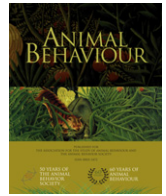




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## Special Issue: Behavioural Plasticity

## Behavioural adjustments for a life in the city

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While human-induced rapid environmental changes are putting many organisms at risk of extinction, others are doing better than ever. This raises the question of why organisms differ in their tolerance to environmental alterations. Here, we ask whether and how behavioural adjustments assist animals in dealing with the urbanization process, one of the primary causes of biodiversity loss and biotic homogenization. Based on a literature review, we present both theoretical and empirical arguments to show that behavioural adjustments to urban habitats are widespread and that they may potentially be important in facilitating resource use, avoiding disturbances and enhancing communication. While a growing number of studies report behavioural differences between urban and nonurban animals, very few studies directly address the underlying mechanisms. In some cases, the changes in behaviour occur very rapidly and involve learning, and hence can be attributed to behavioural plasticity. In other cases, however, it cannot be ruled out that behavioural differences between urban and nonurban animals result from natural selection or nonrandom sorting of individuals by behavioural traits that affect dispersal, habitat selection or establishment. Because the urbanization process is expected to continue to threaten biodiversity in the near future, there is some urgency to improve our understanding of the mechanisms through which behaviour helps animals to cope with such environmental alterations.

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Of all rapid human-induced environmental changes (HIREC, sensu Sih et al. 2011), the urbanization process is currently one of the most important threats to biodiversity (Chace & Walsh 2006; McKinney 2006; Shochat et al. 2006). Urbanization involves a number of important environmental alterations (McKinney 2002, 2006; Shochat et al. 2006): natural vegetation is replaced by built structures and fragmented by buildings and roads; food sources become artificial and often spatially concentrated; disturbance from humans increases; the community of enemies changes; and pollution is more frequent with regards to night-time lights, noise and chemicals. Because these environmental alterations are often drastic and rapid, it is to be expected that the limits of tolerance of many species are exceeded (Hendry et al. 2008; Sih et al. 2011). Indeed, a common outcome of the urbanization process is a dramatic loss of species diversity (Shochat et al. 2010a, b). Nevertheless, a few species seem not only to be little affected by the urbanization process, but appear to perceive urban habitats as ecological opportunities, which has allowed them to proliferate and

expand their range. Although it is generally agreed that the varying response of animals to urbanization reflects differences in their adaptive arsenal to confront environmental changes, controversy still exists regarding the nature of such adaptations.

In this review, we focus on the role of behaviour in the response to alterations associated with the urbanization process. Evidence is accumulating that animals that live in urban environments frequently differ in behaviour relative to those from surrounding habitats. Our first goal is to review the empirical evidence currently available for such behavioural adjustments, and to assess the extent to which they fit expected predictions of ecological theory regarding the demands of the different stages of the urban invasion process. By contrasting theory with empirical data we aim to detect major gaps in our understanding of how behavioural adjustments contribute to the success of animals in urban habitats and to identify important avenues for future research.

Although a growing number of studies provide evidence that behavioural adjustments are needed to persist in urban habitats, the underlying mechanisms remain unclear. The observed behavioural adjustments could in part reflect phenotypic plasticity. Behavioural plasticity is widely believed to be one of the main mechanisms through which animals deal with novel environmental challenges, facilitating population persistence when there is

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a sudden change in the environment (Baldwin 1896; Price et al. 2003; Sol 2003). However, the observation that behaviour differs between urban and nonurban animals is not, in itself, indicative of plasticity because a similar change is also expected as a result of two additional processes. The first is a sorting process in which only individuals or species with proper behaviours are able to colonize urban environments (see also Dingemans & Wolf 2013). The second is an evolutionary response associated with divergent selection, which brings the animal's phenotype closer to the new adaptive peak. Our second goal is to interpret the causes of behavioural adjustments on the basis of these different sources of behavioural variation.

### THE NATURE OF BEHAVIOURAL RESPONSES

Behaviour can be defined as the motor response to sensory information. Because behaviour is an important way animals interact with their environment, the ability to change behaviour in response to changes in the environment is expected to have important consequences. This can be illustrated with the well-known compromise between securing food and avoiding predation (Lima & Dill 1990). When a foraging animal is exposed to a potential predator, the animal (1) can continue foraging because it does not recognize the risk (no responsiveness), (2) can immediately reduce foraging activity and look for a refuge or (3) can adjust its foraging activity to the perceived risk of predation based on previous experience or even develop a new antipredatory tactic to continue foraging in safer conditions. The latter two points are manifestations of behavioural plasticity.

Thus, behavioural plasticity can be divided in two levels: the expression of behaviour and the development of behaviour (see Snell-Rood 2013). The expression of behaviour results from stimuli activating a neural network and eliciting a motor response, whereas the development of a behaviour involves changes in the nervous system that alter motor responses. Because of its immediacy and reversibility, the expression of behaviour allows individuals to efficiently respond to common environmental challenges by enabling rapid modulation of or transitions between behaviours as a function of the individuals' needs. Developmental behavioural plasticity is not so immediate yet it has the advantage to allow the construction of responses to unfamiliar or novel problems. One of the main mechanisms behind developmental behavioural plasticity is learning, the acquisition of new information influencing performance in behaviour (Dukas 2004). Instead of consistently expressing the same behaviour to a particular stimulus, learning allows animals to improve the behavioural response on the basis of their previous experience (Dukas 1998). In our definition of learning we include behavioural innovation, the acquisition of learned behaviours to devise solutions to novel or unfamiliar problems (Lefebvre et al. 1997; Reader & Laland 2003; Ramsey et al. 2007). Thus, learning facilitates movement of the population towards new adaptive peaks (Price et al. 2003). Because the urbanization process is likely to alter the adaptive landscapes for most populations, behavioural plasticity associated with learning appears particularly relevant *a priori* to deal with the challenges posed by urbanized environments.

