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Carnivore Behavior and Ecology, and Relationship to Urbanization

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WHAT IS A CARNIVORE?

Ever since there have been animals, there have been carnivores; that is, organisms that kill and eat animal species and thus live a carnivorous lifestyle. There are carnivorous plants, intertidal anemones, and insects, and in the vertebrate world, any number of fish, snakes, and birds are carnivorous. Even among mammals a variety of species are part-time (e.g., bonobos; Hohmann and Fruth 2008), mostly (e.g., bats; Bonato et al. 2004), or even obligate (e.g., tiger quolls; Belcher et al. 2007; or killer whales; Baird et al. 2006) carnivores. The carnivores we are concerned with here are some of the species that compose the mammalian order Carnivora.

Here we introduce the variety of carnivoran species that occur in the world and try to make clear how diverse a group they are. We consider their taxonomic relationships and give examples of the tremendous variation in carnivore geographic distribution, morphology, ecology, and behavior, including their interactions with prey and with other predators. Finally, we introduce the consequences of this variation in biology with respect to interactions with humans and particularly with urban environments. Specific comparisons between urban and rural populations will be made in the species chapters (4–12) and between species, genera, and families in the taxonomic comparisons chapter (13). Here we provide the basic knowledge of the family and how its members may respond to urbanization.

TAXONOMIC CONSIDERATIONS

The origin of the order Carnivora dates to between 60 and 55 million years ago (mya), and these earliest carnivorans were miacids and viverravids (Flynn 1996). By about 25–35 mya, the extant families of Carnivora had differentiated and are identifiable morphologically through fossil remains and chemically through genetic analyses. An additional family that had differentiated from one of these groups about 20 mya, the Amphicyonidae, or “bear dogs,” died out about 6–9 mya (Hunt 1996). Within the extant taxa, some species are basically monophyletic (e.g., red or lesser panda, although they are most closely related to the raccoon family) and have no current ancestors with any relationship much closer to them than to any other carnivoran. However, others (e.g., cats in the “Ocelot” lineage) have many closely related or sister species with which they share a common ancestor perhaps less than 1 mya (Johnson et al. 2007).

Of the approximately 270 living species in 11 families classified as Carnivora (Wozencraft 1989; but see Dragoo and Honeycutt 1997; Macdonald 2006), 34 or so species are marine carnivorans in 2 families, the Otariidae (sea lions and walruses) and the Phocidae (seals). The other 9 families are considered terrestrial and related as 2 suborders: the Feliformia, including cats (Felidae), civets and genets (Vivveridae), mongooses (Herpestidae), and hyenas (Hyaenidae); and the Caniformia, including dogs (Canidae), bears (Ursidae), raccoons and coatis (Procyonidae), and weasels, otters, and badgers (Mustelidae). Also, recent genetic studies have consistently demonstrated that skunks and stink badgers descend from a common ancestor and together form a separate familial lineage (Mephitidae) that diverged before the split between Mustelidae and Procyonidae (Dragoo and Honeycutt 1997).

Among these terrestrial groups, the Hyaenidae has the smallest number of species ($n = 4$) and has the least size diversity (about fivefold difference in mass between the aardwolf and the spotted hyena), while the Mustelidae number about 55 (Wozencraft 1989) and vary 1,000-fold in size (least weasel vs. sea otter). There are no ursids or procyonids in Africa, though they occur on all other continents except Antarctica (where there are no terrestrial carnivorans) and Australia (where only introduced canids and felids occur; Hunt 1996). Viverrids, herpestids, and hyenids are absent from North and South America but occur in Africa and Asia (and introduced mongooses occur on

some Caribbean and Hawaiian islands). Procyonids and skunks occur only in North and South America, and stink badgers occur only in Java. Canids and felids have worldwide distributions on all continents except Antarctica.

Overall carnivore diversity has been assessed quantitatively in Africa (Mills et al. 2004), the Neotropics (Loyola et al. 2008), and worldwide (Sechrest et al. 2002). In Africa, where 70 species occur, carnivoran diversity is not highest in the biologically diverse rain forests of Central Africa as one might expect; rather, the “hot spots” (top 10% richest areas) for carnivoran species are in East Africa and the northern parts of southern Africa (Mills et al. 2004). In the Neotropics, carnivore phylogenetic diversity is greatest in rain forest ecoregions, whereas for large-bodied carnivores, the tropical Andes are important (Loyola et al. 2008). Worldwide, about 89% of carnivore species occur in at least 1 of 25 previously identified hot spots (Sechrest et al. 2002).

