

Behavioural responses of wildlife to urban environments

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ABSTRACT

Increased urbanization represents a formidable challenge for wildlife. Nevertheless, a few species appear to thrive in the evolutionarily novel environment created by cities, demonstrating the remarkable adaptability of some animals. We argue that individuals that can adjust their behaviours to the new selection pressures presented by cities should have greater success in urban habitats. Accordingly, urban wildlife often exhibit behaviours that differ from those of their rural counterparts, from changes to food and den preferences to adjustments in the structure of their signals. Research suggests that behavioural flexibility (or phenotypic plasticity) may be an important characteristic for succeeding in urban environments. Moreover, some individuals or species might possess behavioural traits (a particular temperament) that are inherently well suited to occupying urban habitats, such as a high level of disturbance tolerance. This suggests that members of species that are less ‘plastic’ or naturally timid in temperament are likely to be disadvantaged in high-disturbance environments and consequently may be precluded from colonizing cities and towns.

Key words: behavioural modification, urban environment, urban adapter, phenotypic plasticity, genetic adaptation, temperament, human disturbance, vocal adjustments.

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I. INTRODUCTION

As the world becomes more urbanized, artificial infrastructure increasingly replaces natural habitats (Hamer & McDonnell, 2010). Wildlife must either adjust to these

human-modified landscapes, or be excluded from urban environments. Currently, urbanization is occurring globally at an unprecedented rate, with predictions that, by 2030, approximately 60% of the world’s human population will be living in urbanized landscapes (United Nations Population

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Fund, 2007). This novel environment presents wildlife with novel challenges, in particular, a loss of natural resources (e.g. habitat and food) and elevated anthropogenic disturbance levels (e.g. pedestrian traffic, vehicular traffic and industrial noise) (Reijnen, Foppen & Veenbas, 1997; Fernández-Juricic & Telleria, 2000). It is well documented that urbanization leads to an overall loss of biodiversity (so called 'biotic homogenisation' *sensu* McKinney & Lockwood, 1999; McKinney, 2006). Numerous species, however, seem to prosper in urban environments and occur in high numbers. Such animals are often described as urban 'adapters' or 'exploiters' (McKinney, 2006). To date, research in urban ecology has tended to focus on resource-based limitations on wildlife inhabiting urban environments (Munyenembe, Harris & Hone, 1989; Lim & Sodhi, 2004; French, Major & Hely, 2005; Gardener *et al.*, 2006). A key question for biologists is what facilitates the success of some species in cities – but the exclusion of others – when resources are not a limiting factor.

There is now a growing body of scientific evidence describing behavioural modifications in urban wildlife, with urban-based animals often demonstrating behaviours that differ from those of their rural counterparts (Cooke, 1980; Traut & Hostetler, 2003; Donaldson, Henein & Runtz, 2007; Evans, Boudreau & Hyman, 2010; Kitchen, Lill & Price, 2010). The ability of an animal to adjust to novel challenges (i.e. human-subsidized resources and anthropogenic disturbance) is likely to be important to its ultimate success in urban environments. Several studies, in particular, have demonstrated behavioural flexibility (or phenotypic plasticity) within urban-adapter species (Lefebvre, 1995; Seferta *et al.*, 2001; Webster & Lefebvre, 2001; Slabbekoorn & Peet, 2003; Slabbekoorn & den Boer-Visser, 2006; Bouchard, Goodyer & Lefebvre, 2007; Levey *et al.*, 2009). There is also some suggestion that genetic differences may be involved in the changed behaviours observed in urban populations (Partecke, Van't Hof & Gwinner, 2004, 2005). More recently, behavioural research has begun to recognize that vertebrates show individual differences in behaviour or temperament, which may have a genetic basis (Bolnick *et al.*, 2003). Thus, some animals might inherently be better suited to urban environments in the first instance (i.e. because they have a 'bold' temperament).

This review comprises three parts. We begin by providing a conceptual framework for understanding the successful colonization of urban environments by wildlife, namely the relative roles of phenotypic plasticity and genetic adaptation, and the role of temperament in facilitating colonization. Next, we review the different ways in which wildlife behaviour is modified in response to different urban stressors and what, in turn, might drive the observed changes. We review how the behaviour of wildlife is modified in response to urban conditions, particularly with respect to reproduction, foraging, and the use of shelter. Finally, we evaluate how some species are able to alter their behaviour(s) to withstand high disturbance levels in urban landscapes.

II. POTENTIAL MECHANISMS INVOLVED IN BEHAVIOURAL ADJUSTMENTS TO URBAN ENVIRONMENTS

(1) Behavioural modification

Urban environments are novel in that they usually present wildlife with selection pressures that are drastically different to those under which they have evolved. Selective pressures ultimately affect an animal's survival, reproduction and fitness (Ibanez-Alamo & Soler, 2010). Accordingly, individuals that can adjust to these new selection pressures should have greater success in urban habitats. These changes can lead to behavioural shifts (or modifications) over time. This has been demonstrated in comparisons of various behavioural traits between urban and rural conspecifics (Cooke, 1980; Traut & Hostetler, 2003). For example, some wildlife demonstrate modifications to common behaviours in urban environments, such as changes to the timing and duration of breeding and altered foraging patterns and diet in response to year-round food resources. Another characteristic of cities is high disturbance levels that can secondarily affect fitness-related traits. For instance, an animal might modify its vigilance or adjust its vocalizations in response to frequent disturbance in urban habitats, thus potentially affecting foraging and breeding behaviours. These modifications can be adaptive or maladaptive depending on how they affect that individual's long-term fitness.

Sometimes the behaviours identified in urban individuals are innovative in that the behaviour is being observed or recorded for the first time (Kark *et al.*, 2007). More innovative species demonstrate greater learning and problem-solving skills in novel conditions. Innovative behaviours are commonly used as a measure of behavioural flexibility and, hence, urban wildlife is at times described as being behaviourally flexible (or phenotypically plastic) (Slabbekoorn & Peet, 2003; Martin & Fitzgerald, 2005; Levey *et al.*, 2009). However, whilst there is a substantial body of research identifying behavioural modifications in urban wildlife, whether the observed behaviours are inherently plastic in nature or the product of genetic adaptations is often unknown.

