Chapter 8 Wildlife Population Dynamics in Urban Landscapes

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Keywords Age structure · Demography · Density · Disease · Genetic structure · Metapopulation · Mortality · Predation · Reproduction · Survival

To say that urban wildlife populations differ from those in other landscapes is, in some ways, to state the obvious, as many studies have well demonstrated how urbanization influences pattern of occurrence and relative abundance of wildlife (e.g., Blair 1996; Marzluff et al. 2001; Sinclair et al. 2005; Chace and Walsh 2006). Identifying the specific ways in which urban and nonurban wildlife populations differ and the drivers of those differences is less understood and requires a more careful examination. The response of a species to urbanization may be the consequence of life history, and behavioral and physiological attributes that promote avoidance, tolerance, or preference for urban systems. For example, urban avoiders, or species that respond negatively to development, tend to be habitat specialists, migratory, and/or sensitive to a wide range of human activities and disturbance (Croci et al. 2008). Species that respond positively to urban development (e.g., synanthropic species, urban exploiters) are often generalists, omnivorous, multi-brooded, and behaviorally flexible. Because these suites of species differ widely in population ecology even in the absence of urbanization, we forgo a direct comparison of these groups of species and, rather, examine how urbanization affects population structure and demography of species occupying both urban and nonurban landscapes (i.e., urban adapters).

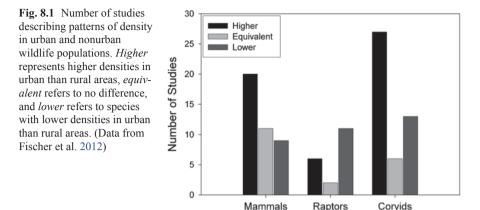
As we synthesize the literature, we recognize the inherent difficulty of clearly defining a "population." What distinguishes a subpopulation from a population? For some species, this may be quite clear because of limited vagility and strong segregation among habitat types; for others, it may be unclear, particularly those with more generalist habitat requirements and extensive mobility across urban

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areas. Although we do not explicitly address population delimitation in our chapter, we alert the reader to the fact that defining a population becomes important when population demography and dynamics, such as vital rates, are the focus.

An important contextual backdrop to studies of urban wildlife is that most have focused on populations, or subpopulations, located within "greenspaces" within the larger urban matrix, or in some cases near the edge of the matrix. Many of the patterns we report are heavily influenced by the preponderance of studies within urban greenspaces, with relatively less attention given to populations living in the developed matrix. Processes we discuss may operate differently, and to different degrees, among populations occurring in the urban matrix proper. We begin this chapter with a review of patterns of population density that are often used to classify species and their relationships with urbanization. Next, we consider how urbanization affects the dynamics (survival and types of mortality, reproduction, and limiting factors) that influence variations in density. We also briefly review metapopulations and genetic structure in urban landscapes, and conclude with a discussion on the importance of understanding the linkages between urbanization and population dynamics for wildlife conservation and management.

8.1 Density

We begin our chapter with an examination of density because, as a noticeable characteristic of urban wildlife, it has been the most common, and oftentimes exclusive, focus of most studies of urban wildlife ecology. In addition, population density or abundance is often the primary indicator used to identify many species as urban exploiters or avoiders, and certainly density has important conservation and management implications.

Many wildlife species reach greater abundances and/or densities in urban than nonurban habitats (Fig. 8.1; Fischer et al. 2012; Møller et al. 2012). The range of

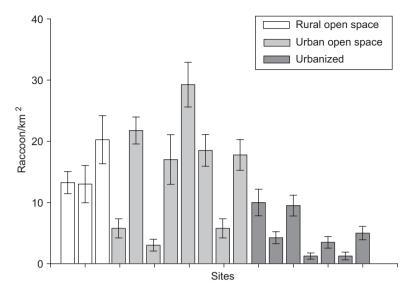


Fig. 8.2 Density estimates for populations of raccoons from 18 sites across the Chicago metropolitan area, based on mark-recapture data, 2005–2006. Populations were classified as occurring in rural natural fragments, urban natural fragments, and those within the urban matrix (urbanized), including industrial sites. (Adapted from Graser et al. 2012)

examples and magnitudes of the differences in density can be striking, with some species reaching $100 \times$ greater densities in cities than rural areas (e.g., blackbird (*Turdus merula*) and magpie (*Pica pica*; Luniak et al. 1997). In general, the greatest shifts in density that occur among mammals in response to urbanization are those of medium-sized, omnivorous species, including European hedgehogs (Erinaceus europeaus) in France (Hubert et al. 2011), and brush-tail possums (Trichosurus vulpecula) in Australia (Stow et al. 2006). A classic urban adapter in the USA, the raccoon (*Procyon lotor*), can reach extremely high densities (>100 raccoons/km²) (Riley et al. 1998; Prange et al. 2003; Hadidian et al. 2010) that are about five times greater than typical nonurban densities (1-20 individuals/km², Gehrt 2003). However, most density estimates are from remnant habitats within cities and estimates for these same species outside preserved areas and within the larger urban matrix are less common. The few extensive mark-recapture studies conducted across urban landscapes, including developed areas, have produced highly variable density estimates. For example, raccoon densities ranged from 37 to 94 animals/km² across the Toronto, Ontario, area (Rosatte et al. 1992; Broadfoot et al. 2001), and 1 to 29 individuals/km² across the Chicago, Illinois, area (Graser et al. 2012). In both systems, densities were highest in forest fragments, and lowest in industrial or built areas, and illustrate the variability in abundance of a species that is often perceived to be ubiquitous across urban landscapes (Fig. 8.2).

On the other hand, decline in abundance of species less suited to anthropogenic disturbance is another hallmark of urban systems. For example, urban landscapes

typically support comparatively few insectivorous and migratory birds relative to nonurban areas (Beissinger and Osborne 1982; Rodewald and Bakermans 2006). Snakes, too, tend to decline in number with urbanization (Patten and Bolger 2003), in part due to vehicular-related mortality and persecution (Akani et al. 2002). Large (>20 kg) mammalian carnivores may occur near the periphery of urban areas, but individuals using developed areas tend to be transitory if they occur at all (Crooks 2002; Iossa et al. 2010; Bateman and Fleming 2012). It is unclear for some species whether they increase or decrease with urbanization, as is the case for urban Eurasian badgers (*Meles meles*) that can occur at low (0–0.04/ha) or high (0.33/ha) densities compared to nonurban populations (Huck et al. 2008; Harris and Cress-well 1987; Harris et al. 2010).