DISTRIBUTIONAL VARIATION OF SPECIES

Aside from domestic dogs and cats, red foxes have the widest geographic variation of any carnivore (70 million km²; Macdonald and Reynolds 2004), but several other species range across multiple continents. For example, brown bears live throughout the Holarctic, striped hyenas occur across Africa and Eurasia, and pumas range from the southern tip of South America into the Rocky Mountains of western Canada (Macdonald 1992; Jackson and Nowell 1996).

In contrast, a number of species have restricted ranges. Seven of the eight carnivore species found on Madagascar (e.g., the fossa, a viverrid) are endemic to the island; the other, the small Indian civet, was introduced there (Hawkins and Racey 2008). Ethiopian wolves are an endangered endemic species restricted to isolated Afro-alpine regions (mountain “islands”) of Ethiopia (Sillero-Zubiri and Marino 2004). Island foxes occur only on six small islands off the west coast of California in the United States (Roemer et al. 2004), and Iriomote cats, the most endangered felid species (a total population of about 100 individuals), are inhabitants of a single island in the western Pacific Ocean about 200 km east of Taiwan (Jackson and Nowell 1996).

Many carnivoran species have experienced major reductions in their geographic range due to persecution and habitat reduction by humans (e.g., African

wild dogs; Woodroffe et al. 2004), but a number of species' ranges have been expanded as a result of introductions (Boitani 2001) or human-caused landscape changes. For example, red foxes are common in Australia but were introduced there (Macdonald and Reynolds 2004). The small Indian mongoose was introduced to several islands in the Caribbean and Hawaii where it also has thrived (Hoagland and Kilpatrick 1999). Introduced raccoon dogs now have a wider geographic range in northern and eastern Europe than their natural range in the Asian Far East (Kauhala and Saeki 2004). Finally, coyotes have greatly expanded their range in North America, not through introduction but rather on their own and likely as the result of land conversion and the removal of wolves since 1900 (Moore and Parker 1992).

On every continent of the world except Antarctica, many species of carnivores are found; plant and animal prey of all sorts are distributed similarly. This also means that many species are well adapted to extremes in temperature, precipitation, and topography. For example, polar bears (Ferguson 2000) spend much of their lives on the Arctic ice pack. The habitat of Ruppell's fox typically includes sand and stone desert across the Sahara of northern Africa and the Middle East (Cuzin and Lenain 2004). Binturongs, a viverrid also known as the Asian bearcat, thrive in the rain forests of Southeast Asia (Grassman et al. 2005). Alternatively, snow leopards live throughout the high, cold mountain ranges of Central Asia (McCarthy and Chapron 2003), and meerkats (or suricates) inhabit all parts of the relatively flat and hot Kalahari Desert in Botswana and South Africa (Clutton-Brock et al. 2001).

The degree of disparity in habitat use within species also varies. Aside from those species whose absolute geographic range, and thus variation in habitat use, is extremely small, there are other species, some of which have rather large geographic ranges, whose habitat preferences are still very narrow. Black-footed ferrets, for example, live only in the grasslands of the Great Plains of North America, where they are obligate predators on prairie dogs, a ground-dwelling rodent (Miller et al. 1996). Similarly, giant pandas live only in bamboo forests of Asia (Schaller et al. 1985). Conversely, wolves range from arctic tundra in Siberia to deserts in the Middle East to rain forests in western Canada (Fuller 2004), and leopards occur in African deserts, Indian jungles, and northern forests in the Russian Far East (Jackson and Nowell 1996).

VARIATION IN ECOLOGY AND BEHAVIOR

Although most differences in species' distributions have a historic, evolutionary genesis, the consequential strategies for continued survival have resulted in tremendous variation in carnivore ecology and behavior. What follows is a cursory review of some of these contrasts.

Morphology and Physiology

Body sizes (weights/masses) of the Carnivora range from the 100-g least weasel to the 800-kg polar bear (Gittleman 1989b). Body weight is not correlated with habitat, activity cycle, or latitudinal gradients, but there are significant differences in body weight among insectivorous, herbivorous, and carnivorous species, and, among predatory carnivores, prey size and diversity increase with body weight (Gittleman 1985).

