**Chapter 6**

# Stay or Leave? Avian Behavioral Responses to Urbanization in Latin America

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## Abstract

Behavioral adjustments are at the forefront of the mechanisms that birds employ to deal with environmental changes. We here review the literature focused on how behavior influences bird responses when faced with the challenges of urbanization in Latin America. Most of reviewed studies assessed for patterns of responses to urbanization with incipient information regarding the behavioral adjustments, as well as the filtering of specific behavioral phenotypes. A common and unsurprising tendency was that several avian species across Latin America are using resources from urban vegetation patches. The few experimental studies performed in urban Latin America focus on the role of personality in adjustments of foraging behavior, as well as the response to noise pollution. Nevertheless, we found no study to directly assess whether or not behavioral adjustments are related to fitness. Even so, studies assessing for the role of behavioral responses to urbanization that explicitly consider their effect on population dynamics are lacking worldwide, despite their importance for fully understanding the differential fate of species having to live in an increasingly built-up planet. Our review allowed us to identify important knowledge gaps of topics related to avian behavioral responses to urbanization, of which the following head the list: (i) behavioral adjustments in both urban greenspaces and highly developed areas; (ii) adaptiveness of avian behavioral adjustments through population dynamics; (iii) metapopulations as one of the process underlying the viability of avian bird populations; and (iv) the role of behavioral changes on evolutionary process in urban areas.

**Keywords** Bird behavior, Personality, Plasticity, Risk-taking, Urban ecology

## 6.1 Urbanization and Bird Behavior

All animals are behaving in one way or another all the time; hence, the task of understanding the role of behavior in how animals adapt to new environments is fundamental due to its relationship with a plethora of aspects related to their ecology (e.g., migration, social behavior, reproduction, feeding, use of space and time, communication, sexual selection). Birds are often used as models for studying animal behavior and, even though the challenge of adjusting to novel environments has been widely studied, many questions still remain and prevent a full understanding of how birds confront life in urban areas and which are the related consequences (Candolin and Wong 2012; Gil and Brumm 2014; Marzluff 2016). For instance, avian behavioral adjustments when faced with a challenging situation have been shown to be essential for explaining whether or not a species is able to cope with the urbanization process (Kark et al. 2007; Lowry et al. 2013; Sol et al. 2013a). Nevertheless, some bird species that thrive in urban environments are not particularly behaviorally flexible, suggesting that there is more than one good strategy for coping with the urbanization process (Sol et al. 2014).

With urban development, many original environmental components are cleared and replaced by human-made structures. This, in turn, leads to a prompt removal of previous habitat conditions and food items, and thus the loss of many of the organisms that depend on them (Marzluff 2001). This could be one of the reasons why most of the urban ecology research has focused on how habitat alterations and urban complexity mold urban bird diversity (Shochat et al. 2006, 2010; Lowry et al. 2013; but see Marzluff 2016 for updated topic trends). As novel types of resources become available with urban development, studies going beyond bird community emergent properties are needed to fully understand the complexity of the phenomenon. For instance, among the set of novel feeding resources, direct food provisioning by people (Galbraith et al. 2015), as well as indirect human sources (e.g., litter), which are virtually ubiquitous across urban systems, head the list (Auman et al. 2008; Crates et al. 2016). Plant material and fruits from exotic and native, often planted, vegetation components are also common in urban greenspaces (Reichard et al.2001; Lafleur et al. 2007; Quesada and MacGregor-Fors 2010). In addition, birds can use buildings for nesting (Møller 2010a) and even as feeding sites by exploiting insects trapped by polarized light pollution (Robertson et al. 2010). The availability of such resources may facilitate the persistence and the recruitment of individuals to the new anthropogenic system, as long as organisms are able to take advantage of these opportunities and can tolerate the disturbances that characterize cities (Emlen 1974; see Chaps. 3 and 4). Thus, urban areas impose new ecological conditions that not all organisms are able to deal with (Møller 2009; Sol et al. 2014), but in which others can persist and even thrive (Sih et al. 2011). These differential responses can be understood by exploring the ability of species, populations, and individuals to use anthropogenic conditions in urban systems (Hulme-Beaman et al. 2016; see Sect. 6.3 in this chapter). The initial response of organisms to altered environmental conditions is probably mediated by behavior and their decisions to leave an urbanized area or stay and colonize, and in doing so, gain the opportunity to adjust to the new environmental scenario (Lowry et al. 2013; Sol et al. 2013a; Wong and Candolin 2015; Fig. 6.1).

## 6.2 Avian Responses to Urbanization

Back in 1996, Robert B. Blair proposed a terminology to characterize the way in which birds respond to urbanization, which has facilitated important insights into the underlying mechanisms of responses to this global environmental change (e.g., Bonier et al. 2007; Kark et al. 2007). This terminology categorized species as ‘avoiders’, ‘adapters’, or ‘exploiters’ based on their presence and abundance in natural, moderately, or highly urbanized areas, respectively. Despite its usefulness, Blair’s terminology rules out, among other things, the fact that the density of a native species in urban environments is, to some extent, related to their density in the surrounding areas (Sol et al. 2013b, 2014). This shortcoming may hamper a fuller understanding of the mechanisms that constrain or promote avian distribution and abundances in urban areas, such as intraspecific responses to different urbanization scenarios (Evans et al. 2011; Sol et al. 2013b, 2014). In this sense, the possibility of birds having metapopulation dynamics in urban systems has also been vaguely considered (Padilla and Rodewald 2015). For instance, despite high abundances of the House Sparrow (*Passer domesticus*) in both urban and industrial areas of a Mexican city, individuals of industrial areas showed physiological parameters that suggest detrimental health status with respect to those from urban conditions (Chávez-Zichinelli et al. 2010). Hence, rather than focusing only on presences and abundances, there is a pressing need to explore for fitness parameters and proxies across urban ecosystems, which may allow to test whether metapopulation growth and persistence are compromised, for example (Hale et al. 2015).

