Chapter 7
Mechanisms of Behavioural Change in Urban Animals: The Role of Microevolution and Phenotypic Plasticity

Ana Catarina Miranda

Abstract A key question in evolutionary behavioural ecology is how species cope with changes in their environments. In the last centuries, humans have caused dramatic changes in our planet that have affected the way many animals behave. In order to live in cities, most animals are forced to adjust their behaviour and life histories to the new urban habitat. While growing evidence reports behavioural differences between rural and urban conspecifics as common and cross-taxonomical, the mechanisms underlying such differences in behaviour remain largely unknown. Recent research using animals with limited experience of their natural urban or rural environments points to the existence of intrinsic differences in behaviour between rural and urban conspecifics. This suggests that phenotypic plasticity might not be the only mechanism explaining behavioural differences between rural and urban individuals and that differences in individually consistent behavioural traits could also be the result of microevolution in the urban environment.

Knowing that urbanization is and will continue to be a major environmental challenge to most living organisms, it is urgent to understand the mechanisms allowing animals to cope with our urbanizing world. In this chapter, I focus on the existence of different behavioural phenotypes between rural and urban animals and on the possible mechanisms leading to such behavioural differences.

Keywords Animal personalities • Anthropogenic environmental change • Behavioural syndromes • Colonization • Microevolution • Phenotypic plasticity • Urbanization

---

A.C. Miranda (✉)
Postgraduate Programme in Biodiversity and Conservation, Universidade Federal do Maranhão, Campus do Bacanga, Av. dos Portugueses 1966, 65080805 São Luís, MA, Brazil

Max Planck Institute for Ornithology, Am Obstberg 1, Möggingen, 78315 Radolfzell, Germany

Department of Biology, University of Konstanz, 78457 Constance, Germany
e-mail: catarina.miranda@gmail.com

E. Murgui, M. Hedblom (eds.), *Ecology and Conservation of Birds in Urban Environments*, DOI 10.1007/978-3-319-43314-1_7

7.1 Introduction

According to the United Nations (2014), two and a half billion people inhabited our planet in 1950. Remarkably, in 2011, little more than 60 years later, that number had almost tripled to seven billion people, and an impressive increase to over nine billion inhabitants is expected by 2050. Along with the world's extreme human population growth, the last few decades have witnessed an unprecedented increase in the number and size of cities. While in the 1950s 30 % of the human population lived in urban areas, that number suffered a drastic growth to 54 % in 2014 and is estimated to further increase to 66 % by 2050 (United Nations 2014).

In the last decades, the significant development of urban ecology as a scientific discipline reflects the now widely accepted fact that the phenomenon of urbanization has a profound impact on ecological systems, being a major threat to many species (Shochat et al. 2006; Gaston 2010).

In their natural habitats, animals are continuously facing environmental challenges, as coping with disturbances, adjusting to shifts in food availability and distribution and interacting and competing with other animals. The manner in which an individual animal responds to such challenges can greatly affect its future chances of survival and reproduction. Over the last centuries, urbanization arose as a new major environmental challenge that may favour individuals consistently behaving in different ways. The colonization of an urban habitat often requires organisms to adapt, among other factors, to increased disturbance levels, shifts in food resources, new species composition, a different microclimate and increased chemical, light and noise pollution (Klausnitzer 1989; Partecke et al. 2006; Brearley et al. 2012; Lowry et al. 2013; Dominoni 2016; Kekkonen 2016). Typically, the changes caused by urbanization occur in a quick and dramatic manner, being thus expectable that many organisms should be unable to cope with these changes, causing their potential exclusion from urban environments (Hendry et al. 2008; Sih et al. 2011). Accordingly, it is well documented that urbanization leads to a drastic loss in species diversity (Shochat et al. 2010; Daniels and Kirkpatrick 2016). On the other hand, it has been argued that urban environments may offer important benefits for certain species, such as warmer temperatures (Arnfield 2003), nocturnally illuminated foraging areas (Lourenço et al. 2008; Santos et al. 2010) and anthropogenic food (Bateman and Fleming 2012; Gleditsch 2016). Supporting this idea, numerous species seem to prosper in urban environments (Case 1996), being therefore crucial to understand how animals cope with urbanization and which are the consequences of living in the new urban habitats. Evidence suggests that, in many species, urban populations differ in several aspects, including timing of reproduction (see Chamberlain et al. 2009 for a literature review), daily activity patterns (Dominoni et al. 2013), stress physiology (Partecke et al. 2006; Fokidis et al. 2009) and even rates of cellular ageing.

Remarkably, urban animals also frequently change the way they behave, and this is the focus of this chapter. In the next sections, I will begin by reviewing the studies documenting shifts in behaviour between rural and urban conspecifics. Next, I will focus on the possible ultimate causes that might lead to such behavioural differences between rural and urban animals, namely, phenotypic plasticity or microevolution in the urban environment. I include some considerations about physiology as a possible proximate cause of shifts in behaviour in urban species. Finally, I will discuss some possible impacts of the observed shifts in behaviour in urban species.