Certain life history or ecological traits may facilitate changes in density. One emerging pattern is that generalist species with high fecundity, strong dispersal ability, omnivorous diets, and nonmigratory behaviors tend to have higher urban than rural densities (Bonier et al. 2007; Kark et al. 2007; Croci et al. 2008; Moller 2009). Yet these attributes fail to fully explain species-specific responses to urbanization, given that only 30–50% of the variation in urban and rural densities was explained by life history and ecological traits (Evans et al. 2011).

At a more proximate level, patterns of densities across rural-urban systems may be driven by a variety of ecological factors associated with urbanization, including changes in food, vegetation, microclimate, and predators. Positive population responses are often attributed to food supplementation, which includes birdseed, trash, and even fruiting ornamental plants (Fedriani et al. 2001; Gehrt 2004; Prugh et al. 2009; Rodewald 2012). Not only can food supplementation affect density through survival and reproduction, but it can also be mediated through behavioral processes. For example, high density of American crows (Corvus brachyrhynchos) in cities was thought to be a behavioral response to rich anthropogenic resources that promoted numbers through reduced space needs of urban crows and immigration to the city by nonurban individuals (Marzluff et al. 2001). Likewise, the rich resources in cities make it possible for Virginia opossums (Didelphis virginiana) to maintain smaller home ranges, which can allow more packing of individuals into smaller spaces (Wright et al. 2012). The behavioral process of habitat selection also can drive densities when urban habitats contain more environmental cues used in habitat selection compared to nonurban areas (Leston and Rodewald 2006; Rodewald and Shustack 2008a, b). In cases where population attributes serve as cues (e.g., conspecific density) positive feedbacks can dramatically affect population dynamics and amplify increases or decreases in density (Schmidt et al. 2010).

Change in predation risk is another potential causal factor of urban-associated changes in density. For example, relaxed risk of predation is another frequently cited driver of high densities of prey and mid-trophic species (Faeth et al. 2005; Shochat et al. 2006). Because cities often lack the apex predators present in nonurban areas (Estes et al. 2011), mesopredator release has been suggested as a mechanism that allows mid-trophic predators to increase in number (Crooks and Soulè 1999; Ritchie and Johnson 2009; Prugh et al. 2009). Indeed, cities usually support greater numbers of some mesopredators (Sorace 2002; Prange and Gehrt 2004; Chace and

Walsh 2006; Rodewald et al. 2011; Fischer et al. 2012), and this may suggest that cities have increased risk of predation for small prey species when compared to nonurban areas (Stoate and Szczur 2006). Despite the conceptual appeal of this hypothesis (McKinney 2002), the mesopredator release hypothesis rests upon the assumption that populations of mid-sized predators are top-down regulated by predation—an assumption that has little or no empirical support for many of the native mesopredator species outside Canidae (Gehrt and Clark 2003; Prange and Gehrt 2007).

Ultimately, the mechanisms driving patterns in density are diverse and sometimes paradoxical. An excellent example is for coyotes in the Chicago area, for which high densities are the result of a combination of contrasting demographic and behavioral traits. The Chicago population exhibits much higher survival rates, and possibly higher reproductive rates, than outlying rural coyotes, so demographic processes are consistent with urban adapters. But these coyotes also exhibit behavioral characteristics more typical of urban avoiders, such as strong temporal and spatial avoidance of people and developed areas, enlarged home ranges in the urban matrix, and resistance to use of available anthropogenic foods or structures (Gehrt and Clark 2003; Prange and Gehrt 2007). Thus, to truly understand a relationship between a species and urbanization, one must go beyond measures of density and examine underlying demographic processes.

8.2 Demography

8.2.1 Age and Sex Structure

The sex and age composition of individuals in a population can provide important insights into the dynamics of the population. For example, populations with an age distribution biased toward young animals tend to have a high intrinsic growth rate, especially if survival is also high. For mammals, a population with a male-biased sex ratio may indicate the population serves as a sink, such as that reported for urban black bears (*Ursus americanus*) in the western USA, where large numbers of bears are attracted to urban food sources and killed at high rates (Beckmann and Berger 2003; Beckmann and Lackey 2008). In polygynous species, a high female-biased sex ratio in a population dominated by young age classes likely reflects a positive growth rate. For example, in an urban fox squirrel (*Sciurus niger*) population with high survival and reproductive rates, the juvenile-to-adult ratio of 0.44 was higher than for rural populations, with all factors combined suggesting that the urban squirrels comprised a source population (McCleery 2009).

In general, urban populations of mammalian carnivores tend to have similar age and sex structures to nonurban populations with relatively minor deviations (Prange et al. 2003; Gehrt and Riley 2010; Rosatte et al. 2010). Similarly, an urban population of Texas horned lizards (*Phrynosoma cornutum*) with apparent stationary growth had a nearly even (1M:1.05F) adult sex ratio, and the age ratio was 74% adult and 26% juvenile (Endriss et al. 2007), which was similar to a rural population (Montgomery and Mackessy 2003). However, in their examination of blackbirds across the western Palearctic, Evans et al. (2009) found that the proportion of first-year birds in urban populations was substantially lower than in rural ones—a pattern that they attributed to higher adult survival rather than reduced reproduction.

Perhaps more effort has been devoted to estimate local population structures of white-tailed deer (*Odocoileus virginianus*) than any other urban species, at least in the eastern half of North America. Such information is critical to develop management goals and to subsequently justify those goals to those segments of the public or policy makers concerned with deer management in their communities. Denicola et al. (2008) reported on the population demography of deer populations in four different urban areas that had been protected from harvest for >10 years. Their results indicated that sex and age structure of nonhunted deer populations may be fairly predictable, such that a typical nonhunted, suburban population is slightly biased toward females (60F:40M), with an age structure of 40% yearlings-to-adults for females and 20% yearlings-to-adults for males, and an overall age structure of the population is made up of 40% fawns to yearling-adult age classes.

8.2.2 Survival

When densities differ between urban and nonurban populations, the pattern is often, though not always, a product of shifts in survival or reproductive rates (Fig. 8.3). Perhaps owing to the difficulty in studying small populations, few studies have documented lower survival rates for species that are negatively associated with urbanization (but see Price et al. 2011). In contrast, several studies provide evidence that elevated survival rates in cities (e.g., Gosselink et al. 2007; McCleery et al. 2008; Lehrer et al. 2012) promote high densities of species, as with raccoons (Prange et al. 2003), fox squirrels (McCleery et al. 2008), eastern long-necked turtles (Chelodina longicollis; Rees et al. 2009), and many birds (e.g., Canada geese (Branta canadensis; Balkcom 2010); northern mockingbirds (Mimus polyglottos; Stracey and Robinson 2012), peregrine falcons (Falco peregrines anatum; Kauffman et al. 2003), and great tits (Parus major; Horak and Lebreton 1998)). On the other hand, a review of carnivores showed equivocal comparisons of survival rates between urban and rural populations, with some species exhibiting greater survival with urbanization (i.e., kit foxes (Vulpes macrotis), raccoons, coyotes, stone marten (Martes foina)) and others with no change or negative trends (i.e., striped skunks, red foxes, bobcats, mountain lions (Puma concolor; Iossa et al. 2010)). Nor are the high densities of urban northern cardinals (Cardinalis cardinalis) explained by demography alone, as survival rates of adults (Rodewald and Shustack 2008a, b) and juveniles (Ausprey and Rodewald 2011) were similar for urban and rural individuals (Fig. 8.4).

