# Chapter 6
# Becoming Citizens: Avian Adaptations to Urban Life

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**Abstract** Although cities have existed for some millennia, it has been only in the last few centuries that they have expanded to become a dominant feature of the landscape. Their growth displaces original habitats and creates new ones, facing birds with the challenge of adjusting their behaviour, physiology and life histories to the novel conditions or be displaced into a shrinking and also increasingly altered rural landscape. Here we identify the salient features—habitat structure, seasonality, interspecific interactions and pollution—in which cities differ from natural environments and to which birds must adjust. Then we describe the several ways in which urban birds have been found to differ from their rural counterparts. Finally, we evaluate whether these differences constitute adaptations to urban conditions or whether they are expressions of pre-existing adaptations to natural conditions, such as behavioural plasticity, which also permit the colonisation of urban habitats.

**Keywords** Urban birds • Adaptation • Cities vs natural areas • Pollution • Urban habitat structure

## 6.1 There Was Once a Country Sparrow

Organisms constantly modify the environment, and it has been argued that virtually every trait they exhibit has consequences on other organisms (Bailey 2012). Indeed, our constant physical and chemical interactions with the surroundings, including the biota, influence in several ways the functioning of the ecosystems. While most such influences may be important, their impact on the environment is usually minor, yet some have major, even drastic environmental effects. The history of life on

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Earth provides several examples of massive effects of organisms on the environment, such as the modification from a reductive to an oxidative atmosphere by photosynthetic cyanobacteria. This biotic influence fundamentally changed the way in which living organisms, erstwhile adapted to an anaerobic atmosphere, reorganised their metabolic pathways to create aerobic respiration, thus using toxic oxygen to extract energy from organic compounds (Kasting and Siefert 2002). Such major effects of organisms on the environment constitute selective pressures that may bring about extinction but also can promote adaptations of species to the changing conditions. In this era, which has been dubbed Anthropocene (Zalasiewicz et al. 2010; Monastersky 2015), urbanisation is becoming a major source of change, as cities sprawl over increasingly larger proportions of the land, facing species with novel ecological conditions in which they may thrive or from which they are displaced (Adams 2005; Goddard et al. 2010). The transformation of natural landscapes into urban zones creates areas with similar ecological conditions through the globe, contributing to biotic homogenisation (Blair 1996, 2001).

Although in the long run new conditions may favour ecological novelty, which is often an engine of speciation (cf. the many adaptive radiations that followed the transformation of the atmosphere from reductive to oxidant), it seems clear that in the short term, the main effect of major environmental disturbances is a loss of biodiversity.

This seems to be the typical consequence of urbanisation, in which environmental alterations are often so drastic and rapid that exceed the limits of tolerance of many species including plants, arthropods, amphibians, birds and mammals (Sih 2013). Yet, some species appear not only to be little affected by the urbanisation process but to take advantage of it, which has allowed them to grow in number and expand their range (Sol et al. 2013). Interestingly, these species seem to have some behavioural attributes in common such as behavioural plasticity, which although not a novelty, that may promote the spread and perhaps the diversification of urban biota. Indeed, there are several examples of avian species that seem to be particularly successful at colonising cities and which have consequently been often studied with the aim of determining what enables them to become good city dwellers.

To explore what distinguishes those bird species that are widespread in cities from those restricted to natural sites and to assess whether phenotypic differences could be due to plasticity or to evolutionary change (see also Chap. 7 by Miranda 2016), we first identify the main factors in which cities differ from rural to natural environments and that are likely to influence avian ecology. We then look into some of the species which have inhabited the cities for longer periods of time trying to identify which attributes they share and which ones allow them the successful colonisation of cities. Finally, we discuss whether differences in the attributes between urban and rural/wild populations or species can be safely regarded as adaptations to urban life.

## 6.2 How Are Cities Different from Natural Areas?

### *6.2.1 Habitat Structure and Seasonality*

Cities represent a local change in habitat structure, climate and productivity, in which the adaptations of local organisms to the pre-existing natural environment may no longer work. Such disturbance alters ecological interactions thus leading to changes in the biological communities (Shochat et al. 2006). Both the identity and the distribution of plant species—sources of food, shelter, nesting places and materials for native birds—are different between the cities and their surroundings (e.g. McDonnell et al. 1997), and bird communities are responsive to those differences (Day 1995; Carbó-Ramírez and Zuria 2011; Becker 2013). Cities are not built to promote biodiversity; thus their plant communities include only a small number of species, often ornamental of exotic origin, which may not cover the needs of the local avifauna (but see Gleditsch 2016). Nevertheless, green islands of vegetation—parks and gardens— which receive regular irrigation, palliate some of the consequences of urbanisation. Urban gardens help to buffer the fluctuations of temperature and humidity due to the dryness and reflection coefficient (albedo) of concrete and asphalt surfaces (Gilbert 1989; Jauregui 1991). Gardens also provide birds with regular food supplies in the form of invertebrates that feed on the irrigated plants and thrive in the thermal conditions provided by the vegetation (Pickett et al. 2001). Finally, gardens offer shelter from the weather and predators to potential nesting places; it is in them that native and exotic avian species alike concentrate (Susca et al. 2011; Lugo et al. 2012). Urban gardens may also be frequented by predators, thus potentially acting as ecological traps (Sorace and Visentin 2007). Because of the constant irrigation, and also from design (as they include many perennial species), these urban green islands can also represent a buffer from seasonality.

