey species increase in abundance with urbanization (McKinney 2006). Some native songbird species reach higher densities in urban areas than in adjacent native habitats, and invasive human commensals such as house sparrows (*Passer domesticus*) often dominate the urban fauna in terms of relative abundance (Marzluff 2001). The hyperabundance of prey could reduce the impact of predation in urban settings if the increase in prey populations is much larger than concurrent increases in the number of prey consumed. Bottom-up forcing driven by the availability of anthropogenic foods in urban environments could support much larger populations of certain prey species than exist in rural habitats. As a result, prey species may escape the predation trap of top-down regulation if their densities remain great enough that predators cannot consume sufficient numbers to limit the prey's population size.

Prey specialization. Carnivorous predators cannot benefit directly from anthropogenic subsidies, but they may be affected indirectly. As was previously discussed, the abundance of some prey species may be greater in urban habitats because of the availability of anthropogenic food. Avian carnivores exhibit diet shifts in urban habitats and focus primarily on the most abundant prey species available, depending on the predator's body size. For example, Cooper's hawks switch from a more generalist diet to one dominated by medium-sized birds such as European starlings (*Sturnus vulgaris*) and dove species (Estes WA and Mannan 2003). The result of such specialization could be a reduction in predation pressure on other potential prey. Because the most abundant species in urban habitats are often exotics,

native species are likely to be the primary beneficiaries of prey specialization (Roth and Lima 2003). If specialization does not occur, the hyperabundance of a few species would probably lead to the population growth of predators and to more depredations on other prey (i.e., *apparent competition*; Bonsall and Hassell 1997).

Predator composition. Stracey (2011) noted that predatory taxa differ in their impacts on prey populations. She hypothesized that nonurban predators have a strong effect on prey dynamics (because of high rates of prey consumption) but are replaced in urban areas by species that exert less top-down control on those prey populations. We found that the composition of predators does change with urbanization. For example, species richness of snakes declines with increasing urban development (Patten and Bolger 2003), whereas exotic predators such as cats are more common in urbanized habitats (Sims et al. 2008). Snakes are one of the primary predators of bird nests in nonurban environments, and their extirpation from cities could lead to a substantial reduction in predation pressure (Patten and Bolger 2003). Cats, on the other hand, reach their greatest densities in metropolitan areas, but their depredations may be insufficient to exert top-down control on avian prey (Sims et al. 2008).

Prey composition. Shochat (2004) proposed that wildlife communities in cities may reflect the "ghost of predation past," whereby urban predators have extirpated all species that were vulnerable to predation. As a result, the prey species that remain are adapted to city predators and experience lower levels of predation than do nonurban prey. We are aware of only one study in which the survival rates of multiple urban and nonurban species have been examined. Møller (2009) compared mortality rates and flight-initiation distances of pairs of related species in which one had colonized urban environments and the other had not. He found that the urban species generally had greater adult survival rates and shorter flight-initiation distances, which suggests that predation pressure may be lower for urban birds because of intrinsic characteristics of the species able to inhabit cities (Møller 2009).

A way forward: A new conceptual model of urban trophic dynamics

The apparent existence of the predation paradox creates the need for a new conceptualization of urban trophic dynamics that reflects the complexity of processes shaping urban wildlife communities. Traditional views of predation and urbanization are focused on two trophic levels: predator and prey. The strength of the interaction between the two is determined by changes in top-down control produced by increases or decreases in predator numbers (Tomialojc 1982, van Heezik et al. 2010). However, the predation paradox reflects a disconnect between predator numbers and predation pressure, necessitating alternative explanations for variation in top-down effects (Rodewald et al. 2011).

The hypotheses proposed to explain the paradox suggest a variety of mechanisms that could be interacting to influence urban trophic dynamics. These potential mechanisms involve altered bottom-up effects on predators and prey, diet shifts of predators, and changes in the community composition of predators and prey that could interact to mediate top-down regulation.