(2) Phenotypic plasticity versus genetic adaptation

Animals are known to vary in their capacity to respond in a phenotypically plastic manner. Phenotypic plasticity describes the tendency of a particular genotype to produce different phenotypes under altered environmental conditions and is relatively common in nature (Thibert-Plante & Hendry, 2011). It allows an animal proximally to adjust its morphology and/or behaviour to suit best the conditions of its immediate environment and thus potentially increase its fitness (Thibert-Plante & Hendry, 2011; Van Buskirk, 2012). Accordingly, a lack of phenotypic plasticity has been postulated as contributing to the exclusion of species from altered environments (Badyaev, 2005). Extreme environments, such as those in cities, have been shown to increase

phenotypic variance, and numerous studies have demonstrated altered behaviours in urban wildlife as individuals respond and adjust to new conditions (Estes & Mannan, 2003; Prange, Gehrt & Wiggers, 2004; Dowding *et al.*, 2010). For instance, several studies have reported modifications to birdsong in urban areas (Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006; Nemeth & Brumm, 2009). In this regard, communicating in urban environments might involve either selection of individuals with specific genotypes within the overall population or exploitation of existing phenotypic potential (Hunter, 2007). Currently, however, there are no studies demonstrating genetic adaptation in the vocalizations of urban birds.

Indeed, convincing evidence of genetic adaptation to urbanization is still relatively rare. In European blackbirds, *Turdus merula*, genetic adaptation has been found in the stress physiology of birds living in urban environments. Specifically, hand-reared, city-born birds showed a lower acute (short-term) corticosterone stress response compared to forest-born birds, although early developmental effects could not be entirely ruled out (Partecke, Schwabl & Gwinner, 2006b). Conversely, research on an urban and a nearby rural population of blackbirds found no evidence of genetic differentiation among adult birds, but disparities in breeding density, daytime activity and migratory behaviour suggest that urban individuals displayed greater phenotypic plasticity (Partecke, Gwinner & Bensch, 2006a). Differences in the timing of reproductive development in urban and rural blackbirds indicated that both genetic and phenotypic changes had occurred in an urban population (Partecke *et al.*, 2004). More recently, Møller (2008) found that disparities in disturbance tolerance (measured as relative flight distance in response to an approaching human) of urban populations of successful urban-adapter bird species were predicted by the estimated number of generations since urbanization. This suggested that genetic adaptation had occurred in these populations.

Whether modified behaviour(s) in urban individuals ultimately leads to genetic divergence between urban and rural populations is dependent on whether dispersal continues between these two populations. Changes to sexual traits and timing of reproductive development enhance the likelihood of genetic divergence by facilitating reproductive isolation between populations (Slabbekoorn & Ripmeester, 2007). Further research is required to determine the extent of genetic adaptation in urban wildlife populations.

(3) The role of temperament

Research suggests that some animals demonstrate consistent individual differences in behaviours (or personality traits), such as boldness, reactivity, exploration, sociality and avoidance of novelty (Dall, 2004; Reale *et al.*, 2007; Stamps, 2007). Accordingly, individuals within a single population may vary in the way they respond to similar situations. These individual differences are referred to as an animal's

temperament, which describes behavioural differences that are consistent over time and across situations (Reale *et al.*, 2007). Such differences are commonly expressed across a wide range of contexts. For example, an individual that is bold may demonstrate bold behaviour in foraging, mating and predation (Dingemanse & Reale, 2005). An animal's temperament can have a direct bearing on how it responds to novel, high-risk or challenging situations and thus temperament has been linked to an individual's ultimate fitness (Reale *et al.*, 2007).

In contrast to behavioural flexibility, which is touted as a major source of phenotypic variation in behaviour, temperament suggests that animals sometimes show limited flexibility in behaviour (Dingemanse & Reale, 2005). Although limited behavioural plasticity would appear to put an individual at a disadvantage to those that are behaviourally flexible, certain circumstances might favour particular temperaments. Therefore, some types of temperament might be naturally suited to certain environments. For instance, an animal with a bold temperament might be predisposed to inhabit high-disturbance urban environments. Accordingly, it has been proposed that temperament is most strongly expressed under extreme conditions (Reale *et al.*, 2007).

(4) Boldness and urban life

Several studies have demonstrated a link between boldness and dispersal. A study of fish comparing behavioural traits of invasive and non-invasive *Gambusia* spp. found that the latter were bolder (took more risks) and exhibited greater dispersal tendencies than their non-invading relatives (Rehage & Sih, 2004). Similar results have been demonstrated in great tits, *Parus major*, and Trinidad killifishes, *Rivulus hartii*, in which bolder (or faster/more explorative) individuals were found to disperse further than their more timid (or slower) counterparts (Fraser *et al.*, 2001; Dingemanse *et al.*, 2003). Boldness reflects the manner in which an individual/population responds to threatening situations: the boldest individuals being willing to take the most risks. Accordingly, for members of a species to disperse into, and thrive in urban environments, one could infer that they would need to have a relatively high disturbance tolerance (i.e. be of bold temperament).

From the limited research investigating temperament in urban wildlife, there is some suggestion that urban individuals show contrasting traits to those of their rural counterparts. A recent study investigating behavioural traits in urban and rural populations of male song sparrows, *Melospiza melodia*, showed that urban birds were bolder and more territorial than rural birds (Evans *et al.*, 2010). Similar results were found for urban noisy miners, *Manorina melanoptera*, in response to a sound stimulus (loud noise) (Lowry, Lill & Wong, 2011). At present, we can only speculate that boldness may predispose an animal to successfully inhabiting urban environments, a hypothesis that warrants further investigation.

