

Chapter 13

Impact of Urbanization on Birds



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Abstract Urban habitats and landscapes are markedly different from nonurban “natural” habitats. The major difference is the transformation of the land, from natural green areas to anthropogenic structures and impervious surfaces. To survive in the urban habitat, birds are forced to either accept or avoid the new conditions. In addition, the urban sprawl has led to a highly fragmented landscape, with islets of suitable bird habitat surrounded by highways and buildings that frequently act as barriers, even for mobile creatures such as birds. These altered conditions have changed the avifauna dramatically, with many species vanishing once an area is urbanized, thus resulting in a significant loss of local biodiversity. However, some species seem to thrive in the city, and these urban-dwelling species often show pronounced phenotypic differences (e.g., in behavior, physiology, and morphology) to their rural conspecifics. These phenotypic changes have been linked to specific urban selective drivers such as air pollution, artificial light at night, noise, different kinds of food, different predation pressures, and human disturbances. However, these drivers are often confounded, and it is hard to separate one urban factor as the main driver for the differentiation. Although the urban habitat is a large threat to biodiversity, it is also an exciting environment for studies of population divergence, evolutionary responses, and ultimately speciation in real time.

Keywords Anthropogenic · Environmental stress · Habitat fragmentation · Light at night · Pollution

13.1 A Brief History of Urbanization

Human exploitation of land dates back to our earliest settlements, with massive, yet local, destruction and deforestation (Diamond 2005). Already the Romans transformed the landscape to the treeless landscape of the Mediterranean that we

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are familiar with today, probably with devastating consequences for the wildlife at that time. Similar scenarios can be found throughout human history and across the world. However, it was not until the Anthropocene that the urban human societies started to grow significantly across the globe. Western industrialization started in the 1700s and with that urbanization and urban sprawl became a significant part of the landscape. Today, urbanization is a global phenomenon with implications for birds as well as for all other animals. Yet, developing countries are still in the early phases of industrial revolution; thus, the impact of global urbanization is expected to increase. Likewise, due to continued growth of the human population, existing urban areas in the western countries are also predicted to intensify and expand in the future.

Together with climate change, urbanization is considered one of the largest threats to wildlife, including the persistence of many bird species. The foremost threat is probably habitat loss and fragmentation, which forces rapid decisions about emigrating (if possible) to more suitable habitats or stay and cope with the new conditions (Marzluff and Ewing 2001; McKinney 2002). The new urban conditions are not only through the process of urbanization per se but also the fact that the existing or remaining “green” areas are often changed, through plantation of non-native plant species, managed lawns, and removal of the mid-story canopy (Luck and Smallbone 2010; Aronson et al. 2014).

Although, the total number of bird species declines once an area is urbanized, many bird species do seem to flourish. In fact, birds are probably the loudest and most visible animal group in the urban habitat. The urban species often exploit anthropogenic resources such as the high abundance of novel food sources and artificial nesting holes, e.g., nest boxes and under roof tiles. In temperate regions, birds can also benefit from the warmer climate caused by the so-called “urban heat island” effect, which is caused by the heat-absorbing properties of the impervious surfaces and buildings together with the scattering effects of air pollution, trapping heat irradiation within the atmosphere of the city. However, in warmer or tropical regions, the urban heating effect can be devastating for birds, leading to heat stress and dehydration (Grimm et al. 2008).

While all anthropogenic change of the landscape (including farmlands and deforestation in sparsely populated areas) is challenging for birds, I will here primarily focus on the anthropogenic disturbance (or urbanization) that is associated with densification of humans and human activities, i.e., cities. Nowadays, up to 54% of the world’s human population live in cities (United Nations 2014). The more humans present in an area, the greater need for buildings and infrastructure, increasing traffic-related air pollution, noise pollution, and artificial light at night. Thus, human population size is a relatively good indicator of city-level impact on birds (Fig. 13.1).

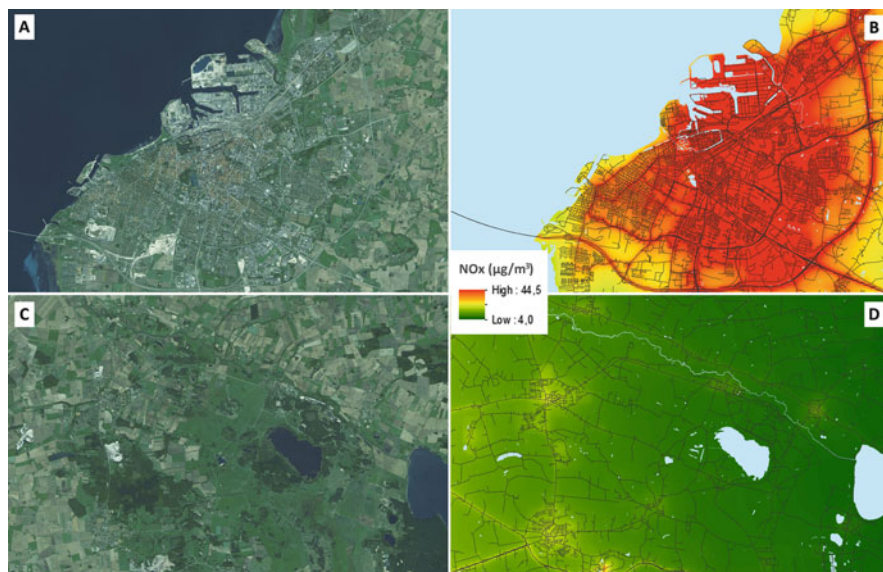


Fig. 13.1 Pollution map over a city and a nearby rural area. (a) Satellite image over Malmö, a city in southern Sweden with around 300,000 inhabitants; (b) pollution image (nitrogen oxides, NO_x) over the same area in Malmö; (c) satellite image over a nearby rural area. The two larger lakes are Krankesjön and Vombsjön; (d) pollution map (NO_x) over the rural area. The picture was produced by Emilie Stroh in 2018 by using ArcGIS (ESRI)

