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Birds in Urban Ecosystems: Population Dynamics, Community Structure, Biodiversity, and Conservation

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Abstract

With the global high rate of urbanization and the rapid loss of wild habitat land, cities are now viewed as challenging ecosystems for sustaining biotic communities and rich diversity. During the 2000s research on urban bird populations and communities focused on global patterns, as well as processes and mechanisms that lead to the two globally recognized patterns: increased overall population densities and decrease in species diversity compared with wildlands. Birds adapt to the urban ecosystem both physiologically (changes in stress hormones), and behaviorally (e.g., changes in foraging behavior, extending the breeding season). The increase in population density is related to the increase in food abundance, and probably to the reduction in predation pressure. The loss of diversity is related to loss of habitat, the high human density, and negative interactions with synanthropic species. Recognizing that the urban habitat will continue to grow, efforts to turn the city into a more friendly habitat for a variety of bird species should focus not only on habitat and vegetation structure, but also on niche opening for subordinate species, by excluding locally aggressive, synanthropic species.

Although the study of urban birds has a fairly long history, urban ecosystems have been largely ignored throughout many decades of ecological research (Miller and Hobbs, 2002; Collins et al., 2000). Since the early 1990s, a different view emerged, accepting urban settings as ecosystems that are structured and function like other natural ecosystems (McDonnell and Pickett, 1990; Rebele, 1994; Grimm et al., 2000; McKinney, 2002; Miller and Hobbs, 2002). This theoretical view represents an emerging realization that by now, most of the world's land is managed and dominated by humans (approximately 50% of the human population lives in cities). Wildlands are continuously converted to agricultural fields

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and urban areas. Consequently, urban environments can no longer be viewed as lost habitat for wildlife, but rather as new habitat that, with proper management, has the potential to support diverse bird communities. During the last decade urban ecosystems have therefore become ecological challenges in conservation, restoration, and reconciliation ecology (Miller and Hobbs, 2002; Rosenzweig, 2003). Designing sustainable urban ecosystems that support species-rich bird communities also includes maintaining key ecosystem services, such as clean air and water, waste decomposition, and pest control.

Knowledge of the patterns of urban bird populations and communities started emerging in the 1970s (e.g., Emlen, 1974). Compared with adjacent, more natural ecosystems, urban settings normally have higher bird abundances (Beissinger and Osborne, 1982; Marzluff, 2001a; Chace and Walsh, 2006). For example, in Tucson, overall bird density increased 26-fold from the Sonoran desert to urban habitats (Emlen, 1974). Patterns of high bird densities have been observed in tropical systems (Sodhi et al., 1999), grasslands (Sodhi, 1992; Bock et al., 2001), temperate forests (Beissinger and Osborne, 1982), deserts (Emlen, 1974), bushland (Sewell and Catterall, 1998), and oak woodlands (Blair, 1996). Increase in food abundance is the most common mechanism described in the literature for the increase in bird densities (Emlen, 1974; Bolger, 2001; Marzluff, 2001; Mennechez and Cleurgeau, 2001). This increase may reflect the combined effect of an increase in exotic vegetation, refuse, and, in many cases, the use of feeders. While all bird guilds increased their densities, the response of seed-eaters to urbanization has been the highest. Emlen (1974) associated this increase with both high supply of seeds in feeders and higher productivity in the urban environment due to urban lawns and weeds. While this "bottom-up control" of population size is accepted as the major cause of population growth in urbanized environments, the contribution of the "top-down control" (i.e., reduction in predation pressure) is still unclear. Cities have high abundance of birds despite the high densities of domestic and feral predators, creating a paradox (Shochat, 2004). We discuss possible solutions to this paradox later in this chapter.