III. BEHAVIOURAL RESPONSES TO ALTERED ENVIRONMENTAL CONDITIONS

(1) Reproduction

Increased year-round food resources attributable to urban plantings, food supplementation (i.e. feeding of wildlife by humans), landfill waste, and artificial watering (or drought-proofing) have all facilitated an extended period of suitable breeding conditions in urban environments. Consequently, changes to the onset and duration of breeding seasons have been observed in numerous animals occupying urban habitats. Changes to breeding behaviours are of particular importance when assessing the viability of wildlife populations in urban environments, successful reproduction being fundamental to an individual's ultimate, long-term success.

Several studies comparing urban and rural populations of avian urban adapters have found that urban individuals may commence breeding earlier, and breed for a longer period, than their rural counterparts. An urban study of silver gulls, *Larus novaehollandiae*, for example, showed that length of the breeding season was positively associated with an increase in the number of humans in the area (Smith & Carlile, 1992). Research on white-winged choughs, *Corcorax melanorhamphos*, also found that urban individuals initiated breeding a month earlier than rural birds (Beck & Heinsohn, 2006). However, the extended breeding period did not necessarily lead to greater productivity in urban individuals. On the whole, silver gulls had low nesting success and fledging rates in cities (Smith & Carlile, 1992), whilst urban white-winged choughs had a poorer reproductive output than rural conspecifics (Beck & Heinsohn, 2006). Reduced success rates were attributed to increased nest predation in urban environments, which counteracted any advantage potentially gained from a longer breeding season (Beck & Heinsohn, 2006). Poorer fledgling success has also been described for urban carrion crows, *Corvus corone corone*, although, in this instance, no significant differences in the timing of breeding were demonstrated between urban and rural birds (Richner, 1989). Urban crows also showed slower growth rates and were significantly lighter at fledging than their rural counterparts (Richner, 1989).

It is unclear to what extent changes in the timing and duration of breeding in urban individuals are a result of genetic differences or phenotypic plasticity. A study comparing reproductive timing and its underlying endocrine control in an urban and rural population of European blackbirds found that urban birds initiated breeding earlier and had a prolonged breeding season. This resulted from an earlier onset of seasonal gonadal growth in males. The authors attributed earlier gonadal recrudescence to changed environmental conditions (i.e. increased food resources and artificial lighting) and social interactions in urban environments (Partecke *et al.*, 2005). Further research on these populations under laboratory conditions showed that the observed differences in reproductive timing did not continue in captivity, indicating that the changed breeding

behaviour in urban individuals was phenotypic (Partecke *et al.*, 2004). Conversely, the same study found differences in plasma luteinizing hormone concentrations in these birds, suggesting that genetic differences might be involved (Partecke *et al.*, 2004). Irrespective of whether observed differences in reproduction in urban birds are genetically or phenotypically driven, differences in the onset of breeding between urban and rural populations could effectively lead to genetic differentiation between populations through reduced integration over time.

(2) Foraging

Urban habitats contrast with more natural habitats in ways that have direct effects on behaviours associated with foraging. Disturbance-related variables, such as pedestrian and vehicular traffic, can negatively affect the foraging efficiency of animals in urban environments. Conversely, greater food availability can buffer urban animals against the seasonal fluctuations in resource availability experienced in natural environments. Nonetheless, disparities in diurnal foraging movements, juvenile feeding patterns and diet have been observed between urban and rural conspecifics of several urban adapter species (Smith & Carlile, 1993; Tigas, Van Vuren & Sauvajot, 2002; Estes & Mannan, 2003; Ross, 2004).

For terrestrial mammals, movement and activity associated with foraging can be a high-risk activity in urban environments (e.g. through collision with vehicles). One way that urban mammals can deal with this is by altering their foraging patterns so that they avoid periods of elevated human activity (i.e. peak pedestrian and vehicular traffic periods). This has been demonstrated, for example, in urban populations of European hedgehogs, *Erinaceus europaeus*. Specifically, individuals changed their nocturnal foraging movements so that they avoided roads and were more active after midnight when human and vehicular traffic were reduced (Dowding *et al.*, 2010). Similar temporal and spatial patterns of avoidance behaviour in response to human activity have been demonstrated in urban coyotes, *Canis latrans*, and bobcats, *Lynx rufus*. Both species were found to be less active and showed avoidance of more developed areas during daylight hours (Tigas *et al.*, 2002). More-urbanized individuals also had larger range sizes than those occupying less-developed sites (Riley *et al.*, 2003).

Interestingly, the increased home range size of more urbanized coyotes and bobcats contrasts with the findings of numerous other urban wildlife studies. Urban animals generally show a reduction in range size compared to their rural counterparts (raccoon, *Procyon lotor*: Prange *et al.*, 2004; key deer, *Odocoileus virginianus clavium*: Harveson *et al.*, 2007; stonemarten, *Martes foina*: Herr, Schley & Roper, 2009). Smaller range sizes in urban wildlife are thought to reflect more stable supplies of localized food resources and greater food resource densities in urban habitats. Riley *et al.* (2003) postulated that the larger range sizes observed in more-urbanized coyotes and bobcats might reflect a tendency for individuals to enter urban areas only for feeding and to return

to surrounding habitat to den, thus travelling further in a night than less-urbanized animals. A comparative study of range size in wholly ex-urban bobcats and coyotes would help resolve this issue. Temporal avoidance behaviour is likely to be an important behavioural modification for animals that are more susceptible to anthropogenic disturbance (i.e. terrestrial mammals), allowing them to forage effectively in urban environments.

Changes to the feeding patterns of adults provisioning juveniles are thought to reflect an increased abundance of food resources often associated with urban environments. A study comparing waterbirds in developed and undeveloped shoreline habitats found higher feeding rates of juveniles by adult ducks (Anatidae) at developed sites (Traut & Hostetler, 2003). The removal of shoreline vegetation by property owners was thought to have promoted foraging conditions favourable to these birds (Traut & Hostetler, 2003). Similarly, research on Cooper's hawks, *Accipiter cooperii*, revealed higher delivery rates of prey items to juveniles in urban than rural habitats (Estes & Mannan, 2003). This study also found that adult birds vocalized less during feeding in urban environments. This was thought to reflect differences in food stress experienced by urban birds, females being less likely to vocalize at the nest when food stress is low (Estes & Mannan, 2003). To what extent other behaviours might change in association with changed feeding rates in urban wildlife is largely unknown and would make an interesting contribution to research in this area.