7.2 Urbanization-Driven Shifts in Behavioural Traits: The Nature of Urban Behaviour

An individual's behavioural phenotype is a set of elements that is crucial for coping with environmental challenges such as urbanization and that might be related with major life history decisions, as whether to colonize new habitats or not and their consequences. Urbanization is a relatively new and strong selection pressure challenging organismal adaptation capabilities. The environmental challenges driven by urbanization can result in various phenotypic shifts, including shifts in behaviour (Sol et al. 2013; Partecke 2013). Indeed, an increasing body of evidence shows that rural and urban conspecifics commonly differ in many behavioural traits (but see literature review in Table 7.1). In specific, a study has assessed how common are shifts in animal behaviour related to the urbanization phenomenon, by reviewing empirical studies comparing rural and urban conspecifics in different behaviours towards stimuli (Miranda et al. 2013). Here, over 2 years later, using the methodology in the aforementioned study (Miranda et al. 2013), I conducted an identical literature search with the objective of finding studies comparing rural and urban populations in the following behaviours: aggression (attacks or other aggressive interactions or displays), alarm (alarm calls in response to disturbing stimuli), escape (retreat behaviours when facing disturbing or threatening stimuli), exploration (exploration of new environments), innovation (ability to solve problems, usually associated with a food reward), neophilia (attraction to novelty), neophobia (novelty avoidance) and risk-taking (exposure to risk). The literature search was performed in ISI Web of Knowledge (http://www.isiknowledge.com) in April 2015, with the following exact search terms: Topic = (Aggression OR Alarm OR Anti-predator OR Behavioural-syndrome OR Bold OR Defense OR Escape OR Exploration OR Fear OR Flight-initiation-distance OR Flush OR Innovation OR Neophilia OR Neophobia OR Novel OR Personality OR Risk-taking OR Shy OR Temperament) AND Topic = (Urbani* OR (Urban NEAR/1 Rural) a OR "Exposure to Humans") AND Topic = (Behaviour) AND Topic = (Animal OR Species). From the retrieved results, I selected all relevant articles in English from appropriate research areas, as well as articles resulting from backward or forward searches of the original search. Statistically significant differences ($P < 0.05$) were classified into 'rural > urban' or 'rural < urban' depending on the direction of the trend. In articles focusing on multiple species or related behaviours, I considered significant differences when these were shown in at least one species and behaviour in the

Table 7.1 Summary of empirical studies comparing rural and urban conspecific populations in behaviours towards different stimuli

Behaviour	Species	Trend	Experiment in the wild or laboratory	Pre-experimental Environment	Repeatability	Behavioural correlation	Refs.
Aggression							
	15 bird species	R < U	Wild	Wild	NA	NA	Møller and Ibáñez-Álamo (2012)
	American crow (*Corvus brachyrhynchos*)	NS	Wild	Wild	NA	NA	Knight et al. (1987)
	Noisy miner (*Manorina melanocephala)*	R < U	Wild	Wild	NA	NA	Lowry et al. (2011)
	Mute swan (*Cygnus olor*)	R < U	Wild	Wild	NA	NA	Józkowicz and Górska-Kłęk (1996)
	Song sparrow (*Melospiza melodia*)	R < U	Wild	Wild	NA	Yes	Evans et al. (2010)
	Song sparrow (*Melospiza melodia)*	R < U	Wild	Wild	Yes	Yes	Scales et al. (2011)
Alarm							
	15 bird species	R > U	Wild	Wild	NA	NA	Møller and Ibáñez-Álamo (2012)
	American crow (*Corvus brachyrhynchos)*	R > U (from a distance) R < U (close distance)	Wild	Wild	NA	NA	Knight et al. (1987)
	Black-tailed prairie dog (*Cynomys ludovicianus*)	R > U	Wild	Wild	NA	NA	Adams et al. (1987)

	Black-tailed prairie dog *(Cynomys ludovicianus)*	NS	Wild	Wild	NA	NA	Magle et al. (2005)
	Eastern grey squirrel *(Sciurus carolinensis)*	R < U	Wild	Wild	NA	NA	Partan et al. (2010)
Escape							
	5 bird species	R > U	Wild	Wild	NA	NA	Clucas and Marzluff (2012)
	10 bird species	R > U (3 species NS)	Wild	Wild	NA	NA	Cooke (1980)
	42 bird species	R > U	Wild	Wild	NA	NA	Carrete and Tella (2011)
	44 bird species	R > U	Wild	Wild	NA	NA	Møller (2008)
	62 bird species	R > U	Wild	Wild	NA	NA	Møller and Tryjanowski (2014)
	American crow (*Corvus brachyrhynchos*)	R > U	Wild	Wild	NA	NA	Knight et al. (1987)
	Black-tailed prairie dog *(Cynomys ludovicianus)*	R > U	Wild	Wild	NA	NA	Adams et al. (1987)
	Black-tailed prairie dog *(Cynomys ludovicianus)*	R > U	Wild	Wild	NA	NA	Magle et al. (2005)
	Black-billed magpies (*Pica pica*)	R > U	Wild	Wild	NA	NA	Kenney and Knight (1992)
	Burrowing owl (*Athene cunicularia*)	R > U	Wild	Wild	Yes	NA	Carrete and Tella (2013)
	Cane toad (*Rhinella marina*)	NS (Novel Prey Exp.) R < U (Novel Object)	Lab	Wild	NA	Yes	Candler and Bernal (2015)

(continued)

Table 7.1 (continued)

Behaviour	Species	Trend	Experiment in the wild or laboratory	Pre-experimental Environment	Repeatability	Behavioural correlation	Refs.
	Cape ground squirrel (*Xerus inauris*)	R > U	Wild	Wild	NA	NA	Chapman et al. (2012)
	Common mynas (*Acridotheres tristis*)	R > U	Wild	Wild	NA	Yes	Ashlee McGiffin (2013)
	Dark-eyed junco (*Junco hyemalis*)	R > U	Wild	Wild	NA	NA	Atwell et al. (2012)
	Eastern grey squirrel (*Sciurus carolinensis*)	R > U	Wild	Wild	NA	No	Engelhardt and Weladji (2011)
	Fox squirrel (*Sciurus niger*)	R > U (adults[a])	Wild	Wild	NA	NA	Mccleery (2009)
	Garden skink (*Lampropholis guichenoti*)	R < U	Wild	Wild	NA	NA	Prosser et al. (2006)
	House finch (*Carpodacus mexicanus*)	R < U	Wild	Wild	NA	Yes	Valcarcel and Fernandez-Juricic (2009)
	Magpie-lark (*Grallina cyanoleuca*)	R > U	Wild	Wild	NA	NA	Kitchen et al. (2010)
	Noisy miner (*Manorina melanocephala*)	R > U	Wild	Wild	NA	NA	Lowry et al. (2011)
	Song sparrow (*Melospiza melodia*)	R > U	Wild	Wild	Yes	Yes	Evans et al. (2010)
	Song sparrow (*Melospiza melodia*)	R > U	Wild	Wild	Yes	Yes	Scales et al. (2011)