Although learning may offer advantages when the environment changes (see reviews in this issue: Foster 2013; Mason et al. 2013; Sih 2013; Slabbekoorn 2013; Snell-Rood 2013), it also involves costs. The costs include time and energy invested in the production and maintenance of neural and cognitive functions that could otherwise be used for reproduction. Thus, in both birds and primates, learning seems to be primarily limited by the size of the brain, relative to body size, and particularly by the relative size of the association areas of the brain (e.g. the mesopallium in birds and the isocortex and

striatum in primates; reviewed in Lefebvre et al. 2004; Lefebvre & Sol 2008). In addition, the propensity to learn can be influenced by emotional temperament traits (e.g. degree of boldness or activity levels), motivational states (e.g. hunger), degree of ecological specialization (e.g. morphological architecture to perform some motor patterns) and life history strategies that increase or decrease the value of learning (Dukas 1998). Because the capacity to plastically adjust behaviours is limited by many factors, the changes in behaviour can often be insufficient to cope with new environmental pressures and, on occasions, can even lead to incorrect decisions.

Behaviours that show little plasticity may provide fitness benefits in the context for which they have been developed or selected, but such benefits are predicted to generally decrease when the context changes. Thus, it is tempting to conclude that such behaviours are of little relevance for coping with novel environmental pressures compared with more plastic behaviours. However, this is not necessarily true. Some behavioural types considered to be highly consistent across time and contexts, including personality traits like exploratory behaviour, aggression towards conspecifics and boldness in risky situations, are also expected to provide advantages for invading new environments (Phillips & Suarez 2012), both directly (e.g. if they facilitate encountering novel resources) and indirectly influencing the production of plastic behavioural responses (Sol et al. 2011). Moreover, if variation in behavioural types exists within a population, then this may also assist in the response to novel challenges by increasing the chances that some behaviours are suitable to deal with the novel challenges (the so-called 'skill pool effect', sensu Giraldeau 1984) and by facilitating evolutionary adjustments when there is heritable variation.

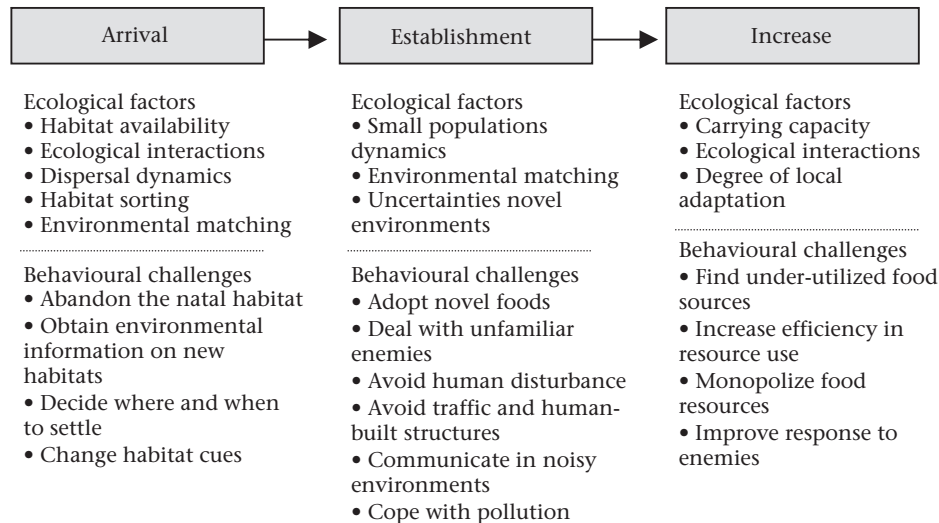
### HOW CAN BEHAVIOURAL ADJUSTMENTS INFLUENCE THE PROCESS OF BECOMING AN URBAN DWELLER?

As shown in Fig. 1, the colonization of urban environments may be described in four main ecological stages: arrival, establishment, and increase/spread (see Evans et al. 2010). The role of behaviour in geographical spread has nicely been reviewed elsewhere (Phillips & Suarez 2012), and hence we focus here on arrival, establishment and increase. In each of these stages the ecological challenges vary, and so does the role of behavioural adjustments. Consequently, we discuss each stage separately, even though we acknowledge that some behavioural responses may be influential in more than one stage.

#### Arrival Stage

For a species colonizing an urban environment, the first step is arrival. Because not all animals are able to reach and settle in urbanized environments, the arrival stage is a first filter that contributes to differences in biodiversity between urban and surrounding habitats (Ostling 2005). Indeed, the high success of many introduced species in urban habitats (Case 1996) suggests that urban communities could contain many more species if there were no arrival limitations.

Arrival is essentially a combination of two processes, dispersal and habitat selection. Both processes may lead to nonrandom arrival of individuals or species as a function of their behavioural plasticity and variation in personality types. Dispersal behaviour is generally regarded as highly plastic (Chaine & Clobert 2012), but habitat selection is often not. In general, we would expect individuals to attain higher fitness in habitats similar to their dispersal habitats, either because they are already phenotypically adapted, or because they have previous experience (habitat training; Stamps 2001). This should generally reduce the motivation to adopt different habitats,



**Figure 1.** Schematic representation of the main stages of the colonization of urban environments, with their ecological factors involved and the main behavioural challenges involved in dealing with them. Note that not all species need to pass all the stages to become an urban exploiter. For example, the dispersal stage is absent in species that thrive during the transformation of the natural habitat into an urban habitat or that are introduced by humans.

increasing niche conservatism. Because urban environments are so different from natural environments, the expectation for many species is to simply avoid settling in such habitats.

However, there are reasons to think that animals that base their lifetime in learning new things should be more likely to change their habitat than less plastic animals. First, these animals should show a higher tendency to explore and adopt novel ecological opportunities, and hence to develop generalist-opportunistic lifestyles (Klopfer 1967; Greenberg 1990). Indeed, many urban dwellers are regarded as highly opportunistic in their ecology (Møller 2009; Sol et al. 2012a). In contrast, less behaviourally plastic species should avoid novel situations, which would make them less prone to change their habitat.

Second, and related to the first point, animals with high behavioural plasticity should be less restrictive in the cues they use to choose the habitat. Although the use of environmental cues is believed to be partially genetically determined (Seppänen et al. 2011), some animals may learn to use new cues to decide where to best settle. For example, European flycatchers (*Ficedula* spp.) are able to acquire a preference for new nest site cues, an arbitrary sign situated in a nestbox (Seppänen et al. 2011), through associative learning. In some species, individuals may even use information inadvertently produced by the presence or breeding performance of individuals of other species to assess habitat quality, provided that the species share similar environmental needs (Parejo et al. 2008). This can result in increased arrival of immigrants until the costs of interspecific competition override the benefits of heterospecific attraction (Mönkkönen & Forsman 2002).