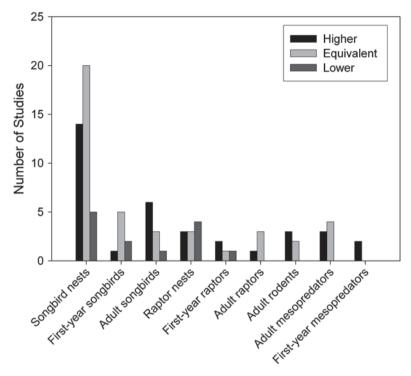
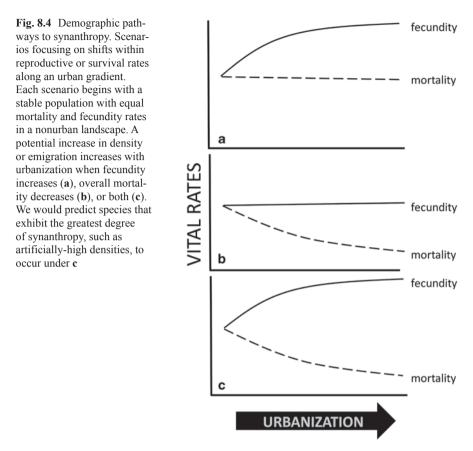


Fig. 8.3 Numbers of studies indicating higher, lower, or equivalent rates of survival in urban compared to rural habitats. (Adapted from Fischer et al. 2012)

Complicating the matter is the fact that there may be high spatiotemporal variation in survival rates across different life stages. For example, adult and nestling survival for Florida burrowing owls (Athene cunicularia floridana) declined along a development gradient, but juvenile survival improved (Millsap and Bear 2000; Millsap 2002). Survival rates of songbird nests and juveniles tended to be equivalent, but adult survivorship generally greater, in urban than rural habitats (Fig. 8.3; Fischer et al. 2012). Similarly, in urban areas, survival of white-tailed deer fawns and black bear cubs were lower than adults (Beckmann and Lackey 2008; Piccolo et al. 2010), and juvenile raccoons may have a greater susceptibility to vehicle collisions than adults (Hadidian et al. 2010). Heterogeneity in urban-associated ecological changes can produce spatial variation in survival rates even within cities. Gray catbirds (Dumatella carolinensis) illustrate how heterogeneity in urban-associated ecological changes can drive spatial patterning in juvenile mortality, which was most related to, and depressed by, local abundance of domestic cats (Felis catus; Balogh et al. 2011). There also can be striking differences in survival rates between the developed matrix and remnant habitat patches within cities (Whittaker and Marzluff 2009; but see Rosatte 2000; Gross et al. 2012; Gehrt unpublished data).



8.2.3 Mortality Causes

Sources of mortality can vary widely between urban and nonurban populations, and can also vary dramatically within the city between exclusively terrestrial and flying species, the latter of which are more vulnerable to collisions with buildings and windows. The death toll of migrating birds attracted to tall lighted buildings can be staggering, especially in foggy conditions (Longcore and Rich 2004). Even for local breeding populations, collisions can have important population-level consequences. For example, the greatest cause of mortality of Cooper's hawks (*Accipiter cooperii*) in Tuscon, Arizona was collisions (70%), primarily with windows (Boal and Mannan 1999).

8.2.3.1 Roads

Arguably the greatest challenge for exclusively terrestrial species to overcome in exploiting the urban landscape is roads and the associated vehicles. The implications

that roads have for urban wildlife are addressed in more detail in another chapter (Chap. 15), but we briefly summarize its relevance to population demography here. The importance of vehicles as a mortality source across a range of terrestrial taxa is shown in Table 8.1. In some cases, vehicle mortality is so high that it represents the greatest limitation to population growth, and may exceed reproduction, such as for black bears (Beckmann and Lackey 2008) and some reptiles (Cureton and Deaton 2012). Some turtle species are highly susceptible to road mortality because they are not able to adjust or avoid road traffic, and their relatively low fecundity does not allow for replacement of individuals killed by cars. Turtle populations affected by road mortality are those that are male biased and occur at low densities (Cureton and Deaton 2012).

Some urban adapted species appear to make behavioral adjustments to roads and traffic. Although vehicle-related mortality is common for white-tailed deer, raccoons, kit foxes and coyotes (Table 8.1), each of these species appear to reduce the risk of collision by avoiding roads or avoiding traffic when they do cross (Etter et al. 2002; Cypher 2010; Gehrt unpublished data). Notably, raccoons and coyotes that live exclusively in the urban matrix, and consequently cross many roads regularly, have the same risk of collision as individuals living in the urban parks that are exposed to fewer roads and less traffic (Gross et al. 2011; Gehrt unpublished data). However, in contrast to deer and coyotes, juvenile raccoons may be susceptible to vehicle mortality and this may be an important density-independent limitation to their population growth (Hadidian et al. 2010).

8.2.3.2 Predation

The combined effects of urban habitat fragmentation and elevated native and nonnative predator abundance can produce high levels of predation on terrestrial and flying species alike. Predation levels from mammalian mesopredators can threaten herpetofauna and shift community structure in suburban and urban aquatic systems (Mitro 2003; Eskew et al. 2010). Increased predation levels on avian populations are well-documented in some, but not all urban systems (Chamberlain et al. 2009; Fischer et al. 2012). Large numbers of nonnative species, such as domestic cats, prev on small mammal and avian species (Beckerman et al. 2007; van Heezik et al. 2010; Loss et al. 2013). Predation rates for some species may decline with urbanization, especially for mammals such as rodents (Table 8.1). For example, woodchucks (Marmota monax; Lehrer et al. 2012) and fox squirrels (McCleery et al. 2008) are more likely to die from predation in rural areas, but mortality risk shifts from predators to vehicle collisions with urbanization. Likewise, covote killing of foxes, due to intraguild competition, decreases with urbanization in those cities where coyotes are not as abundant as adjacent rural areas (Gosselink et al. 2007; Cypher 2010). The noise of cities also may indirectly reduce predation in cases where predators avoid the loud environments (Francis et al. 2009).