Many organisms adaptively time several aspects of their life history to the predictable periodic changes that are caused by geophysical cycles (Lack 1968; Murton and Westwood 1977; Nicholls et al. 1988). In addition to internal rhythms, such tracking of the seasons occurs in response to changes in environmental variables (e.g. temperature, photoperiod, rainfall and food availability; Dawson 2008). In cities, however, seasonality is buffered, and the cues that birds use to track it may be blurred by gardening activities (Haggard 1990; Shochat et al. 2006). Also urbanisation could alter phenology through altered photic conditions due to artificial lights at night. Yet, reduced seasonality does not necessarily need to be bad for birds and may be the key to the success of some urban birds. For instance, bird assemblage composition in parks of Valencia is maintained through the constant arrival of migrant species through the year, arguably favoured by the stability of the conditions, including food availability (Murgui 2007). These circumstances favour resident species that can become dominant by excluding others from their urban park territories and also contribute to the lack of functional response, by which population size responds to fluctuations in food production.

For other species, however, becoming urban residents is not an option, either because they are migrants who need to reach their breeding or wintering grounds on time or because the seasonality of key elements of their ecology (e.g. food or predators) is not influenced by the conditions in the cities. Therefore, it is crucial for them to correctly read the changes in the season in order to not risk local extinction through the timing of food, shelter and other resources (Lugo et al. 2012).

### 6.2.2 *Interspecific Interactions*

Urbanisation modifies the structure of animal communities and the way in which organisms interact. Cities do harbour a much reduced diversity of vertebrate predators than natural environments (McKinney 2002). This is somewhat counterbalanced by the very high numbers of those predators that are found in cities, particularly domestic cats (*Felis catus*), whose reported effect on urban birds can range from minor (e.g. Gering and Blair 1999; Gillies and Clout 2003) to severe (e.g. Woods et al. 2003; Loss et al. 2013), often compromising the persistence of urban bird populations (e.g. Baker et al. 2005; Van Heezik et al. 2010). The latter may be particularly true for native bird species in areas where cats are not originally native (Sorace 2002). Predation by cats may influence the composition of the urban bird assemblage, with the least susceptible species becoming dominant (e.g. Noske 1998); it is intense, affecting millions of birds every year, although perhaps not more so than in nonurban environments (Baker et al. 2008), and it appears to afflict birds in low condition (old, diseased, injured), as would be expected elsewhere (Baker et al. 2008).

The responses of avian predators to urbanisation vary between species and as a function of the urbanisation process. Specialist predators, being more sensitive to changes in the prey community, are typically much less frequent in cities than in the surrounding habitats (Blair 2001; Mckinney 2006), which is not the case of more generalist predators (Sorace and Gustin 2009). It has been argued that since predator size is positively correlated with flight distance (from humans), large predators are less likely to colonise urban habitats, thus allowing some relative large prey species to settle there (Møller et al. 2012). This process would not apply to nocturnal predators, as human activity is much reduced at night (Chace and Walsh 2006; Sorace and Gustin 2009).

An impoverished community of large predatory birds (see Møller et al. 2012) appears to contribute to the settlement of large corvids in some cities (e.g. Vuorisalo et al. 2003). Corvids, in turn, are often responsible for high rates of nest predation in cities (Major et al. 1966). Other known nest predators such as snakes and small carnivores (i.e. viverrids or procyonids) are also scarce in most cities, which instead harbour unnaturally high concentrations of cats.

Th evidence of how urbanisation affects the interaction between birds and predators is not uniform, probably due to the fact that the planning of urban landscapes varies across cities, thus affecting the assemblage and functioning of urban biological communities. Some authors report that predation decreases with urbanisation (e.g. Møller 2010), which is consistent with the fact that the density of breeding birds is higher in urban areas than in their surroundings (although the diversity of breeding species follows the opposite trend; Lancaster and Rees 1979; Beissinger and Osborne 1982; Shochat 2004). However, other works report that in the cities, there is a higher risk of predation, particularly on nests (Haskell et al. 2001; Sorace 2002; Jokimäki et al. 2005; Chace and Walsh 2006), which constitutes a crucial limiting factor for avian populations (Martin 1993; Conway and Martin 2000). Again, cats frequently prey on fledglings, and it has been argued that they have a major negative impact on breeding success of urban birds (Sorace 2002; Woods et al. 2003; Baker et al. 2008).