In most cases, diversity in urban habitats decreases or remains similar to wildlands (Marzluff, 2001; Chace and Walsh, 2006). Although urbanization increases total bird densities, it appears that only a few species contribute to this increase. Cities consist of mixtures of built habitats and green patches. Only a few species can exist and thrive in the most built parts of the city where vegetation is almost absent, such as business districts and industrial zones. Thus, urbanization increases the abundance of feral pigeons, swallows, swifts, and a few other species that breed in walls. As vegetation cover increases toward the rural parts of the city, species diversity increases (Emlen, 1974; Mills et al., 1989; Chace and Walsh, 2006; Sandstrom et al., 2005). In areas of intermediate disturbances (i.e., suburban development) diversity also increases (Blair, 1999). Because the vegetation is usually exotic, the increase in diversity is attributed to many human-commensal or alien species, whereas native vegetation allows, in some cases, a higher proportion of native species (Emlen, 1974; Mills et al., 1989; Chace and Walsh, 2006; Daniels and Kirkpatrick, 2006). Since the majority of urban bird research addresses basic patterns of abundance and distribution, the generality and consequences of these patterns in urban bird ecology remain unclear. *Evenness*, a term denoting the similarity in relative abundance of all species in the community, appears to decrease with urbanization, although only few studies

address this issue (Edgar and Kershaw, 1994; Marzluff, 2001). The reduction in evenness is the result of a few species becoming highly dominant in urban environments (Shochat et al., 2010). Exotic and synanthropic species generally thrive in the novel urban ecosystem, while many native species avoid it. This might lead to a loss of diversity if the dominant species "monopolize" resources. While these patterns have been described in many studies (reviewed by Chace and Walsh, 2006), the mechanisms underlying this community pattern have not been addressed (Shochat et al., 2006).

Until the early 2000s, an experimental and mechanistic approach had rarely been taken in urban bird research (Shochat et al., 2006). Currently, ecologists are trying to better understand the drivers of urban bird population dynamics and community structure, the role of habitat and vegetation profile vs. predator–prey interactions, and interspecific competition for food and other resources. In this chapter, we describe recent findings from a more process-oriented type of research on urban bird communities.

Physiological and Behavioral Adaptations to Urbanization

Birds respond to urban ecosystems by either avoiding cities or by adapting or exploiting the urban landscape. Many of the species able to adapt to or exploit the urban landscape undergo behavioral and/or physiological adaptations to survive and sometimes thrive in urbanized areas. If urbanization induces stress, one should expect to find differences in stress hormone levels and blood parasites between urban and wildland birds. Yet, it is not intuitive how these variables should change along the wildland–urban gradient due to the scant research on urban bird physiology. In Germany, urban blackbirds (*Turdus merula*) showed lower levels of corticosterone stress levels than forest birds. This may suggest that individuals that modify their stress response can adapt to the high stress level in cities (Partecke et al., 2006b). Yet, other studies show somewhat opposite trends. Urban male white-crowned sparrows (*Zonotrichia leucophrys*) sampled in Washington and California had higher corticosterone levels than rural ones, while no differences were found in females (Bonier et al., 2007). Furthermore, a comparison in several stress-associated variables between urban and desert birds in central Arizona indicated opposite trends for different species. At least two species, northern mockingbird (*Mimus polyglottos*) and curve-billed thrasher (*Toxostoma curvirostre*), appeared to be more stressed in the urban habitat (Fokidis et al., 2008).

Similarly to physiological adaptations, behavioral adaptations to urbanization do not show a general pattern. In some cases, urban birds appear more adapted to the presence of humans than rural birds. Such is the case of the black-billed magpie (*Pica pica*) in Colorado, where flushing response and flight distance were lower in urban than in rural habitats (Kenney and Knight, 1992). In contrast, the same species showed avoidance behavior in China, where birds built nests higher in urban than in rural and wildland habitats (Wang et al., 2008). Avoidance behavior can also occur temporarily. For example, in Madrid, Spain, the abundance of foraging individuals of several species decreased with an increase in the number of pedestrians in urban parks (Fernández-Juricic, 2000), suggesting that birds avoid foraging patches when their perceived risk increases. Species able to exist in the urban habitat enjoy higher resource