	Two-banded plover (*Charadrius falklandicus*)	R > U	Wild	Wild	NA	NA	St Clair et al. (2010)
	White-fronted plover (*Charadrius marginatus*)	R > U	Wild	Wild	NA	NA	Baudains and Lloyd (2007)
	Woodchuck (*Marmota monax*)	NS	Wild	Wild	NA	Yes	Lehrer et al. (2012)
	Woodlouse (*Porcellio laevis*)	R > U	Lab	Wild	NA	NA	Houghtaling and Kight (2006)
Exploration							
	Dark-eyed junco (*Junco hyemalis*)	R < U	Lab	Lab since juveniles	NA	NA	Atwell et al. (2012)
Innovation							
	House sparrow (*Passer domesticus*)	R < U	Lab	Wild	NA	No	Liker and Bókony (2009)
	House sparrow (*Passer domesticus*)	NS (3tests) $U_{large} > U_{Small} + R_{Small}$ (1 test)	Lab	Wild	Yes (Rural = Urban)	NA	Papp et al. (2014)
Neophilia							
	Blackbird (*Turdus merula*)	R > U	Lab	Brought as nestlings to the lab	Yes	Yes	Miranda et al. (2013)
Neophobia							
	Blackbird (*Turdus merula*)	R < U	Lab	Brought as nestlings to the lab	Yes	Yes	Miranda et al. (2013)
	Cane toad (*Rhinella marina*)	NS (Novel Prey and Novel Food)	Lab	Wild	NA	NA	Candler and Bernal (2015)

(continued)

Table 7.1 (continued)

Behaviour	Species	Trend	Experiment in the wild or laboratory	Pre-experimental Environment	Repeatability	Behavioural correlation	Refs.
	Eastern grey squirrel *(Sciurus carolinensis)*	R > U	Wild	Wild	NA	NA	Bowers and Breland (1996)
	House sparrow *(Passer domesticus)*	NS	Lab	Wild	NA	No	Liker and Bókony (2009)
	House sparrow *(Passer domesticus)*	NS	Lab	Wild	NA	Yes	Bókony et al. (2012)
Risk-taking							
	American crow (*Corvus brachyrhynchos*)	R < U	Wild	Wild	NA	NA	Knight et al. (1987)
	Black-tailed prairie dog (*Cynomys ludovicianus*)	R < U	Wild	Wild	NA	NA	Adams et al. (1987)
	Cane toad (*Rhinella marina*)	R > U (Novel prey and Novel object)	Lab	Wild	NA	NA	Candler and Bernal (2015)
	Cape ground squirrel (*Xerus inauris*)	R < U	Wild	Wild	NA	NA	Chapman et al. (2012)
	Eastern grey squirrel (*Sciurus carolinensis*)	NS	Wild	Wild	NA	No	Engelhardt and Weladji (2011)
	Garden skink (*Lampropholis guichenoti*)	R < U	Wild	Wild	NA	NA	Prosser et al. (2006)
	House sparrow *(Passer domesticus)*	R < U (juveniles) R > U (adults)	Lab	Wild	NA	NA	Seress et al. (2011)
	House sparrow (*Passer domesticus*)	NS	Lab	Wild	NA	Yes	Bókony et al. (2012)

	House sparrow *(Passer domesticus)*	NS	Lab	Wild	Yes	Yes	Vincze et al. (2014)
	White-fronted plover (*Charadrius marginatus*)	R < U	Wild	Wild	NA	NA	Baudains and Lloyd (2007)
	Woodchuck (*Marmota monax*)	NS	Wild	Wild	NA	Yes	Lehrer et al. (2012)

The column ‘trend’ reports differences in average trait values between rural (R) and urban (U) individuals, where the reported trends are significant ($P < 0.05$), and the non-significant results are reported as ‘NS’. For details on the methodology, see Miranda et al. (2013). The literature review was conducted in April 2015

[a] Juveniles possibly with no difference

same category. For clarity, only studies that focused both on rural and urban populations of the same species, excluding studies focusing on gradients of urbanization, or disturbance in only rural or urban environments. Nonetheless, the concept of rural and urban certainly differs in many of the retrieved studies regarding characteristics of the habitat and degree of anthropogenic disturbance.

The literature review reinforces the idea that only individuals able to behaviourally cope with the new urban selection pressures can be successful in urban habitats. However, with the few number of studies available for each species, we can only speculate about the specific behavioural traits that could benefit a specific city dweller. Most likely, there are various ways for an animal to be successful in an urban habitat, and the optimal behavioural strategies might also vary according to different stages of colonization (for a review on the theme, see Sol et al. 2013) or to the characteristics of each urban habitat. It should be noted that not all urban species are urban colonizers in the true sense of the word; instead, for many populations, their natural habitats are 'colonized' by urban settings. Birds seem to be an ideal taxa to study the urbanization-related shifts in behavioural traits, with two thirds of the studies from our literature review focusing on this group (Fig. 7.1).