Because urbanisation brings about major changes in the composition of biological communities, it is reasonable to expect that it has an effect on parasite-/pathogen-host interactions. In the case of birds, this possible link has not been very extensively investigated (c.f. Delgado and French 2012), but available information suggests that the effect of urbanisation on the prevalence of avian parasitic infections is a function of the parasites' life cycle. On the one hand, both helminth parasite richness and prevalence (Aponte et al. 2014; Calegaro-Marques and Amato 2014) and diversity of blood parasites have been found to decrease with urbanisation, arguably due to loss of intermediate hosts (Fokidis et al. 2008; Geue and Partecke 2008). Conversely, viral infection (*Avipoxvirus*) and the severity of coccidial (*Eimeria* spp.) infection are positively associated with the degree of urbanisation in the house finch (*Haemorhous* [= *Carpodacus*] *mexicanus*; Giraudeau et al. 2014). These two pathogens are directly transmitted, and their prevalence may be linked to the high density of finches in the cities and possibly also to the abundance of bird feeders that promote contagion. This latter effect is worrying, since high densities of parasitised urban birds may spill infection to the wild bird living in the neighbourhood of cities (see Bradley and Altizer 2007).

It is unclear why intermediate hosts (mainly ectoparasites) should be less abundant in the cities than in rural areas, given that a large proportion of avian ectoparasites complete their life cycles in the bird nests (López-Rull and Macías García 2015) or on their plumage, while small water deposits that act as breeding sites for *Diptera* (mainly mosquitoes) are normally abundant in urban areas. As indicated above, most studies suggest that the effect of urbanisation on avian parasite biology depends on the life cycle of the parasites, yet other factors such as pollution may mediate this link. For instance, Bichet et al. (2013) found that lead pollution, which is high in cities, is linked with prevalence of *P. relictum*. This protozoan is responsible for one type of avian malaria, and since it requires an intermediate (arthropod) host, it would not have been expected to be too prevalent in cities.

### *6.2.3 Pollution*

Pollution by chemicals, light and sound is a defining attribute of cities that can negatively affect the physiology and disrupt the communication of birds. Organisms inhabiting anthropogenic environments are exposed to both inorganic and organic pollutants (see Kekkonen 2016) that often get into the tissues of birds (e.g. lead accumulation in the kidneys of pigeons (*Columba livia*); Johnson et al. 1982). This has prompted the use of urban birds to monitor pollution (e.g. house sparrows [*Passer domesticus*] used to track heavy metals in cities; Swaileh and Sansur 2006). At high concentrations, heavy metals can promote hatchling mortality (Scheuhammer 1987), but even sublethal concentrations can compromise bird condition (e.g. reducing both song repertoire and song output in great tits [*Parus major*]; Gorissen et al. 2005) or increase susceptibility to disease (Bichet et al. 2013). The progressive abandonment of leaded fuel has stalled the accumulation of lead in the cities, although it persists in the soil and finds its way into birds via earthworms and possibly other food (Scheifler et al. 2006). Currently the risk of heavy metal intoxication is probably greatest in areas where metals are extracted (see, for instance, Eeva and Lehikoinen 1996) than in cities, thus adaptations to contend with metal pollution—if they do exist—may not be particular to urban birds.

City birds are exposed to organic pollutants such as insecticides and rodenticides which are toxic to birds. These are often endocrine disruptors and as such can have a variety of effects in birds (Giesy et al. 2003), from interfering with sex determination to promoting the expression of sexually selected attributes, as in some British populations of common starlings (*Sturnus vulgaris*; Markman et al. 2008). Insecticides were first implicated in raising the mortality of urban birds by Carson (1962) in his inspirational *Silent Spring* and were famously recognised as the main cause of peregrine falcon (*Falco peregrinus*) decline in eastern USA (Peakall 1970; Cade et al. 1971). This rose concern about the ecological consequences of organochlorine insecticides (DDT in particular) and was partly responsible for the drive to develop less persistent organophosphorous insecticides. As with heavy metals, bird exposure to insecticides is not greater in cities than in rural areas, and thus any adaptation that may arise to contend with them would not be particular to the cities. Similarly, rodenticides are widely used in agriculture to control voles and other rodents, but also in cities, where they are ingested and damage several species of both rural and urban birds (see Godfrey 1986).