In contrast to the aforementioned studies, urban European starlings, *Sturnus vulgaris*, had a low food provisioning rate of nestlings and correspondingly poor nestling success rates in urban areas (Mennechez & Clergeau, 2006). The authors suggested that more-specialized species, which demonstrated a shift in food selection in urban environments, might do better in the long term than more-generalist species (i.e. omnivores) that continued to feed on similar food resources to those of rural conspecifics [see Fearn *et al.* (2001) and Kubler, Kupko & Zeller (2005) for examples of shifts of principal prey items in urban-based specialist species]. This is in contrast to the widely accepted view that generalist species are inherently better suited to the urban environment than specialist species (Chace & Walsh, 2006), and highlights the importance of incorporating behavioural assays, such as food innovations into urban wildlife research.

(3) Use of human-subsidized resources

Another way in which wildlife alters their foraging behaviour(s) in urban environments is by utilizing human-subsidized resources. Provisioning of food for wildlife by humans in urban areas is a popular pastime, but it can sometimes lead to significant and unexpected changes to behaviour in animals that utilize this resource. For example, Australian magpies, *Gymnorhina tibicen*, that exploited feeding stations in urban areas, commenced breeding earlier than those that fed entirely on natural food resources (O'Leary & Jones, 2006). Another study investigating effects of food supplementation in great tits found that food-supplemented

males changed the timing of their dawn chorus until after sunrise, whereas unsupplemented males did not (Saggese *et al.*, 2011). The authors suggested that the delayed singing in these birds could potentially affect the reproductive success of urban great tits if females base mate selection on dawn song performance (Saggese *et al.*, 2011).

Behavioural shifts resulting from food supplementation have also been described for urban-adapted mammals. For example, chipmunks, *Tamias striatus*, altered their seasonal behaviour patterns in urban environments. Reduced activity levels normally observed in this species during summer in natural environments were absent in urban landscapes due to human-supplied food resources (Ryan & Larson, 1976). Notably, in all of the aforementioned studies, focal animals fed on natural resources when supplemented food items were no longer available. Conversely, research on wildlife feeding activities devised for tourism purposes has shown ongoing negative effects on food-supplemented animals. These include reliance on supplemented foods, disruption to normal activities, habituation to humans and nutritional problems (Newsome & Rodger, 2008). Long-term feeding of urban wildlife by humans is likely to produce similar outcomes.

Utilization of landfill sites by animals in urban landscapes is well documented (Gabrey, 1997). Gulls, due to their scavenging habits, are undoubtedly one of the most successful animals at exploiting these sites (Smith, 1992; Smith & Carlile, 1992, 1993). Six thousand silver gulls per hour, for example, were recorded leaving a single urban landfill site (Smith & Carlile, 1993). The stomach contents of silver gulls revealed that 85% of birds sampled contained only human refuse in their stomachs (Smith & Carlile, 1993). Poor waste management practices in urban landscapes have also led to increased numbers of Australian white ibis, *Threskiornis molucca*, a species that is particularly adept at taking advantage of this novel food resource (Ross, 2004). Although adult birds often utilize these anthropogenic food resources effectively, there is some suggestion that these types of resources can be detrimental to nestlings. For instance, research on American crows, *Corvus brachyrhynchos*, found that urban nestlings were significantly smaller (and more nutritionally deficient) than rural nestlings (Heiss, Clark & McGowan, 2009). Whether the former survive due to other advantages obtained in urban environments (e.g. reduced competition for food) remains unclear.

Learning ability and tolerance of novel objects (both assays of behavioural flexibility) are likely to be important traits in animals that utilize novel foods in urban environments, with more-innovative species generally being better at problem-solving and learning in challenging situations (Kark *et al.*, 2007). Accordingly, high levels of feeding innovations and reduced neophobia have been described for several successful urban-adapted species in both field and laboratory studies (Lefebvre, 1995; Seferta *et al.*, 2001; Webster & Lefebvre, 2001; Martin & Fitzgerald, 2005; Echeverria, Vassallo & Isacch, 2006; Bouchard *et al.*, 2007). In line with this, behavioural flexibility has been identified as an important

predictor of invasion success in animals, with successful invaders showing a higher frequency of foraging innovations in their region of origin than unsuccessful ones (Sol & Lefebvre, 2000; Sol, Timmermans & Lefebvre, 2002). Thus naturally innovative species might be predisposed to inhabit urban environments due to their inherent ability to respond more rapidly to altered conditions (see Section II.1).

(4) Use of shelter

Urban environments are novel habitats in that natural vegetation is largely replaced by exotic plants and artificial structures. In addition, anthropogenic climate change in urban environments, such as higher ambient temperatures in city centres and artificial watering of gardens, creates a new set of environmental variables that can have both positive and negative effects on wildlife (Pickett *et al.*, 2001).

Changed roosting behaviours have been observed in several wildlife species in cities. Warmer conditions and fewer frosts in a city centre were thought to have facilitated the successful establishment of the grey-headed flying-fox, *Pteropus poliocephalus*, outside of its natural habitat (Parris & Hazell, 2005). Changes to roosting behaviour have also been observed in urban Torresian crows, *Corvus orru*, which engage in aggregated roosting, a behaviour not seen in this species in natural environments (Everding & Jones, 2006). Although the authors were unable to explain the development of communal roosting behaviour in these birds, they suggested that local enhancement (use of the same local feeding areas) and network foraging (group feeding) strategies may operate in these populations. However, why these behaviours would benefit urban and not rural birds is not clear. A more detailed comparison of roosting-associated behaviours in urban and rural crows might help resolve this issue.