Finally, in animals with high behavioural plasticity, the trade-off between continuing to search for a high-quality habitat versus settling in a worse habitat should be lower (Stamps 2001). This is because animals that show high learning abilities tend to have a longer life span (van Schaik & Deaner 2003; González-Lagos et al. 2010; Barton & Capellini 2011). Thus, for these species, the costs of delaying or skipping a reproductive event are lower, increasing the opportunities to explore new environments. Moreover, these species are more likely to experience habitat alterations throughout their lives, increasing the likelihood that they will be forced to change their habitat.

While these lines of argument suggest that the arrival stage may sort individuals according to their behavioural plasticity, this is not necessarily true in all cases. One reason is that long-lived animals should be more risk averse when exploring, as their life history strategy relies on increasing the value of adults over the value of offspring. Thus, the final decision to settle in a new environment may be contingent on the risk perceived in the sampled environments.

The arrival stage may also sort individuals according to personality types if there is heritable variation in a population for behaviours affecting dispersal or habitat selection. Behavioural types that have been associated with dispersal and habitat selection include boldness and exploration (Marchetti & Drent 2000; Overington et al. 2011). Interestingly, individuals that arrive earlier, when the density of conspecifics is low, will tend to mate assortatively with respect to their behaviour (Phillips & Suarez 2012). This process can accentuate behavioural differences between urban and nonurban populations.

Whether the arrival stage sorts individuals according to their behavioural plasticity or particular personality types is likely to depend on the ecological factors that drive individuals to change their habitat. According to classical habitat selection models (e.g. Fretwell & Lucas 1970), there are a number of situations that may force individuals to decide to settle in a habitat different from the natal habitat. In most cases, they are related to density-dependent effects that reduce the rewards of the current habitat, either because an increase in density has raised the degree of competition for resources or because the old habitat has been altered. Natural habitats surrounding human settlements are often deteriorated and fragmented by human activities, which may increase the animals' motivation to search for alternative habitats. If having a low status in the social hierarchy increases the chances that individuals abandon their natal area, this could result in an over-representation of the most behaviourally plastic individuals among those settling in urban habitats. This is because individuals ranking low in the social hierarchy (e.g. juveniles) are often pressed to be more innovative in behaviour, an idea known as the 'necessity drives innovation' hypothesis (Laland & Reader 1999; Biondi et al. 2010; Overington et al. 2011; Morand-Ferron et al. 2011). Alternatively, being bold and aggressive could be regarded as more advantageous for voluntary dispersal (Fraser et al.

2001; Dingemanse et al. 2003; Duckworth & Badyaev 2007; Cote et al. 2010), although this can limit behavioural plasticity (Marchetti & Drent 2000). Likewise, as noted above, a generalist-opportunistic lifestyle may also facilitate a voluntary change in habitat.

#### *Establishment Stage*

The choice to settle in an urbanized environment does not guarantee the establishment of a self-sustaining population, even when individuals are able to survive and reproduce there. The probability of establishment is driven by population dynamics in the context of small populations and novel environments (Leung et al. 2012; Sol et al. 2012b).

Concerning small population dynamics, some species may fail to establish in urbanized environments because they arrive in low numbers and hence they are highly vulnerable to extinction by demographic and genetic stochasticity as well as Allee effects (Simberloff 2009). Whether and how plasticity and personality types influence small population dynamics remains controversial, however. The most obvious nexus is the classical fecundity–survival trade-off, which defines a life history continuum from ‘highly reproductive species’ (fast-lived) to ‘survivor species’ (slow-lived). As already mentioned, animals that base their lifetime in learning new things tend to be at the slow extreme of this continuum (van Schaik & Deaner 2003; González-Lagos et al. 2010; Barton & Capellini 2011). On the contrary, animals that are bold and aggressive, traits often positively associated with productivity, have been suggested to be at the fast extreme (Biro & Stamps 2008). Whether a species is fast- or slow-lived can have important consequences for the extinction in the context of small populations. A fast-lived strategy can reduce extinction by allowing the population to grow faster and hence to reduce the period during which it will be threatened by demographic stochasticity (Lewontin & Cohen 1969). However, these advantages may be in part countered by an increased risk of extinction through population fluctuations resulting from demographic stochasticity. Furthermore, the fitness costs of losing a breeding attempt tend to be higher in short-lived species, which have fewer opportunities to reproduce in the future. Thus, the importance of behavioural plasticity and personality types is contingent on the size of the founder population and the risk of reproductive failure (Sol et al. 2012b).

Concerning population dynamics in novel environments, the risk of extinction comes from the difficulty for individuals to survive and reproduce in unfamiliar contexts to which they have had no opportunity to adapt. This should generally decrease the mean fitness of the population, which can in turn lead to a negative population growth and eventually to extinction (Chamberlain et al. 2009).

As already discussed, behavioural plasticity associated with learning is considered one of the main mechanisms by which animals can avoid extinction in novel environments (see also Snell-Rood 2013), and it is thus expected to also be key for their establishment in urban environments (e.g. Møller 2009). Through plastic behaviours, animals can better track environmental variation, find new food opportunities, use hard-to-extract foods, deal more efficiently with unfamiliar enemies or change the way they communicate with conspecifics, among many other issues (Sol 2003). Indeed, evidence from reptiles (Amiel et al. 2011), birds (Sol et al. 2005) and mammals (Sol et al. 2008) suggests that animals with higher learning capacities, whether directly measured or indirectly inferred by their disproportionately larger brains, are more likely to survive in novel environments (but see Drake 2007).

Variation in personality types within populations is also expected to be important in the establishment of animals in urban habitats. On one hand, it increases the chances that the population

contains individuals with appropriate behavioural types to survive and reproduce in the new environment. On the other hand, such variation will be the raw material for natural selection to better adjust the population to the new adaptive landscape (see Dingemanse & Wolf 2013). Whether or not the species can adapt to the new environment will depend on a variety of factors, such as the strength of selection and population size. The strength of selection will vary in turn according to the degree of environmental matching between the natural and novel habitats. If selection is strong and the population is small, the risk of extinction is expected to be high and genetic variation may be insufficient in traits that are relevant to survive and reproduce in the novel environment.