abundances than species in wildlands. For example, in arid environments, birds have higher water availability (Shochat et al., 2006). Furthermore, fluctuations in these resources are minor compared with wildlands (Shochat, 2004). This allows some species to extend their breeding season, as seasonality does not restrict resource availability as in wildlands. For example, relying on food abundance as a cue, suburban Florida scrub jays (*Aphelocoma coerulescens*) start breeding earlier than wildland birds (Schoech and Bowman, 2001). Similarly, urban magpies begin breeding earlier than wildland magpies in Poland, taking advantage of higher food abundance and more advantageous microclimate conditions in cities. In addition, urban magpies also re-nested more often than wild magpies (Jerzak, 2001). In Germany, urban blackbirds extend their breeding season by developing their gonads 3 wk before forest individuals (Partecke et al., 2006a), again, due to the increase in food subsidies.

While food density is normally high in urban settings, the main source is low quality, anthropogenic refuse. Sauter et al. (2006) showed that although adult Florida scrub jays prefer to feed their nestlings with natural food (i.e., arthropods), they are forced to feed their nestlings with low quality food in suburban areas because of a low density of arthropods. This may negatively affect nestling growth and development. Thus, although the high density of resources may support high densities of birds, the low quality of these food resources may have costs in terms of bird health and growth. Pierotti and Annett (2001) showed how "urban diet" can lead to lower fitness in western gulls (*Larus occidentalis*). Gulls that nested close to urban areas relied mostly on refuse and had relatively low nesting success, whereas birds that nested far from urban areas relied on scavenging in marine habitats and had higher nesting success (Pierotti and Annett, 2001).

Another stressor birds have to cope with in urban settings is noise. The urban ecosystem is characterized by elevated noise levels, which can interfere with vocal communication (Warren et al., 2006). Birds use vocalizations to warn of danger, defend a territory, and attract mates. The most prominent noise source in urban ecosystems is traffic, and consequentially, the majority of urban acoustic studies concentrate around roads. The noise within urban ecosystems is at low frequencies, usually below 2000 Hz (Patricelli and Blickley, 2006; Warren et al., 2006); therefore, birds with higher frequencies or those with the ability to shift their frequency (Slabbekoorn and Peet, 2003) will have an advantage to communicate amid the urban noise. However, the interaction between responses to noise and resultant fitness is not well understood. A recent study showed that house finches (*Carpodacus mexicanus)* adjusted their songs in response to noisy areas within a city by raising the low frequency of their songs and decreasing the number of notes per song (Fernández-Juricic et al., 2005), which could potentially decrease their mating opportunities because females are generally more attracted to males with longer songs (Nolan and Hill, 2004). When communicating with their young, adults use low-frequency contact calls near the nest. Forman et al. (2002) suggested fledglings and nestlings cannot hear warnings from their parents because of the traffic noise. This interference may negatively impact reproductive success. In addition, urban noise might influence bird distribution. Rheindt (2003) demonstrated a strong correlation with song frequency and distance to roads, where birds with higher frequencies had a greater abundance closer to roads than birds with lower frequencies.

Top-Down and Bottom-Up Control of Urban Bird Populations

Urban bird densities are normally extremely high (Emlen, 1974; Marzluff, 2001; Chace and Walsh, 2006; Rodewald and Shustack, 2008). Increase in bird densities may be the result of high food density (bottom-up control), low predation pressure (top-down control), or the combination of both (Shochat, 2004). Although food abundance is normally difficult to quantify, the bottom-up concept has been accepted as the major driver of urban bird densities (Marzluff, 2001). Exotic vegetation, refuse, and bird feeders all provide food sources for urban birds. In a study on northern cardinals (*Cardinalis cardinalis*) in Ohio, food abundance was found to be 2.6 times higher in urban than in rural habitats, although based on bird densities total food abundance was expected to be four times higher in the urban habitat (Rodewald and Shustack, 2008). Fuller et al. (2008) also found a positive correlation between urban bird feeding stations and bird abundance in Sheffield, UK.