Fischer et al. (2015) proposed a characterization of how organisms deal with the urbanization process based on Blair's (1996) terminology. This characterization recognizes the existence of urban 'avoider', 'utilizer', and 'dweller' organisms. While urban 'avoiders' rarely inhabit urban areas, Fischer et al. (2015) suggest they may persist in such environments by using the resources from natural areas that are scattered across the urban matrix. Urban 'utilizers' and 'dwellers' are defined based on the relative importance of natural and urban environments to their population dynamics, whereby 'dwellers' are located at one extreme of this gradient of response and their persistence in urban areas is independent of extra-urban resources. Population responses to urbanization of particular species can fully fall within a particular category or span multiple categories, which recognize the dynamic nature of the adjustment of organisms to this environmental change (Sol et al. 2014; Fischer et al. 2015).

Based on the above, we believe that the study of interactions between organisms and their environments under a behavioral framework could strengthen the understanding of avian responses to urbanization. Taking into account that behavior affects key demographics parameters and population dynamics, an ethological scope could shed light on whether organisms are potential ‘avoiders’, ‘utilizers’, or ‘dwellers’. In this chapter, we pinpoint the importance of avian behavior in urban areas as a key element in the study of the mechanisms that animals use to confront not only urbanization, but also other rapid human-induced environmental changes such as biological invasions, overharvesting, pollution, and climate change (Sih et al. 2011; Maxwell et al. 2016).

For Latin American cities in particular, the study of avian behavior offers unprecedented opportunities for research into the behavioral repertories of its generally understudied avifauna. This knowledge may not only help our understanding of the differential fate of organisms based on their behavioral profiles and performances, but may also encourage more predictive knowledge that, for instance, could promote better urban planning for sustainable urban development, as well as conservation strategies that are so urgently required in the region (United Nations 2015; see Chaps. 1, 2, and 8). Here, we provide an overview of avian behavioral research in urban areas, drawing from studies worldwide. We then review avian behavior studies in urban Latin America and contrast them with the findings of the behavioral literature from the rest of the world, highlighting insights, identifying potential knowledge gaps, and suggesting future directions on avian behavior research in an increasingly urbanized Latin America.

### *6.2.1 Ethological Adjustments to Novel Environments*

The current wave of human-induced rapid environmental changes, including urbanization (Sih et al. 2011), requires appropriate adaptive responses from organisms to persist despite the new challenges. As noted above, behavior is the first tool that birds, as well as other animals, have when they confront new scenarios (Tuomainen and Candolin 2011), and it can be described and studied using a variety of approaches (e.g., descriptive, experimental, correlational). Thus, the literature vastly illustrates behavioral comparisons between urban and nonurban populations of focal species, finding striking differences among them (Candolin and Wong 2012; Gil and Brumm 2014; Wong and Candolin 2015; see Sect. 6.3 in this chapter). These changes may be the product of individual selection or a plastic response to new scenarios (Sol et al. 2013a). Yet, disentangling these two effects is fraught with difficulties as the two processes may be occurring simultaneously. On the one hand, to survive to increased urbanization intensity or to successfully establish in urbanized areas may require the selection of particular phenotypes from the original population that can 'perform well' in these environments (Carrete and Tella 2011; Miranda et al. 2013; Partecke 2014). For instance, the frequency of certain genes within a population may favor the ability to withstand urban life (Müller et al. 2013) or to establish in new areas (Edelaar et al. 2015). However, genetic selection, even though it is always active to some extent within a population (Carrete et al. 2016), may take longer and requires stable selection pressures, and not necessarily be the most parsimonious way for responding to quick changes occurring during urbanization processes (van Buskirk 2012). On the other hand, many different behavioral responses may emerge as a consequence of a particular plastic response. If we consider the distinct components of plasticity, it is important to recognize the cases in which the same genotype provokes a variety of responses to different environments. In the context of behavioral plasticity, this has been termed developmental plasticity (sensu Snell-Rood 2013) or reaction norm (Levis and Pfennig 2016).

Developmental plasticity is the range of ways that a particular behavior may express itself in a particular situation (Snell-Rood 2013); thus, some behavioral syndromes may be selected as they perform well in cities without any direct influence from genetic selection (Dingemanse and Wolf 2013). Indeed, although the House Sparrow is a species whose urban and nonurban populations differ behaviorally (Seress et al. 2011; Bókony et al. 2012), studies have failed to find any significant genetic differences between individuals from both environments (Vangestel et al. 2011). Another type of behavioral plasticity that may be observed in birds is activational plasticity (sensu Snell-Rood 2013), which refers to the variable response that an animal exhibits to the same stimulus through its life. It is clear that, after an initial experience with a certain stimulus, an organism may adjust its responses and improve its efficiency in successive encounters until it reaches an optimal response. One of the main mechanisms responsible for this intraindividual change in behavior is learning (Sol et al. 2013a), understood as the alteration of behavior as a result of individual experience (Shettleworth 2010). Birds can acquire experience through two main nonexclusive mechanisms, individual and social learning. In individual learning, acquiring new information occurs through experiences based on trial and error and successful rewards. Social learning, on the other hand, is related to information acquisition through the observation of other individuals and the consequences of their behavior (Brown and Laland 2003), which has been suggested to be a useful spreading mechanism for behavioral innovation and thus a useful skill for thriving in cities (Brown 2012). It is relevant to notice that innovative problemsolving may also be achieved by simple behavioral persistence without the need to invoke demanding cognitive processes, such as learning (Guez and Griffin 2016). Regardless of the origin of behavioral changes, the effectiveness of ethological adjustments is thought to have several properties that make them ideal for explaining many ecological and adaptive changes for the urban living. For example, behavioral adjustments can occur more quickly than any physiological or morphological changes that are mediated by genetic mechanisms; so, the time lag in the expression of the phenotype that fits the new situation is shorter (see Hendry et al. 2008 and references therein). Nonetheless, there is an additional advantage: some behavioral changes can be reversed, which is particularly useful in changing environments such as built-up systems (West-Eberhard 1989).