#### *Increase Stage*

Once a species has established itself in an urban area, its long-term persistence and spread will depend on whether or not the population size increases. As in the case of establishment, an increase in population size also results from population dynamics. Unlike establishment, however, changes in abundance are more related to carrying capacity and ecological interactions than to dynamics in small populations and novel environments (Leung et al. 2012).

In urban habitats, some animals may reach extremely high densities. Analysing multiple populations of the same species across Europe, Møller & Ibáñez-Álamo (2012) found that population density was on average 30% higher in urban than in rural habitats, and it was as much as 100-fold higher in some species. There are at least four demographic processes that can lead to higher densities of animals in cities (Stracey & Robinson 2012): (1) increased offspring production, (2) higher adult survival, (3) higher site faithfulness and (4) higher immigration from dispersing individuals. Current evidence is insufficient to assess which of these processes (or combination of processes) is more relevant. For example, evidence in birds suggests that urban species tend to have lower productivity per nesting attempt than their nonurban counterparts (Chamberlain et al. 2009), suggesting that productivity is unlikely to explain their higher densities in cities. However, this is not necessarily true because individuals may compensate for such reduced productivity by beginning breeding earlier than nonurban birds and extending their breeding season (Johnston & Janiga 1995; Yeh & Price 2004). Regardless of differences in the underlying demographic processes, there is some agreement that subsidized food resources and reduced predation pressure may be crucial in allowing high population densities of some urban species (Anderies et al. 2007).

Plastic behavioural adjustments may potentially contribute to population increase by helping secure novel resources and avoid unfamiliar enemies. These include finding under-utilized food sources, increasing efficiency in novel resource use, facilitating coexistence with competitors and developing new responses to enemies (Sol 2003). However, if behavioural flexibility is costly, we also expect it to be lost as the population becomes further adapted to the new ecological niche. If so, we should not detect any correspondence between abundance and behavioural plasticity.

Variation in personality types may also contribute to increased species' density if the individuals that succeed in both the arrival and the establishment stage possess behaviours that allow a more efficient use or partitioning of resources and a better avoidance of enemies. Pintor et al. (2009), for example, in the context of biological invasions, suggested that an ‘aggression syndrome’ may be important to successfully confront heterospecific contest encounters and attain high densities. In fact, some of the most abundant species in urban environments are also very aggressive against other species (Sol et al. 2012a).



## EVIDENCE OF BEHAVIOURAL ADJUSTMENTS IN URBAN HABITATS

Table 1 shows examples of behavioural changes observed between urban and nonurban animals (for the full data set, see [Supplementary Table S1](#)). In the next sections, we will briefly describe current evidence for behavioural adjustments related to the most important challenges animals face in urban environments.

### Obtaining Food Resources

One of the major challenges for animals in urbanized environments is the need to acquire food supplies. Newcomers are likely to be confronted more often with novel foods than with familiar ones, so they run the risk of starvation if they are unable to adjust their behaviour to adopt new foraging opportunities. A number of studies provide evidence that urban animals often shift to using foods associated with human activities, including human refuse, artificial feeders and ornamental fruiting shrubs and trees ([Tanner et al. 2010](#)). The importance of behavioural shift is further suggested in a number of field and laboratory experiments showing that urban animals show shorter latencies to explore and adopt novel food opportunities than those from less urbanized environments ([Liker & Bókony 2009](#); [Sol et al. 2011, 2012b](#); but see [Bókony et al. 2012](#)). Although gregariousness is known to enhance the acquisition of novel foods (e.g. increasing the chances that some group members are particularly innovative or exploratory, reducing neophobic responses and the time devoted to scan for predators, and facilitating the transmission of learnt behaviours; [Kijne & Kotrschal 2002](#); [Liker & Bókony 2009](#); [Morand-Ferron & Quinn 2011](#)), very few studies report changes in social foraging behaviour in urban animals. One of the few cases is that of zenaida doves, *Zenaida aurita*, from Barbados, in which individuals that settled in the port area have shifted from aggressive territoriality to feed in large unaggressive groups with conspecifics ([Carlier & Lefebvre 1997](#)).

The use of human-derived food resources is often considered to have important population consequences. For example, there is some evidence that an increased availability of human-provided food improves blackbird, *Turdus merula*, survival during the winter ([Batten 1978](#)) and increases the density of other birds like pigeons and gulls ([Coulson et al. 1987](#); [Haag-Wackernagel 1995](#)). In Australia, field experiments suggest that the nonindigenous birds that attain higher population densities are those more likely to adopt food opportunities provided by humans ([Sol et al. 2012a](#)). In mammals, the capacity of opossums to survive in latitudes where they usually do not survive ([Kanda 2005](#)), or of black bears to decrease their hibernation period ([Beckmann & Berger 2003](#)) has also been related to a more regular temporal availability of food resources derived from human activities. A possible consequence of a more regular food provisioning is the tendency of some animals to increase sedentarism, which can further increase their densities ([Partecke 2007](#); [Evans et al. 2012](#)) and even facilitate genetic divergence ([Evans et al. 2012](#)). Behaving aggressively against other species has also been suggested to facilitate population increase by allowing monopolization of resources ([Anderies et al. 2007](#)), a possibility supported by some evidence (e.g. [Sol et al. 2012a](#)). However, we found no evidence that aggressiveness increases in urban dwellers.

### Avoiding New Predators

Predators may affect the distribution and abundance of their prey directly by increasing mortality rates, and indirectly by forcing individuals to allocate more time and energy to antipredator

behaviours. In urban habitats, species are often released from many of their main enemies, including predators and parasites ([Shochat et al. 2006](#)). Optimal foraging theory predicts that when perceived predation risk is reduced, individuals should spend less time engaged in antipredator behaviour and more time engaged in other fitness-dependent activities, such as foraging ([Lima & Dill 1990](#)). Such a beneficial change in behaviour is reported in a few studies. For example, highly urbanized fox squirrels, *Sciurus niger*, invest less time in vigilance behaviour and react less to predator vocalization than do less urbanized squirrels ([McCleery 2009](#)).