Fig. 7.1 Some of the main bird species used in studies assessing behavioural shifts related with the urbanization process (**a**) European blackbird *Turdus merula* (female and nestlings at an urban nest, picture taken by A.C. Miranda); (**b**) dark-eyed junco *Junco hyemalis thurberi* (picture taken by Jonathan Atwell/www.juncoproject.org); (**c**) house sparrow *Passer domesticus* (picture taken by P.R. Monteiro); (**d**) *Melospiza melodia* (picture taken by C.D. Santos)

The literature review retrieved 36 empirical studies comparing rural and urban conspecifics in aggressive, alarm, escape, neophilic, neophobic, innovative and risk-taking behaviours towards different types of stimuli (Table 7.1). Most of the studies were made in the wild, with only nine studies made under controlled laboratory conditions and only two of these studies using individuals with limited experience of their natural rural or urban environment (Atwell et al. (2012) made a common garden experiment using birds caught as juveniles; Miranda et al. (2013) made a common garden experiment using birds caught as nestlings). Of the 36 studies, 33 showed significant differences between rural and urban populations for at least one of the behaviours and species analysed. Urban populations seemed to be more aggressive (5 of 6 studies in the wild) and showed reduced escape behaviour (24 of 26 studies), having mixed results regarding risk-taking behaviour (6 of 11 studies found that urban populations incurred in higher risk-taking behaviours). For the other considered behaviours, 9 of 12 studies showed differences between rural and urban conspecific populations. Repeatability was only assessed in five studies, in which four found the behaviours under study to be repeatable. Eleven studies assessed correlations between different behaviours, finding that most of the behaviours were correlated.

Although it is now unquestionable that the conquest of urban habitats by animals is linked to intraspecific behavioural shifts, the underlying mechanisms of this changes remain unclear. Are behavioural changes in urban animals due to phenotypic plasticity or to microevolution? Although behavioural plasticity is likely to play an important role in helping animals to cope with the urban environment, recent studies suggest that behavioural differences between rural and urban individuals might be intrinsic, potentially resulting from divergent selection pressures on rural and urban populations (Atwell et al. 2012; Carrete and Tella 2013; Miranda et al. 2013). Next, I will focus on the two possible responsible mechanisms for behavioural shifts in urban animals, behavioural plasticity and microevolution of behavioural traits.

It should be noted that, while throughout this chapter I portray behavioural plasticity and microevolution of behavioural traits separately for the sake of simplicity, I believe that in most cases both mechanisms contribute in some extent to the behaviour observed in urban animals.

7.3 Behavioural Plasticity in Urban Environments

Phenotypic plasticity is a common phenomenon in nature that can be defined as the capacity of an individual with a particular genotype to alter its phenotype under certain environmental conditions (Thibert-Plante and Hendry 2011). Phenotypic plasticity is the primary mechanism enabling individual organisms to adjust their morphology OR physiology OR behavior OR phenology to better suit changes in their environmental conditions, thereby potentially increasing fitness (Thibert-Plante and Hendry 2011; Van Buskirk 2012).

Behaviour, which consists of a motoric response to a sensorial input, is an essential function for animals to interact with their surrounding environment. Being able to adjust behaviour in response to environmental changes can have important life history consequences for an organism. It is generally assumed that behavioural plasticity plays a critical role for the success of city dwellers, as it enables organisms to more efficiently and rapidly deal with the different challenges of the novel urban environment, as finding new resources and effectively using them and coping with unfamiliar and potentially dangerous animals, objects or situations (Sol et al. 2013; Lowry et al. 2013). Under rapid environmental changes as urbanization, behavioural plasticity can be advantageous over evolutionary changes because it can emerge immediately in response to a new environment. It has been suggested that organisms lacking phenotypic plasticity might be naturally excluded from altered environments (Badyaev 2005).

Although having flexibility in behaviour might be advantageous in specific circumstances, it involves an investment of time and energy, implying important costs that might ultimately have a negative effect on reproduction and survival (Sol et al. 2013). Another potentially negative side effect is that behavioural plasticity, by uncoupling the genotype from the phenotype, might decrease the efficacy of evolutionary responses to selection (Van Buskirk 2012). It is important to note, however, that behavioural plasticity is not independent of the mechanisms involving evolution and adaptation: plasticity can evolve in response to changes in the environment if selection acts on reaction norms or if the trait means are correlated with plasticity (Van Buskirk 2012).

7.4 Microevolution of Behaviour in Urban Environments

In many species, certain individuals exhibit behavioural traits that might make them inherently well suited to occupy urban environments. Behaviours that are consistent across time and contexts for one individual (personality traits) might indeed provide important advantages for invading new environments. Animal personalities are taxonomically widespread, being documented in over 100 species (Wolf et al. 2008). In the last years, a number of studies revealed the variation in (van Oers et al. 2004; Schielzeth et al. 2011).

Despite the generalized evidence showing behavioural differences between urban and rural conspecifics, the vast majority of studies so far were not able to disentangle microevolution from behavioural plasticity (Table 7.1). Nevertheless, two recent common garden experiments conducted with urban and rural conspecific bird populations indicate that consistent behavioural traits differ intrinsically between rural and urban individuals (Atwell et al. 2012; Miranda et al. 2013). These differences are likely the result of microevolutionary changes, although the experimental setups could not fully exclude early developmental influences.

The idea of a genetic basis for behavioural shifts in urban individuals is further supported by a recent comparative study that assessed candidate genes for behavioural traits on several rural and urban blackbird populations across Europe (Mueller et al. 2013). In the above-mentioned study, a candidate gene for harm avoidance behaviour (the SERT gene) exhibited a significant association with habitat type.