(5) Use of artificial structures

Utilization of artificial structures provides wildlife with an alternative form of shelter in urban environments. Brushtail possums, *Trichosurus vulpecula* (Statham & Statham, 1997), stone martens (Herr *et al.*, 2010) and chipmunks (Ryan & Larson, 1976) frequently use buildings rather than natural sites for denning in urban habitats. For example, individual stone martens were recorded using artificial structures as den sites 97.1% of the time (Herr *et al.*, 2010). Seasonal shifts in use of these sites have also been observed. Fox squirrels, *Sciurus niger*, for instance, use the inside of buildings more during the colder months, with female squirrels exploiting them during the rearing of young (McCleery *et al.*, 2007).

Artificial structures have also allowed more vulnerable species to inhabit urban environments. The blue-tongued lizard, *Tiliqua scincoides*, described as one of the few large reptiles to occupy urban areas successfully, has been observed exploiting artificial structures as shelter sites in cities (Koenig, Shine & Shea, 2001). Similarly, little penguins, *Eudyptula minor*, occupying coastal urban habitats have adjusted their nesting behaviour by utilizing rocky crevices and human-made structures in the absence of natural nesting sites, such

as tussock grass and sandy substrata (Bourne & Klomp, 2004). A review by Bolen (1991) suggests that structural components of the urban environment can be viewed as analogs (i.e. of similar function, but different origin) of exurban habitats, and should therefore be considered when assessing the viability of urban habitats for wildlife. The ability to exploit artificial shelter sites is considered an important factor in the success of some animals in urban environments and, again, suggests that urban wildlife exhibit behavioural flexibility (see Sections III.1 and III.2 for other examples of behavioural flexibility in urban adapters).

IV. BEHAVIOURAL ADJUSTMENTS TO DISTURBANCE

Disturbances to wildlife in urban environments are many and varied, from replacement of habitat with anthropogenic land cover (i.e. buildings) to novel predators (i.e. cats and dogs). In this review, we focus on studies that investigate the impact of human activity (i.e. pedestrian and vehicular traffic) and noise disturbance on urban animals.

(1) Disturbance from human activity

At the landscape scale, research suggests that disturbance resulting from human activity is one of the most important factors affecting species richness (Schlesinger, Manley & Holyoak, 2008). Accordingly, a fundamental question in urban ecology is to understand why some species adjust well to the presence of humans while others do not (Levey *et al.*, 2009). In a study comparing elevational and latitudinal distributions of urban birds with those of rural congeners, Bonier, Martin & Wingfield (2007) found that urban birds showed markedly broader environmental tolerance. The authors suggested this might be attributed, in part, to behavioural and physiological flexibility. Quantifying the effects of human disturbance on animals is based on measuring the trade-off between resource use and risk of disturbance. An individual must assess the cost of responding to a perceived threat (energy expenditure and time diverted from resource acquisition) against the cost of ignoring the risk (potential death) (Frid & Dill, 2002). The ‘resource-use-disturbance trade-off’ hypothesis was demonstrated in urban house sparrows, *Passer domesticus*. Breeding densities and consumption of food peaked at intermediate pedestrian traffic rates, whilst food consumption levels decreased when traffic rates were high (Fernández-Juricic *et al.*, 2003). It was suggested that house sparrows might associate humans with sources of artificial foods (i.e. refuse and leftovers), therefore preferring to inhabit sites much visited by people (Fernández-Juricic *et al.*, 2003). However, constant high pedestrian traffic rates might also increase the probability of disruption of foraging and breeding activities, creating a limit to the level of disturbance that the sparrows can tolerate. A similar effect was demonstrated in pink-footed geese, *Anser brachyrhynchus*, in response to vehicular traffic disturbance, where the level

of disturbance affected the extent to which fields were exploited (rate of feeding) (Gill, Sutherland & Watkinson, 1996).

A perceived threat, such as an approaching human, induces a similar response to that which prey species have evolved to predators. Hence, when an animal is approached by a human it will eventually flee (Frid & Dill, 2002). Understanding the factors that control flight responses among species can help to predict which species are likely to tolerate high-disturbance, urban environments (Frid & Dill, 2002). Several factors have been associated with variations in flight initiation distance (FID), the distance between an animal and an approaching human when the animal flees (Fernández-Juricic, Jimenez & Lucas, 2001). Body size (Cooke, 1980; Fernández-Juricic *et al.*, 2001; Blumstein *et al.*, 2005; Blumstein, 2006), age at first reproduction (Blumstein, 2006) and availability of escape options (Fernández-Juricic *et al.*, 2001) have all been shown to affect FID in birds. Blumstein (2006) postulated that the greater alert distances (or increased wariness) exhibited by larger-bodied birds might reflect a greater vulnerability to predation (i.e. they have poor agility and high visibility). Alternatively, the cost of flight might be less than it is in smaller-bodied species, due to smaller birds having comparatively greater mass-specific energy requirements. However, as highlighted by Blumstein (2006), this explanation fails to take into account the possible effect of habituation in these birds, i.e. a reduction in response to a stimulus through a learning process in which the stimulus ceases to be regarded as dangerous after repeated exposures (Mirza, Mathis & Chivers, 2006). Animals are known to vary in their tendency to habituate to disturbance, and there are numerous examples of larger-bodied, avian urban adapters that appear highly resilient to human disturbance in urban environments (e.g. Australian magpie: Cilento & Jones, 1999; Warne & Jones, 2003; white ibis: Ross, 2004; silver gull: Smith & Carlile, 1992, 1993).

A number of avian studies comparing disturbance tolerance between urban and rural individuals have found that urban birds are less wary than rural conspecifics (Cooke, 1980; Traut & Hostetler, 2003; Donaldson *et al.*, 2007; Møller, 2008; Evans *et al.*, 2010; Kitchen *et al.*, 2010; Lowry *et al.*, 2011). Whether this disparity is wholly explained by habituation to humans in urban individuals is contentious. Møller (2012), for example, postulates that consistency in flight-initiation distances and the correlation between time since colonization and disturbance tolerance in urban birds points to micro-evolutionary adaptation rather than habituation *per se*. A review by Frid & Dill (2002) suggests that animals will tend to maximize their fitness by overestimating, rather than underestimating risk. Although both strategies involve a cost to the animal, overestimation might result in a lost feeding opportunity whereas underestimation could result in death. Thus even though habituation occurs, it is often only partial, and there are several studies that have demonstrated changed behaviours in urban adapters that cannot be explained by habituation alone (Rodriguez-Prieto *et al.*, 2009; Lowry *et al.*, 2011).