13.2 Birds and the City

Among the over 10,000 recognized bird species in the world, around 2000 (nearly 20%) occur in cities (Aronson et al. 2014). Although some bird species are cosmopolitan and thus occur in cities across the globe (e.g., Feral Pigeon *Columba livia*, House Sparrow *Passer domesticus*, Common Starling *Sturnus vulgaris*, Barn Swallow *Hirundo rustica*; Aronson et al. 2014), most urban species are representatives of the regional biogeographical species pool. Depending on their reliance on human resources, birds can be divided into three groups: urban avoiders, urban (suburban) adapters, and urban exploiters (Blair 1996, see further details below). Due to these different species-level responses to urbanization, once an area is urbanized, the species composition will change, with some species vanishing and others flourishing. In the sections below, I will start by reviewing the underlying drivers for these contrasting species-level responses and then continue with population divergence within a species as a result of urbanization and its implications for the species.

13.2.1 *Species Vanish from the City*

The urban avoiders are the species that immediately vanish when an area is urbanized. These species are generally characterized by ecological features such as having low natal dispersal, migratory behavior, fear toward humans (long flight-initiation distance), insectivory, and/or low yearly fecundity (Møller 2009 and references therein). This has, on a large geographic scale, led to a species-homogenizing effect (Clergeau et al. 2006) and a general lower species richness in the urban areas (e.g., Chace and Walsh 2006; MacGregor-Fors et al. 2012; Aronson et al. 2014). The main driver of this decline in avian biodiversity (i.e., that species vanish) is habitat loss, and there is a clear negative association between density of avian species and urban land cover (Chace and Walsh 2006; Aronson et al. 2014). However, cities that maintain native vegetation composition and structures will retain more native bird species than those that do not (Chace and Walsh 2006). Singapore is a good example of a megacity that has maintained a relatively high avian biodiversity. In a worldwide survey of bird species across 54 cities, 36 bird species were identified to be on the IUCN global Red List for threatened species, and 12 were recorded in Singapore (Aronson et al. 2014). Thus, cities like Singapore have an important conservational role for maintaining these species in the future—to defeat the species homogenization effect and to maintain suitable habitats for them. Since the human population continues to increase, so will urbanization; hence, the urban threat for birds is likely to be even more alarming in the future, and urban city planners and conservationists have an important task to maintain existing biodiversity.

The species that vanish immediately upon urbanization are relatively easy to identify. However, many species show a slower response to urbanization, with population decline over time as a result. To identify these species can be more difficult and requires long-term studies of populations and their dynamics (e.g., dispersal, fecundity, and survival). For studies of population dynamics, it will be important to (1) identify species for which the city act as an ecological trap, and (2) to establish, whether the urban population is a sink or source population. Both scenarios can result in impoverishment of the urban bird populations through lower lifetime fitness compared to birds in the surrounding nonurban habitats (Lepczyk et al. 2017). However, if the urban environment acts as an ecological trap, it can have implications for the persistence of the whole species. As the word *trap* indicates, an ecological trap acts by luring and attracting birds to a specific area. The city attracts many birds with its higher abundance of resources (i.e., food and nesting opportunities for cavity-nesting birds) and, in temperate regions, also with its milder winter climate compared to the surrounding nonurban habitats (Lepczyk et al. 2017). These factors make birds to evaluate the city habitat as a “high-quality” habitat, thus a preferred habitat compared to more natural habitats (Donovan and Thompson 2001). However, through the high rate of nest predation (e.g., by corvids and eastern gray squirrels *Sciurus carolinensis*), predation at feeding tables (e.g., by feral cats and dogs), poor nutritional value of the food sources, exposure to high pollution levels, and the high incidence of collisions with windows and cars reduce the overall fitness

of the population in the urban habitat (e.g., Donovan and Thompson 2001; Erritzoe et al. 2003; Bonnington et al. 2015). Hence, if the ecological trap (city preference) is strong, the urban habitat will continue to attract rural birds to the city where they will suffer the negative consequences, ultimately reducing the species future chances of survival (Donovan and Thompson 2001). The second scenario, the source-sink scenario, can result in both positive and negative effects on the population depending on whether the urban population is a source or a sink. However, if the urban population is a sink (without being a trap), birds do not prefer the urban habitat over nonurban habitats. Instead, surplus individuals can be forced into the city due to lack of free niches in the natural habitat. However, since the urban habitat is not preferred, there will not be as severe effects on the species level as with the ecological trap (Dias 1996; Lepczyk et al. 2017). That argument, however, relies on the existence of natural habitats; thus, the continuation of habitat destruction and deforestation could be devastating also for source-sink dynamics across the urban/rural landscape.

13.2.2 *Species Flourish or Persist in the City*

Although many species vanish from urbanized areas, some species thrive or persist in the city. The group of urban exploiters comprise species that seemingly flourish in the city. They have exploited the human resources to such a degree that they now depend on them to maintain current population densities. Many of the avian urban exploiters are invasive species, for example, Feral Pigeons, House Sparrows, and Common Mynas *Acridotheres tristis*. In fact, urban areas have greater abundance of birds (or biomass) per sampling unit than nonurban habitats (e.g., Chace and Walsh 2006; MacGregor-Fors et al. 2012). This is something that many raptor species have gained from, and some are now becoming increasingly common in urban areas, e.g., Great Horned Owl *Bubo virginianus*, Peregrine Falcon *Falco peregrinus*, and Black Sparrowhawks *Accipiter melanoleucus* (Chace and Walsh 2006; Kettel et al. 2017; Suri et al. 2017).