Two different evolutionary processes could be responsible for heritable differences in personality traits between rural and urban conspecifics (Miranda et al. 2013): (1) microevolution in personality traits as an adaptation to new urban selective pressures that shift the behavioural optima (post-colonization adaptation) or (2) microevolution of personality traits via non-random gene flow, through a personality-dependent colonization of the urban habitat (pre-colonization adaptation, Edelaar and Bolnick 2012). The two processes might occur concurrently and potentially under distinct selection pressures indifferent stages of colonization (Martin and Fitzgerald 2005).

7.5 Differences in Physiology as Potential Precursors of Differences in Urban Behaviour

The endocrine system is an essential causal mechanism behind animal behaviour. To understand how hormones might shape behaviours under different selection pressures, it is essential to investigate the covariation between hormonal and phenotypic traits and how those could relate to fitness. It has been suggested that differences in suites of behaviours might be influenced by modifications of the two main endocrine axes, the hypothalamic-pituitary-adrenal axis (HPA axis, related with the production of corticosteroid hormones) and the hypothalamic-pituitary-gonadal axis (HPG axis, related with the production of estrogens or androgens) (van Oers et al. 2011). Understanding if and how the endocrine system relates to differences in behaviours between rural and urban conspecifics should be a crucial focus of research in behavioural urban ecology.

In recent years, several studies have focused on differences between rural and urban conspecifics on hormones associated with the hypothalamic-pituitary-adrenal axis (HPA), such as corticosterone, which might improve the chances of survival under adverse environmental conditions. Studies with captive bird populations suggest the existence of an intrinsically reduced acute corticosterone stress response in urban animals (Partecke et al. 2006; Atwell et al. 2012). However, field studies on the subject provided less clear results (Schoech et al. 2004; French et al. 2008; Fokidis et al. 2009). One recent common garden experiment with rural and urban dark-eyed juncos (*Junco hyemalis*) simultaneously assessed differences in behavioural traits and in HPA responsiveness in rural and urban conspecific, concluding that intrinsic differences in exploratory behaviour might be correlated to differences in the corticosterone stress response (Atwell et al. 2012).

The lack of knowledge is even greater when considering hormones associated with the hypothalamic-pituitary-gonadal axis (HPG), such as estrogens or androgens (Buchanan and Partecke 2012). An existing study suggests that, in the wild, male rural blackbirds have higher levels of plasma testosterone and luteinizing hormone than urban males (Partecke et al. 2005). However, virtually no study assesses simultaneously differences in behavioural traits and in HPG responsiveness in rural and urban conspecifics.

Although the existence of correlations between baseline or maximum hormone levels and individual consistent behavioural traits have been suggested, they have rarely been found (Johnsen 1998; McGlothlin et al. 2007; but see Atwell et al. 2012). It is possible that correlations between behavioural and hormonal traits are not stable during the annual cycle but rather transient (reviewed in Adkins-Regan 2005). Moreover, while some studies found differences in hormone concentration between rural and urban animals, there is a lack of comparisons of other factors involved in the HPA and HPG axis. In fact, many of the reported differences in behaviour between rural and urban conspecifics could be related to aspects of the HPA and HPG axis, not only hormone concentration but also to differences in transport proteins, differences in the number or sensitivity of hormone receptors or cofactors or hard-wired (neural) differences that are not under hormonal control. All these aspects should be addressed in future studies.

7.6 Synthesis and Directions for Future Research

In this chapter, I revised the literature showing that urban animals across many taxa exhibit differences in behaviour when compared to their rural counterparts. I further focused on how behavioural shifts in urban animals can arise from plasticity or from microevolutionary changes and on the possible relations between differences in physiology and in behaviour in urban animals.

On one hand, species in which individuals show high plasticity in behaviour have an inherent capacity to quickly adjust to altered conditions and, in consequence, might be particularly predisposed to occupy urban environments. On the other hand, microevolution of individually consistent behavioural traits (personality traits) as an adaptation to the urban environment could also explain the observed shifts in behavioural traits in urban animals. By allowing populations to flexibly adjust their behaviours to environmental changes, behavioural plasticity can potentially decrease the need for selection to act on behavioural traits (Price et al. 2003). Conversely, it is also possible that the selection of individuals presenting only specific behavioural traits that are beneficial under urban environmental conditions might be associated with a reduction in behavioural plasticity (Martin and Fitzgerald 2005).

Variation in behaviour, either plastic or intrinsic, is an essential aspect that allows species to respond to environmental challenges as urbanization. Individuals from species with a large variation in their behavioural phenotypes are thought to better cope with urbanization when compared to species with narrower ranges of behavioural phenotypes (Sih et al. 2010). To understand the role of evolution versus plasticity in shaping behavioural traits, we would ideally need to separate the genetic and environmental components of the behaviour and to assess its fitness value in urban and rural habitats. Although these data might be difficult to obtain, studies with repeated measures of behavioural elements in which family effects can be estimated could be the foundation for revealing the basis of variation in behaviour. In the future, behavioural ecologists working with urbanization should more thoroughly address behavioural variation within individuals (plasticity), between individuals (personality), within populations and between populations (Araya-Ajoy and Dingemanse 2013; Dingemanse and Dochtermann 2013). By gaining knowledge about the variation in behaviour and the environmental correlates, we will be able to better understand which are the species that will be excluded from urban habitats and which will be the ones successfully colonizing them, maybe even being able to foresee the shifts in behaviour in our ever changing world.

If microevolution acts in the urban environment through selection pressures favouring specific personality traits, the decrease in between-individual variation (or lower heritability) could lead to the reduction in genetic diversity that is commonly observed in anthropogenically impacted animal populations and usually attributed to genetic drift (Carere and Maestripieri 2013). To date, few publications have focused on assessing the effects of urbanization on shaping the strength and direction of behavioural syndromes, but it has been suggested that urbanization might act on behavioural syndromes by changing the correlations between behaviours via correlational selection (Bell and Sih 2007) or directly by disrupting certain behavioural traits (Scales et al. 2011; Bókony et al. 2012; Royauté et al. 2013). Variation in syndrome structures between different populations may reflect adaptation to local environmental conditions (Bell 2005; Dingemanse et al. 2007). However, selection can also act on independent behavioural traits. In either case, proving that these traits are adaptive would require the evaluation of selection gradients, such as estimating the survival of each behavioural type in natural conditions (Bell and Sih 2007; Sweeney et al. 2013).