Despite all of the highlighted advantages, it is worth underlining that not all behavioral responses are favorable in terms of fitness and, for example, maladaptive behavioral responses may also occur when urbanization erodes the reliability of the cues that animals use to assess the quality of resources or mates (Wong and Candolin 2015, see Sect. 6.3 in this chapter). Finally, behavioral changes in urban individuals and populations must translate into an improvement or upholding of fitness so that a population can persist in the new environment. Establishing direct links between the development of a particular behavioral response and its impact on population dynamics is a difficult task (Pelletier and Garant 2012), as is whether or not behavioral adjustments are sufficiently vigorous to be able to deal human-induced environmental changes (Wong and Candolin 2015).

## 6.3 Behavioral Challenges in Urban Areas

Urbanization creates new environments that force birds to tackle important challenges (Shanahan et al. 2014). Among the drastic changes given by the urbanization process, situations that are stressful in nonurban areas (e.g., predators eliciting acute responses) may become commonplace and persistent in cities. These situations can turn into chronic stress, affecting the allostatic condition in birds (e.g., Canyon Towhee—*Melozone fusca*; Chávez-Zichinelli et al. 2013), thereby hampering their ability to benefit from anthropogenic resources. For instance, corticosterone plays a key role in behavioral and physiological modulation during stressful situations that could influence on whether a bird adjusts or not to the urban life (Bonier 2012). Nevertheless, no consistent patterns regarding the relationship between urban life and this hormone have yet been established (Bonier 2012; Buchanan and Partecke 2012).

In addition to the replacement of preexistent systems with artificial structures and the intrinsic urban disturbances, cities are often characterized by high levels of noise, chemical, and light pollution (Forman 2014). These urban features have been shown to influence avian physiology including the endocrine, nervous, and immune systems, which can lead to important behavioral changes (Gil and Brumm 2014). For instance, chemical pollution is an important disruptor of the endocrine and nervous systems that control many aspects of sexual and social behavior (e.g., aggressiveness, courtship). Indeed, birds subject to high concentrations of heavy metals are more aggressive (Janssens et al. 2003) and more dominant (Hogstad and Pedersen 2007), states that may affect their breeding performance (Eeva and Lehikoinen 2000; Dods et al. 2005). Chemical pollution may also affect signaling indirectly. For example, birds exposed to DDT significantly change brain structures that are related to song (Iwaniuk et al. 2006), and animals with higher mercury concentrations in their blood are known to modify their song repertoires (Mckay and Maher 2012). Artificial lighting is another of the common extended forms of pollution in urban areas that directly affect the endocrine system (Dominoni et al. 2013; Da Silva et al. 2015) and is also a good example of how cities induce changes in wildlife use of space and time (Dominoni 2015).

Probably one of the most studied sources of behavioral change in urban areas is the use of novel resources resulting from human activities (see 6.1 in this chapter). A classic example is the Great Tit (*Parus major*), which starts to open milk bottles to feed on the cream. The first observations of this technical innovation were recorded near Southampton (England). Afterward, the innovative behavior became widespread across many regions of the United Kingdom (Fisher and Hinde 1949). The mechanisms underlying the transmission of these innovations are frequently based on social learning and cultural transmission, in which social interaction plays a crucial role (Bókony et al. 2009). Since sociality is mediated by external factors such as predation risk and resource abundance, social dynamics are expected to change in cities because these external factors differ between urban and nonurban areas (Blumstein 2014). Density-dependent processes are often mediated by cost/ benefit relationships and, thus, social interaction is expected to have an influence on fitness and, ultimately, on population dynamics (Blumstein 2014). Both sexual and social interactions are frequently performed via signaling, where song, integuments, and plumage usually work as cues of quality (e.g., dominance status, foraging ability, body condition). However, cues that work in original habitats may not be informative in urban systems and could even result in maladaptive behavioral responses. For example, certain urban features may compromise not only signal production but also their transmission. One of the most studied such cases is that of song transmission in noisy urban environments (Slabbekoorn and Peet 2003; Laiolo 2010; Gil and Brumm 2014). Urban areas are characterized by noise that overlaps with the song frequencies of many birds, which has driven individuals to adjust their behavior to overcome sound interference. Adjustments that may be beneficial for communicating in a noisy environment include changes in spatiotemporal activity, song frequencies, and song structures (Rosenthal and Stuart-Fox 2012); yet, these behavioral adjustments do not necessarily guarantee the ability to persist and thrive in urban areas (Moirón et al. 2015). Visual signals can also be masked in a city, and signaling traits may thus mislead messages with serious consequences for the receptor's fitness. For instance, Senar et al. (2014) showed that the black tie in Great Tits, a sexually selected trait that signals parental ability (Norris 1990), is positively related to survival in nonurban habitats; however, the relationship between survival and the size of the black tie is negative in cities. Thus, if urban females use big ties as a quality signal during mate choice (see Norris 1993, Quesada and Senar 2009), they are, in fact, eliciting a maladaptive response and selecting the least viable males, and consequently may succumb to an evolutionary trap (Senar et al. 2014).