Rodriguez-Prieto *et al.* (2009) tested some of the predictions of the 'risk allocation' hypothesis put forward by Lima & Bednekoff (1999), which postulates that an animal will decrease its anti-predator effort in response to increasingly frequent high-risk situations. To test this, Rodriguez-Prieto *et al.* (2009) simulated attacks on urban European blackbirds through either a pedestrian approach or an approach by a radio-controlled toy truck. In support of the risk allocation hypothesis, blackbirds adjusted their anti-predator behaviour according to the rate of pedestrian traffic, with a greater FID when pedestrian traffic rates were lower. Habituation, however, was also important, with birds being less responsive to pedestrians than to the radio-controlled truck (i.e. a novel stimulus).

In contrast to the aforementioned study, research on urban house finches, *Carpodacus mexicanus*, found that highly urbanized individuals were more wary of human approach (i.e. flushed at larger distances) than those occupying less-urbanized landscapes (Valcarcel & Fernández-Juricic, 2009). The authors suggested that house finches might perceive urban environments as more dangerous, despite there being smaller numbers of native predators, possibly due to the presence of human activities (Valcarcel & Fernández-Juricic, 2009). Whether these birds would eventually habituate or remain sensitised to human disturbance remains to be seen.

There is some evidence to suggest that the social context in which an animal finds itself may also play a role in how it will respond to human disturbance. Parker & Nilon (2008) investigated the inter-relationships among population density, intraspecific aggression, and reduced fear of humans in urban populations of grey squirrels, *Sciurus carolinensis*. A positive association was found between squirrel density and intraspecific aggression, and a negative relationship between density and wariness. Risk-taking behaviour has also been shown to vary with social context in great tits, which showed bolder behaviour in the presence of a companion (Van Oers, Klunder & Drent, 2005). These studies suggest that reduced wariness might stem from greater numbers, as more individuals are available to provide warnings about predators.

Recently, behavioural researchers have begun to recognize that consistent individual (within-species) differences in behaviour traits (or temperament) exist among animals (Runyan & Blumstein, 2004; Van Oers *et al.*, 2004; Reale *et al.*, 2007; Martin & Reale, 2008; Evans *et al.*, 2010). Individuals may habituate to or become sensitized to different levels of disturbance in urban environments. A study investigating rates of habituation in yellow-bellied marmots, *Marmota flaviventris*, showed that individuals varied in how quickly they became sensitized to disturbance (an approaching human) (Runyan & Blumstein, 2004). Another study investigating associated behaviours in eastern chipmunks found that more explorative and docile chipmunks occupied the sites that experienced the highest rates of human disturbance (Martin & Reale, 2008). The authors suggested that temperament might cause animals to distribute themselves in a non-random way in response

to human disturbance. Accordingly, some animals that inhabit urban environments might have an innately higher disturbance tolerance (or bold temperament) than non-urban individuals, and this has been demonstrated in several urban avian adapters (see Section II.4). If, in fact, urban environments do select for, or favour, bolder individuals, this could occur through bolder animals being more able to colonize urban environments in the first instance. Alternatively, urban individuals might habituate to high-disturbance urban environments through learning and, in so doing, become bolder with time.

Being bold in temperament might allow an animal to live close to humans without experiencing chronic stress. Consequently, bolder individuals inhabiting urban environments might not suffer the detrimental effects typically associated with chronic physiological long-term stress responses (characterized by the release of glucocorticoid steroid hormones) that more timid animals experience in high-disturbance environments. Thus urban animals ought to have a weaker stress response than rural conspecifics. For example, hand-reared blackbirds taken from urban populations had a lower acute corticosterone stress response than hand-reared rural conspecifics (Partecke *et al.*, 2006b). Given that both study groups were raised under identical conditions, the difference was likely to be genetically based. Similarly, urban Florida scrub-jays, *Aphelocoma coerulescens*, had lower blood corticosterone concentrations than their rural counterparts (Schoech, Bowman & Reynolds, 2004). The authors postulated that access to more stable, year-round food resources in urban environments might result in less food stress (Schoech *et al.*, 2004). In contrast to these findings, urban rufous-collared sparrows, *Zonotrichia capensis*, had higher primary (acute) and secondary (chronic) physiological stress characteristics and lower body mass than rural individuals (Ruiz *et al.*, 2002). Due to the limited research available on stress responses in urban wildlife, it is difficult to know exactly what level of stress urban animals might be experiencing and what the underlying causes might be (i.e. temperament *versus* resource-related stress). Future studies may wish to investigate whether there are associated differences in stress levels, boldness, and body condition in urban adapters and their rural counterparts.

Aggression is a behavioural trait that is often associated with boldness in animals (Dingemanse & Reale, 2005). A review of the ecology of the urban vertebrate fauna of Australia identified urban areas as being dominated by behaviourally aggressive species (Gardener *et al.*, 2006). This association has been demonstrated in several studies, which showed elevated aggression levels in successful urban adapters (Australian magpie: Cilento & Jones, 1999; Warne & Jones, 2003; white ibis: Ross, 2004; noisy miner: Lowry *et al.*, 2011). Warne *et al.* (2006) described this phenomenon as the ‘urban wildlife syndrome’, whereby wildlife species undergoing synurbanization (the process of becoming urbanized) exhibit increased densities, increased aggression and a reduced fear of humans. It is unclear, however, whether these animals become more aggressive

as a result of becoming urbanized or are just inherently aggressive.