Nest predation has probably been better studied than any other type of predation in urban areas. Although cities generally have greater numbers of generalist and opportunistic predators that prey upon bird nests (Sorace 2002; Prange and Geh-

Table 8.1 Cause-specific mortality for terrestrial vertebrates derived from radiotelemetry. Number of mortalities (n) and the percentage of mortalities by three types of mortality. We have highlighted three types of mortality, therefore total percentages for each species will not be equal to 100%. The location of the study site is noted as occurring within a habitat fragment (urban fragment), within the urban development or matrix (urban matrix), or a combination of fragments and matrix (mixed)

Species	n	Landscape type	Vehicles (%)	Predation (%)	Disease (%)	Source
Horned lizard	9	Urban fragment	11	44	0	Endriss et al. (2007)
Fox squirrel	26	Urban fragment	57	4	0	McCleery et al. (2008)
Woodchuck ^a	26	Mixed	19	27	0	Lehrer et al. (2012)
Red fox	173	Mixed	36	9	39	Gosselink et al. (2007)
Red fox (premange)	80	Mixed	62	0	17	Soulsbury et al. (2010)
Red fox (postmange)	67	Mixed	32	0	61	Soulsbury et al. (2010)
Kit fox	56	Mixed	45	30	0	Cypher (2010)
Raccoon	18	Urban fragment	17	0	50	Riley et al. (1998)
Raccoon	13	Urban fragment	23	0	77	Prange et al. (2003)
Raccoon	18	Suburban fragment	56	0	39	Prange et al. (2003)
Raccoon	16	Urban matrix	56	0	19	Gross et al. (2012)
Striped skunk	23	Urban fragment	17	0	70	Gehrt (2005)
Bobcat	49	Mixed	69	0	22	Riley et al. (2010)
Coyote	68	Mixed	62	0	10	Gehrt et al. (2011)
Black bear	156	Mixed	57	0	0	Beckmann and Lackey (2008)
White-tailed deer	40	Suburban fragment	72	0	0	Etter et al. (2002)

^a Study occurred along an urban-rural gradient; mortality was primarily vehicles, and less due to predation, for urban animals (Lehrer et al. 2012)

rt 2004; Rodewald et al. 2011; Fischer et al. 2012), there is paradox in that links between urbanization and nest predation are surprisingly weak with mixed empirical support (Chamberlain et al. 2009; Fischer et al. 2012). Rural nest survival has been similar (Reidy et al. 2009; Burhans and Thompson 2006; Rodewald et al. 2013), greater (Newhouse et al. 2008; Ryder et al. 2010; Stracey and Robinson 2012), and

lower (Phillips et al. 2005; Vigallon and Marzluff 2005; Bakermans and Rodewald 2006) than urban nest survival. Part of the variation may result from different scales of study, as research examining remnant patches of habitat in urban and rural land-scapes usually finds similar rates of nest predation, whereas research comparing developed and undeveloped areas within the urban matrix finds higher nest survival within the developed areas (Fischer et al. 2012). Ongoing research comparing nest survival in suburban yards and adjacent forest parks shows that early-season nest survival is greater within the developed matrix than the remnant forest patches even within the city alone (J. Malpass and A. Rodewald, unpublished data). Temporal patterns of nest depredation also can vary with urbanization. Suburban Florida scrub-jays (*Aphelocoma coerulescens*) experienced lower rates of depredation during egg stage but higher depredation during nestling stage than nonurban populations, though overall rates of success were similar (Bowman and Woolfenden 2001).

The "predator paradox", where high predator numbers in cities are not matched with correspondingly high rates of nest predation, is supported both empirically in demographic studies (Rodewald et al. 2011; Stracey 2011) as well as in literature reviews (Fischer et al. 2012). A 10-year study of nearly 5000 nests of five songbird species breeding in forests along a rural-to-urban gradient in Ohio provides an excellent illustration. The nest predator community of the study system was diverse with 21 video-documented predator species, most of which were generalist species (Rodewald and Kearns 2011). Despite greater numbers of nearly all documented predators within urban compared to rural landscapes, there were no consistent relationships between avian nest survival and urbanization for any of the focal bird species (Rodewald et al. 2013). Moreover, although increasing predator detections were associated with nest survival in rural landscapes, predator-prev relationships were decoupled in urban landscapes such that predator activity failed to predict nest survival rate. Similar patterns have been detected in European cities, where superabundant hooded crows (Corvus cornix) (Weidinger 2009) and magpies (Chiron and Julliard 2007) were less important nest predators than in nonurban landscapes. This apparent disconnect between rates of nest predation and predator activity in urban landscapes may arise because many urban predators are heavily subsidized by anthropogenic food sources (Gehrt 2004; Prange et al. 2004; Marzluff and Neatherlin 2006; Withey and Marzluff 2009; Rodewald et al. 2011) and therefore may depredate fewer nests than less subsidized rural predators.

There is growing evidence that the species most responsible for nest depredation differs between urban and nonurban areas. Nests of understory birds, including northern cardinal, Acadian flycatcher (*Empidonax virescens*), gray catbird, and wood thrush (*Hylocichla mustelina*), were three times more likely to be depredated by mesopredators in cities compared to rural areas (35% vs. 13% of nests; Rodewald and Kearns 2011). On the other hand, rural nests were most likely to be depredated by small passerine birds (e.g., brown-headed cowbird (*Molothrus ater*) and common grackle (*Quiscalus quiscula*) and raptors. Reidy et al. (2008) also documented that the dominant avian nest predator of golden-cheeked warbler (*Dendroica chrysoparia*) shifted from the western scrub-jay (*Aphelocoma californica*) in urban areas to the American crow in rural landscapes. Domestic cats were the most important predators of northern mockingbird nests (Stracey 2011) and juvenile gray catbirds within cities (Balogh et al. 2011). However, the impact of cats may not be similarly distributed across cities. Ongoing work video-documenting nest predation in forest parks vs. adjacent backyards shows that domestic cats are more likely to depredate nests in yards than nests in adjacent forests (J. Malpass and A. Rodewald, unpublished data).

8.2.3.3 Disease

For most mammals, disease influences population dynamics in all systems to varying degrees, but in urban systems it is most apparent for mammalian mesopredators (Table 8.1, see Chap. 10), and it usually takes the form of transmissible diseases because of artificially-high host densities and consequent interactions between individuals. For example, rabies is an important disease that can dramatically reduce host density in urban areas and other notable epizootics in urban areas have been reported for raccoons, striped skunks, and red foxes (Riley et al. 1998; Rosatte 2000). Much like rabies, epizootics of sarcoptic mange (*Sarcoptes scabei*) impact high-density canid populations, and these can be dramatic in urban areas where populations are subsidized with anthropogenic foods and buffered from predation (Gosselink et al. 2007; Soulsbury et al. 2010).