Despite the negative impacts of urbanization, some bird species have shown to benefit from urbanized systems. For instance, tolerance to human disturbance may improve productivity as living in close proximity to humans may discourage potential predators (Møller 2010a). This may be determinant for commensal species that increase their breeding success dramatically in cities (Hulme-Beaman et al. 2016). Comfortable ecological conditions in cities may also affect bird movements like migratory behavior, such as urban populations that become more sedentary than nonurban ones (Evans et al. 2012), presumably due to the synergistic effect of the greater availability of feeding resources coupled with climatic amelioration (Plummer et al. 2015). Recent evidence has also shown that cities can influence migrant phenology, and migrants from urban areas arrive relatively earlier than their nonurban counterparts (Tryjanowski et al. 2013).

Finally, many aspects of reproduction and breeding performance may also vary between urban and nonurban environments (Chamberlain et al. 2009; Shanahan et al. 2014). For instance, highly abundant food sources in cities may potentially make urban birds more productive; yet, evidence shows that the breeding output of urban birds is lower when compared with their performance in original habitats (Chamberlain et al. 2009). Nevertheless, in San Diego (CA, USA), milder climatic conditions enabled Dark-eyed Juncos (*Junco hyemalis*) to advance and even extend their breeding phenology (a plastic adaptive response), increasing fitness and productivity in this population by changes in their reproductive behavior (Yeh and Price 2004).

## 6.4 Behavioral Background of ‘Avoiders’, ‘Utilizers’, and ‘Dwellers’

A fundamental question that must be raised when talking about urbanization is: what leads organisms to avoid, utilize, or dwell within an urban area? Some authors have approached this problem by suggesting that the processes involved in the arrival of a species to a city resemble those than occur when exotic species invade new environments (Blackburn et al. 2009; Evans et al. 2010; Sol et al. 2013a; Møller 2014). From a behavioral point of view, we can examine this question from many different perspectives, all of which are related to the final decision taken by the animal: ‘stay’ or ‘leave’. The choice must probably be based on a fitness cost–benefit analysis (Chaine and Clobert 2012). If ‘stay’ is the response, organisms must deal with the new environmental challenges and maximize their fitness (e.g., survival, reproduction), considering factors that differ from their natural environments such as food, mates, nesting sites, predators, humans, parasites, and the disruption of communication, among others (Candolin and Wong 2012; Gil and Brumm 2014). However, there are certain scenarios where, despite that birds decide to stay or colonize urban areas, they may show negative population growth rates, as happens in source–sink dynamics (Padilla and Rodewald 2015; see Sect. 6.2 in this chapter).

Adjustments via behavioral responses and adaptation through genetic changes are two possible strategies for accommodating, stabilizing, or improving population status (i.e., growth in numbers; Evans et al. 2010; Chaine and Clobert 2012; Sol et al. 2013a). Consequently, the first step for assessing avian responses to urban life is to understand if birds leave their original natural habitats and disperse into builtup areas (Evans et al. 2010; Sol et al. 2013a; Møller 2014), or whether resident species avoid cities as a way to compensate for the negative impact of built-up environments where some important ecological requirements may no longer be fully satisfied (Biamonte et al. 2011; Chaine and Clobert 2012). Once the urban environment has been reached, or once the system has been urbanized, individuals must evaluate the feasibility of staying (Fig. 6.1). As has been noted by Fischer et al. (2015), there is a possibility that some resident species will decide to stay in patches with original habitats or novel systems that resemble them across cities, which may still satisfy their ecological requirements. However, individuals that stay ought be able to withstand urban-related perturbations through adjustments, such as their flight initiation distances (Møller et al. 2013) and home range sizes (Chiang et al. 2012). Hence, we hypothesize that for such individuals, behavioral responses may be much more important than genetic changes in the short and medium terms. In scenarios under which individuals are urban ‘utilizers’ or ‘dwellers’, their ability to ‘choose’ among conditions will be pivotal because it cannot depend anymore, or at least not entirely, on nonurban resources. In fact, behavioral plasticity and genetic changes are probably more important in these cases, with a crucial role on bird ability to use anthropogenic niches (Hulme-Beaman et al. 2016). Thus, birds unable to choose among the array of available conditions will probably become urban ‘avoiders’ from an ethological perspective (Hulme-Beaman et al. 2016; Sih et al. 2016; Fig. 6.1). Recognizing the existence of this intraspecific variation between ‘avoiders’ and ‘dwellers’ may shed important light on identifying and understanding the influence of demographic parameters driving urban bird ecology. Despite the existence of variations between populations in response to urbanization, these are lower than those observed between species, which supports the idea that the ability to thrive in cities is a species-level trait (Sol et al. 2014). Indeed, some traits have been identified as being more closely associated with avian species inhabiting cities, including: high dispersal ability (Møller 2009), low propensity to migrate (Croci et al. 2008), and high fecundity (Møller 2009). However, fitting into one or more of the aforementioned traits does not automatically turn a bird species able to become an urban ‘utilizer’ or ‘dweller’. Adaptive traits may only be pivotal if they generate a positive impact on population dynamics (Pelletier and Garant 2012; Wong and Candolin 2015). The population size of 'incomers' facing urban challenges is usually small and determined by environmental stochasticity, which may easily lead to local extinction. Indeed, population abundance in surrounding nonurban environments can directly be related to species abundance in urban areas, suggesting that some species that are present in urban areas are there due to random dispersal (Sol et al. 2014), and would also be classified as urban 'utilizers'.