Although the diversity of predators generally decreases in urban habitats, the densities and/or activity levels of some generalist and opportunistic predators may increase ([Rodewald et al. 2011](#)). The changes in the community of predators may also elicit a number of additional behavioural changes. [Møller & Ibáñez-Álamo \(2012\)](#), for example, found that when captured by a human, birds from an urban population showed different antipredator responses than a distant, more rural population. The authors argued that the response reflects differences in the community of predators and the need to use different antipredatory responses.

### Dealing with Human Disturbance

Humans themselves are an important source of disturbance for animals. These disturbances may be ecologically important. [Burger \(1993\)](#) found that in areas of limited human activity, shorebirds devoted nearly 70% of their time to foraging and 30% of their time avoiding people or predators; however, when the population of people increased, shorebirds foraged less than 40% of the time. Thus, the frequency of human visits generally decreases the frequency of resource use by animals ([Fernández-Juricic & Sallent 2003](#)).

Some animals can behaviourally respond to direct human disturbances by changing spatial activity. [Vines \(1992\)](#) reported that, in Florida, oystercatchers, *Haematopus palliatus*, shifted their foraging and nesting activities to offshore islands in response to an increase in people on the beaches. Even a species like the house sparrow, *Passer domesticus*, which is highly dependent on human-derived food resources, tends to avoid very high human densities ([Fernández-Juricic & Sallent 2003](#)). Alternatively, some species shift their diel activity patterns to avoid humans. [Burger & Gochfeld \(1991\)](#), for example, found that sanderlings not only concentrated their foraging activities in areas with fewer people but also increased time spent foraging nocturnally. Some carnivores, like bobcats and coyotes ([Tigas et al. 2002](#)) and black bears ([Beckmann & Berger 2003](#)), are also able to change the timing of their activity in response to human presence. Marmosets, *Callithrix penicillata*, even adjust their behaviours to the day of the week in accordance to human activities ([Duarte et al. 2011](#)).

One of the most commonly reported responses of animals to human disturbance is shorter flight initiation distances (FIDs) to approaching humans. Within species, this has been reported in a variety of animals, mostly birds and mammals (see [Supplementary Table S1](#)). In common blackbirds, for example, individuals from parks with higher pedestrian rates show lower FIDs than individuals from parks with lower pedestrian rates ([Rodríguez-Prieto et al. 2009](#)).

Human presence is not always perceived as a threat by animals, however, and learning who is and who is not a threat may be beneficial. In many cities, for example, pigeons rely to a great extent on food provided by people, which has favoured their overpopulation ([Haag-Wackernagel 1995](#)). Experiments have revealed that individuals can learn to recognize those humans that provide food on a regular basis ([Belguermi et al. 2011](#)).

**Table 1**

Examples of studies reporting behavioural differences between urban and nonurban animals, tentatively organized by invasion stage

Ecological challenges	Taxa	Approach	Type of comparison	Findings	Source
<b>Arrival</b>	b	FE	ws	European flycatchers, <i>Ficedula hypoleuca</i> , learned to acquire a preference for arbitrary nest site cues of a human-made structure (nestbox) for nesting	Seppänen et al. 2011
	b	FE	ws	Highly aggressive male western bluebirds, <i>Sialia mexicana</i> , were more likely to displace mountain bluebirds, <i>Sialia currucoides</i> , from nestboxes, allowing them to increase their density	Duckworth & Badyaev 2007
<b>Establishment</b> Obtaining food resources	b	LE	bp	Urban common mynas, <i>Acridotheres tristis</i> , were less neophobic, more exploratory and more likely to innovate and learn a technical foraging task than were suburban mynas, but they did not differ in their latency to adopt novel foods	Sol et al. 2011
	b	LE	bs/ws	Group-feeding zenaida doves, <i>Zenaida aurita</i> , learned a foraging task slightly faster than did territorial doves	Seferta et al. 2001
	b	FD/FE	bp	Urban birds tended to show lower latencies to respond to a novel food opportunity than did suburban and wildland birds	Sol et al. 2012b
	m	FD/M	ws	Foraging innovation by taking profit from human resources allowed opossums, <i>Didelphis virginiana</i> , to live in much colder urban areas than predicted by models	Kanda 2005
	m	FD	ws	Smaller home range sizes for urban badgers, <i>Meles meles</i> , was related to the high productivity of gardens and backyards	Davison et al. 2009
Avoiding new predators	m	FE	ws	More urbanized fox squirrels, <i>Sciurus niger</i> , invested less time in vigilance behaviour and reacted less to predator vocalization	Mccleery 2009
Dealing with direct human disturbances	b	C	bs	FIDs of birds increased from urban to rural sites, with distances being shortest in places where human residents encouraged birds with food supplies	Clucas & Marzluff 2012
	b	FD/FE	ws	Urban dark-eyed juncos, <i>Junco hyemalis</i> , had shorter FIDs than did wild conspecifics	Atwell et al. 2012
	b	FE	ws	Feral pigeons, <i>Columba livia</i> , were able to recognize individual human faces and learned to use this information to modify their foraging behaviour in urban areas	Belguermi et al. 2011
	b	FE	ws	Northern mockingbirds, <i>Mimus polyglotta</i> , distinguished individual humans that posed a threat to their nests from humans that had not previously behaved in a threatening way	Levey et al. 2009
	b	FD	ws	White-fronted plovers, <i>Charadrius marginatus</i> , breeding in more human-visited beaches returned to incubate faster after human-derived disturbances	Baudains & Lloyd 2007
Avoiding traffic and human-built structures	m	FD	ws	Urban red foxes, <i>Vulpes vulpes</i> , modified their ranging activity based on traffic intensity	Baker et al. 2007
	m	FD	ws	Urban Eurasian hedgehogs, <i>Erinaceus europaeus</i> , avoided actively foraging near roads with high human traffic	Dowding et al. 2010
Communicating in noisy environments	b	FE	ws	Great tits, <i>Parus major</i> , used more higher-frequency singing types when environmental noise was experimentally manipulated	Halfwerk & Slabbekoorn 2009
	b	FD	ws	Urban noisy miners, <i>Manorina melanoccephala</i> , showed a noise-level-dependent change in sound signal amplitude to avoid alarm call masking	Lowry et al. 2012
	b	FD	bp	Urban ash-throated flycatcher, <i>Myiarchus cinerascens</i> , increased singing frequency in noisy areas, but range occupancy did not change	Francis et al. 2011
	b	FD	ws	Urban serins, <i>Serinus serinus</i> , changed their singing behaviour as a function of noise levels	Díaz et al. 2011
	b	FD	ws	Black-capped chickadees, <i>Poecile atricapillus</i> , used shorter, higher-frequency songs when traffic noise was high, and longer, lower-frequency songs when noise abated	Proppe et al. 2011
	m	FE	ws	In male humpbacks, <i>Megaptera novaeangliae</i> , mating song duration was longer during exposure to man-made noise (i.e. low-frequency active sonar) but returned to normal following exposure	Miller et al. 2000
	m	FE	ws	Urban eastern grey squirrels, <i>Sciurus carolinensis</i> , shifted to rely more on visual antipredator signals in noisy environments	Partan et al. 2010
Avoiding habitat fragmentation	m	FD	ws	Racoons, <i>Procyon lotor</i> , had smaller ranges and less seasonal changes in their ranging behaviour in urban and suburban areas compared with rural areas, as a consequence of high and regular food availability	Prange et al. 2004
<b>Increase</b> Efficiency in resource use	ar	LE	bs	Introduced red-eared sliders, <i>Trachemys scripta</i> , hid less from simulated predation than did native Spanish pond turtles, <i>Mauremys leprosa</i> , contributing to their greater competitive ability in disturbed environments	Polo-Cavia et al. 2008
	b	LE	ws	Urban house sparrows, <i>Passer domesticus</i> , showed constant feeding motivation irrespective of predation risk	Tsurim et al. 2010