Plastics and other materials discarded by humans also constitute a form of pollution that can affect birds, particularly when used as nest materials. Thus crows and probably many other birds bring plastic debris to their nests. This often leads to entanglement and entangled chicks fail to fledge (Townsend and Barker 2014). Interestingly, the probability of entanglement for nestling crows is a function of the length of the plastic stripe/thread, which is larger in rural habitats where plastic mesh and wiring are widely used in agriculture-related activities (Townsend and Barker 2014).

Light pollution is present within and outside the cities, yet while it only affects a small proportion of rural birds, virtually every bird in the cities has to contend with it. Human sources of light are unlikely to match the quantity of light that birds are exposed to during the daylight hours, but can generate light that is qualitatively different to sunlight, and, more importantly, extend the period during which birds are exposed to light (see Dominoni 2016). Conventional low-frequency fluorescent tubes emit light that flickers at a rate below 100–120 Hz. When the rate is too low, the flicker can be perceived by and be stressful for some birds, particularly of fast flying species (as they need to update the visual scene frequently; Evans et al. 2012). This effect may be of concern for captive birds maintained under artificial light, yet although urban birds may be exposed to low-frequency fluorescent light, this would only occur by night and may have negligible effect on them.

Artificial light in cities and roads extends the perceived day length. This has several physiological effects on urban birds which are covered by Dominoni (2016, and see also references therein). Briefly, urban light can affect the circadian rhythms, reduce the age at maturity, advance the laying date and interact with other anthropogenic pollutants such as noise and chemicals. It can compromise the foraging efficiency and limit the foraging time of nocturnal birds dependent on light-sensitive prey (but see Weaving and Cooke 2010).

The effect of sound pollution—from traffic and other forms of anthropogenic noise—on organisms other than humans has been intensively studied, particularly since the seminal paper by Slabbekoorn and Peet (2003). In contrast to natural environments, the impervious surfaces of cities scatter sound waves and create multiple reverberations that can cancel and distort acoustic communication (Slabbekoorn et al. 2007). We now know that sound pollution causes major disruptions in the communication of many taxa (insects (Schmidt and Balakrishnan 2014), fish (Popper and Hastings 2009), amphibians (Hanna et al. 2014), mammals (Richardson et al. 1995; Schaub et al. 2008) including birds (see a recent review by Gil and Brumm 2013). Noise masking has led to shifts in the composition of local avian fauna (Francis et al. 2012) and has a major effect on the onset of the dawn chorus (Gil et al. 2015).

## 6.3 Which Avian Species Thrive in Cities?

Because of the challenges that birds face in urban environments, not all species seem to be able to thrive in cities, but of those that do, some seem to perform even better in urban areas than in the wild. Bird communities in the cities tend to include a large proportion of omnivores, granivores and aerial/ground insectivores, and often the resident species dominate over noninvasive immigrants (Allen and O'Connor 2000; Kluza et al. 2000; Poague et al. 2000; also see Lepczyk et al. 2016; Chen and Wang 2016). Invasive species such as the house sparrow, on the other hand, often outcompete ecologically similar native species such as the North American House finch (*Carpodacus mexicanus*; Bennett 1990), and they can breed explosively and become noxious pests, such as the common pigeon, which transmits disease and is harmful to buildings (but note that in some areas, notably in western Europe, house sparrow populations seem to be collapsing; see Summers-Smith 2003). Such preponderance of a few species also hints at different processes structuring avian—and possibly biological—communities in cities and in the wild.

The distributions of birds such as the house sparrow (*Passer domesticus*) and the pigeon (*Columba livia*; Driscoll et al. 2009) have become global as they moved from the relatively few ancient Eurasian cities to virtually all the cities that sprawled around the globe in the last 2000 years or so (Cocker and Tipling 2013). In part because of this ubiquity, they have been thought to possess particular attributes that favour life amongst humans. Yet even if they do have some traits that facilitate their living in urban environments, the subsequent colonisation of non-Eurasian cities by local fauna—which constitute most of the biodiversity in those cities (Aronson et al. 2014)—suggests that whatever attributes facilitate city dwelling, they are not exclusive of the few original urban species.

## 6.4 Recognising Adaptations

Since in this chapter we are exploring possible avian adaptations to urban life, it is crucial to distinguish between attributes that evolved in nature but allow birds to thrive in cities (e.g. noise and avian song; Brumm and Naguib 2009), from those that may have evolved in response to the selective forces acting in the cities. Normally, an adaptation is defined as the consequence of natural selection promoting the reproduction of organisms with particular heritable attributes which then become better represented in the next generation. Of the ten methods to detect natural selection listed by Endler (1986), only two (or three; see below) have been used to evaluate whether attributes in which urban bird differs from their rural counterparts amount to adaptations to life in the cities. Such differences are systematically referred to as adaptations (see Diamond 1986), yet in most cases, alternative explanations have not been ruled out. Demonstrating that natural selection has been involved is not the only way to determine whether an attribute is an adaptation. When phenotype and environment (e.g. urban/rural) are correlated, common-garden experiments provide the method of choice to infer that the differences are the consequence of adaptation, and not of phenotypic plasticity, trans-generational epigenetic effects or constitute preadaptations that evolved in natural contexts where the selective agents are similar to those found on sites. For instance, the surroundings of large waterfalls, which can be as noisy as the streets of a city, have an influence on bird song that is comparable to that of anthropogenic noise (see Brumm and Slater 2006).