Similarly to above, when comparing city-dwelling species from the Western Palearctic with urban avoiders from the same region, the urban birds shared several ecological features (Møller 2009). Urban bird species are characterized by large breeding distributions, high propensity for dispersal, high rates of feeding innovation (novel ways of acquiring food), less fear toward humans (short flight-initiation distance), and a life history characterized by a high annual fecundity and high adult survival rate (Møller 2009). Urban species also have a larger size of the *bursa of Fabricius*, a specialized organ in birds that is part of the immune system, which suggests that they have the capacity to mount a stronger immune response compared to urban avoiders (Møller 2009). In addition, urban species have higher levels of dietary antioxidants (vitamin E and carotenoids) than the urban avoiders, which may help them to defeat oxidative pollution better, see below (Møller et al. 2010). Other studies have also concluded that urbanization favors omnivorous,

granivorous, and cavity-nesting bird species but that it depends on geographical location and climate (Chace and Walsh 2006).

Although these features are common to species that are regularly seen in urban habitats, they are not indicative of whether a particular species is an exploiter or adapter species. Similar to the two scenarios above—the ecological trap and source-sink dynamic—to know whether a species is an adapter or an exploiter species can be very important for understanding species resilience to urbanization, the associated urban stressors, and also its dependence on humans. The urban adapter species are not dependent on human resources, but are happy to utilize them from time to time. Urban adapters include, for example, many of the small perching birds such as Great Tit *Parus major*, Blue Tit *Cyanistes caeruleus*, and House Finch *Haemorhous mexicanus* but also species such as the endemic New Zealand Tui *Prosthemadera novaeseelandiae*. A change in human behavior, the waste disposal system, or the urban landscape could potentially quite rapidly change the composition between urban adapter and exploiter species within an urban area, where adapters can outcompete the exploiters, if the resources decrease; however, the opposite scenario is probably more common.

As mentioned above, urban areas have overall lower species richness than nonurban habitats. However, a higher species richness is seen in Palearctic (European) cities as compared to cities in the Nearctic and Australasia (Aronson et al. 2014). This difference could be related to time since urbanization, i.e., the birds have had more time to adapt to the urban environment in the older cities. In the rest of this chapter, I will look into individual- and population-level responses to urbanization, which ultimately provide a platform for selection to act upon and for population divergence to appear, with potential implications for sexually selected traits and speciation.

13.2.3 Species Change

Urban environments provide an intriguing opportunity for studies of evolution in real time. Many, if not all, animal species show some phenotypic difference between the urban and nonurban counterparts. These phenotypic differences have been documented in all sorts of traits, from physiology and behavior to morphology, with potential effects on life-history traits and ultimately fitness. The drivers of these phenotypic changes are multiple and not always easy to disentangle. Likewise, the mechanistic underpinnings of the changes and whether they are caused by “non-genetic” phenotypic plasticity or genetic divergence (discussed below) are not always known.

Phenotypic plasticity here refers to the direct response of organisms to an environmental change like urbanization. In other words, a certain genotype will give rise to a different phenotype when in a urban compared to a rural environment. The term is broadly used to describe all phenotypic responses and includes, for example, physiological acclimatization and learning (West-Eberhard 1989). Some of

these responses can change once and then persist throughout an individual's life or change continuously in response to environmental cues. Although I here refer to phenotypic plasticity as a "non-genetic" trait, plasticity itself can be an inherited trait. How much genes are expressed and the timing of the expression are important determinants of a species' or individuals' plasticity or, in other words, potential to phenotypically change. To date, there is only one study that has compared transcriptomes of urban and rural birds (Watson et al. 2017). The differentially expressed genes revealed to be involved in gene regulation (such as DNA methylation), innate and adaptive immune responses, DNA repair, heavy metal detoxification, and fat metabolism. Furthermore, two species of the well-known Darwin's finches *Geospiza* sp. showed dramatic differences in DNA methylation patterns between urban and rural populations (McNew et al. 2017). Although the functional significance of these mechanistic differences is yet unknown, it is promising to find variation here for species capacity to rapidly change in response to urbanization (West-Eberhard 1989).

13.3 Urban Environment as a Barrier for Movement

A population needs to be reproductively isolated from other populations of the species to diverge genetically. For a long time, urban habitats were not considered a barrier for mobile species such as birds. However, habitat loss through intensification of urbanization or urban sprawl has been proven problematic for species with sedentary habits or limited vagility, i.e., the ability to move freely and migrate (reviewed in Delaney 2014). As a result, populations get trapped. Indeed, among the studies that have found strong genetic differentiation between urban and rural populations are those of relatively sedentary species such as the Wren Tit *Chamaea fasciata* (Delaney et al. 2010). However, also the Song Sparrow *Melospiza melodia*, which is a more mobile species, shows a weak (yet significant) divergence (Unfried et al. 2013). In addition to dispersal ability, the strength of genetic structuring can also be associated with city characteristics and urbanization intensity (habitat fragmentation) (Delaney et al. 2010). The Great Tit, which is a fairly sedentary species, has shown mixed results in different cities. In Barcelona (Spain), the urban individuals show strong genetic divergence from those in the surrounding forest habitats (Björklund et al. 2010), whereas in Montpellier (France), there was a low yet significant genetic differentiation from individuals in the more rural sites (Perrier et al. 2017). However, when Great Tits were simultaneously screened from nine European cities and corresponding rural sites close to the city, the overall pattern was that Great Tits are very similar, genetically, across the whole of Europe and there was no divergence in relation to urbanization (Salmón 2017). However, the study could also reveal signals of selection on certain genetic regions, suggesting that the urban environment does pose a selective pressure on this common European species.