Table 1 (continued)

Ecological challenges	Taxa	Approach	Type of comparison	Findings	Source
	b	FE	ws	Urban house finches, <i>Carpodacus mexicanus</i> , increased foraging efficiency in response to reduced foraging time resulting from human disturbance	Valcarcel & Fernández-Juric 2009
	b	FE	ws	Fast explorers and noninnovative individual great tits had significantly more access to artificial food supplies than did slow explorers and solvers	Cole & Quinn 2012
	b	FD/FE	bs	Species that were more opportunistic foragers tended to show higher densities in urban habitats	Sol et al. 2012b
	b	FD	bs	An increase in black vultures, <i>Coragyps atratus</i> , partially driven by learning to take profit from human-derived resources, hindered population growth of other species through interspecific competition	Carrete et al. 2010

b: birds; m: mammals, ar: amphibians and reptiles; FE: field experiment; FD: field data; LE: lab experiment; C: comparative; M: model; bs: between species; ws: within species; bp: between populations; FID: flight initiation distance.

### Avoiding Traffic and Human-built Structures

The proliferation of cars, electric lines, buildings and windows might make urban areas unsuitable for some species. The most obvious effect is on mortality rates. In Toronto, over 30 000 lethal collisions of birds have been recorded for only 20 buildings, according to the Fatal Light Awareness Program (<http://www.flap.org>). Reproductive activity can also be altered. For example, grassland birds breeding at airports have high rates of nest failure caused by mowing (Kershner & Bollinger 1996). In urban habitats, most evidence of behavioural adjustments associated with such disturbances relate to shifts in hours of daily activity. For example, red foxes, *Vulpes vulpes*, cross streets less in the early hours of the night presumably because of the increased traffic (Baker et al. 2007).

Species that are able to adopt human-made structures to reproduce may be more likely to settle, persist and increase in urban habitats. Møller (2010), for example, found that, in species inhabiting urban environment, those with the ability to breed in human-made structures showed a significant decrease in nesting failure due to predation, compared to species breeding outdoors. Finding appropriate places to reproduce may be problematic for many species, however. Kriska et al. (1998), for example, showed that some types of asphalt polarize light horizontally and as a result are much more attractive to mayflies than the surface of a pond or stream. Thus, mayflies end up laying their eggs on an inappropriate substrate where they are unable to hatch successfully. Such ecological traps may have important negative effects on population dynamics (Dwernychuk & Boag 1972; Robertson & Hutto 2006). However, some species are able to change some components of their breeding behaviour. Urban American crows, *Corvus brachyrhynchos*, for example, have been reported to be less aggressive at nest defence than rural individuals (Knight et al. 1987).

### Communicating in Noisy Environments

Anthropogenic noise may have negative effects on acoustic communication because it interferes with animals' acoustic signals, limiting the distance at which individuals may efficiently communicate with each other (Miller et al. 2000; Slabbekoorn & den Boer-Visser 2006; Halfwerk et al. 2011). Some animals, notably birds, whales and insects, use acoustic signals to attract mates, defend territories, recognize species and advertise dangers (Catchpole & Slater 2008). Thus, anthropogenic noise may have important fitness effects for these species (Catchpole & Slater 2008).

As a way to avoid the masking of songs in noisy conditions, birds can change their acoustic signals, for example by using signals with

higher frequencies (Slabbekoorn & den Boer-Visser 2006; Halfwerk et al. 2011; see also Slabbekoorn 2013) and/or longer duration (Miller et al. 2000). An increased number of studies report differences in song frequency between urban and nonurban birds (Table 1). Such adjustments in song features are likely to be beneficial, although current evidence is admittedly limited (Nemeth et al. 2012). And even when the response is beneficial, it may not be sufficient. In a study in reed-buntings, *Emberiza schoeniclus*, acoustic adjustments did not prevent more males from remaining unpaired at a noisy location than at a quiet location throughout the breeding season (Gross et al. 2010).