One can easily imagine that, given the badger's digging, the otter's fishing, or the cheetah's chasing, the skeleton and thus body proportions of carnivores also vary tremendously (Ewer 1973). Ambulatory bears and digging badgers have plantigrade (heel-on-ground) stances and relatively shorter legs than, for example, cursorial canids, which are digitigrade (toe-runners; Taylor 1989). It also follows that the variation in dental adaptations of carnivores is great as well; felids are often pure meat eaters with large cutting carnassial teeth, whereas frugivorous/plant-eating bears or shell-crunching otters have broad, grinding molars, and bone-crushing spotted hyenas have stout conical premolars and molars (Van Valkenburgh 1989).

In general, the digestive system of carnivores is simple, especially for those species (e.g., cats) consuming mainly easily digested meat; their gut length is only four times their body length (Ewer 1973). Some species have relatively long guts (e.g., sea otters), and others (e.g., spotted hyenas) produce copious hydrochloric acid to help dissolve bones (Macdonald 1992). The caecum, or gut pocket, of carnivores is usually absent or relatively small, though in canids it is prominent (Ewer 1973).

Some carnivores, like the canids, are typically seasonal breeders that regularly come into estrus (spontaneous ovulators), mate, and produce pups fifty to seventy days later (Ewer 1973). Others, like American mink and striped skunks, are induced ovulators (eggs released after behavioral, hormonal, or physical stimulation; Larivière and Ferguson 2003), with similar-length gestation periods. However, some ursids

and mustelids and both "pandas," though spontaneous ovulators, have delayed implantation, or embryonic diapause and, as a result, have gestation periods lasting 95–365 days (Mead 1989).

Highly efficient sense organs seem essential for predators, both for capturing prey and for interacting successfully with one another. The eyes of nocturnal species usually have a relatively large anterior chamber with a large, curved lens and a highly convex cornea, as well as the presence of one or more layers of reflecting cells, the tapetum lucidum, outside the receptor layer of the retina (Ewer 1973). Carnivores also often have binocular vision, as well as a nictitating membrane, further enhancing visual acumen. The potential for carnivores to hear well is reflected in the facts that red foxes need to listen for rodents, aardwolves for termites, and hyenas for prey calling in distress (Mills et al. 2001). From a social perspective, it is not uncommon to hear wolves howl, lions roar, dholes whistle, hyenas whoop, or African wild dogs twitter to maintain communication among their kind (Peters and Wozencraft 1989). Similarly, olfaction plays a key role in prey capture (Cushing 1985) and carnivore social organization (Gorman and Trowbridge 1989).

Population Ecology

The rate at which an animal population could potentially increase is a result of several factors, all of which vary widely among carnivore species. The first age of reproduction of many species is 1-year-old, but for other large species, such as black bears, it may be as old as 6 years (Kasworm and Thier 1994). Similarly, number of offspring produced per reproductive event (litter size) varies from only 1 (e.g., giant panda) to 19 in arctic foxes (Ovsyanikov 1993). Most small- or medium-sized carnivores, especially in temperate areas, produce a litter every year after reaching maturity, but bears only reproduce every 2, 3, or 4 years, depending on species and location (Dahle and Swenson 2003). In monogamous species (e.g., red foxes), every adult of breeding age could potentially breed; for some social species, however, reproductive suppression of subordinates can result in a substantial portion of adults not producing offspring in a given year (e.g., >80% for dwarf mongooses; Creel 1996). Given this variation in parameters, it is easy to understand that populations of monogamous species with an early age of first reproduction, a large litter size, and young that disperse and breed quickly have a high potential of increase (e.g., 1.5- to 2.0-fold/year for wolves; Mitchell et al. 2008).

Conversely, some species with low reproductive rates (old age at first reproduction, small litters, long intervals between litters) have a low potential rate of increase (e.g., 5%–10%/year for brown bears; Garshelis et al. 2005).

Within species, the density of carnivores varies from one to over three orders of magnitude, and though obviously affected by intensity of mortality, a species' density is ultimately determined by the availability of food (Fuller and Sievert 2001); in fact, a comprehensive analysis of the entire order of carnivores indicated that, in general, 10,000 kg of prey supports about 90 kg of a given species of carnivore, irrespective of body mass (Carbone and Gittleman 2002). Food affects a species' density because relatively more abundant food resources result in better physical condition and thus affect reproduction by lowering first age of reproduction, increasing litter size, and/or lowering mortality rate of juveniles (Fuller and Sievert 2001). Poor food resources result in increased mortality of adults, larger home ranges, and increased rates of movement (Fuller and Sievert 2001).