Canine distemper is a morbillivirus commonly found in urban mesopredator populations, especially raccoons and skunks (Gehrt 2004). In fact, canine distemper virus is probably enzootic in most urban North American raccoon populations as a result of high host densities (Roscoe 1993; Gehrt 2003), and periodic outbreaks of new strains may occur that impact domestic animals as well as native hosts (Cleave-land et al. 2000; Hadidian et al. 2010).

Although transmissible diseases may have less impact on urban avian populations than predation or accidents, novel pathogens introduced to urban systems can severely limit populations of some species, as in the case of West Nile Virus and American crow populations (*Corvus brachyrhynchos*; LaDeau et al. 2007). An alarming 72% of the crow population in Stillwater, Oklahoma, was lost to this disease in 1 year (Caffrey et al. 2005). Moreover, avian exposure to West Nile Virus can be greater within urban than nonurban areas, as shown in the Chicago region (Hamer et al. 2012). A recent literature review showed that urbanization could be positively or negatively associated with the diversity and prevalence of bird parasites (Delgado and French 2012). Comparing urban and rural blackbird populations across Europe, Evans et al. (2009) found that prevalence of both ticks and avian malaria was lower in cities.

8.2.3.4 Other Mortalities

Urban wildlife die from many causes in addition to those mentioned above, including electrocution, drowning, poisoning, nuisance removal, and entombment, but we have highlighted those that have been reported to have population-level effects. However, one cause of mortality that is notable because of its *absence* from urban systems is harvest or the hunting and trapping of game species. In North America, most of the mammals common to urban systems, and many that are considered overabundant, are game animals with legal harvest outside of cities. The annual harvest of some of these species is substantial; for example, during a single year (the 2010–2011 harvest season) 110,415 opossums, 216,663 coyotes, 74,223 striped skunks, and an impressive 801,335 raccoons were harvested across 13 states in the Midwestern USA (source: Association of Fish and Wildlife Agencies). Indeed, across the USA approximately 1 million raccoons are harvested from primarily rural areas each year. For these species it is harvest, rather than predation from apex predators, that typically represents the primary form of mortality in rural areas, in contrast to the frequent assumption by others claiming mesopredator release as a primary mechanism (McKinney 2002).

Similarly, for white-tailed deer harvest is the primary cause of death in rural areas (Nixon et al. 2001). For example, hunting-related mortality of white-tailed deer in rural Illinois makes up 60% of all causes of mortality for does, and 78% for bucks, of all ages, compared to 18 and 13% (does and bucks, respectively) vehicle-related mortality. Consequently, annual survival across subadult-adult age classes ranged 56–92% for does and 35–76% for bucks (Nixon et al. 2001), which was much lower than annual survival rates for deer in suburban Chicago where auto collision was the primary cause of mortality (Etter et al. 2002). The same situation likely occurs for waterfowl, particularly giant Canada geese that become nonmigratory in urban systems. Thus, it is not surprising that generalist species already well-equipped for urban landscapes exhibit accelerated population growth and attain relatively high densities when the primary mortality agents are removed.

8.2.3.5 General Mortality Patterns

The highly generalized patterns that emerge from reviews of the mammalian and avian literature to date (Chamberlain et al. 2009; Fischer et al. 2012, this chapter) reveal that for either taxa, anthropogenic-related mortality increases quickly with urbanization as would be expected (Fig. 8.5), although the specific causes may differ between the groups (i.e., vehicles for mammals, buildings and other structures for some birds). However, mortality rates associated with predation and disease tend to change more strongly with urbanization for mammals than for birds (Fig. 8.5). For mammals, there is a "strong" negative curve as predation or more likely harvest declines or disappears with urbanization consistently across species, whereas changes in predation rate for birds are mixed across species and systems, with predation often remaining an important form of mortality even if it trends slightly downward with urbanization. Disease often exceeds predation as a mortality factor for urban mammals, whereas disease does not commonly exceed predation of ruban birds. These are generalizations, and the relative risk of predation or

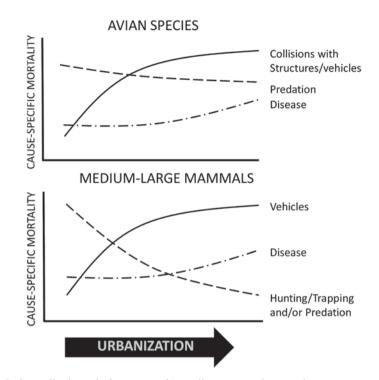


Fig. 8.5 Generalized trends for causes of mortality among urban species, as one moves along a rural-to-urban gradient. The curves are merely conceptual based on the literature and do not represent a formal meta-analysis. Curves exhibiting extreme changes in mortality rates (such as vehicles) represent the "strength" (or consistency) of the pattern among studies, whereas a slight curve (such as disease) reflects mixed results and a more complex relationship with urbanization

disease may change with life stage, such as higher predation for nestlings/fledglings than for adults, whereas risk from disease may be greater for adults.

8.2.4 Reproduction

8.2.4.1 Phenology

Urban populations often initiate breeding earlier in the season than their rural counterparts. A review of avian reproductive phenology by Chamberlain et al. (2009) showed that urban egg-laying was earlier in 16 of 19 studies. Although breeding early is thought to improve reproductive success (Perrins 1970; Norris 1993; Verhulst et al. 1995), some urban breeders may advance reproductive timing by 7–10 days with no detectable benefit in terms of reproductive output (Shustack and Rodewald 2011). Although the federally threatened Florida scrub-jay initiated breeding earlier in suburban than rural populations due to the protein-rich anthropogenic subsidies in suburban areas (Schoech and Bowman 2003; Fleischer et al. 2003), advanced laying dates resulted in greater hatching failures due to increased exposure of eggs to low ambient temperatures (Aldredge et al. 2012). While most studies have demonstrated advanced phenology of residents and short-distance migratory birds in cities (Eden 1985; Antonov and Atanasova 2003; Schoech and Bowman 2003), urban birds also may initiate breeding later. At higher levels of urbanization, Acadian flycatchers, a Neotropical migratory bird, arrived and initiated clutches later and finished nesting earlier (due fewer breeding attempts) than in forests within more rural landscapes (Rodewald and Shustack 2008b; Shustack and Rodewald 2010).

The causes of phenological shifts are unknown for most species but include a wide variety of social and ecological factors. In the aforementioned study of delayed reproduction for urban Acadian flycatchers, evidence suggested that urban forests were less desirable and selected later by smaller individuals, which initiated first clutches later in the nesting season than larger birds (Shustack and Rodewald 2010). For European blackbirds, a captive-rearing experiment indicated that earlier breeding in cities was primarily due to plasticity in hormone secretion and gonadal development (Partecke et al. 2004) likely related to social interactions and environmental conditions (Partecke et al. 2005). Artificial night lighting was implicated as the driver of advanced phenology of five common forest-breeding songbirds, with blue tits laying eggs 1.5 days earlier when territories included street lights than without (Kempenaers et al. 2010). Environmental conditions related to climate (e.g., temperature accumulation, leaf phenology) explained the timing of breeding of northern cardinals (Shustack 2008) and great tits and blue tits (*Parus caeruleus*; Nilsson and Kallander 2006).