Two very successful avian urban-adaper species, Australian magpies and noisy miners, are described as aggressive in both urban and rural habitats and have more behaviours associated with aggressive interactions than in any other context (Australian magpie: Brown & Veltman, 1987; noisy miner: Higgins, Peter & Steele, 2001). However, in both species, differences were found between levels of aggression in urban and rural individuals; urban birds were significantly more aggressive and demonstrated higher disturbance tolerance than rural conspecifics (Australian magpie: Cilento & Jones, 1999; Jones & Nealson, 2003; noisy miner: Lowry *et al.*, 2011). The research on Australian magpies looked at aggression toward human intruders, whereas the study on noisy miners found that they responded aggressively to a single exposure to a startling sound stimulus (loud noise). The latter is a surprising observation, especially given that adult birds were not associated with juveniles during testing, a context in which they might be expected to demonstrate elevated aggression levels.

Aggression towards humans by urban Australian magpies does not appear to be random. A study by Warne & Jones (2003) found that 71% of magpies attacked only one of three types of intruder (pedestrians, cyclists and mail deliverers), with about half attacking only pedestrians. Aggressive magpies also actively selected particular individuals to attack. Another urban-based study examined the response of northern mockingbirds, *Mimus polyglottos*, to nest approach by humans and found that individuals very quickly learnt to identify particular humans as potential threats (Levey *et al.*, 2009). It was suggested that this level of perception and rapid learning (or behavioural flexibility) might predispose mockingbirds and other species to exploit urban environments successfully.

Research suggests that two main factors might drive the observed differences in behavioural responses to human disturbance in urban wildlife. First, behavioural flexibility appears to allow some animals to habituate or become desensitised to frequent, novel threats in urban environments more readily than others (see Sections II.1 and II.2). Second, some urban-colonizer species or individuals may be inherently bolder in temperament and thus have a greater disturbance tolerance in the first instance than those that fail to colonize urban habitats. The latter would give these animals a natural advantage over more timid (low disturbance-tolerant) species or individuals in the urban environment (see Section II.4).

(2) Sensory disturbance

Urban environments create a number of sensory disturbances, such as chemical and light pollution and constant, ubiquitous, background noise. Research on the effects of sensory disturbance on urban wildlife has largely focused on noise disturbance that can negatively affect species diversity and richness (Stone, 2000; Rheindt, 2003; Francis *et al.*, 2011). In particular, constant background noise in

urban environments can affect communication through vocal masking. Here, we focus on research into the behavioural responses of wildlife to anthropogenic urban noise.

In cities, acoustically communicating animals need to find ways to avoid vocal masking of their signals by constant, low-level, anthropogenic noise. Animals can improve signal transmission in noise by altering or adjusting their acoustic communication patterns (Catchpole & Slater, 2008). One vocal mechanism that mitigates the effect of noise in urban habitats is a shift in the frequency of a signal above the main frequency range of anthropogenic noise (described as 1–2 kHz; see Slabbekoorn & Peet, 2003). There are numerous studies demonstrating such frequency shifts in the songs of urban birds. For example, urban great tits (Slabbekoorn & den Boer-Visser, 2006) and European blackbirds (Nemeth & Brumm, 2009) sing at higher minimum frequencies (kHz) than their rural counterparts [see also Slabbekoorn & Peet (2003), Wood & Yezerinac (2006), Slabbekoorn, Yeh & Hunt (2007) and Hu & Cardosa (2009) for examples of frequency adjustments].

More recently, research has found that several birds and a single frog species can adjust the sound frequency of other types of vocalisations in urban environments (Parris, Velik-Lord & North, 2009; Hu & Cardosa, 2010; Potvin, Parris & Mulder, 2011; H. Lowry, A. Lill & B. B. M. Wong, in preparation). Whereas songs are learned, other call types are usually innate and therefore expected to show limited plasticity. Notably, for both the southern brown tree frog, *Litoria ewingii* (Parris *et al.*, 2009) and the noisy miner (H. Lowry, A. Lill & B. B. M. Wong, in preparation), the observed increases in minimum frequency were relatively small compared to those observed for bird song and were not actually sufficient to avoid masking by low-frequency, anthropogenic noise. It is possible that vocal adjustment to noisy urban habitats is still developing in these species. Alternatively, there may be other plausible explanations for sound-frequency adjustments in urban birds that could throw the whole anti-masking argument into question. For instance, it has been suggested that increased song pitch might not be an adaptation that reduces sound masking in cities, but rather a physiological side-effect of birds singing at higher amplitudes in urban environments (Nemeth & Brumm, 2010). Research into the possible association between frequency and amplitude adjustments of signals encompassing both songs and calls would be a worthwhile extension of research in this area.

Several studies have demonstrated disparities in frequency adjustments between cohabiting species with contrasting 'higher'- or 'lower'-pitched songs. Parris & Schneider (2009) investigated the effect of traffic noise and volume on two bird species occupying roadside habitat. The lower-pitched song of the grey shrike-thrush, *Collurincinclia harmonica*, was sung at a higher dominant frequency in the presence of traffic noise. By contrast, the naturally higher-pitched song of the grey fantail, *Rhipidura fuliginosa*, remained unaffected by greater noise disturbance. A similar pattern was demonstrated in flycatchers (grey, *Emionax wrightii*, and ash-throated, *Myiarchus*

cinerascens, flycatchers), although in this case, the shift was in the minimum frequency of the signal (Francis, Ortega & Cruz, 2011). A study by Hu & Cardosa (2009) found that passerines with lower frequency songs were more likely to adjust the pitch of their signals in urban environments. This study also identified a trend for urban bird species to vocalize at a higher dominant frequency than strictly non-urban species. Katti & Warren (2004) postulated that noise effects would favour those species with sufficient behavioural (learning or temporal patterning of behaviour) or genetic flexibility (innate variation in vocal frequency range) to adjust to changed noise conditions, such as those encountered in cities.

Although birds in urban environments sometimes adjust the sound frequency of their vocalizations in response to anthropogenic noise, less is known about the long-term nature of frequency modification. Luther & Baptista (2010) conducted the first long-term study of urban bird song in this context. They investigated three adjacent dialects in the songs of white-crowned sparrows, *Zonotrichia leucophrys*, over a 30-year period. It was found that the minimum frequency of songs increased both within and among dialects over this period. Thus, the dialect with the highest minimum frequency is in the process of replacing a lower frequency song dialect in urban individuals. Further investigation is needed, however, to identify to what extent the described shifts in signal frequency in urban birds are leading to vocally distinct urban and rural populations. Nevertheless, some researchers have suggested that these shifts could even lead to speciation (Warren *et al.*, 2006).