Food Habits

Not all Carnivora are carnivorous. In fact, most are omnivorous. In addition to animal prey, some vegetation (often high-calorie fruits or nuts) is also consumed. Felids are usually considered the most obligate of carnivores (Ewer 1973), and canids, bears, viverrids, and perhaps procyonids are the most omnivorous and have the most generalized diet. Many carnivores scavenge (DeVault et al. 2003), yet cats rarely do so (but see Bauer et al. 2005); canids do so fairly frequently (e.g., Schrecengost et al. 2008), and hyenas do so quite often (e.g., brown hyenas; Mills and Mills 1978). Some species are mostly myrmecophagous in that they specialize in feeding on ants and termites (e.g., aardwolf; Richardson 1987; Kruuk and Sands 1972; and sloth bear; Joshi et al. 1997). Similarly, giant pandas are bamboo specialists (Schaller et al. 1985), and black-footed ferrets eat only prairie dogs (Miller et al. 1996). Within a species, diet can vary greatly, depending on the resources available (e.g., Iriarte et al. 1990), and for many carnivore species, what they eat depends on "what they can get" (Ewer 1973). Even within an area, diet may change as prey availability changes (e.g., O'Donoghue et al. 1998; Corbett and Newsome 1997).

Overall, it is doubtful that there are animal prey species that some type of carnivore does not eat. Size certainly doesn't matter; wolves kill 1,000-kg bison (Smith

et al. 2000), tigers kill 1,500-kg gaur (Karanth and Sunquist 1995), and lions even hunt young elephants (Loveridge et al. 2006), but bat-eared foxes eat termites (Clark 2005). Massive brown bears feast on army cutworm moths (*Euxoa auxiliaries*; White et al. 1998); and 300-g stoats prey on >2,000-g lagomorphs (McDonald et al. 2000). Skunks eat bird eggs and nestlings, insects of various sorts, and apparently even clams (Cuyler 1924), and various viverrids and other small carnivores eat fish, reptiles, amphibians, and crustaceans (Ewer 1973; Wang and Fuller 2003).

Behavior

The daily activity patterns of carnivores range from almost exclusively nocturnal (e.g., large-spotted genets; Fuller et al. 1990), to crepuscular (active mostly at dawn and dusk; e.g., African wild dogs; Fuller and Kat 1990), to almost exclusively diurnal (e.g., cheetahs; Caro 1994). Species often are active throughout the day and night but at varying levels (e.g., spotted hyenas; Kolowski et al. 2007). Activity patterns within a species may also vary with levels and kinds of human activities (e.g., coyotes; Kitchen et al. 2000; red foxes; Baker et al. 2007) or with the composition of competing carnivore species (e.g., jackals; Fuller et al. 1989). With regard to seasonal activity patterns, some carnivore species have highly regularized breeding and denning dates (e.g., wolves; Fuller 1989a), but others have no fixed breeding season (e.g., lions; Haas et al. 2005). Home ranges vary in size between winter and summer for some species (e.g., wolves; Fuller 1989b), largely in relation to changes in prey distribution and thus changes in habitat use (e.g., Koehler 1991).

Most small, nocturnal carnivores and all felids (except for lions and domestic cats) are solitary except for females with offspring (raising them alone) and during mating season (Bekoff et al. 1984; Eisenberg 1989). This does not mean that they do not communicate through vocal olfactory or even visual signals but rather that they don't regularly travel together or interact directly. Many species in other taxa, however, have evolved various levels of sociality from monogamous pairings (e.g., maned wolves; Rodden et al. 2004) to groups, clans, packs, or prides of >25 members (e.g., white-nosed coati; Gompper 1997). Additional group members may provide extra provisioning for offspring, increase hunting efficiency, or provide increased protection (Bekoff et al. 1984; Gittleman 1989b). Intraspecific variation in social organization, primarily due to differences in food resources and habitat (Bekoff et al. 1984), is at least

as large as that among species (e.g., golden jackals; Macdonald 1979a).

Carnivores hunt for and kill prey in different ways, constrained by inheritance expressed by morphological specializations and dependent on prey type and behavior (Sunquist and Sunquist 1989). Searching for prey likely always involves traveling through patches of habitat where success has previously occurred, regardless of capture technique. For many carnivores hunting among thick vegetation or other cover, prey are typically captured from ambush or a stalk and short rush or chase (Sunquist and Sunquist 1989). Such hunting may be carried out singly (e.g., a weasel or snow leopard) or in large groups (e.g., lions). Conversely, groups of wolves, African wild dogs, and spotted hyenas employ long-distance chases of prey, some covering as much as 20 km (Mech and Korb 1978). Still, foxes pounce on mice they hear through the snow, bears turn over logs and lick up ant pupae, and many individual carnivores hunt in several ways during the same foraging bout, depending on the food types that are available.