Regardless of the underlying mechanism, ecological differences between birds living in cities and those living natural sites are notable and ubiquitous. This suggests that species exploiting urban environments typically adjust their phenotype to face the new challenges imposed by urbanisation. In the next section, we will review some examples of phenotype changes following urbanisation and the nature of them.

## 6.5 Adapting to Life in the Cities

### 6.5.1 Habitat Structure and Seasonality

Responsiveness to attributes that indicate seasonality varies amongst and between species and depends on phenotypic plasticity, which allows colonisation of different environments (Lambrechts et al. 1996). As we saw above, cities buffer the seasonal changes in the weather and in food availability. Cities also blur some of the cues that can be used by birds to adjust their physiology/behaviour to changes of the season. These changes should have led urban birds to become less seasonal. One demonstration that this is the case comes from studies showing increased sedentariness in urban blackbirds (*Turdus merula*; Partecke and Gwinner 2007). The authors looked at the pattern of nocturnal activity and fat deposition, two variables tightly linked to predisposition to migrate, of hand-reared birds from urban to nonurban localities and found that the former had a significantly reduced tendency to migrate. An earlier common-garden experiment by the same group (Partecke et al. 2004) demonstrated that, although the timing of reproduction was not different between birds from urban to nonurban areas, the former initiated earlier (both sexes) and finished also earlier (females) their reproductive hormonal activity, implicating a genetic difference in their physiological response to environmental cues (see also Partecke et al. 2005). As the authors recognise (Partecke and Gwinner 2007), these experiments do not quite preclude the possible influence of early developmental (e.g. maternal) effects, yet taken together they constitute one of the most convincing cases so far of adaptation by birds to urban life. As indicated above, light pollution is associated with the adaptive shift in the timing of breeding and sedentariness of urban blackbirds (Dominoni and Partecke 2015), yet other ecological variables are associated with life-history differences between city and field blackbirds in Spanish populations (Ibáñez-Álamo and Soler 2010). Since membership to different lineages suggests that blackbirds have invaded European cities several times independently (Evans et al. 2009), it is conceivable that different processes have led to subtly different adaptations to urban life in different cities, although to date only the case of the Munich population (Partecke et al. 2004; Partecke and Gwinner 2007) constitutes a demonstration of life-history adaptation of blackbirds to life in the cities.

Other environmental variables may also drive changes in seasonality or migratory patterns of urban birds. For instance, regular food availability promotes earlier breeding in urban than rural populations of Florida scrub jays (*Aphelocoma coerulescens*; Schoech and Bowman 2001), possibly because it reduces the production of corticosterone, a hormone with negative effects on reproduction. The fact that supplementing food to wild jays advanced their breeding time (Schoech and Bowman 2001) shows that this is a plastic attribute, and thus there is no indication of adaptation of breeding time in urban Florida scrub jays.

Adaptation may be implicated in changes of migratory habits. In particular, the famous example of central European populations of the blackcap (*Sylvia atricapilla*) migrating to Britain and Ireland to overwinter there instead than in the traditional Mediterranean wintering grounds (Berthold and Terrill 1988) may represent an adaptation to urban life. Blackcaps overwintering in Britain make extensive use of feeding stations (bird tables and bird feeder) which are much more abundant in the cities of the British Isles than in those around the Mediterranean. Recent evidence has demonstrated that migratory direction is heritable and controlled by only a few genes (Helbig et al. 1994) and can diverge rapidly due to substantial additive genetic variance (Berthold and Pulido 1994). Populations overwintering in Britain and Ireland arrive earlier at their breeding ground and thus are temporally segregated from those migrating southwards (Rolshausen et al. 2009). The two groups have diverged genetically (as assessed using neutral markers) and phenotypically, westward-migrating birds having rounder wings, slenderer bills (presumably linked to generalist-feeding habits at bird tables) and a darker back colour than those that migrate to the south (Rolshausen et al. 2009). Based on data from Fiedler (2003), Rolshausen et al. (2009) suggest that similar processes may be taking place in as many as 50 bird species. If, as seems the case in the blackcap history, exploitation of urban resources is a causal factor, then shifts in avian migratory behaviour may be the most frequent avian adaptation to urban conditions.