8.2.4.2 Reproductive Output

Even if rates of nest predation are no higher in urban than nonurban habitats, reproductive output can be lower within cities due to other factors. In the central Ohio system, urban Acadian flycatchers produce fewer young annually despite similar rates of nest predation in urban and rural forests due to a combination of flycatcher behavior (i.e., fewer nest attempts) and brood parasitism (Rodewald and Shustack 2008b; Shustack and Rodewald 2010). Despite increased breeding densities within cities, reproductive performance within urban areas was lower than those surrounded by rural land for great tits (Hedblom and Soderstrom 2012), American crow (Marzluff et al. 2001), and house sparrows (*Passer domesticus*; Schroeder et al. 2012; Seress et al. 2012). Differences in productivity may reflect poorer food quality or nutrient restriction in urban compared to nonurban habitats (Solonen 2001; Antonov and Atanasova 2003; Heiss et al. 2009; Ibanez-Alamo and Soler 2010).

For some species, reproductive performance is greater within than outside of metropolitan areas for other species. In their review of the avian literature, Chamberlain et al. (2009) reported that annual productivity was greater in urban than nonurban habitats for seven of eight urban adapting species though nestling weight was lower in urban than rural areas for nine of ten urban adapters. Brood size of

northern goshawks (Accipeter gentilis; Solonen and Ursin 2008) as well as number of young fledged by northern mockingbirds (Stracey and Robinson 2012) and house wrens (Troglodytes aedon; Newhouse et al. 2008) was greater in urban than rural sites. Urban adapting mammalian species that are able to exploit anthropogenic resources also tend to have elevated reproductive rates compared to rural populations. Reproduction was relatively higher for urban black bears (Beckmann and Lackey 2008), white-tailed deer (Etter et al. 2002), raccoons (Prange et al. 2003), kit foxes (Cypher 2010), San Clemente Island foxes (Urocyon littoralis clementae, Gould and Andelt 2011), and fox squirrels (McCleery 2009) than for rural populations. Apparently the artificially-abundant food allows females to continue to reproduce without density-dependent effects manifesting at population sizes similar to those found in nonurban areas. For example, it is well-established that canid reproductive success is closely tied to food abundance, and small-tomedium sized canids readily use anthropogenic foods in urban areas (Iossa et al. 2010). Higher fecundity for urban kit foxes than for nonurban foxes is attributed to the constant, predictable supply of anthropogenic foods in urban areas compared to the highly variable natural prev supply in natural or rural systems (Cypher 2010). Although reproductive output is often treated as a useful indicator of habitat quality, an important caveat is that for species occurring at densities near carrying capacity, as may be the case for urban-adapted species, density-dependent regulatory mechanisms may result in equivalent reproductive rates in urban and rural habitats (Rodewald and Shustack 2008a).

A New Classification System for Urban Wildlife Seth P. D. Riley and Stanley D. Gehrt

Urban ecologists frequently classify wildlife based on their relationship to urbanization. Throughout this book, you will see the use of a three-category system of urban exploiters, urban adapters (originally "suburban adaptable" species), and urban avoiders, developed by Blair (1996, 2001) for urban birds and later adapted for other taxa (McKinney 2002). This system has three problems: (1) coarse partitioning, (2) exclusive partitioning, and (3) "urban adapter" has erroneous evolutionary connotations. Accordingly, we propose a new way of categorizing wildlife to address these problems. This system replaces the original three categories with four to facilitate greater precision in understanding how different wildlife populations interact with urban processes. In contrast to the commonly used classifications, our categories are meant to be fluid in relation to individuals, species, populations, and time; the same species may belong to different categories in different situations, different individuals within the same population may belong in different categories, and specific individuals may even belong in different categories at different times in their lives.

Our proposed classification of species in urban areas is:

Urban dependents: Wildlife that are dependent on humans for food and shelter, even though humans do not provide it intentionally (as they do for livestock and pets). These animals are small and cryptic enough (rats and mice) or mobile enough (pigeons and house sparrows) to avoid humans even in urban cores.

Examples: house mouse (*Mus musculus*), Norway rat (*Rattus norwegi-cus*), rock pigeon (*Columba livia*), house sparrow (*Passer domesticus*).

Location: Typically found at greatest densities in or near the urban core, quickly decline in occurrence in the suburbs, and generally are rare in natural landscapes.

Urban exploiters: Wildlife able to exploit anthropogenic resources available in urban areas, but not dependent on these resources. These animals typically have generalized ecological niches with flexible behavior that allows exploitation of food and shelter that humans provide.

Examples: raccoon (*Procyon lotor*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), stone marten (*Martes foina*), eastern cottontail (*Sylvilagus floridanus*), gray squirrel (*Sciurus carolinensis*), white-footed mouse (*Peromyscus leucopus*), house finch (*Haemorhous mexicanus*), peregrine falcon (*Falco peregrinus*), northern cardinal (*Cardinalis cardinalis*), house gecko (*Hemidactylusfrenatus*).

Location: Found to varying degrees throughout the urban landscape, but likely reach greatest densities in areas with green fragments interspersed within the urban matrix, or in low to medium density residential areas. Can reach greater densities in urban landscapes than in nonurban ones.

Urban tolerant: Wildlife that may use some anthropogenic resources and may reside in parts of the urban landscapes but do not generally exploit urban areas to reach greater densities. In some cases, density may be misleading in that urban populations may be sinks, with relatively high mortality or low reproduction.

Examples: bobcat (*Lynx rufus*), black bear (*Ursus americanus*), leopard (*Panthera pardus*) in India, some bat species, white-tailed (*Odocoileus virginianus*) and mule (*Odocoileus hemionus*) deer (but may sometimes be exploiters), some songbirds (e.g., red-eyed vireo (*Vireo olivaceus*), generalist or cryptic reptile and amphibian species such as American toad (*Anaxyrus americanus*), brown snake (*Storeria decayi*), green anole (*Anolis carolinensis*), legless lizards (*Anniella pulchra*), alligator lizards (*Elgaria spp.*), some small plethodontid salamanders (*Batrachoseps attenuatus* and *B. nigrventris* in California, *Plethodon cinereus* in the eastern USA).

Location: They generally occur in low density residential areas with vegetated yards, or medium density residential areas in close proximity to patches of natural landscape. Their occurrence declines quickly toward the urban core.