An individual's home range size (the area regularly used by an individual) is determined by several factors. First, range size increases with metabolic needs, and thus larger individuals, all else being equal, have larger ranges (Gittleman and Harvey 1982); it also follows that ranges of groups are larger than for individuals. Furthermore, trophic level affects range size; in particular, meat eaters of a given body mass have larger ranges, and intraspecific variation in feeding patterns causes variation in range size (Gittleman and Harvey 1982). Within a species, range size increases in proportion to prey density (e.g., bobcats; Knick 1990), and distribution of patches of food within a range also affects its size (e.g., Cape clawless otters; Somers and Nel 2004).

Ranges of some carnivores overlap considerably among individuals, depending largely on resource density and distribution (e.g., leopards; Bailey 1993; Marker and Dickman 2005) and genetic relatedness (e.g., black bears; Moyer et al. 2006). Many carnivores have individual- or group-specific defended ranges (i.e., territories) that often do not overlap among the same sex but do overlap between sexes (e.g., fishers; Arthur et al. 1989). Where prey distribution is stable, these territories are often stable, but under other circumstances, they drift (e.g., red foxes; Doncaster and Macdonald 1991) or either move with migrating prey (e.g., wolves; Walton et al. 2001) or are fixed but temporarily left by

individuals to find prey (e.g., spotted hyenas; Hofer and East 1993).

Community Ecology

Aside from interacting with others of their own species and with prey species, carnivores must regularly deal with other species of carnivores (e.g., chapter 14). In circumstances in which food habits do not overlap, resources are distributed widely, and size differences are small, competition is relatively low, and these interactions are relatively benign. In other circumstances, carnivore species may compete intensively, and the results usually are manifested in differences among species with respect to size, diet overlap, habitat-specific abundances, activity patterns, and behavioral dominance (e.g., Fuller et al. 1989; Johnson et al. 1996; Fedriani et al. 2000). Under some circumstances, interspecific killing (Palomares and Caro 1999) takes place, and this can lead to species population regulation and restriction in distribution (e.g., gray foxes; Farias 2000; Farias et al. 2005).

Infectious diseases of carnivores are emerging as an important factor in population viability (Murray et al. 1999). In addition to outbreaks that may decimate specific populations (e.g., lions; Roelke-Parker et al. 1996) and change community structure, noninfectious diseases may act as factors modifying resistance and susceptibility to other diseases (Funk et al. 2001). Some disease risk assessments have been carried out for large, endangered carnivore species (e.g., Ethiopian wolves; Sillero-Zubiri and Macdonald 1997), but small carnivores have been largely neglected, as have disease interactions among carnivore species (Funk et al. 2001).

Carnivores interact with humans in a variety of ways (Clutton-Brock 1996). Historically, many carnivore species were considered competitors for prey, a natural resource in the form of fur and food, or pests because of depredation on livestock (or humans) or as carriers of disease. As a consequence, many species were persecuted relentlessly, and their populations and distribution reduced dramatically. They have served as totems, icons, entertainment, and political "footballs," and some have been domesticated and now number in the millions.

More recently, the role that carnivores play in ecosystem process and stability has been investigated and debated (Ray et al. 2005), giving them yet another, perhaps essential, perceived value. Thus, the need to conserve carnivores, even in the face of perpetual con-

flict with many, has led to wide-ranging discussion of options and strategies for management (Sillero-Zubiri and Laurenson 2001). Aside from the practical reasons for learning more about carnivores to manage them efficiently and reasonably, there is still the point that they are amazing and wondrous organisms that humans unabashedly admire once they have observed them in natural circumstances (Macdonald 2001).

EFFECTS OF URBANIZATION

So, given the amazing variation in carnivore biology and ecology, how might the relatively recent effects of human urbanization affect carnivores? Clearly, the specifics of such interactions will be covered in detail in the chapters that follow. But in terms of general expectations, we might consider the following.