The role of top-down control, however, is more complex. Predators are known to affect prey on three different temporal scales: in the short term, prey may change its behavior; in the long term, prey population size may decrease; and in an evolutionary time scale, prey may show morphological adaptations to the presence of predators. Of these three possible responses, the second—the population level—is the most straightforward to address logistically, and thus, the most studied of the three levels. While many natural predators avoid urban areas, at least during daytime, when birds are active (Tigas et al., 2002), other feral or domestic predators that inhabit cities in high densities, especially cats (Haskell et al., 2001), can affect bird population regulation. In Britain, cats have been shown to hunt millions of birds per year (Woods et al., 2003). Baker et al. (2005) studied the impacts of cats on urban animals, including birds in Bristol, UK, and noted a prey preference for juvenile birds. In particular, house sparrows (*Passer domesticus*), dunnock (*Prunella modularis*), and robin (*Erithacus rubecula*) had a higher predation rate compared to their relative productivity. Thus, cat predation could negatively impact dispersal and recruitment in urban areas particularly. Other researchers (e.g., Sorace, 2002) suggested that due to the high densities of cats in urban ecosystems, predation pressure should be higher than or equal to that in wildlands. Yet, observations on bird behavior and population size do not appear to concur with the idea of strong top-down controls on urban bird populations (Shochat et al., 2006). For example, while direct top-down control predicts a negative correlation between predator and prey density, studies in urban settings consistently indicate that despite high cat densities, urban bird populations are denser than wildland populations. Thus, when correlated versus each other, cat and bird densities are positively correlated in urban settings (Sims et al., 2008). Shochat (2004) suggested that urban bird community composition may therefore represent the "ghost of predation past"; urban environments may have selected a small group of cat-resistant species. Having available water, high density of food, and a lack of native predators allows these species to flourish in the city.

The most effective way to test behavioral or survival responses of prey to predators is to manipulate predator abundance. Removal of black-billed magpies from city parks in Paris, France demonstrated that these nest predators have a minor effect on the abundance of 14 bird species or their reproduction (Chiron and Julliard, 2007). The only obvious effect of magpies appeared to be the shift in

foraging niches by some of these species. Another study also showed that magpies in urban parks in Madrid influenced the antipredator behavioral responses of some bird species by reducing the number of species (and their neighbor distance) within a patch when magpies were present (Fernández-Juricic et al., 2004). This was attributed to the fact that magpies were opportunistic predators of adult birds; however, their capture success was relatively low (5%). Interestingly, differences in prey vigilance behavior were related to the probability of being attacked rather than mortality rate by magpies. A preferentially attacked prey species in relation to its abundance (e.g., blackbirds) enhanced their vigilance effort (i.e., increase in scanning time and scanning rate with magpies present) relative to a species (e.g., house sparrow) attacked infrequently in relation to its abundance, which showed no vigilance responses when magpies were present (Fernández-Juricic et al., 2004).

At the behavioral and morphological levels, the effect of predation on birds has not been studied thoroughly, and the few studies conducted showed mixed results regarding the low predation pressure hypothesis. Studies on foraging behavior of birds and squirrels in urban and wildland habitats suggest that the urban habitat is probably less risky than the wild habitat, whether it is forest or desert (Bowers and Breland, 1996; Shochat et al., 2004). In both cases, individuals quit foraging on artificial food patches earlier in wildland or rural habitats than in the urban habitat, as the costs of predation are apparently lower in the urban habitat. Furthermore, contrary to desert habitat, urban birds in Phoenix, AZ showed no differences in foraging behavior between food patches that are close to shelters (under bushes), and patches that are out in the open (Shochat et al., 2004). These findings suggest that animals view the urban habitat as safe from predators. However, other studies found that urban habitats are not as safe for some bird species as previously thought. Valcarcel and Fernández-Juricic (2009) found that house finches in more urbanized areas formed larger flocks, had less tolerance to human approaches, and increased their pecking rates to compensate for the lower amount of foraging time than those in less urbanized areas in Southern California. Interestingly, avian predator richness and abundance was lower in urban areas. These results suggest that urban house finch's perceived risk of predation is regulated by human activities, which could increase risk or decrease the ability to detect predators.