Urban avoiders: Wildlife that have narrow ecological niches or other traits that conflict with urbanization. These animals may occur at the margins of

urban areas, but rarely occur in suburban or urban zones, unless large natural fragments occur near edges. If they are in urban landscapes, it is generally temporary or a transient individual (although over time, an individual may become an "urban tolerant.")

Examples: mountain lion (*Puma concolor*), gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos horribilis*), many native small mammals, habitat-specific birds associated with recent burn areas (e.g., Bachman's sparrow, *Peucaea aestivalis*), early-succession areas (e.g., prairie warbler (*Setophaga discolor*)), or longleaf pine forest (e.g., red-cockaded woodpeckers, *Picoides borealis*).

Location: If they are found in urban or suburban areas, it's generally near open space.

Finally, there are some species that are likely never to be found in urban landscapes or even close to urban areas, even transient individuals, because they are very specific to certain natural habitats and highly sensitive to anthropogenic processes including habitat fragmentation, noise, and altered ecological systems. This group, which we would call "urban impossibles," might include species such as tailed frogs (*Ascaphus truei*) that require cold streams in old growth northwest forest, spotted owl (*Strix occidentalis*), mountain gorilla (*Gorilla beringei beringei*) in Africa, or snow leopard (*Panthera uncia*) in Asia. However, over time, even these species may come increasingly into contact with urban areas (Fig. 8.6).

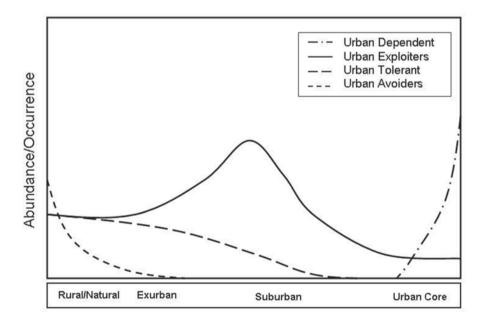


Fig. 8.6 Conceptual model illustrating the ways that wildlife species respond to urbanization, as indicated by abundance across the urban gradient

8.3 Limiting Factors

8.3.1 Density-Independent Factors

It has been long understood that populations are regularly affected by density-independent and density-dependent limiting factors. In nonurban systems, density-independent factors typically involve weather or other environmental conditions. Within urban systems, many of these traditional factors are ameliorated to various degrees. For example, drought in nonurban systems is buffered in the urban landscape with artificial sources of free-standing water, and climate-induced swings in natural food availability are buffered by anthropogenic foods. This overall pattern of buffering from extreme environmental conditions may explain why few urban wildlife studies have identified density-independent factors as important for limiting populations. One notable exception would be the heat island effect in large urban centers reducing the limiting effect of winter weather at northern latitudes for some species (e.g., opossums, Kanda et al. 2009). Other possible density-independent factors may include roads and toxins, such as rodenticides (Chaps. 10, 15).

8.3.2 Density-Dependent Factors

Many urban adapters occur at relatively high population densities, so it may seem that density-dependent processes are minimized for these populations through urban drivers, such as an anthropogenic food supply that seems unending. However, as intuitive as this seems, the perception that density dependence is not as important in "overabundant" urban populations may be wrong. Density-dependent processes are notoriously difficult to document, and may be obfuscated by other factors that are more easily observed, especially when demographic processes that have been identified for a species in nonurban areas are severely altered in urban systems. More likely, density dependence for urban populations occur at different points in the trajectory of population growth, or primary regulatory mechanisms may switch with urbanization. The following examples illustrate the importance of density-dependent factors even for "overabundant" urban species.

For urban white-tailed deer at high population densities, food and water seem not as limiting as in nonurban sites as suggested by the high adult survival rates and fecundity of urban deer (Etter et al. 2002). An exception to the pattern is that canid predation on fawns appears to be density-dependent factor that that increases vulnerability of deer neonates. Through browsing abundant deer reduce the cover available for neonates, increase their predation risk and reducing fawn survival from 0.78 to 0.26 at densities of 100 adults/km² (Piccolo et al. 2010). Low fawn survival explains why deer populations at high densities in some urban greenspaces appear to experience no additional population growth, despite continued high adult survival and fecundity (Etter et al. 2002).

For other species not affected by predation, especially medium-sized mammals, disease may act in a density-dependent mechanism, such as sarcoptic mange. Sarcoptic mange often becomes epizootic at high host densities, and urban red fox populations may cycle as source and sink, depending on the prevalence of this disease (Gosselink et al. 2007). In peak years of the mange cycle, urban populations may serve as sinks, where mortality rates exceed reproduction and limited dispersal occurs, but during periods of low mange incidence survival in urban areas is relatively high and urban populations serve as sources with considerable juvenile dispersal into rural areas (Gosselink et al. 2007).

Although the abundant anthropogenic resources and reduced predation pressure may change when density-dependent factors manifest, many urban wildlife populations appear stable and experience some regulation such that they fluctuate less than rural populations (e.g., some rodent species, McCleery 2009; Chiappero et al. 2011). The apparent lack of an obvious density-dependent mechanism for a high-density species was evident in a raccoon population intensively monitored for 8 years, during which 647 individuals were captured 1452 times (Prange et al., 2003; Gehrt 2004). This population resided in an urban park with access to abundant and predictable sources of anthropogenic food, as the park received between 1.5 and 3 million human visitors annually (Gehrt 2004). Spring densities were quite consistent over the years whereas autumn densities fluctuated wildly (Fig. 8.7). The autumn densities were driven by juvenile recruitment, thus reflecting successful reproduction that year. Coefficient of variation for the autumn densities (48%) was nearly four times that of spring densities (14%), and there was clearly a disconnect between spring densities and the number of juveniles per adult female in the subsequent autumn (r=-0.48, P=0.28). Nevertheless, some process occurred between autumn and the following spring (that is, over winter) that regulated the population. This process likely involved juveniles as they were not radiocollared, and probably involved over-winter survival or emigration, neither of which is mutually exclusive. Genetic evidence for this population, and others like it, indicated there was little immigration into the population (<5% of the study population originated outside the study area, Santonastaso et al. 2012), which was consistent with field data (Gehrt unpublished data), suggesting a general flow outward from the population and a possible density-dependent mechanism that is difficult to observe in this species.

Emigration is likely another important component of population regulation for urban adapter mammals (McCleery 2009; Soulsbury et al. 2010). Dispersal appears to be an important density-dependent mechanism in urban foxes (Gosselink 2002; Soulsbury et al. 2010), given their highly-structured social systems. Similarly, dispersal of young coyotes from urban populations with high survival and reproductive rates helps to maintain local densities at carrying capacity (Gehrt unpublished data).