There are exceptions to every rule in ecology, and attempts to generalize within a large and varied taxonomic group such as carnivores often fall short of reality. However, having acknowledged this, it seems clear that carnivores that do well in urban and suburban areas often share several common characteristics. First, it seems like most of the carnivores that inhabit urban and suburban ecosystems tend to be small to medium sized (see chapter 13). The largest carnivores in North America, such as wolves, grizzly bears, and mountain lions, are not usually found within highly developed human landscapes, though they are sometimes nearby (Dickson and Beier 2007; chapter 11). Many urban and suburban carnivores have relatively high reproductive potential; that is, they are capable of having and raising large numbers of young and could be classified as *r*-selected ("fast"-reproducing) species. Coyotes, raccoons, and red foxes fit this description. Females can breed at an early age, can have relatively large litters, and can breed every year, thus potentially producing a large number of offspring in their lifetimes. The black bear, however, is a key exception to these generalizations. It is a large-bodied species with low reproductive potential increasingly inhabiting suburban environments (Lyons 2005).

Perhaps most important, the carnivores that are most well adapted to urban and suburban environs seem to be the ones that are diet generalists (Nilon and Pais 1997; Pickett et al. 2001); that is, they are not picky about what they eat and consume plant or vegetable matter, human refuse, and living or dead animals, depending on availability. A generalist diet, in fact, can lead to many negative interactions between

people and carnivores. Intentionally feeding carnivores table scraps, unintentionally feeding carnivores by not properly containing garbage or leaving out pet food, or mistakenly feeding carnivores by leaving birdfeeders out year-round often leads to human intolerance of carnivores (DeStefano and DeGraaf 2003; Ditchkoff et al. 2006).

What else then, beyond life history, defines the success of urban carnivore species? Perhaps behavioral characteristics such as a tolerance for or lack of avoidance of humans account for the success of many urban carnivore species. Tolerance for humans may be an intrinsic trait ("Species X is more afraid of people than species Y"), but it is more likely a trait with the capacity for plasticity and adaptation both intra- and interspecifically. Synurbanization (Adams et al. 2005; Ditchkoff et al. 2006) is thought to involve an increase in animals' tolerance and even affinity for humans. Many examples of variation in tolerance can be found in this book. For example, some populations of coyotes are more willing to occupy urban lands than are others (Gompper 2002; chapter 7).

Shifts in the behavior of populations or species might occur as a consequence of phenotypic plasticity (e.g., behavioral flexibility) or through genetic evolution, given sufficient opportunity for selection to act. Contemporary evolutionary change (often thought of as occurring within human lifetimes) is generally facilitated by an increase in the strength of selection (e.g., from a disturbance or other environmental change; Stockwell et al. 2003) as well as by genetic isolation of the affected population (Slabbekoorn and Peet 2003). For many carnivores experiencing habitat fragmentation from suburbanization, conditions are likely ripe for facilitating evolutionary responses to the novel urban environments they are encountering (Hendry et al. 2008).

Perhaps even more likely is the possibility that humans both directly and indirectly facilitate adaptation (either phenotypic or genetic) of urban carnivores. People provide food resources to carnivores in all sorts of ways, whether directly (as noted earlier) or indirectly (e.g., providing food and cover to prey species like rabbits and deer). These elevated food resources generally lead to increased densities for species able to occupy urbanized lands (McKinney 2002; Shochat et al. 2006). In addition, urban environments frequently ameliorate climate effects (Kanda et al. 2005; Parris and Hazell 2005) and may even provide refugia for some species from predators (Faeth et al. 2005). Some spe-

cies are already showing behavioral shifts in response to human provisioning (e.g., black bears with reduced hibernation intervals; Beckmann and Berger 2003a). Finally, changes in human behavior, such as reduction in hunting pressures, have been suggested as leading to relaxing previously strong selection pressures on species to avoid humans (Gompper 2002; Geist 2008). All of these factors, from intrinsic behavioral flexibility to altered selection pressures from humans, may lead to surprising shifts in tolerance of humans. This makes us wonder whether there are any species, given adequate resources, truly lacking the capacity to adapt to urban or suburban environments.

CONCLUSION

The aim of this chapter is to illustrate the biological and ecological diversity of carnivore species. Combined with the often amazing capacity for adaptation in carnivores, this diversity makes it difficult to identify more than generalizations regarding their responses to urbanization. We suggest that one project for readers of this book is to extract and to synthesize facts from the growing body of research presented here and then define new, more generalizable predictions about the vulnerability or success of carnivores in response to global urbanization. As understanding grows of the mechanisms limiting the distribution of carnivores in urban settings, we may also find ways to facilitate the success of the more vulnerable species in the face of growing human influences.