### 6.5.2 Food Availability

Food availability has also been implicated in the marked phenotypic-dependent mortality of urban pigeons. Haag-Wackernagel et al. (2006) found that, in comparison with wild populations, the proportion of urban pigeons with a colour pattern known as checker decreased, whereas that of pigeons with bronze colour pattern augmented. Although the causal link between juvenile colour and survival is unclear, other authors have suggested that by remaining continuously in breeding condition, dark-morph feral pigeons cannot accumulate fat reserves between breeding periods and are therefore more vulnerable to food shortage than lighter morphs (e.g. Murton 1970). It is unclear, nevertheless, whether this differential mortality of urban pigeons leads to adaptation to city life.

The distribution of food resources differs markedly between cities and rural/wild environments. Food of various types is abundant in urban environments, yet apart from the case of the westward-migrating European blackcaps (which appear to have evolved a beak morphology to suit the exploitation of a variety of seeds offered in British and Irish bird tables; see above), there seems to be no examples of adaptation of birds to human-provided food. Food processed for humans contains various toxicants and has generally a low ratio of nutritional to energetic content. This might have promoted adaptations in generalist urban birds to avoid less nutritious/more toxic food as well as physiological adaptations in food-supplied urban birds (such as hummingbirds which are commonly attracted to feeders) to cope with a diet rich in refined sugars.

Reports abound of birds starting to exploit anthropogenic food sources, from the opening of milk bottles by tits in Britain to the cracking of nuts using cars by Japanese crows (*Corvus macrorhynchos*; Nihei and Higuchi 2001). Blue (*Cyanistes caeruleus*) and great tits (*Parus major*) were originally found in 1921 to open milk bottles to consume the cream accumulating under the lid. At the time fresh milk was customarily delivered at the doorstep in glass bottles fitted with a flexible metal lid (tin and more recently aluminium). As bottles remained some time before being taken indoors, this provided opportunity for birds to approach, inspect and exploit this source of fat. The spread of this behaviour was mapped and quantified by Fisher and Hinde (1949; Britain) and Hinde and Fisher (1951; Europe). This enabled Lefebvre (1995) to evaluate the spread rate with models used in the study of human cultural transmission (Cavalli-Sforza and Feldman 1981). That bottle opening by Paridae was culturally transmitted which was not certain, particularly since Sherry and Galef (1984, 1990) demonstrated that American parids (*Parus* [= *Poecile*] *atricapillus*) are very likely to spontaneously open a bottle and that the probability that this happened was not influenced by the presence of an experienced tutor. Lefebvre (1995) found that accelerating (e.g. exponential) functions best described the spread of bottle opening by tits in Britain and in Belfast. This is consistent with the cultural transmission assumption of an autocatalytic increase in the rate of spread over time. The idea that cultural transmission is involved was further supported by the fact that data only poorly fitted the linear wave-of-advance model which would describe the spread of the behaviour as a function of a constant rate of untutored learning.

We devoted some time to this phenomenon as it is a textbook example of how birds adjust their behaviour to exploit anthropogenic food sources. The controversy regarding the mechanism of spread of milk bottle opening could be framed in the wider discussion of whether such examples are genuinely novel traits that reflect adaptation to cities or whether they represent exaptations (the expression in a novel context of a pre-existing adaptation to deal with similar conditions; in this case the adaptive behaviour of tits to uncover food items under lichens and bark). As seems to be the case, this exemplifies two different exaptations: a tendency to seek food under lichens and bark and a predisposition for cultural transmission. Also it illustrates the transient nature of cities and the challenges and opportunities they pose to colonising birds (and other organisms). The capability of learning—whether socially or otherwise—and thus adjusting the behaviour to novel conditions may be a key factor enabling some species to colonise urban environments (although we note that cognitive abilities such as problem-solving need not necessarily be better in urban than in rural populations; Papp et al. 2015). Maklakov et al. (2011) demonstrated that brain size was positively associated with the probability that members of passerine bird families, as well as individual species, bred in European city centres. These comparative analyses were prompted by the idea that cities present birds with new challenges, and the previous demonstrations that big brains facilitate the colonisation of novel environments, and that this effect is due to the cognitive consequences of having a big brain (Sol et al. 2005). In their work, Sol et al. (2005) used, as proxy of cognitive ability, the number of foraging novelties reported for the species included in their study. This is a widely used index, yet it is not exempt of problems, for it relies on perfect knowledge of foraging strategies. For instance, the finding that *Parus* (= *Poecile*) *atricapillus* spontaneously opens bottles suggests that this is likely to be an exaptation rather than a genuine urban novelty. Still, employing behaviours evolved in one environment to exploit resources encountered in a novel, one may require a degree of behavioural plasticity. Since both technological and cultural changes ensure that the conditions confronted by urban birds change constantly, it is likely that some degree of behavioural plasticity is required to remain a successful urban coloniser. However, even if behavioural plasticity requires large brains, the reported link between brain size and urbanism (Maklakov et al. 2011) is as likely to be a consequence of differential colonisation of cities by large-brained species as it is of being the result of adaptation to urban life.