Furthermore, a newly colonized urban population can start to grow from an initially small or large gene pool. If the urban population starts to grow from a

small number of individuals, this small population can be very different from the surrounding populations, the so-called founder effect, resulting in rapid population divergence (Delaney et al. 2010). Urban habitats may attract a certain kind of individuals such as those that are more explorative and bold (Riyahi et al. 2015; Audet et al. 2016; Charmantier et al. 2017; Senar et al. 2017). In the Great Tit, genes that are associated with exploration behaviors show the highest expression in the urban (from Barcelona) compared to the rural birds (Riyahi et al. 2015). Thus, colonization of urban habitats by a certain type of individuals rather than a subset of the population being trapped can more rapidly lead to genetic divergence but also loss of genetic diversity.

Studying genetic diversity is another common approach to explore the strength of a genetic barrier. Both isolated populations and populations showing founder effects are expected to show relatively low genetic diversity compared to their conspecifics. Indeed, this has been shown in urban populations of a number of species such as Dark-eyed Junco *Junco hyemalis*, Common Kestrel *Falco tinnunculus*, and Common Blackbird *Turdus merula* (Rasner et al. 2004; Rutkowski et al. 2006; Evans et al. 2009a). In the Blackbird study, the structure of the genetic signals suggested that this species has colonized urban environments multiple times (i.e., several independent founder effects) rather than one colonization event followed by local adaptation and dispersal (a leapfrog colonization model) (Evans et al. 2009a). A low genetic diversity is a concern, since it can lead to many negative effects. One example is the negative effects of inbreeding, which increases the occurrence of malformations and genetic disorders. A lower genetic diversity also means that natural selection has a reduced variation to act on; consequently populations of low genetic diversity are more sensitive to environmental perturbations. Interestingly, the genetic diversity in the abovementioned Great Tit populations from Barcelona and Montpellier showed contrasting results. The genetic diversity was higher for city birds in Barcelona and lower for city birds in Montpellier compared to their respective rural populations, suggesting that different population dynamics are in place in this species in these two European cities (Björklund et al. 2010; Perrier et al. 2017).

13.4 The Urban Drivers

There are at least four drivers (or environmental stress factors) that are directly related to urbanization and that are general across all geographical zones, namely, chemical pollution, noise, artificial light at night (ALAN), and human presence (Fig. 13.2). These four factors have led researchers to suggest that urban environments are relatively homogenous in the selection pressures that they might enforce.

The chemical pollutants that urban areas have in common are generated by traffic—the combustion of fossil fuels give rise to especially high levels of nitrogen oxides (NO_x) and soot (Fig. 13.1; Salmón et al. 2018). Many Chinese cities have particularly high levels of these pollutants (Grimm et al. 2008). But pollution levels of a standard city of Sweden, which is a much more sparsely populated region, are also high enough to have negative impacts on birds as well as humans (Fig. 13.1;

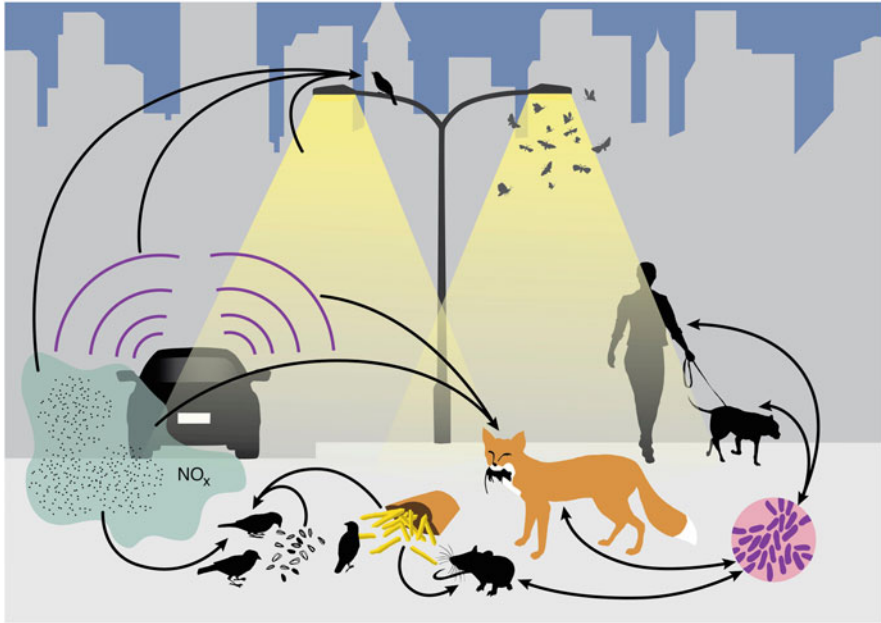


Fig. 13.2 An illustration of the multiple urban stressors/drivers. When an area is urbanized, the habitat is changed in many ways; apart from habitat fragmentation and the increased number of buildings and impervious surfaces which affect the climate of the area, there are also increased noise levels, traffic-related pollution, and artificial light at night. In addition, we (humans) and our pets disturb birds. We also provide birds with food which may not always be of the best quality. All these urban stressors likely generate selection pressures on urban birds. Illustration made by Anna Persson. From Isaksson (2015), *Functional Ecology*. Copyright © 2015 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc.