We propose a conceptual model that integrates the hypotheses as a framework for understanding and further examining trophic interactions and their ramifications for community structure in urban environments (figure 2). The greater abundance of anthropogenic foods in cities relative to nonurban areas could support larger populations of omnivorous mesopredators and could lead to diet shifts away from vertebrate prey (*predator subsidy consumption*). Human-provided foods may also increase the numbers of

prey species to the point that predators can no longer exert top-down control (*prey hyberabundance*). Abundant prey could lead to an increase in the number of carnivorous mesopredators and their consumption of the most common prey species, thereby reducing predation pressure on other urban vertebrates (*prey specialization*). In addition, predatory species that regulate prey populations in nonurban areas may decline in abundance with urbanization and may be replaced by other predators that consume fewer vertebrates (*predator composition*). The types of prey species may also change with urbanization, such that urban prey may be less vulnerable to predation than species inhabiting nonurban environments (*prey composition*). Finally, the extirpation of top predators from cities could release mesopredators from top-down control, which might lead to larger population sizes (*mesopredator release*; Prugh et al.
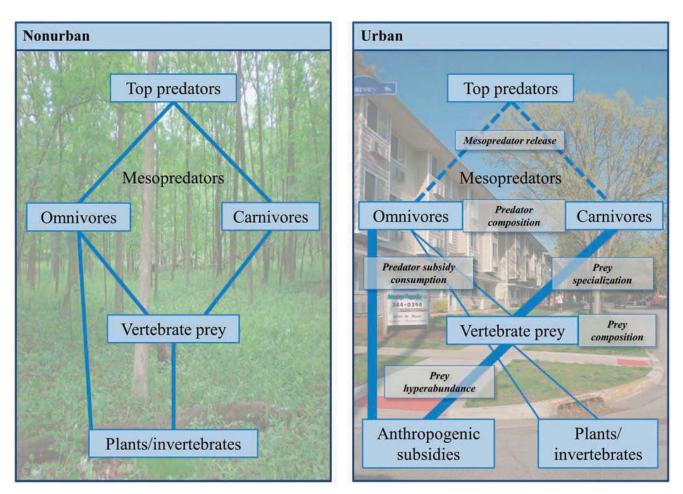

Figure 2. A conceptual model of the differences in trophic dynamics between urban and nonurban habitats and the hypotheses (in italics) proposed to explain these differences. The lines represent connections among trophic levels, and line thickness in the urban panel indicates an increase or decrease in the strength of the trophic interaction relative to nonurban environments. The dashed lines refer to an interaction that does not occur in the urban context. The hypotheses situated on top of the interaction lines indicate the connections and trophic levels to which a particular hypothesis pertains. Two hypotheses (predator and prey composition) are located within a particular trophic level to indicate that they refer to alterations in trophic dynamics that are driven by changes in the identity of the species in nonurban and urban habitats. See the "Predation paradox revisited" section for more details on the hypotheses. Photographs: Sarah H. Cleeton.

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Box 1. Predictions derived from hypotheses represented in the model of trophic dynamics of urban vertebrates (figure 2).

Predator subsidy consumption
The proportion of anthropogenic food in the diet of mesopredators will increase with urbanization.
Predation rates on vertebrates preyed on by mesopredators will decline with urbanization.

Prey hyperabundance
The proportion of anthropogenic food in the diet of some prey species will increase with urbanization.
The abundance of these species will increase with urbanization.
The predation rate on these species will decline with urbanization.

Prey specialization
The diet of carnivorous mesopredators will be increasingly dominated by a few species with urbanization.
These prey species will be hyperabundant within cities.
The predation rate on prey species that are not hyperabundant will decline with urbanization.

Predator composition
The abundance of species of predators with a high proportion of vertebrate prey in their diet will decline with urbanization.
The abundance of species of predators with a low proportion of vertebrate prey in their diet will increase with urbanization.
Predation rates on vertebrate prey will decline with urbanization.

Prey composition
The abundance of species of prey experiencing high predation rates will decline with urbanization.
The abundance of species of prey experiencing low predation rates will increase with urbanization.

Mesopredator release
The abundance of large-bodied predators will decline with urbanization, whereas the abundance of mesopredators will increase.

See the "Predation paradox revisited" section for more details on the hypotheses.
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about trophic changes in city centers. Consequently, the proposed model is most applicable to a comparison of rural or natural habitats with urban landscapes that reflect a mixture of residential neighborhoods, commercial developments, and managed open space (e.g., parks).

From nonurban to urban habitats, the hypotheses summarized in the conceptual model predict changes in community structure and the strength of trophic interactions (box 1). These predictions can be tested with detailed data on the diets and abundances of predators and prey along gradients of urbanization. Such information is necessary to further support or refute the existence of the predation paradox and to determine which of the alternative hypotheses are shaping trophic dynamics in cities. For example, the predator subsidy consumption hypothesis predicts changes in diet with urbanization for a given predatory species, whereas the predator composition hypothesis posits that it is the relative abundance of different predators that varies with development rather than a variance in species-specific diets. However, most of the hypotheses are not mutually exclusive and may act synergistically. For example, increasing anthropogenic food in the diets of both mesopredators and prey could contribute to reduced predation rates and increases in prey abundance in cities.