After their initial arrival to the city, some species increase their numbers dramatically in comparison with the nonurban system in which they inhabit, a process whose underlying mechanisms are still subject to debate (Møller 2009; Evans et al. 2011; Jokimaki et al. 2014). Studies that take into account the influence of the population size in surrounding nonurban environments have shown that the association of some traits previously related to the presence of avian species in cities provide little support as drivers of differential avian success in urban areas (Evans et al. 2011; Sol et al. 2014). Likewise, larger brains and associated cognitive abilities turn out to be less important (Evans et al. 2011; Møller and Erritzøe 2015). These findings do not mean that behavioral flexibility is not relevant for a life in the city; rather, a number of different strategies including behavioral flexibility may assist when it comes to thriving in an urban environment (Sol et al. 2014).

## 6.5 Avian Behavior in Urban Latin America

To summarize the literature that covers several dimensions of avian ecology in urban Latin America and implicitly or explicitly discuss bird behavior, we conducted a bibliographic search in the Web of Science platform (www.webofknowl- edge.com) and Google Scholar (http://scholar.google.com) seeking for peer-reviewed publications, theses, conferences, and congress proceedings, as well as magazines published by local universities and ONGs. We used a set of keyword combinations, both in Spanish and English, including the terms ‘urban’, ‘urbanization’, ‘city’, ‘bird’, and ‘avian’, with refining keywords, such as ‘behavior’, ‘behavioral syndrome’, ‘personality’, ‘risk-taking’, ‘temperament’, ‘copying styles’, ‘behavioral flexibility’, and ‘behavioral plasticity’. From the list of articles obtained with the combinations using the aforementioned keywords, we selected those that were performed in urbanized areas from Latin America. We retreived a total of 86 publications from 11 countries that met our search criteria including additional publications from the references cited in some of the gathered documents (Table 6.1). To analyze the gathered literature, we explored the role of avian behavior when it comes to confront some of the main challenges to persist or colonize urban areas in Latin America (see Shanahan et al. 2014). Specifically, we focus on five types of urban challenges: (i) habitat loss and fragmentation; (ii) resource availability; (iii) pollution; (iv) species interactions; and (v) human activities.

### ***6.5.1 Habitat Loss and Fragmentation***

Under the context of the urbanization process, examples focused on the behavioral adjustments of vertebrates, including birds, to habitat loss and fragmentation are scarce (Lowry et al. 2013; Sol et al. 2013a). Although behavior adjustment has been recorded in relation to human disturbances (Salinas-Melgoza et al. 2013), we did not find any study directly assessing avian behavioral adjustments to habitat loss and fragmentation in urban Latin America. Yet, we found studies that suggest that some native species take advantage of these urban conditions, such as the Rufoustailed Hummingbird (*Amazila tzacatl*) in Costa Rica (Biamonte et al. 2011), Rufouscollared Sparrow (*Zonotrichia capensis*) and Monk Parakeet (*Myiopsitta monachus*) in Argentina (Bellocq et al. 2011; Bucher and Aramburú 2014; see Chaps. 2 and 3). Despite the high abundances of these species, whether they persist, thrive, and finally become urban ‘dwellers’ in the long term remains unknown (Sol et al. 2013a; Wong and Candolin 2015). Indeed, individuals from urban populations of the Rufous-collared Sparrow—which are highly abundant in some Chilean (Ruiz et al. 2002) and Argentinean urban centers (Bellocq et al. 2011) have lower body weights, and several of their physiological blood parameters suggest they live in more stressful environments than their nonurban counterparts, as has been recorded in central Chile (e.g., Ruiz et al. 2002). Accordingly, the Common Ground-Dove (*Columbina passerina*) was highly abundant in gardens and open areas from San Jose in Costa Rica up to the late 1990s, but nowadays has almost disappeared from urban areas from this region (Biamonte et al. 2011). These findings reinforce the need to assess not only species presence and abundance in urban areas but also their behavioral responses and whether or not they are sufficient to confront the habitat change produced by urbanization.

### *6.5.2 Resource Availability*

Based on the retrieved studies, we identified at least two ways of how birds use resources available in cities. First, in most of the reviewed studies, species use food items that are not directly generated by anthropogenic activities (referred to as natural food hereafter) that are mostly present in urban greenspaces. For instance, the presence of patches of native vegetation scattered throughout Brazilian urban areas allow the presence of plant–frugivorous mutualistic networks with birds remaining as important seed dispersers (Andrade et al. 2011). A study performed in Mexico indicates that Nearctic–Neotropical migrant birds may also make use of natural food resources and shelter in urban greenspaces, emphasizing the importance of greenspaces in cities (Charre 2013). Other examples of species using natural food items in urban areas include the Yellow Warbler (*Setophaga petechia*) and Summer Tanager (*Piranga rubra*) in Colombia (Caicedo-Argüelles and Cruz-Bernate 2014), seven species of hummingbirds and two passerines in a university campus in Brazil (Mendoça and dos Anjos 2006), and a terrestrial bird assemblage from an urban park in Venezuela (Sainz-Borgo 2016), among others. Not just food, but nesting sites on natural components scattered across the urban area are also chosen by birds. For example, Zuria and Rendón-Hernández (2010) followed nests of six bird species in a greenspace of the city of Pachuca (Mexico), recording differential substrate preferences (i.e., native, exotic vegetation).