Salmón et al. 2018). In addition, many urban areas are also polluted with heavy metals; however the difference between urban and rural sites in heavy metal contamination seems to vary widely, depending on local industry and history (Binkowski and Meissner 2013; Manjula et al. 2015; Orłowski et al. 2014). For example, in India many of the polluting industries are located in rural areas such as metal fabrication industries and leather tanning, which result in no differences between urban and rural populations in heavy metal incorporation in feathers (Manjula et al. 2015). Thus, the urban exposure to heavy metals is less tightly linked to level of urbanization as compared to NO_x and soot exposure.

To find a silent place within an urban landscape is difficult. Constantly, cars are honking, sirens are alarming, hammering from construction work, and airplanes are taking off. This is jointly called urban noise pollution. Birds' responses to noise will depend on its loudness, frequency, consistency, and duration. Similarly, darkness is a rare thing in cities. Satellite images of the globe at night clearly illustrate the lit urban hotspots worldwide (Fig. 13.3). Europe, USA (mid- to eastern parts), and Asia, especially Japan and India, are lit hotspots on the map, whereas northern South



Fig. 13.3 A global map showing artificial light at night

America, central Africa, Russia, and Australia are still experiencing limited ALAN pollution (Fig. 13.3). All three pollution sources (chemical, noise and light pollution) are linked to phenotypic changes, which will be exemplified below, and also to costs in terms of reduced health, number of surviving offspring, and/or survival.

The last general urban driver is human presence. Birds perceive humans as a threat, and this threat is something that urban birds need to handle, since they interact and are exposed to humans constantly (Senar et al. 2017). Encounters with humans are likely to stress birds, in particular during the breeding season. Human behaviors toward birds are also likely to differ depending on species, for example, small birds are generally accepted to stay close, whereas larger species are vigorously scared away and even hunted in the city. Also human behavior toward birds are context-specific; we want them close when we choose to for example actively feed them (Fig. 13.4), but we do not want them too close while eating outside ourselves.

Apart from the abovementioned drivers, there are a few other factors that have been highlighted, namely, food abundance, pathogens, and predation (Fig. 13.2). However, these seem to be more affected by regional conditions, geography, and culture compared to the abovementioned factors. For example, food availability for urban birds can vary greatly across the globe. Supplementary feeding of birds is very common in western countries but more or less absent in eastern countries (Fuller et al. 2008). Thus, western urban birds seem to have plenty of food, whereas eastern urban birds may not (at least not from intentional feeding). Also, people living in sparsely populated farmlands can supplement birds heavily; thus food access is not directly linear to urbanization per se. However, poorer food quality, of both the natural and the anthropogenic sources, and reduced diversity of food items (e.g., grain and insect species) are also likely to be general across cities (e.g., Isaksson and Andersson 2007; Pollock et al. 2017).

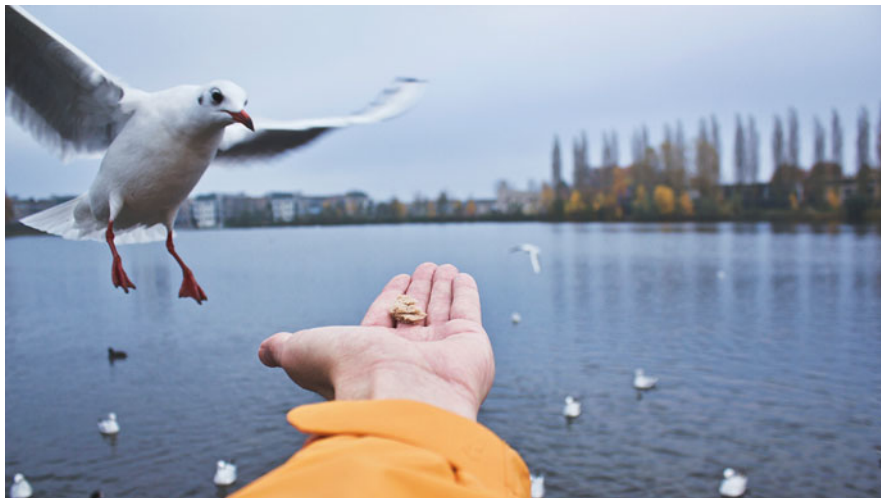


Fig. 13.4 Anthropogenic food sources for birds. The abundance of food in the urban environment is one of the key factors that attract birds into the cities. However, the food that we provide them with is not always the most nutritional food

Pathogen abundance and diversity show also great geographic variation and even variation across cities from the same region (e.g., Evans et al. 2009b; Delgado-V and French 2011). Climate and presence of water bodies are the two main factors that affect pathogen abundance and diversity in the city. However, transmission of disease may be more rapid in urban areas due to the higher densities of birds and gathering of birds at feeding tables.

Predation pressures may ease or increase depending on the characteristics of the city and the region. On the one hand, there are presumably fewer natural predators (e.g., large mammals and raptors) in the urban areas compared to natural nonurban areas. On the other hand, corvids, feral cats, and American minks *Neovison vison* are more common. Likewise, many smaller raptors such as Peregrine Falcons and Lesser Kestrels *Falco naumanni* perform very well nowadays in the urban setting (Chace and Walsh 2006; Kettel et al. 2017). Also the presence of artificial nests seems to attract predators significantly more in urban than in rural areas (Wilcove 1985; Jokimäki and Huhta 2000). However, in a comparative study of multiple urban species, it was shown that feathers of urban birds were more difficult to pluck (i.e., an anti-predation response), which was interpreted as reduced pressures from natural selection caused by predation in urban habitats (Møller 2009). Although these three last factors are more variable across cities, when present, they are likely to be strong drivers of population-level shifts in phenotypic traits.