2009). This last hypothesis was not discussed as an explanation of the predation paradox because it predicts greater predation pressure in urban areas in contrast to the central tenet of predation relaxation. Nonetheless, it could contribute to predator proliferation in cities and was therefore included in our conceptual model.

We recognize that our model is a simplification of urbanization. Development does not proceed along a linear path from nonurban to urban but, rather, encompasses a series of processes that result in diverse landscape configurations between the extremes of wilderness and highly developed city centers (Ramalho and Hobbs 2011). Nevertheless, we propose that vertebrate communities generally respond to urbanization in consistent ways, culminating in differences between nonurban and urban habitats that are reflected in the model (figure 2). It is possible that vertebrate responses to urbanization change in the most highly developed portion of cities (Marzluff 2001), but because limited empirical data are available for this habitat, we do not speculate

The key to testing the predictions derived from the hypotheses (box 1) will be investigating multiple predator and prey species simultaneously. Previous work has been focused on single species (e.g., Estes WA and Mannan 2003), which makes it difficult to understand species-specific and cumulative impacts of different predators on their prey. The vertebrates to be investigated will vary by region, but certain cosmopolitan species, such as the domestic cat or the house sparrow, will be central to most investigations of trophic dynamics. Gathering multispecies data on diet and abundance will allow for correlative studies that can support or refute the proposed hypotheses (box 1). Experimental and modeling projects will be crucial to exploring causal links between trophic dynamics and community structure. By manipulating the population sizes of particular predators or anthropogenic food availability and by tracking the consequent changes in predation rates and abundances (e.g., Stoate and Szczur 2006), the impacts of top-down and bottom-up factors may be teased apart. Predator exclosures

around nests, dens, burrows, or roosts may also be effective ways to experimentally reduce species-specific predation (e.g., Newhouse et al. 2008). Where such manipulations are not feasible for ethical and cultural (e.g., introducing or removing predators; Sims et al. 2008) or practical (e.g., convincing homeowners to stop providing food for wildlife; Jones 2011) reasons, modeling can be used to explore population responses to changing food availability, diet composition, and predator abundance (e.g., van Heezik et al. 2010).

Perhaps the reason such multispecies investigations have yet to be conducted is the difficult and time-consuming nature of traditional diet studies. Methods for this type of research rely on radio tracking or observing prey and predators to record depredations (e.g., Roth and Lima 2003) or on obtaining diet samples by lethal sampling, stomach flushes, or fecal analysis (Valentini et al. 2009). Techniques for recording depredations require a great deal of time and yield small sample sizes. Processing diet samples requires expert knowledge to identify dietary components on the basis of morphology, and the results are often biased because of the differential digestibility of various food types (Valentini et al. 2009). Recent technological advances may make investigations of diet more tractable, however. Stable isotope analyses can reveal changes in consumption at different trophic levels (including anthropogenic foods) but generally cannot provide more detailed information on diet composition (Newsome et al. 2010). DNA barcoding can give a more complete and accurate taxonomic resolution of dietary components than can other methods, but assessing the proportion of different foods in the diet remains a challenge (Valentini et al. 2009). Despite the limitations of these techniques, they offer the potential to characterize larger numbers of diet samples more rapidly than would be possible under traditional methodologies.

Conclusions

The evidence to date suggests that a predation paradox may be occurring in the cities of North America and Europe, although more research is needed in different climatic zones throughout the world to determine to what extent predation relaxation and predator proliferation are characteristic features of landscapes undergoing urbanization. Regardless of the universality of the paradox, traditional conceptualizations of predation and urbanization are overly simplistic, and a new research framework is needed to advance the study of urban trophic dynamics. We believe that the interplay between increased bottom-up forcing and reduced top-down control is key to understanding trophic interactions in metropolitan environments. Comprehensive studies of the diets and abundances of predators and prey, coupled with experimental manipulations and modeling efforts, will be required in order to assess the relative importance and interaction of different potential mechanisms that could be shaping trophic dynamics in cities. Finally, more research in all the various habitats produced by urban development is warranted to determine whether the model proposed here is adequate or must be replaced with a more complex conceptualization of trophic dynamics.

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