Other examples regarding birds nesting in urban areas include those of the Rufous-tailed Hummingbird (*Amazila tzacatl*), Bananaquit (*Coereba flaveola*), and Yellow-headed Caracara (*Milvago chimachima*), among many other Colombian species (Borrero 1965; De La Ossa and De La Ossa-Lacayo 2011). The descriptive nature of the above studies precludes us to categorize these urban birds as 'avoiders' or 'dwellers', as there is no available information regarding their behavioral decisions. This is not surprising as most of the reviewed studies were observational (see Table 6.1). Additionally, some species have been identified to have the ability to change their usual foraging strategies and hence able to incorporate vegetable material or fruit from exotic trees to their diets, or take profit from artificial food items such as food waste or direct feeding by people. These behavioral adjustments have been more commonly recorded in harsh environmental conditions. For instance, during winter, several fruit-eating bird species from Brazil, such as the Rufousbellied Thrush (*Turdus rufiventris*), Pale-breasted Thrush (*Turdus leucomelas*), Purple-throated Euphonia (*Euphonia chlorotica*), among others, change their movement patterns and visit urban areas for feeding on fleshy fruits of nonindigenous species from urban greenspaces, but then return to their natural areas to breed (Guix 2007). A similar situation has been described for the Black-chinned Siskin (*Carduelis barbata*) in Chile, where individuals of this species have been recorded feeding on seeds from exotic trees and using them as refuges in built-up areas in winter (San Martín 2009). Other examples of the ability to choose nonhabitual resources in an urban context include the nest built on an open-sky telephone by Azure-crowned Hummingbirds (*Amazilia cyanocephala*) in Mexico (EscobarIbáñez and MacGregor-Fors 2015) and the nectarivorous behavior of House Sparrows as function of temporal variability in human disturbance in Argentina (Leveau 2008). Both behavioral plasticity and personality traits may help to explain their ability to use novel urban resources in Latin America. For instance, a field study using experimental feeders in an extra-urban area in Argentina showed that granivorous birds not related to urbanization did not use the feeders, regardless of their feeding preference, underlining their aversion to novel situations (e.g., neophobia; Echeverría et al. 2006). Likewise, another experimental study performed in Argentina showed that the Chimango Caracara (*Milvago chimango*) is characterized by its tendency to explore, showing lack of neophobia and great ability to innovate (Biondi et al. 2010). These personality traits and learning skills give this species the impressive capacity to obtain food in novel situations by opening garbage bags and raiding trash cans (Biondi et al. 2008; CG-L pers. obs.; Fig. 6.2). Even within species, different levels of neophobia have been found in relation to a bird's original habitat. Related to the latter, Ducatez et al. (2016) conducted field experiments on nine avian species in Barbados and found that urban birds are bolder, less neophobic, and have shorter flight distances than their less urbanized conspecifics. Even so, less neophobia in urban birds is not a consistent pattern and, unexpectedly, clear generalist and urban species such as the House Sparrow, Eared Dove (*Zenaida auriculata*), and Shiny Cowbird (*Molothrus bonariensis*) are usually neophobic (Echeverría et al. 2006; Echeverría and Vassallo 2008). These differences have also been recorded within species, such as the study of Audet et al. (2016), who found that urban Barbados Bullfinches

(*Loxigilla barbadensis*) are highly neophobic, but bolder and better at problem-solving than nonurban individuals. Discrepancies in the degree of neophobia in birds that usually inhabit urban areas may be due to the modification of fear, which is directed to regularly encounter objects rather than a general phenotypic characteristic to deal with the urban habitat (Greggor et al. 2016).

### *6.5.3 Pollution*

With the exception of two studies focused on artificial night lighting in urban Latin America (i.e., MacGregor-Fors et al. 2011; Dorado-Correa et al. 2016), noise has been the most studied type of pollution affecting birds (Bermúdez-Cuamatzin et al. 2011). The reviewed studies focused on noise have revealed several ways in which birds adjust their songs to urban life. For example, some species modify the frequency of a specific syllable (Bermúdez-Cuamatzin et al. 2011) or combine changes in the length of songs with changes in frequencies (León et al. 2014; PachecoVargas and Losada-Prado 2015; Soto-Gamboa et al. 2015). Some studies also provide evidence of individual song plasticity (Bermúdez-Cuamatzin et al. 2009; Ríos-Chelén et al. 2013). Of all the types of song modification, changes in frequencies are the most studied behavioral responses to noise. For instance, by considering the variation present in five frequency parameters, Laiolo (2011a) showed that Rufous-collared Sparrows sang significantly higher pitched songs (with higher minimum frequencies) in noisy than in quiet areas in Bahía Blanca, Argentina. A similar pattern was recorded for this species in Chile (Soto-Gamboa et al. 2015), as well as for other species, such as the House Finch (*Haemorhous mexicanus*) in Mexico (Bermúdez-Cuamatzin et al. 2009; Bermúdez-Cuamatzin et al. 2011), House Wren (*Troglodytes aedon*) in Costa Rica (Redondo et al. 2013), Saffron Finch (*Sicalis flaveola*) in Argentina (León et al. 2014), and Rufous-browed Peppershrike (*Cyclarhis gujanensis*) and Scrub Greenlet (*Hylophilus flavipes*) in Colombia (Pacheco-Vargas and Losada-Prado 2015).

The relationship between noise and shifts in song frequency showed to be stronger in oscines than in suboscines from Mexico and Brazil, showing that suboscines may be more vulnerable to acoustic pollution than oscines and thus less capable of entering cities, as well as to acoustically novel habitats (Bermúdez-Cuamatzin et al. 2009). In terms of variability, a study from Argentina revealed that neighboring Rufous-collared Sparrows in gardens sang similarly when compared with those from nonurban environments, thereby suggesting that the filtering and homogenization of singing behavior can occur in urban areas (Laiolo 2011b).