A different type of vocal adjustment that can mitigate the effects of background noise in urban environments is signal amplitude adjustment. The Lombard effect describes an animal maintaining the broadcast area of its vocalizations by increasing vocal amplitude in response to an increase in the background noise level (Brumm, 2004). Although numerous studies have found this type of vocal adjustment under laboratory conditions (Cynx *et al.*, 1998; Manabe, Sadr & Dooling, 1998; Brumm & Todt, 2002; Kobayasi & Okanoya, 2003), only two have shown amplitude adjustments in animals occupying urban habitats. The songs of the common nightingale, *Luscinia megarhynchos*, were sung more loudly by individuals inhabiting noisy locations than by those living in quieter places (Brumm, 2004). Similarly, noisy miners on noisy arterial roads consistently called at higher amplitudes than those occupying quieter residential streets (Lowry, Lill & Wong, 2012).

Nemeth & Brumm (2010) modelled the relative benefits of amplitude and pitch adjustments on signal transmission in noise. They showed that amplitude increases were five times more effective at increasing the communication distance of a signal than an elevation in vocal pitch under analogous sound conditions. The authors postulated that an increase in song amplitude would therefore be the more effective modification for improving signal transmission in urban landscapes. Thus noise-level-dependent adjustments in signal amplitude are conceivably widespread phenomena

in animals communicating acoustically in noisy urban environments.

There are several other temporal (or short-term) vocal mechanisms that are thought to mitigate background-noise effects that have been identified in wildlife inhabiting urban environments. Research on sound transmission indicates that longer signals undergo greater degradation than shorter signals due to echo effects, which often occur in highly structured urban environments (Wiley & Richards, 1982). Accordingly, several studies have demonstrated that urban birds sang shorter, faster songs compared to their rural counterparts (Slabbekoorn & den Boer-Visser, 2006; Nemeth & Brumm, 2010). Song-switching, whereby vocalizing birds favour song types that do not overlap with anthropogenic noise (Halfwerk & Slabbekoorn, 2009), and changes to the timing of vocal activity (Sun & Narins, 2005; Fuller, Warren & Gaston, 2007) have also been demonstrated in urban animals. The latter does not require animals to alter the structure of their vocalizations and has been demonstrated, for example, in anurans inhabiting a pond in central Thailand (Sun & Narins, 2005). They found that individuals of three species (*Microhyla butleri*, *Rana nigrovittata* and *Kaloula pulchra*) significantly reduced their calling rate during playback of motorbike and aeroplane flyby noise (Sun & Narins, 2005). However, one species, *Rana taipensis*, increased its calling rate throughout periods of elevated noise. Sun & Narins (2005) suggested that the reduction in calling rates in the other cohabiting species actually stimulated calling in *Rana taipensis*, a secondary effect of anthropogenic acoustic interference on anuran communication.

Diurnal shifts in the timing of vocal activity have also been demonstrated in cities. Urban European robins, *Erithacus rubecula*, reduced acoustic interference from traffic noise by singing at night (Fuller *et al.*, 2007). Other studies have shown that light pollution can also cause diurnal birds to sing at night, adjust the timing of their dawn chorus or even change reproduction and mating patterns (Miller, 2006; Kempenaers *et al.*, 2010). However, for urban European robins, the effect of light pollution on singing behaviour was much weaker than that of daytime noise (Fuller *et al.*, 2007).

Modification of behaviour in response to noise disturbance in cities can involve costs. For instance, it has been postulated that anthropogenic noise pollution can negatively impact on the sexual signals of some wildlife (i.e. fishes, amphibians, birds and mammals). This, in turn, may have direct negative influences on reproduction and consequently population growth (Laiolo, 2010). Altering a signal important in mate attraction in response to noise pollution may affect an individual's chances of attracting a mate. On the other hand, song adjustment to such pollution might orientate females preferentially to adjusted males, leading to reproductive divergence in urban birds (Slabbekoorn & Ripmeester, 2007). However, by not making vocal adjustments, males risk not being heard. This has been demonstrated in male ovenbirds, *Seiurus aurocapilla*, where interference effects on song at noisy compressor sites had a significant negative impact on male breeding success (Habib, Bayne & Boutin,

2007). In addition, short-term adjustments to sound signals, such as amplitude changes, are likely to be energetically costly (i.e. due to an increased rate of oxygen consumption) (Oberweger & Goller, 2001) and some species may simply lack the physiological capacity to make this type of vocal modification (e.g. through limitations of the communication system). Changes to the timing of vocalizations may result in species which cease vocalizing during periods of elevated anthropogenic background noise being replaced by those that continue to vocalize during noisy periods. Increasing our understanding of the mechanisms driving such changes in communication in urban environments and their ultimate costs to wildlife will help us to predict better which species will ultimately be more adept at inhabiting noisy urban environments.

V. CONCLUSIONS

(1) Urban environments expose wildlife to selection pressures that often differ drastically from those under which they have evolved. Individuals that can respond behaviourally to the new selection pressures presented by cities should have greater success in urban habitats when resources are not a limiting factor.

(2) Research suggests that two main factors might drive the observed differences in behavioural responses by wildlife to urban environments, namely behavioural flexibility (or phenotypic plasticity) and an animals' temperament. Behaviourally flexible (and therefore naturally innovative) species may be particularly predisposed to inhabiting urban landscapes due to their inherent ability to respond more rapidly to altered conditions. However, whether behaviour adjustments are the product of phenotypic plasticity or genetic adaptation remains largely unknown. By contrast, temperament implies that animals sometimes show limited flexibility in behaviour. However, urban-living might favour individuals or species with particular temperaments (e.g. boldness).

(3) By expanding research into the behaviours of urban wildlife we will gain a better understanding of which species will be able successfully to colonize cities and towns and which will ultimately be excluded from them (Sutherland, 1998; Warren *et al.*, 2006).

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