From a population perspective, the evidence supports a reduction in predation pressure in urban areas. The behavioral evidence is less conclusive and points to different mechanisms (predation risk, human disturbance, intra-guild predation) acting simultaneously, which can complicate interpretations. Furthermore, we should bear in mind that cats still cause damage to bird populations and that many cities are inhabited with natural predators (Chace and Walsh, 2006). Altogether, additional research is required to establish the role of top-down effects on urban bird populations.

Urban Bird Community Structure and Composition

Species interactions and the mechanisms underlying community structure in urban settings are the least studied issues in urban ecology. The presence of a few abundant synanthropic or alien species in cities may affect native species at different levels—behavioral, population size, and species diversity. Hints for such

effects can be drawn from evenness, which is normally low in urban environments (Marzluff, 2001). The low evenness may be the result of a few synanthropic species that thrive and account for a high proportion of the whole community (Shochat et al., 2010).

To understand community structure, Shochat et al. (2004) studied foraging efficiency in urban and desert birds in Phoenix, AZ. Foraging efficiency is defined in terms of the ability to deplete food patches, especially in low resource density habitats. Inefficient species need to dominate over more efficient species to coexist. Using artificial food patches, Shochat et al. (2004) found that urban birds were more efficient foragers than desert birds. From a series of field experiments they concluded that the combination of high food and water resource density combined with low predation pressure allowed urban birds to increase their food intake.

In many cases, temporal partitioning is required for species coexistence. In this mechanism of coexistence, subordinate species are more efficient foragers than dominant species (Ziv et al., 1993). Thus, once dominant species quit food patches, they leave behind enough food for subordinate species in subsequent patch visits. However, it appears that in urban habitats, this situation changes. Shochat et al. (2010) demonstrated that the most efficient foragers in urban settings are probably the more dominant species in the community. Such a situation may constrain subordinate species, limit their population sizes, and in extreme cases, lead to local extinction.

Species Diversity

According to the random sampling hypothesis (Connor and McCoy, 1979), urban environments should have higher species diversity because cities attract more individuals from the regional species pool. However, most studies on urban bird species diversity detect a low diversity for the number of individuals "sampled" (Emlen, 1974; Mills et al., 1989; Sewell and Catterall, 1998; Marzluff, 2001; Chace and Walsh, 2006). These findings indicate that urban ecosystems do not draw a random set of species from the regional pool, but rather favor a small group of birds that appear to adapt well to this novel ecosystem. Indeed, cities are normally inhabited with high densities of human commensal or synanthropic species, many of which are invasive or alien (e.g., house sparrow, feral pigeon, Eurasian starling). Because such species were introduced by humans to many parts of the world, it has been argued that humans create a homogeneous avifauna in cities (Blair, 2001; McKinney, 2006).

Relatively few studies to date have tried to thoroughly investigate the mechanisms for the loss of species in urbanized areas. Whereas habitat fragmentation or destruction leads to extinction of many native species, urbanization also creates new habitat for other species. Yet, regardless of large-scale landscape composition or geography, urbanization results in low species diversity on a global scale. Two different mechanisms have been suggested for these phenomena. Using island biogeography as a framework, Marzluff (2005) suggested that the overall sum of bird species should be lower in the most urbanized parts of the landscape. In Seattle, bird diversity peaked at intermediate levels of urbanization, where the proportion of forest was still relatively high. The high number of species in these habitats was mostly the result of an increase in richness of early successional birds—species that are found in a variety of habitats around the area.

Extinction rates of native forest species and immigration rates of synanthropic species played a minor role in influencing species diversity.