### Dealing with Light Pollution

Increased artificial lighting is another anthropogenic factor that may alter activity patterns of animals. Some of the examples in the literature describe the detrimental consequences of being inflexible in behaviour. Witherington (1997), for example, reported that sea turtle hatchlings, which normally rely on light cues from the open horizon to orient after emerging, may migrate inland instead of towards the ocean due to light pollution from beachfront structures. However, the effects for the species may sometimes be positive. Perhaps the most obvious beneficial changes in behaviour associated with artificial lighting are those described in bats and birds that have learned to improve performance in prey capture by feeding on insects attracted to artificial lights. Likewise, light allows some diurnal birds like gulls and pigeons to forage during the night, thus extending the period available to meet their daily food requirements. Another common alteration is dawn singing in birds, which occurs earlier in birds close to artificial lightning (Miller 2006; Kempnaers et al. 2010). In blue tits, *Cyanistes caeruleus*, singing earlier has been shown to increase reproductive rates and opportunities for extrapair copulations for males because singing earlier is a sign of male quality (Kempnaers et al. 2010).

### Avoiding Habitat Fragmentation

Habitat fragmentation is a usual outcome of the urbanization process, affecting both the temporal and spatial patterns of habitat use in animals (Tigas et al. 2002). As a response to fragmentation, it has been suggested that individuals may expand their home ranges to include several fragments that together provide adequate resources (Redpath 1995). However, the opposite pattern seems to be more common in urban animals, including raccoons, *Procyon lotor*, coyotes, *Canis latrans*, Florida Key deer, *Odocoileus virginianus clavium*, and Eurasian badgers, *Meles meles* (Supplementary Table S1). This pattern may occur because some urban habitats may have increased resource abundances such that individuals can

meet their energetic requirements in smaller areas. In Eurasian badgers, for example, smaller home ranges are associated with the high productivity of gardens and backyards (Davison et al. 2009).

### CAUSES OF BEHAVIOURAL ADJUSTMENTS

For most behavioural adjustments we found in the literature (see [Supplementary Table S1](#)), there is no unequivocal evidence to conclude whether they reflect plasticity, a sorting process, or an evolutionary response. To distinguish between the different proposed mechanisms we would ideally need to estimate the genetic and environmental components of the behaviour and its fitness value in urban and nonurban habitats. However, even if such information was available, it would be insufficient unless those measurements were conducted during the early stage of the colonization of urban habitats. All of these pieces of evidence are difficult to obtain in practice.

Despite these limitations, there are three lines of evidence suggesting that some of the observed behavioural adjustments reflect phenotypic plasticity. The first is the rapidness with which some of the behavioural changes occur. Adjusting the communication system to current noise levels is a clear example. In male humpbacks, *Megaptera novaeangliae*, mating songs were longer when exposed to man-made noise (i.e. low-frequency active sonar) but returned to normal duration after exposure (Miller et al. 2000). Some birds also change song activity as a function of different noise levels (e.g. Díaz et al. 2011; Francis et al. 2011). Interestingly, there are notable differences in song plasticity between species, and this may have important consequences. Grey flycatchers, *Empidonax wrightii*, for example, do not adjust their vocal frequency in response to noise, but instead avoid highly noisy places. In contrast, habitat occupancy of the ash-throated flycatcher, *Myiarchus cinerascens*, seems to be unaffected by noise, but individuals in areas with greater noise amplitudes vocalize at a higher frequency when noise levels are high (Francis et al. 2011). Other examples of behaviours that show plasticity include FID (Rodríguez-Prieto et al. 2009) and the latency to adopt novel foods (Sol et al. 2012a).

The second line of evidence is that some of the reported behavioural adjustments are known to involve innovation and/or learning, like for example, using novel food opportunities (Bouchard et al. 2007) or responding to human threats (Lee et al. 2011). Eurasian magpies, *Pica pica*, for example, reduce their aggressive response towards individual humans that do not pose a threat to their nests (Lee et al. 2011). This is facilitated by the ability of magpies to recognize human individual features (Belguermi et al. 2011), an ability also known in some other urban exploiters like northern mockingbirds, *Mimus polyglottos* (Levey et al. 2009), and feral pigeons, *Columba livia* (Belguermi et al. 2011). Indeed, there are a number of experiments in birds suggesting enhanced learning propensity in urban birds compared to nonurban birds (Carlier & Lefebvre 1997; Seferta et al. 2001; Sol et al. 2011; Liker & Bókonyi 2009). Lefebvre and coworkers, for example, found that urban zenaida doves were less neophobic and faster at learning a foraging task than less urbanized doves and, in line with their social foraging experience, learned more readily from conspecifics than from heterospecific demonstrators (Carlier & Lefebvre 1997; Seferta et al. 2001). More general evidence comes from comparative analysis reporting that urban-dwelling birds tend to have larger brains and are more innovative in feeding behaviour than nonurban dwellers (Møller 2009; Carrete & Tella 2011; Maklakov et al. 2011). However, it is worth noting that neither Kark et al. (2007) nor Evans et al. (2011) found evidence that innovation propensity and brain size influence species responses to urban environments.

The last line of evidence for behavioural plasticity is a recent meta-analysis by Hendry et al. (2008), which suggests that much of

the phenotypic changes observed in anthropogenic contexts (mostly involving human-aided range expansions) may be partly the result of phenotypic plasticity. This conclusion is based on the finding that the difference in phenotypic change between anthropogenic and natural contexts was greater when evaluated using wild-caught individuals than when using common garden or quantitative genetic methods. Although this may reflect that common garden environments lack the stresses needed to release important genetic variation, Hendry et al. (2008) argued that the observed pattern is easier to interpret if the greater environmental challenges associated with anthropogenic change are more easily dealt with via plasticity than with genetic change.

Compared with behavioural plasticity, the possibility that behavioural differences between urban and nonurban animals reflect a sorting process has received less attention. The only evidence we found is the finding of Carrete & Tella (2011) that in a recently built South American city, the degree of urbanization was not significantly related to species' average rural FIDs but to inter-individual variability in FID. This opens the possibility that urban invaders are not individuals from apparently tame species, but rather tame individuals from species with a variable response regarding fear of people (Carrete & Tella 2011). The importance of assortative mating in shaping behavioural differences between urban and nonurban animals has not been investigated, but Cardoso & Atwell (2011) found evidence that behavioural differences may be accentuated by cultural transmission. These authors estimated that the input of cultural transmission in an urban songbird population explained about half the extent of the population divergence in song frequency.