However, another study of the same species in Chile found great individual variability in repertoire size and song cues in urban environments (Soto-Gamboa et al. 2015). It is possible that these differences are given by different colonization stages, with the reduction in repertoire size at initial stages and subsequent increases in variability (see Møller 2010b for a similar example but for avian fear responses); however, methodologies could also lead to such differences. Finally, a recent study on the same species explored why urban individuals start singing earlier than individuals from nonurban areas. The authors found that noise—but not lighting levels—determined variations in this behavior in Rufous-collared Sparrows in Bogota, Colombia (Dorado-Correa et al. 2016).

### *6.5.4 Species Interactions*

Studies focused on avian behavioral changes related to competition for resources, predation, and parasitism were scattered, but present, in urban Latin America. For example, the increase in abundance of some potential preys in cities has been recorded to be beneficial for avian predators such as the Harris's Hawk (*Parabuteo unicinctus*) that feed on bats in Mexico City (Ortega-Álvarez and Calderón-Parra 2014), as well as Peregrine Falcons (*Falco peregrinus*) recorded preying on the highly abundant exotic and invasive Monk Parakeets in Santiago de Chile (Fig. 6.3). Supplementary food in urban centers may also determine hierarchical relationship among birds, as reported in Venezuela, where a nonrandom order of access to an artificial food patch was recorded for several avian species (Levin et al. 2000). This type of subsidized urban food may also alter bird–plant interactions. For instance, two studies in Mexico show that the presence of nectar feeders decreases plant visitation rates of all studied hummingbirds (Arizmendi et al. 2007, 2008). Behavioral shifts in the urban context may also affect the relationship between parasites and their hosts, as has been shown in Mexico where two widely distributed urban birds started to use cigarette butts to build their nests, a behavior that was found to be associated with a decrease in the number of nest-dwelling parasites (SuárezRodríguez et al. 2012, see Chap. 5). A recent study has reported that despite this behavior decreases parasite load on nests, it might increase breeding costs for urban birds as a consequence of the genotoxic damage produced by cigarette butts (SuárezRodríguez et al. 2017). Finally, as recorded in other parts of the world (Shanahan et al. 2014), results of nest predation along urbanization gradients are contradictory. For example, a study from Mexico reveals that nest survivorship was higher in nonurban than in urbanized environments; nevertheless, the speed at which nests were depredated did not change along the gradient of urbanization intensity (LópezFlores et al. 2009). By contrast, a study conducted in Bolivia showed that the predation and destruction of artificial nests did not differ between urban and nonurban sites (Salazar and Garitano-Zavala 2015). These contrasting observations maybe related to the findings of Rivera-López and MacGregor-Fors (2016), who showed that artificial nest predation was driven by the interaction between spatial location and degree of urban development, where visual predators were most frequent. This may help to explain contrasting results between studies in terms of nest predation, the dynamics of which can be diverse within the same urban area (both predation 'relaxation' and intensification within the same area; Rivera-López and MacGregorFors 2016).

### *6.5.5 Human Activities*

The increase of human population density and high environmental disturbance regimes in urban areas are other challenges shown to drive bird behavior in urban Latin America. In fact, compared with their nonurban conspecifics, urban birds of several species from southeast Brazil have shown higher levels of tolerance to human disturbance and shorter flight initiation distances (Piratelli et al. 2015). The same pattern has been recorded for Burrowing Owls (*Athene cunicularia*; ReboloIfrán et al. 2015; Cavalli et al. 2016). Variability in flight initiation distances has also been associated with the number of predators that approach the implied birds (Piratelli et al. 2015; Cavalli et al. 2016), as well as their body mass (Piratelli et al. 2015), but has not been related with predator type (Fabiano et al. 2015). Interindividual variability in flight initiation distances and the relative brain size of a given species could be good predictors of the ability to colonize a city, as indicated for 42 avian species from Argentina (Carrete and Tella 2011). Despite that habituation has been claimed as the main mechanism behind the above-described patterns (Møller 2008, 2010b), studies focused on the Burrowing Owl in Argentina found high consistency in the fear of humans throughout the adult life span of both urban and nonurban birds (Carrete and Tella 2016). This supports the existence of heritability or resemblances between relatives and that selection pressures on flight initiation distances may be an important evolutionary force in this species when confronting urbanization (Carrete et al. 2016). Moreover, a study focused on the potential physiological mechanisms behind flight initiation distances found no support that corticosterone, a glucocorticoid related to stress responses in birds (Wingfield et al. 1998), drives such behavioral response by the Burrowing Owl in Argentina (Rebolo-Ifrán et al. 2015).