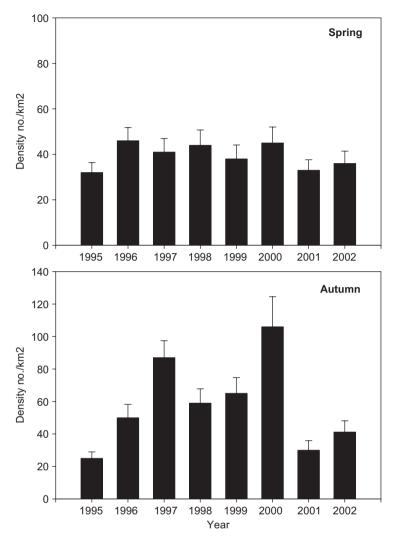


Fig. 8.7 Seasonal density estimates (+SE) for a raccoon population in an urban park with abundant and predictable anthropogenic foods in the Chicago metropolitan area, 1995–2002 (Gehrt 2004). Note the different scale on the y-axis. The population appeared to be at an artifical carrying capacity, as spring estimates exhibited little annual variability, whereas autumn estimates varied substantially across years

8.4 Metapopulations and Genetic Structure

Populations within metropolitan areas may occur as disjunct subpopulations with limited exchange of individuals. We would expect such a pattern to be especially extreme in terrestrial, sedentary species with specific habitat requirements.

Amphibians exhibit these characteristics (Hamer and McDonnell 2008), and genetic evidence suggests that they are susceptible to urban fragmentation of habitat, resulting in limited gene flow and reduction of genetic heterogeneity within subpopulations (Hitchings and Beebee 1997; Noël et al. 2007; Tsujia et al. 2011). For example, genetic differentiation of the common frog (*Rana temporaria*) between town ponds separated on average by only 2.3 km was nearly twice as high as that found for rural sites separated on average by 41 km (Hitchings and Beebee 1997). Similar genetic patterns occur in urban aquatic reptiles such as turtles (Rubina et al. 2001) and terrestrial lizards (Delaney et al. 2010).

Urban fragmentation of natural habitats also affects the dispersal abilities and genetic structure of small mammal populations (Gortata et al. 2012) and semi-fossorial medium-sized mammals (Huck et al. 2008). In a comparison of Sigmodontine rodent *Calomys musculinus* populations in an urban and agroecosystem environment in Argentina, urban subpopulations were genetically isolated and had higher level of relatedness than the subpopulations in the agricultural landscape (Chiappero et al. 2011). For species of small mammals that attain high densities in urban fragments such as the white-footed mouse (*Peromyscus leucopus*), genetic heterogeneity also occurs across subpopulations indicating limited dispersal between fragments, but genetic variability may remain relatively high within subpopulations because of high local densities (Munshi-South and Kharchenko 2010). As Munshi-South and Kharchenko (2010) assert, given that white-footed mice display genetic structuring over vast geographic regions outside the city, the substantial genetic structuring over short distances in the New York City system illustrates the power of urban processes even on "urban adapter" species.

It is perhaps intuitive that urbanization may fragment populations or limit dispersal of small-bodied species or those restricted to natural habitat fragments such as Eurasian badgers (Huck et al. 2008), but the strength of urbanization to fragment or structure populations is clear even when species with high mobility are considered. Genetic and behavioral data for foxes in Melbourne, Australia, and Zurich, Switzerland, revealed limited dispersal and relatively low genetic heterogeneity among urban foxes when compared to outlying rural populations (Robinson and Marks 2001; Wandeler et al. 2003). Extensive mark-recapture data across the urban landscape of Scarborough, Ontario, and recent genetic analysis of subpopulations across Chicago revealed metapopulation structure with limited dispersal and gene flow for raccoons, despite that species being the most abundant native mesomammal in both systems (Broadfoot et al. 2001; Santonastaso et al. 2012). However, gene flow was still sufficient to prevent loss of genetic diversity or drift due to limited dispersal in the Chicago system (Santonastaso et al. 2012). Similarly, genetic evidence suggests a limited, male-biased, dispersal among brush-tail possums in Australian cities (Stow et al. 2006). More surprising is when urbanization reduces population connectivity for birds such as wrentits (Chamaea fasciata; Delaney et al. 2010), and especially highly vagile avian species such as song sparrows (Melospiza melodia; Unfried et al. 2013) and house sparrows (Passer domesticus; Vangestel et al. 2012).

8.5 Conservation and Management Implications

Conservation and management of wildlife generally takes place at the population level, and this makes knowledge of population dynamics within cities important from a practical perspective. Understanding population dynamics of species negatively impacted by elements of urbanization is necessary to identify effective conservation activities (Hamer and McDonnell 2008), as well as to communicate to decision makers and the general public the need for controversial measures, such as removal of non-native vegetation from habitat fragments and control of domestic animals such as feral cats (Chap. 11). Knowledge of demographic parameters is often essential for effective management of "overabundant" urban wildlife. For example, deer (Odocoileus sp.) are typically the largest vertebrates inhabiting urbanized landscapes across North America. Consequently, they are quite obvious to the public, providing viewing opportunities, while at the same time causing substantial property damage and collisions with vehicles (Warren 2011). In particular, the proliferation of white-tailed deer in urban parks and residential areas has presented management challenges (Chap. 17). As a result, municipalities and management agencies expend considerable effort and expense to estimate population demographics of deer populations to determine acceptable population levels and to provide support for deer management to the public or decision makers (Jones and Witham 1995; De Nicola et al. 2000; LaBonte et al. 2004; DeNicola et al. 2008). Reliable estimates of population density and demographic structure are critical for identifying management goals such as harvest numbers for culling programs or for justifying such management to the public (LaBonte and Barclay 2007).

Understanding population dynamics of urban wildlife also has implications for human health, which is increasingly subject to emerging zoonoses. In this case, demographic information and dispersal patterns are instrumental for the management of certain wildlife diseases, such as rabies and canine distemper (Rosatte et al. 2007a). Rabies management typically involves culling or baiting programs (Rosatte et al. 2007b), and density estimates are necessary to determine the number of animals to remove and the number of vaccine baits to distribute (Rosatte et al. 1992, 1997).

Conclusion

We extol the value of explicitly considering the population ecology of urban wildlife, yet we recognize that demographic studies are time- and resource-intensive and, hence, not always possible. Application of general rules of thumb can sometimes be a reasonable surrogate for place-based studies, but this may prove difficult within urbanizing systems. One of the most striking patterns to emerge from our review was the absence of any clear "rules" governing population ecology of urban wildlife. Though there are several common patterns in density and/or demography, sufficient exceptions exist to preclude widespread generalization. This fact at once makes urban wildlife populations especially interesting from a scientific perspective and especially challenging from a conservation and management one.

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