### *6.5.3 Interspecific Interactions*

Nest predation influences both nesting strategy (cavity, open, etc.) and patterns of nest attendance (e.g. Conway and Martin 2000) and determines the nature of urban bird assemblages (Jokimati and Huhta 2000). But is there evidence that birds adapt to the particular predation regimes found in cities?

A first line of defence against predation is avoiding encounters with predators. Birds may achieve this by selecting safe/secluded perching, roosting and nesting places (see Marzluff 2001). We are not aware of adaptive differences in those behaviours between wild and urban bird populations; birds in forests and cities alike take readily to breeding in nest boxes, and birds nesting in building crevices are probably even safer than their rural, cliff-nesting counterparts.

Encounters with predators can also be avoided by preventing detection, for instance, through cryptic colouration. There is no suggestion, however, that the reported cases of difference in colour between urban and rural birds (e.g. Haag-Wackernagel et al. 2006; see above) are the consequence of difference in predation regimes. Also, although adaptation is suspected in the case of rapid evolution of geographic colour races of *P. domesticus* in North America, as it parallels the pattern of geographic variation of other species it is now sympatric with (Johnston and Selander 1964), there is no evidence that this is a response to predation, nor that it constitutes an adaptation to urban life.

Early detection of predators in the neighbourhood may allow the birds to either avoid the place altogether (e.g. Amo et al. 2015) or to monitor its behaviour and take evasive action as necessary. In birds, evasive action means to fly, and the distance at which a bird decides to fly is a function of both its fleeing tendency and of the cost of leaving the place (Blumstein 2006). When low-risk encounters are too frequent, tolerance would be advantageous, as it may allow birds to exploit feeding resources efficiently. Accordingly, Møller (2008) found that urban birds have a reduced flight distance than their rural conspecifics. Further, Møller (2009) found that rural populations of bird species that have successfully become city dwellers have shorter flight distances than sympatric populations of nonurban species. This suggests that short flight distance may preadapt species to life in the city, although the possibility that flight distance in rural populations has been influenced by gene flow from urban populations cannot be ruled out. Mutually supporting evidence strongly suggests that this is useful for city birds to have a short flight distances and that a short flight distances enable colonisation of urban habitats. Yet there is no evidence so far demonstrating that flight distance of a particular species has been reduced following colonisation of cities and that such modification is genetically based, i.e. short flight distance appears to be and exaptation, not an adaptation to life in the cities.

Urbanisation also affects the interaction between parasites and their hosts. One intriguing possibility is that cities provide some effective means for birds to deal with ectoparasites. Indeed, urban birds have been reported to collect discarded cigarette butts, rip them open and use the tar-loaded filter fibres as lining material for their nest, thus bringing about a reduction in the number of ectoparasites recovered from the nests (Suárez-Rodríguez et al. 2013). Since a similar effect is achieved by wild birds using green material from plants with known repellent activity (Dubiec et al. 2013), such behaviour may not be an adaptation to life in cities but a modification of the materials used for antiparasitic defence. This assumes that similar cues at the nest trigger the use of green aromatic plants and discarded cigarette butts and that similar cues are also used to find and gather both materials. On the other hand, the effectiveness of both aromatic plants and discarded cigarette butts as ectoparasites repellent has not been compared. It may be that the high concentration of substances in the smoked-through filters makes them more effective at repelling ectoparasites (and also toxic; Suárez-Rodríguez and Macías Garcia 2014), thus further promoting their use. The impact of urban nest materials on ectoparasites abundance and diversity, and hence on the prevalence of the pathogens they transmit, remains hypothetical.

### *6.5.4 Pollution*

Pollution may, in principle, select for advantageous physiological traits to detoxify (chemical), adjust response thresholds (light) or modify the emission of signals to avoid masking (noise). Although chemical pollution has diverse impacts on bird populations, both within and outside the cities, we found no reports of novel adaptations to contend with it, but there is one possible case of an exaptation (Chatelain et al. 2015). The capture of zinc (and other heavy metals) by feather melanin makes advantageous for birds to be dark in areas polluted with heavy metals. Urban pigeons have been found to be darker than their suburban counterparts (Chatelain et al. 2015), and this seems to represent an example of directional selection in cities of an attribute evolved earlier in the lineage of vertebrates. Work in this area is likely to become more common as avian genomic tools become more abundant (see Zhang et al. 2014), which will allow the characterisation of urban-rural differences, if any, on the expression of genes involved in detoxification.