13.5 Phenotypic Changes and Responses as a Result of Urban Life

With this chapter, I do not intend to cover all kinds of phenotypic changes or drivers. In fact, in many cases the causal relationship between a driver and a phenotypic change is not known or difficult to single out from the ocean of possible urban drivers. Thus, many studies of phenotypic changes are linked to urbanization per se rather than to single drivers. The phenotypic changes documented can be both a result of (1) population-level changes in the genetic pool (see above) or through (2) “nongenetic” responses of an individual (phenotypic plasticity). It should be noted that these two sources for population-level variation are not mutually exclusive. In fact, a genetic change can give rise to a change in phenotypic plasticity, and changes in phenotypic plasticity can lead to a new phenotype for natural and sexual selection to act upon, changing the genetic pool to the coming generations.

13.5.1 *Physiology*

13.5.1.1 Stress Physiology and Its Implications

The main physiological responses investigated in relation to urbanization or to single urban stressors is stress physiology (oxidative stress and corticosterone, commonly referred to as a stress hormone). Oxidative stress is the key target for toxicological research but also in relation to cost of life, since oxidative stress is part of the unavoidable aging process (Isaksson et al. 2011; Isaksson 2015). Environmental influences on oxidative stress can be multiple, e.g., pollution, radiation, disease, and food intake. However, the main factor in the urban environment is probably chemical pollution (such as NO_x and soot, Fig. 13.1). Many of the urban air pollutants act as prooxidants, which will react with and cause damage to life-sustaining molecules such as proteins, lipids, and DNA, unless they are detoxified by the protective antioxidants. Oxidative damages are commonly used as biomarkers of poor health, leading to premature death. The first response to pollution or prooxidants is to increase the antioxidant responses, and this is also what birds, as well as humans, generally do in urban environments (Isaksson 2010, 2015; Salmón et al. 2018). However, the upregulation is not always sufficiently high to avoid oxidative damage and species’ as well as individuals’ capacity to deal with oxidative stress varies. For example, some sparrow species (Passeridae) have a poorer capacity to block generation of oxidative damages to proteins and lipids in the urban environment compared to the tit species (Paridae) living in the same urban environments (Isaksson et al. 2017; Salmón et al. 2018). Consequently, the physiological response and capacity vary across urban-dwelling species and, ultimately, the negative physiological effects related to urbanization.

Another aging biomarker that may be linked to oxidative stress is the shortening of telomeres (von Zglinicki 2002; Boonekamp et al. 2017). Telomeres are the outer protective ends of the chromosomes, which shorten throughout an individual's life and can shorten more rapidly if exposed to stress such as irradiation, malnutrition, or pollution. When the telomeres reach a critical length, the cell cannot function, ultimately leading to cellular death. Early life in an urban environment has proven particularly challenging for Great Tits. In a cross-fostering experiment of 2-day-old chicks, half broods were swapped between an urban city park and a forest. Twelve days later, a blood sample was taken and analyzed for telomere length. The Great Tits that grew up in the urban habitat (independent of population origin) had significantly shorter telomeres than the chicks that grew up in the forest (Salmón et al. 2016). These individuals were followed to the next season, and it was clear that only the individuals with relatively long telomeres were recaptured the following breeding season, indicating that individuals with short telomeres had not survived the winter and this effect was significantly stronger in the urban environment (Salmón et al. 2017). This suggests that telomere length matters and that urban environmental stress significantly affects survival. To date, all studies on oxidative stress and telomeres are linked to urbanization and not to a specific urban driver; however, it is clear that regardless of source, the urban environment is challenging for birds and their physiological responses do not always circumvent the negative effects.

Another pathway to remove toxic heavy metals has been proposed for birds, namely, their incorporation into feathers. Melanin-pigmented feathers seem to incorporate more heavy metals, specifically zinc and lead, compared to feathers that are paler (non-melanin-pigmented). This was shown in pigeons of different color morphs which suggests that the dark melanin-pigmented Feral Pigeons could benefit in urban areas since they detoxify the blood stream from heavy metals, thereby reducing the potentially negative effect from pollution (Chatelain et al. 2014). Indeed, several studies have shown that the dark morph is more common in cities across Europe (Obukhova 2007; Jacquin et al. 2013).

Hormones have also been of great interest in relation to how birds respond to urbanization (Bonier 2012), especially stress and reproductive hormones. This is because hormones trigger behavioral and other physiological responses, thus representing key targets for selection. Changes in hormones have been associated with resource availability, conspecific interactions, predation, night light (see below), and human disturbance (Bonier 2012). Baseline levels of corticosterone seem to depend highly on sex, life-history stage, and/or species (Bonier 2012). Thus, studies on avian stress hormones have so far not been able to reveal any consistent pattern in relation to urbanization. Regarding hormones that affect reproduction, gonadotropin-releasing hormone is stimulated by day length. Due to the artificial night lighting in urban habitats the day becomes longer than in areas lacking street lights. Indeed, in urban environments gonadotropin-releasing hormone and other reproductive hormones are more stimulated which is the likely mechanistic explanation for the advancement of the timing of mating behaviors and reproduction (Deviche and Davies 2014).