As in the case of the sorting process, the importance of evolutionary divergence to explain behavioural differences between urban and nonurban animals has not been studied in detail. Evolutionary responses to human disturbances have been reported in some studies, yet few of the studied traits were behaviours (Hendry et al. 2006). Moreover, studies examining genetic differentiation with neutral markers do not generally support the existence of evolutionary divergence between urban and nonurban animals (Partecke et al. 2006; Partecke 2007; Potvin et al. 2013). A few studies in birds provide evidence that behavioural differences between urban and nonurban individuals reflect genetic differences (Partecke & Gwinner 2007), but this does not necessarily imply natural selection; it could merely reflect a sorting process for behavioural types. The most serious attempt to identify selection as a cause of behavioural differences is the classic study of Yeh & Price (2004) showing that dark-eyed juncos, *Junco hyemalis*, extended their breeding season following their colonization of a novel urban environment in San Diego, an increase in reproductive effort that contributed substantially to the persistence of the population. A selection analysis revealed that selection was mostly operating on a nonheritable component, and hence that the extension of the breeding season reflected behavioural plasticity rather than evolutionary divergence. In a more recent common garden experiment, however, Atwell et al. (2012) did report evidence of rapid adaptive shifts in both stress physiology and correlated boldness behaviours in San Diego's dark-eyed juncos. Thus, evolutionary responses can also be a factor behind the differences in behaviour observed between urban and nonurban animals, although current evidence is insufficient to assess its real importance.

### SYNTHESIS AND FUTURE PROSPECTS

Our literature review indicates that behavioural adjustments are common in animals living in cities, and that these adjustments may have contributed to their success in such environments (see also reviews lead by Mason et al. 2013). While the fitness benefits



of these behavioural adjustments have rarely been quantified, there is evidence that not adjusting behaviour to the new environmental demands may have important detrimental consequences.

However, our review is not exempt of biases (see also Evans et al. 2010). On one hand, most studies involve birds and mammals, which arguably contain some of the most behaviorally flexible species. Studies of behavioural changes have probably been mostly focused on these groups because theory predicts that learning is favoured in species or clades that are long-lived, live in coarse-grained environments and have complex social structures (Whitman & Agrawal 2009). On the other hand, there is a dominance of research on northern temperate regions, where the urbanization process is older and more extensive.

Bearing these limitations in mind, we find that the most consistent changes in behaviour are related to the use of new foraging opportunities, enhanced communication and reduction of fear to humans. Some of these changes occur very rapidly and/or involve learning, and hence can be attributed to behavioural plasticity. While some of the most elaborate plastic behaviours have been observed in urbanized environment (L. Lefebvre, unpublished data), most do not seem to require highly sophisticated cognitive skills (e.g. Sol et al. 2011). Indeed, many just involve modulations of pre-existing behaviours, such as altering activity patterns or adjusting FID. This may indicate that the challenges posed by urban habitats do not require substantial changes in behaviour. However, the fact that some studies report a link between brain size and the use of urban habitats suggests that, at least for some organisms, cognitive limitations may partially explain the varying success of species in these habitats. Moreover, although different behaviours appear to be useful at different stages of the invasion of urban habitats (see Table 1), a general ability to develop plastic behaviours in a variety of contexts may potentially assist in all the stages.

Although there is an emergent interest in linking behaviour to the urbanization process, as indicated by the fact that most publications we found were published in the last 5 years, a number of issues remain insufficiently resolved. Below, we propose several avenues for future research.

First, very few studies directly address the underlying causes of behavioural differences between urban and nonurban animals. We need detailed studies where the effects of selection, plasticity and sorting may be disentangled (e.g. Yeh & Price 2004). Especially informative would be the study of animals from less human-altered, biodiverse regions that are still in the early stages of becoming urban dwellers.

Second, the importance of neophobic responses and exploration in the production of plastic behaviours points to the need to study behavioural adjustments as part of a behavioural syndrome (Sih et al. 2004; Sih & Del Giudice 2012). To date, the search for behavioural syndromes of urban species has yielded no consistent patterns (Bókonyi et al. 2012). Although this may reflect that there is not a unique way to be an urban dweller (Sol et al. 2012a), whether different syndromes assist animals in different stages of the invasion of urban habitats requires further attention.

Third, studies that investigate the population consequences of behavioural adjustments in urban environments are scarce. For example, the mechanisms that make a species select or avoid urban habitats have rarely been investigated. Likewise, few studies have addressed the fitness consequences of adjusting behaviours to urbanized environment. Consequently, in most cases we ignore whether the behavioural responses to urban environments have had any population impact.

Fourth, the importance of evolutionary responses in the process of becoming an urban dweller remains unclear. Although behavioural plasticity can facilitate population persistence, high levels of plasticity

may also reduce the likelihood of genetic change because the plastic response itself places the population close to the novel adaptive peak (Price et al. 2003). Evolution may in turn affect the degree of behavioural flexibility. A loss of behavioural flexibility may be a usual outcome for populations that are well adjusted to their environment, like that reported in house sparrows introduced in America (Martin & Fitzgerald 2005). However, because the urban environment continuously exposes individuals to new challenges, it is possible that populations never become well adapted to urban environments and always require some degree of behavioural flexibility.

Finally, future work should evaluate whether the behavioural responses of animals to urbanization are relevant to understanding their response to other forms of HIREC. Understanding this is important because environmental alterations associated with urbanization, habitat loss, climate change and biological invasions often act in concert, and hence whether the responses are similar or different may have great consequences for the future of many organisms. Concerning climate change, for example, it is expected that the effect of extreme weather events on winter mortality is lower if animals rely on human-supplemental food (Zuckerberg et al. 2011). The field of biological invasions may also benefit from a better understanding of how organisms adjust their behaviour to survive and reproduce in urbanized environments. Because many nonindigenous species reach their highest success in human-disturbed habitats, we would expect that tolerance to urbanization is a good predictor to forecast the success of future biological invasions. To date, however, there is little evidence that urban dwellers are better invaders than nonurban dwellers.

Given that the impact of urbanization on biodiversity loss and alteration is expected to increase further in the near future, and because there is a renewed interest in the role of behavioural flexibility in response to HIREC, we anticipate that all the above issues will represent important avenues of future research.

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## Supplementary Material

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