Shochat et al. (2010) suggested a different scenario, involving competitive exclusion. They used data from Phoenix and Baltimore to link this phenomenon to community structure and species interactions. In their scenario, the increase in resource abundance, combined with the decrease in predation pressure, results in a "winner take all" situation. Not only do cities offer high amounts of resources to birds, resource input into the ecosystem is highly predictable, owing to human activity routines (Shochat, 2004). Bird species that cannot exist in less predictable or resource-poor environments may be able to flourish in cities, where these hurdles associated with food and water resources are removed. Growing in numbers, they dominate resource patches and out-compete many native species or cause a significant reduction in others. Such changes may be the reason for the low evenness pattern of urban bird communities.

Conservation

The changes in bird community structure and composition discussed here are summarized in Fig. 4–1. The role of species interactions in urban bird population dynamics and community structure may suggest that solutions for the loss of diversity cannot be based on habitat alteration per se. Creating proper habitat for a given species may not be sufficient to attract it into the city if it suffers from aggressive interactions from local urban species or human disturbance. Urban conservation ecology should therefore seek creative solutions based on the evolutionary differences between dominant and subordinate species, creating special breeding or feeding niches for the latter. Such solutions already exist and are widely used—e.g., squirrel-proof feeders. Their basic concept is that whereas dominant, aggressive species are impossible to control, we can still open a niche
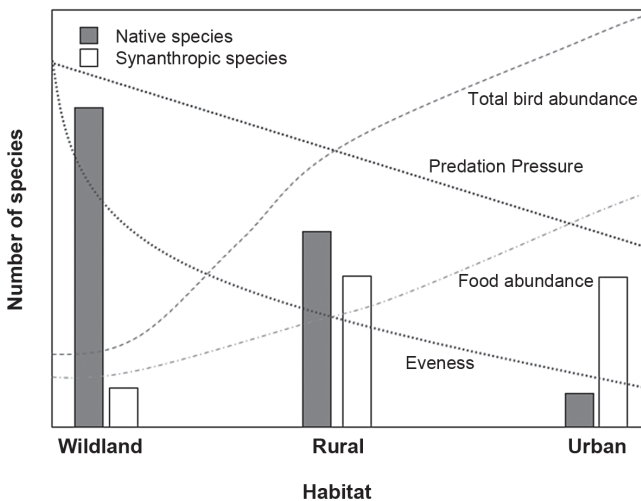

Fig. 4–1. Changes in bird community structure and composition along a wildland–urban gradient. As food abundance increases and predation pressure decreases, total bird abundance increases. This increase results from a few thriving synanthropic species, while many native species are lost due to habitat changes and competitive exclusion. These changes in community composition lead to lower evenness.

for subordinate species with simple manipulations that exclude the dominant species from a small but important part of the urban habitat. Squirrels are aggressive toward birds, but-squirrel proof feeders based on body mass turn a squirrel's advantage in adapting to the urban ecosystem into a disadvantage. Feeders allowing seed access only for animals below a given threshold body mass, such as small birds, allow for species coexistence by opening a niche to granivorous birds, which in turn increase local diversity. The same concept is used with nest boxes, where hole size prevents dominant species like starlings from occupying them, creating more available nesting sites for smaller, native cavity nesters. The foraging "niche opening" principle has been taken one step further with sparrow-proof feeders that allow small finches to persist in the urban habitat. This suggests that the principle can be applied for other species or on larger scales and presents an alternative to expensive programs to eradicate abundant aggressive synanthropic species (Shochat et al., 2010).

Whether one considers loss of habitat or negative interactions, addressing the mechanisms leading to the loss of diversity in urban settings is one of the fundamental challenges in conservation biology because of the widespread distribution of urbanized habitats on the planet. The above-described frameworks of Marzluff (2005) and Shochat et al. (2010) concerning the role of landscape structure, top-down, and bottom-up effects should be treated as starting points for future research on this topic, with the ultimate conservation goal of transforming urban environments into species-rich ecosystems.

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