13.5.1.2 Nutritional Physiology and Its Implications

Birds are provided with a great deal of anthropogenic food. This food can be either provided on bird feeders (e.g., peanuts, bread, sugar-water, sunflower seeds), or birds can scavenge from for example garbage bins or restaurant terraces. It is clear that many of the gregarious urban exploiter and invasive species take advantage of this resource (e.g., Robb et al. 2008; Galbraith et al. 2017). Food abundance and reliability change many phenotypic characters such as fat storage and flight-initiation distance, i.e., the tameness of the birds (Liker et al. 2008; Andersson et al. 2015; Møller et al. 2015). However, in relation to nutritional physiology, it is only recently that it has gained interest among ornithologists (e.g., Isaksson 2015). This goes hand in hand with human nutrition and the many negative health effects documented from our increased fat and sugar intake. Regarding fat intake, it is not only the increased consumption that is negative but also the changed composition of fatty acids, which affects, for example, inflammatory responses and metabolic rate. For example, in urban Great Tits there were less functionally important polyunsaturated fatty acids in yolks compared to yolks from eggs laid in the forest (Toledo et al. 2016). In addition, adult Great Tits show seasonal differences in fatty acid composition which reflect the differences in availability of anthropogenic food sources (Andersson et al. 2015). Furthermore and interestingly, the proportions of fatty acids were frequently in opposite directions when comparing species from the two families—Paridae and Passeridae. These patterns suggest that sparrows and tits feed on different food sources across the urban-rural gradient (Isaksson et al. 2017). Although the diet items were not quantified for fatty acids in any of the studies, certain polyunsaturated fatty acids are essential, i.e., they need to be obtained through the diet. The impact of these dietary differences shown in the birds' physiology is still unknown, but given the large-scale feeding of birds, it screams for attention (see, e.g., Harrison et al. 2010; Plummer et al. 2013).

Dietary antioxidants have also received attention in relation to urbanization, especially carotenoids (Isaksson and Andersson 2007; Møller et al. 2010). Carotenoids are synthesized by plants; thus birds need to obtain carotenoids through their diet. During the breeding season, many passerines rely on caterpillars for raising their brood, and these leaf-eating caterpillars represent a rich source of carotenoids (Isaksson and Andersson 2007). In cities, caterpillars are generally of lower abundance due to the high pollution levels and lack of native tree species (e.g., Pollock et al. 2017; Isaksson unpublished). However, it has also been shown that urban trees of birch *Betula* sp. and oak *Quercus* sp. (native to Northern Europe) produce less carotenoids (Isaksson 2009), which affects the carotenoid concentration of caterpillars and, ultimately, the carotenoid availability for birds (Isaksson and Andersson 2007). Carotenoids are important nutrients for proper development, the immune system, night vision, and yellow-red plumage pigmentation. Lack of carotenoids has been shown to affect breeding success, through smaller clutch sizes and reduced fledging success (Blount et al. 2002; Ewen et al. 2009). Nutritional limitation for breeding females and developing chicks is probably one of the reasons for the often-lower breeding success in urban environments (e.g., Chamberlain et al. 2009; Charmantier et al. 2017; Meyrier



Fig. 13.5 Urban (pale yellow) and rural Great Tits *Parus major* (yellow). The dietary pigments, carotenoids, that make feathers yellow are limited for urban birds. Hence the paler plumage coloration of this urban Great Tit. Photo: Caroline Isaksson

et al. 2017; Pollock et al. 2017). Moreover, carotenoid pigmentation is often used as an indicator of individual quality (i.e., nutritional quality and/or immunocompetence) used during mate choice. Urban Great Tits and also Great Tits living close to a copper smelter have a paler yellow (carotenoid-based) plumage coloration compared to their rural conspecifics (Eeva et al. 1998; Isaksson et al. 2005; Fig. 13.5). A paler plumage coloration affects the males' attraction potential (i.e., sexual signal value), and females may want or need to evaluate other characters, which may reduce female choice based on pigmentation and instead enhance the "sexiness" of other characters, which could lead to population divergence and reproductive isolation in the long run.

13.5.2 Behavior

13.5.2.1 Behavioral Responses to Chemical Pollution

Most responses documented to chemical pollution are physiological; however, also behavioral responses have been shown. In China, Li and colleagues documented the time it took for homing pigeons to find their way home. This race was conducted in an area with considerable air pollution, and it was shown that pigeons were homed faster when the air pollution level was especially high (Li et al. 2016). By doing this, the birds escape the high pollution levels, which can have negative effects on their performance and health. Another novel behavior is the use of cigarette butts in nests.

Both House Sparrows and House Finches have been shown to include cigarette butts as nest materials. The nicotine appears to work as an effective insect repellent against ectoparasites and the more cigarette butts the less infested was the nest (Suárez-Rodríguez et al. 2013). However, this repellent seems to come with physiological costs to the parent birds which show increased genotoxic damage (Suárez-Rodríguez et al. 2017).