Birds undoubtedly adapt to prolonged exposure to light in the cities, as they sleep through the night (albeit less than in wild conditions; see above). Yet this is likely sensory adaptation and is unlikely to be different from that undergone through the year by birds living at high latitudes. But this sensory adaptation is not complete, and as we saw above, hormonal activity, circadian rhythms, length of breeding season and onset of maturity are all affected by urban light patterns in a way that suggest that no evolutionary adaptation to light pollution is taking place.

Sound pollution in cities evokes a variety of responses from birds. When exposed to noise that may mask their vocalisations, birds can modify the song output (Díaz et al. 2011), increase the duration of their songs (Ríos-Chelén et al. 2013) or otherwise modify their structure (Francis et al. 2011), and they may be uttered at different times (Fuller et al. 2007) and/or have some frequency components altered (see reviews in Slabbekoorn 2013; Gil and Brumm 2013). A small but growing number of papers also report that some bird species can adjust in real time their songs in response to sudden bursts of noise (Bermúdez-Cuamatzin et al. 2009, 2010; Gross et al. 2010; Verzijden et al. 2010), whereas only a handful involve species which lack (or appear to lack) the capability to vary their songs (Francis et al. 2011; Ríos-Chelén et al. 2013). These later cases may be examples of adaptation to urban conditions by non-learning songbirds, although some degree of vocal plasticity in suboscine birds cannot be ruled out (e.g. Ríos-Chelén et al. 2005, 2012), and other mechanisms such as differential habitat use (discussed in both Francis et al. 2011 and Ríos-Chelén et al. 2013) could explain the difference in song attributes between urban and rural populations of non-learning bird species.

Halfwerk et al. (2011) provide perhaps the best case for the adaptive value of song adjustment to overcome masking of vocalisations by urban noise. They showed experimentally that although low-frequency songs are preferred by females and linked to female fecundity, exposure to urban noise impairs their effectiveness and favours higher-pitched songs. Yet, this convincing evidence of the fitness value of adjusting the frequency of song to prevent masking does not demonstrate adaptation to cities, because male great tits can adjust the frequency of their songs in real time (i.e. this is an adaptive plastic response, presumably evolved elsewhere, that is also useful in cities).

## 6.6 Conclusion

We have seen that most differences between rural and urban birds can be explained as being consequence of either phenotypic plasticity or of differential colonisation by individuals or species with sufficient behavioural plasticity to move into novel environments. These two patterns raise the question of whether cities in fact represent novel, more complex environments than birds would have experienced in their evolutionary past. It is possible, instead, that cities are as challenging as any novel environment that may confront birds, and the relative paucity of globally successful urban species is the result of the rapid overtaking of other environments by the cities. Still, it may be that the very speed at which urban landscapes spread at the expense of natural ones poses a particular novel challenge to would-be urban birds. We also saw that biodiversity within the cities, although lower than in their surroundings, is dominated by local species.

We argue that, in terms of complexity, cities cannot compare with forest ecosystems, particularly with those in the tropics. Cities do not have the vast numbers of species (and hence of potential interactions) of tropical forests, and their physical complexity is also probably lower. Seasonality is buffered in the cities, and many links to parasite transmission are therein disrupted. It is also unlikely that cities expose birds to physical or biological conditions that are genuinely novel, in the sense of not having being experienced by birds over their evolutionary past. Yet in one attribute, these environments pose a fundamentally different challenge, cities keep changing. The urban conditions that house sparrows confronted in the cities of the Fertile Crescent some 10,000 years ago are much more similar to current rural conditions than to anything the same species confronts in the midst of contemporary cities. Yet this urban species persists, suggesting that it has kept pace with urban change (but see below). Whether being possessed of a large brain has been the key to such behavioural plasticity is an open question. Another open question is whether the current urban species will persist, and the answer to this question seems to be negative in the case of one of the earliest city dwelling birds, the house sparrow currently declining in Europe (Summers-Smith 2003). Even as birds adapt—or adjust—to living in cities, the cities continue changing; waste management modifies every few human generations the distribution and availability of food, while environmental awareness means that measures are taken to promote both the number and the diversity of species in our cities (e.g. green roofs and walls, Baumann 2006; Chiquet et al. 2013). As successful city dwellers become enormously numerous compared with their rural conspecifics, the rural environment shrinks. This may lead to a constant flow of inadequate phenotypes or maladaptive genes from the city to wild, which arguably may drive to extinction the rural populations and seal the destiny of such species that have colonised them, to that of the cities.

Finally, in spite of an already large and rapidly increasing number of works centred on potential bird adaptations to urban life, there is a dire need of studies that use in the cities the same tools traditionally used for detecting adaptation in nature, the direct measure of fitness in relation to the putative urban-adapted traits, together with measures of its genetic underpinning.

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