## 6.6 Conclusions, Research Gaps, and Future Directions

Given that behavior is one of the most immediate skills available to confront environmental challenges and it influences several aspects of animal ecology, avian urban ecology will undoubtedly be strengthened by the consolidation of a behavioral approach. However, most of the reviewed studies from urban Latin America are observational, with the behavioral component of avian responses nonexplicitly evaluated. For instance, many of the reviewed studies report an increase in the abundance of some species following the loss of natural habitat by urbanization, a common pattern worldwide (see Aronson et al. 2014; Sol et al. 2014). Due to the lack of direct assessments of behavioral responses under a more mechanistic framework, we can only speculate either behavioral adjustments or the filtering of specific phenotypes underly the apparent success of some urban birds. Additionally, a common and unsurprising tendency was that several avian species across the region are using resources from remnant patches of natural habitat within the urban matrix. On the one hand, this suggests that the presence of birds in urban areas is supported by this type of resources. Nevertheless, whether or not birds are dependent on these resources, and thus fall on the 'avoider' or 'utilizer' categories, remain as open questions. The study of bird behavior in urban greenspaces also represents a bias in Latin America (Chap. 9). Regarding studies focused on behavioral changes between urban and nonurban populations, we found experimental studies showing the importance of specific personality traits in foraging adjustments that agree with findings from research performed across the globe. Experimental studies were also targeted to evaluate how birds confront the challenge of urban pollution, recording a wide array of singing adjustments, also in agreement with the global literature (reviewed by Sol et al. 2013a). Among the identified research gaps, the impact of behavioral adjustments on population dynamics has not been evaluated in Latin America (nor has been assessed in other regions; Marzluff 2016). Moreover, whether metapopulation dynamics are involved in the persistence of avian populations in urban areas is unknown, despite representing critical information to generate conservation strategies (Padilla and Rodewald 2015).

To advance our knowledge regarding the urban drivers and consequences of urbanization on birds, we must identify the role of behavioral responses to determine the varying fate of avian species, populations, and individuals confronting the urbanization process. To do so, studies evaluating the response in areas with different urbanization intensities, ideally throughout urban systems (see Chap. 9 for a detailed analysis on citywide surveys), are crucial. Specifically, we recognize the importance of understanding the interactions of birds with anthropogenic resources with the main goal of disentangling their relationships with the urban scenarios and their related components. After identifying the behavioral responses of birds to urbanization, we ought to assess their impacts on population dynamics, unraveling whether such adjustments are advantageous or maladaptive in terms of fitness (Sol et al. 2013a; Fischer et al. 2015; Wong and Candolin 2015).

Among the approaches to study avian responses to urbanization, behavioral and evolutionary frameworks allow to assess how birds thrive or fail in these novel environments. In particular, the behavioral framework is undoubtedly more plastic than morphological or physiological ones, leading to a wide spectrum of evolutionary inquiries for which birds are excellent models. Behavioral modifications in urban areas are thought to occur under selective regimes, and so may promote adaptive changes involving genetic, physiological, and morphological modifications in future generations (Bateson and Laland 2013). However, whether or not behavior promotes evolution in urban systems is still subject to debate since behavioral plasticity may also buffer evolutionary change (Duckworth 2009). Due to its flexibility and, in some cases, reversibility, behavior is not subject to the same degree of evolutionary pressure as morphological or physiological traits (van Buskirk 2012, Rosenthal and Stuart-Fox 2012). Behavioral changes without genetic transmission may be selected, so that some phenotypes are directed toward an adaptive peak (Lopez-Sepulcre and Kokko 2012). Thus, transmitted learned behaviors may eventually become genetically stabilized in subsequent generations (e.g., Baldwin effect; Badyaev 2009). It is noticeable that these topics represent important research challenges not only in Latin America, but globally (Evans et al. 2015; Marzluff 2016). Untangling the role that behavior has on birds in urban Latin America may not only contribute to the design of conservation strategies and a better urban planning, but also to reveal basic, and still understudied, questions related to animal behavior and evolution in general.

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**Table 6.1** Behavioral studies from Latin America addressing the different challenges for an urban life

| Topic[a] | Countries | Experimental (%) | Observational (%) |
|---|---|---|---|
| Habitat loss and fragmentation (19) | Argentina, Brazil, Chile, Colombia, Costa Rica, Ecuador, Mexico | 16 | 84 |
| Resources availability (24) | Argentina, Barbados, Brazil, Chile, Colombia Mexico, Peru, Venezuela | 33 | 67 |
| Pollution (14) | Argentina, Brazil, Chile, Colombia, Costa Rica, | 71 | 29 |
| Species interaction (9) | Argentina, Bolivia, Mexico, Peru, Venezuela | 44 | 66 |
| Human activities (20) | Argentina, Barbados, Brazil, Colombia, Mexico | 40 | 60 |

[a] Number of studies of each topic in parenthesis

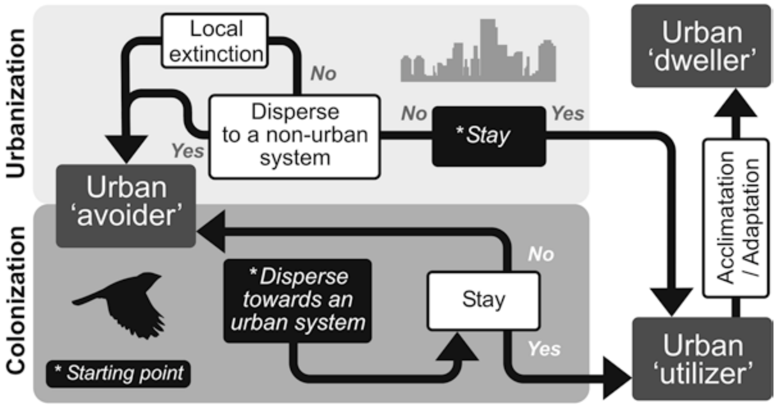

**Fig. 6.1** Decision-making model depicting the chances of living in urban areas and the behavioral challenges during each state. See Sect. 6.4 (this chapter) for details on the behavioral challenges related to the response of birds to urbanization

**Fig. 6.2** Chimango Caracara (*Milvago chimango*) exploring on garbage bags (*above*) and group of individuals of the same species feeding on leftovers in an asphalt street (*below*) (Photo: CG-L)

**Fig. 6.3** Peregrine Falcon (*Falco peregrinus*) preying on an invasive Monk Parakeet (*Myiopsitta monachus*) in Santiago de Chile (Photo: Romina Benzi)