13.5.2.2 Behavioral Responses to Noise

The list of behavioral responses to noise is long and includes changes in, for example, (1) vocal communication, (2) avoidance responses, and (3) fight-flight responses (e.g., Ortega 2012; Nemeth et al. 2013; LaZerte et al. 2017). The key feature of urban background noise is the low frequency, hence masking songs in this frequency range. Thus, a shift to higher frequency songs should be favored in the city. This is exactly what has been found in Great Tits (among many other species) in noisy natural environments (e.g., Slabbekoorn and Peet 2003). The higher minimum frequency song of urban Great Tits could also be experimentally induced, suggesting a highly plastic response (Halfwerk and Slabbekoorn 2009). However, a recent study challenges that plasticity is the cause for song differences across noisy habitats (Zollinger et al. 2017). The study by Zollinger and colleagues found that Great Tits sang consistently on pitch and with the same mean minimum frequencies in all noise conditions. This suggests that the observed changes between urban and forest populations may not be the result of individuals' plastic response, but instead be the outcome of slower, population-wide changes through selection (Zollinger et al. 2017). These population-level shifts in song could be driven by sexual selection, however, it could also be driven by body size and/or beak morphology (i.e., a smaller body and beak would lead to higher frequency songs). Urban environments have different food items available which repeatedly has been shown to affect beak morphology (e.g., Badyaev et al. 2008; Bosse et al. 2017). For example, urban House Finches were shown to feed on larger, harder foods than their counterparts in natural Sonoran Desert habitats (e.g., sunflower seeds *versus* cacti and grass seeds, respectively) (Badyaev et al. 2008). This led to a selection for larger bills in the urban population, which ultimately affected courtship song. This was suggested to give rise to a novel trade-off between bill size and song characteristics in urban environments. Possibly, these novel trade-offs between morphology and song in different environments could result in a nonoptimal song and mask the effect of noise on song.

Moreover, also species characters can influence the strength of vocal responses to urbanization. These species characters can, for example, be degree of vocal communication within species that use vocal communication to attract a mate, to defend a territory, or to warn for predators. Species also vary in their hearing capacity—some bird species hear certain frequencies and amplitudes better than other species, sometimes even within the ultrasonic range (Ortega 2012). Some species have solved the masking issue of their song and calls by changes in their daily rhythm. This is the case for European Robins *Erithacus rubecula*. The urban Robins reduce their

acoustic interferences by singing during night, and the effect of daily noise was indeed a stronger driver of this change in behaviour than the night-light pollution through changed sleep patterns (see also below) (Fuller et al. 2007).

13.5.2.3 Behavioral Responses to ALAN

The effects on the navigation and orientation system of nocturnally migrating birds are the most well-known negative effects caused by ALAN. The migrating birds are attracted to urban ALAN, hence they appear more frequently in urban lit areas during autumn migration than during other seasons (La Sorte et al. 2017). Apart from the general ALAN, light installations are very popular nowadays; unfortunately, the light beams from installations can “trap” birds, i.e., birds are attracted to the beam and, while in the beam, they get disorientated and fly around in circles within the beam—they get trapped. This was shown for the light installation put up in New York as memorial tribute to the 9/11 victims. Over a billion birds were affected during a few days count repeated over multiple years (van Doren et al. 2017). Migrating birds were in 20 times higher densities in the light beams compared to the nearby surroundings. Nowadays, the city of New York turn off the light installations when the bird densities get too high within the beam. Another sensitive group for ALAN are seabird fledglings. During their first flight to the sea, they can get disorientated by ALAN and end up grounded at lit highways and roads (Rodriguez et al. 2014). By turning off road light during fledging it reduces the number of birds that ground on the road (dead or alive) (Rodriguez et al. 2014).

Reproductive timing and mating behaviors are also affected by ALAN (e.g., Kempenaers et al. 2010; Dominoni et al. 2013a). A study of city and forest Common Blackbirds revealed that when exposed to ALAN in captivity, the reproductive system developed one month earlier than in individuals that were kept with dark nights. However, even more interesting was the fact the bird that originated from the city responded stronger to ALAN treatment compared to the forest birds, i.e., they had an even earlier start than the forest birds (Dominoni et al. 2013b).

Furthermore, correlational studies of ALAN have for long suggested that birds start their dawn singing earlier in urban lit areas; however, recently a large-scale experiment using different light colors could not confirm this for the 14 species investigated (Da Silva et al. 2017). In another experimental study, Blue Tits responded to ALAN by advancing their daily activity onset and more so for red and white light than for green light (de Jong et al. 2017). Similarly, experimental lighting progressively advanced the dawn singing of Robins (Da Silva et al. 2016). Thus, at least for some bird species, urban influences through ALAN can be mitigated by changing the spectral characteristics and intensity of outdoor lighting.

Another concern with ALAN is the effect it might have on sleep. Anyone who has tried to sleep with the lights on knows how disruptive that can be. The sleep hormone, melatonin, is affected by light and a decline in melatonin with ALAN has been shown in Great Tits and Blackbirds (Dominoni et al. 2013a; de Jong et al.

2016) and female Great Tits spend a greater proportion of the night awake (Raap et al. 2015).

13.6 Concluding Remarks

Urbanization has led to an immense change of the avifauna. Species have fled and vanished in response to urbanization but also flourished and changed. It is clear that urbanization is a huge threat to biodiversity and the existence of many bird species and urbanization is not expected to slow down in any close future, rather the opposite (United Nations 2014). Thus, conservationists and city planners have an important task for the future. Their actions can in fact have great positive effects on the bird community, if the urban green space areas are managed well through plantation of native flora and enhanced complexity and if they enhance the urban green space or limit construction in key areas (e.g., Chamberlain et al. 2007; Aronson et al. 2014; Kang et al. 2015). Many political actions are also taken to reduce the impact of the different pollution sources, e.g., electric cars and LED lights that can be turned off or dimmed during sensitive periods, which will probably also show a positive effect on urban-dwelling species. However, much remains unknown about urban bird species resilience to urbanization and how plastic these species can be in their stress resistance responses to multiple stressors, before they reach a threshold with a population crash as a result (Watson et al. 2015). Future studies will entail, whether urbanization will be an opportunity for species radiation or if it will continue to be a habitat of species eradication and homogenization.

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