It is also particularly important to assess the individual consistency of the behavioural phenotypes. In theory, selection should only act on traits where the intra-individual variation is larger than the between-individual variation (Boake 1989). Repeatability of a behavioural trait is the proportion of the variance of the trait that is explained by differences among individuals, and in most cases the repeatability of a behavioural trait sets the upper limit for heritability (Falconer and Mackay 1996). Thus, in general, genetically determined traits on which selection is able to act are repeatable.

The majority of studies in urbanization has been done on temperate northern regions, where the process of urbanization is older and more widespread (Sol et al. 2013). But research is also needed on regions where the urbanization process is still at an early stage.

Currently, we only have rudimentary knowledge about the mechanisms that allow some species to cope with anthropogenic environmental change. Developing a realistic interpretation of the mechanisms behind differences in behaviour in urban animals requires an integrative approach, of behaviour, physiology, ecology, genetics and evolution of urban populations. The answers are likely to be complex, but we will hopefully be able to contribute to unravelling the evolutionary ecological consequences of urbanization.

Although understanding organismic behavioural adaptations to urbanization is a topic of major importance, the most crucial achievement should be changing human behaviour itself. The consequences of human environmental change are so devastating that none of our research efforts will be relevant if humans keep destroying natural habitats and depleting natural resources at the current pace.

Acknowledgements I thank the editors, Enrique Murgui and Marcus Hedblom, for the kind invitation to contribute to this book.

References

Adams RA, Lengas BJ, Bekoff M (1987) Variations in avoidance responses to humans by black-tailed prairie dogs (*Cynomys ludovicianus*). J Mammal 68:686–689. doi:10.2307/1381606

Adkins-Regan E (2005) Hormones and animal social behavior. Princeton University Press, Princeton

Araya-Ajoy YG, Dingemanse NJ (2013) Characterizing behavioural “characters”: a conceptual and statistical framework. Proc R Soc B 2014 281 20132645. doi:10.1098/rspb.2013.2645

Arnfield AJ (2003) Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. Int J Climatol 23:1–26. doi:10.1002/joc.859

Ashlee McGiffin AL (2013) Tolerance of human approaches by Common Mynas along an urban-rural gradient. Emu 113:154. doi:10.1071/MU12107

Atwell JW, Cardoso GC, Whittaker DJ et al (2012) Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. Behav Ecol 23:960–969. doi:10.1093/beheco/ars059

Badyaev AV (2005) Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. Proc Biol Sci 272:877–886. doi:10.1098/rspb.2004.3045

Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. J Zool 287:1–23. doi:10.1111/j.1469-7998.2011.00887.x

Baudains TP, Lloyd P (2007) Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Anim Conserv 10:400–407. doi:10.1111/j.1469-1795.2007.00126.x

Bell AM (2005) Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). J Evol Biol 18:464–473. doi:10.1111/j.1420-9101.2004.00817.x

Bell AM, Sih A (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett 10:828–834. doi:10.1111/j.1461-0248.2007.01081.x

Boake CRB (1989) Repeatability: its role in evolutionary studies of mating behavior. Evol Ecol 3:173–182. doi:10.1007/BF02270919

Bókony V, Kulcsár A, Tóth Z, Liker A (2012) Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). PLoS One 7:e36639. doi:10.1371/journal.pone.0036639

Bowers MA, Breland B (1996) Foraging of gray squirrels on an urban-rural gradient: use of the gud to assess anthropogenic impact. Ecol Appl 6:1135. doi:10.2307/2269597

Brearley G, McAlpine C, Bell S, Bradley A (2012) Influence of urban edges on stress in an arboreal mammal: a case study of squirrel gliders in southeast Queensland, Australia. Landsc Ecol 27:1407–1419. doi:10.1007/s10980-012-9790-8

Buchanan KL, Partecke J (2012) The endocrine system: can homeostasis be maintained in a changing world? In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world: mechanisms and consequences. Oxford University Press, Oxford, pp 145–158

Candler S, Bernal XE (2015) Differences in neophobia between cane toads from introduced and native populations. Behav Ecol 26:97–104. doi:10.1093/beheco/aru162

Carere C, Maestripieri D (2013) Animal personalities – behavior, physiology, and evolution. University of Chicago Press, Chicago, IL

Carrete M, Tella JL (2011) Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. PLoS One 6:e18859. doi:10.1371/journal.pone.0018859

Carrete M, Tella JL (2013) High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. Sci Rep. doi:10.1038/srep03524

Case TJ (1996) Global patterns in the establishment and distribution of exotic birds. Biol Conserv 78:69–96. doi:10.1016/0006-3207(96)00019-5

Chamberlain DE, Cannon AR, Toms MP et al (2009) Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151:1–18. doi:10.1111/j.1474-919X.2008.00899.x

Chapman T, Rymer T, Pillay N (2012) Behavioural correlates of urbanisation in the Cape ground squirrel *Xerus inauris*. Naturwissenschaften 99:893–902. doi:10.1007/s00114-012-0971-8

Clucas B, Marzluff JM (2012) Attitudes and actions toward birds in urban areas: human cultural differences influence bird behavior. Auk 129:8–16. doi:10.1525/auk.2011.11121

Cooke AS (1980) Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biol Conserv 18:85–88. doi:10.1016/0006-3207(80)90072-5

Daniels G, Kirkpatrick J (2016) Ecology and conservation of Australian urban and exurban avifauna. In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer, Heidelberg, pp 343–370

Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol 82:39–54. doi:10.1111/1365-2656.12013

Dingemanse NJ, Wright J, Kazem AJN et al (2007) Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. J Anim Ecol 76:1128–1138. doi:10.1111/j.1365-2656.2007.01284.x

Dominoni DM (2016) Ecological effects of light pollution: how can we improve our understanding using light loggers on individual animals. In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer, Heidelberg, pp 251–270

Dominoni DM, Helm B, Lehmann M et al (2013) Clocks for the city: circadian differences between forest and city songbirds. Proc R Soc B Biol Sci 280:20130593. doi:10.1098/rspb.2013.0593

Edelaar P, Bolnick DI (2012) Non-random gene flow: an underappreciated force in evolution and ecology. Trends Ecol Evol 27:659–665. doi:10.1016/j.tree.2012.07.009

Engelhardt SC, Weladji RB (2011) Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). Can J Zool 89:823–830. doi:10.1139/Z11-054

Evans J, Boudreau K, Hyman J (2010) Behavioural syndromes in urban and rural populations of song sparrows. Ethology 116:588–595. doi:10.1111/j.1439-0310.2010.01771.x

Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Longman, Essex, England

Fokidis HB, Orchinik M, Deviche P (2009) Corticosterone and corticosteroid binding globulin in birds: relation to urbanization in a desert city. Gen Comp Endocrinol 160:259–270. doi:10.1016/j.ygcen.2008.12.005

French SS, Fokidis HB, Moore MC (2008) Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban-rural gradient. J Comp Physiol B 178:997–1005. doi:10.1007/s00360-008-0290-8

Gaston KJ (2010) Urban ecology. Cambridge University Press, Cambridge

Gleditsch J (2016) The role of invasive plant species in urban avian conservation. In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer, Heidelberg, pp 413–424

Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. Mol Ecol 17:20–29. doi:10.1111/j.1365-294X.2007.03428.x

Houghtaling K, Kight S (2006) Turn alternation in response to substrate vibration by terrestrial isopods, *Porcellio laevis* (Isopoda: Oniscidea) from rural and urban habitats in New Jersey, USA. Entomol News 117:149–154. doi:10.3157/0013-872X(2006)117[149:TAIRTS]2.0.CO;2

Johnsen TS (1998) Behavioural correlates of testosterone and seasonal changes of steroids in red-winged blackbirds. Anim Behav 55:957–965. doi:10.1006/anbe.1997.0642

Józkowicz A, Górska-Kłęk L (1996) Activity patterns of the mute swans *Cygnus olor* wintering in rural and urban areas: a comparison. Acta Ornithol 31:45–51

Kekkonen J (2016) Pollutants in urbanized areas – direct and indirect effects on bird populations. In: Murgui E, Hedblom M (eds) Ecology and conservation of birds in urban environments. Springer, Heidelberg, pp 227–250

Kenney SP, Knight RL (1992) Flight distances of black-billed magpies in different regimes of human density and persecution. Condor 94:545–547. doi:10.2307/1369231

Kitchen K, Lill A, Price M (2010) Tolerance of human disturbance by urban magpie-larks. Aust Field Ornithol 27:1–9

Klausnitzer B (1989) Verstädterung von Tieren. A. Ziemsen, Wittenberg Lutherstadt

Knight RL, Grout DJ, Temple SA (1987) Nest-defense behavior of the American crow in urban and rural areas. Condor 89:175–177. doi:10.2307/1368772

Lehrer EW, Schooley RL, Whittington JK (2012) Survival and antipredator behavior of woodchucks (*Marmota monax*) along an urban–agricultural gradient. Can J Zool 90:12–21. doi:10.1139/z11-107

Liker A, Bókony V (2009) Larger groups are more successful in innovative problem solving in house sparrows. Proc Natl Acad Sci USA 106:7893–7898. doi:10.1073/pnas.0900042106

Lourenço PM, Silva A, Santos CD et al (2008) The energetic importance of night foraging for waders wintering in a temperate estuary. Acta Oecol 34:122–129. doi:10.1016/j.actao.2008.04.005

Lowry H, Lill A, Wong BBM (2011) Tolerance of auditory disturbance by an avian urban adapter, the noisy miner. Ethology 117:490–497. doi:10.1111/j.1439-0310.2011.01902.x

Lowry H, Lill A, Wong BBM (2013) Behavioural responses of wildlife to urban environments. Biol Rev Camb Philos Soc 88:537–549. doi:10.1111/brv.12012

Magle S, Zhu J, Crooks KR (2005) Behavioral responses to repeated human intrusion by black-tailed prairie dogs (*Cynomys ludovicianus*). J Mammal 86:524–530. doi:10.1644/1545-1542(2005)86[524:BRTRHI]2.0.CO;2

Martin LB, Fitzgerald L (2005) A taste for novelty in invading house sparrows, *Passer domesticus*. Behav Ecol 16:702–707. doi:10.1093/beheco/ari044

Mccleery RA (2009) Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. Landsc Ecol 24:483–493. doi:10.1007/s10980-009-9323-2

McGlothlin JW, Jawor JM, Ketterson ED (2007) Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. Am Nat 170:864–875. doi:10.1086/522838

Miranda AC, Schielzeth H, Sonntag T, Partecke J (2013) Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Glob Change Biol 19:2634–2644. doi:10.1111/gcb.12258

Møller AP (2008) Flight distance of urban birds, predation, and selection for urban life. Behav Ecol Sociobiol 63:63–75. doi:10.1007/s00265-008-0636-y

Møller AP, Ibáñez-Álamo JD (2012) Escape behaviour of birds provides evidence of predation being involved in urbanization. Anim Behav 84:341–348. doi:10.1016/j.anbehav.2012.04.030

Møller AP, Tryjanowski P (2014) Direction of approach by predators and flight initiation distance of urban and rural populations of birds. Behav Ecol. doi:10.1093/beheco/aru073

Mueller JC, Partecke J, Hatchwell BJ et al (2013) Candidate gene polymorphisms for behavioural adaptations during urbanization in blackbirds. Mol Ecol 22:3629–3637. doi:10.1111/mec.12288

Papp S, Vincze E, Preiszner B et al (2014) A comparison of problem-solving success between urban and rural house sparrows. Behav Ecol Sociobiol 69:471–480. doi:10.1007/s00265-014-1859-8

Partan SR, Fulmer AG, Gounard MAM, Redmond JE (2010) Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. Curr Zool 56:313–326

Partecke J (2013) Mechanisms of phenotypic responses following colonization of urban areas: from plastic to genetic adaptation. In: Gil D, Brumm H (eds) Avian urban ecology. Oxford University Press, Oxford

Partecke J, Van't Hof TJ, Gwinner E (2005) Underlying physiological control of reproduction in urban and forest-dwelling European blackbirds *Turdus merula*. J Avian Biol 36:295–305. doi:10.1111/j.0908-8857.2005.03344.x

Partecke J, Schwabl I, Gwinner E (2006) Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecology 87:1945–1952. doi:10.1890/0012-9658(2006)87[1945:SATCUA]2.0.CO;2

Price TD, Qvarnström A, Irwin DE (2003) The role of phenotypic plasticity in driving genetic evolution. Proc R Soc B Biol Sci 270:1433–1440. doi:10.1098/rspb.2003.2372

Prosser C, Hudson S, Thompson MB (2006) Effects of urbanization on behavior, performance, and morphology of the garden skink, *Lampropholis guichenoti*. J Herpetol 40:151–159. doi:10.1670/38-05A.1

Royauté R, Buddle CM, Vincent C (2013) Interpopulation variations in behavioral syndromes of a jumping spider from insecticide-treated and insecticide-free orchards. Ethology. doi:10.1111/eth.12185

Santos CD, Miranda AC, Granadeiro JP et al (2010) Effects of artificial illumination on the nocturnal foraging of waders. Acta Oecol 36:166–172. doi:10.1016/j.actao.2009.11.008

Scales J, Hyman J, Hughes M (2011) Behavioral syndromes break down in urban song sparrow populations. Ethology 117:887–895. doi:10.1111/j.1439-0310.2011.01943.x

Schielzeth H, Bolund E, Kempenaers B, Forstmeier W (2011) Quantitative genetics and fitness consequences of neophilia in zebra finches. Behav Ecol 22:126–134. doi:10.1093/beheco/arq184

Schoech SJ, Bowman R, Reynolds SJ (2004) Food supplementation and possible mechanisms underlying early breeding in the Florida scrub-Jay (*Aphelocoma coerulescens*). Horm Behav 46:565–573

Seress G, Bókony V, Heszberger J, Liker A (2011) Response to predation risk in urban and rural house sparrows. Ethology 117:896–907. doi:10.1111/j.1439-0310.2011.01944.x

Shochat E, Warren P, Faeth S et al (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191. doi:10.1016/j.tree.2005.11.019

Shochat E, Lerman SB, Anderies JM et al (2010) Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60:199–208. doi:10.1525/bio.2010.60.3.6

Sih A, Stamps J, Yang LH et al (2010) Behavior as a key component of integrative biology in a human-altered world. Integr Comp Biol 50:934–944. doi:10.1093/icb/icq148

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4:367–387. doi:10.1111/j.1752-4571.2010.00166.x

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. Anim Behav 85:1101–1112. doi:10.1016/j.anbehav.2013.01.023

St Clair JJH, Garcia-Peña GE, Woods RW, Székely T (2010) Presence of mammalian predators decreases tolerance to human disturbance in a breeding shorebird. Behav Ecol 21:1285–1292. doi:10.1093/beheco/arq144

Sweeney K, Gadd RDH, Hess ZL et al (2013) Assessing the effects of rearing environment, natural selection, and developmental stage on the emergence of a behavioral syndrome. Ethology 119:436–447. doi:10.1111/eth.12081

Thibert-Plante X, Hendry AP (2011) The consequences of phenotypic plasticity for ecological speciation. J Evol Biol 24:326–342. doi:10.1111/j.1420-9101.2010.02169.x

United Nations (2014) World urbanization prospects: the 2014 revision. Department of Economic and Social Affairs, Population Division, United Nations, New York

Valcarcel A, Fernandez-Juricic E (2009) Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? Behav Ecol Sociobiol 63:673–685. doi:10.1007/s00265-008-0701-6

Van Buskirk J (2012) Behavioural plasticity and environmental change. In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world: mechanisms and consequences. Oxford University Press, Oxford, pp 145–158

van Oers K, Drent PJ, de Goede P, van Noordwijk AJ (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc R Soc B Biol Sci 271:65–73. doi:10.1098/rspb.2003.2518

van Oers K, Buchanan KL, Thomas TE, Drent PJ (2011) Correlated response to selection of testosterone levels and immunocompetence in lines selected for avian personality. Anim Behav 81:1055–1061. doi:10.1016/j.anbehav.2011.02.014

Vincze E, Papp S, Preiszner B et al (2014) Does urbanization facilitate individual recognition of humans by house sparrows? Anim Cogn 18:291–298. doi:10.1007/s10071-014-0799-z

Wolf M, van Doorn GS, Weissing FJ (2008) Evolutionary emergence of responsive and unresponsive personalities. Proc Natl Acad Sci USA. doi:10.1073/pnas.0805473105