

**Behavioural traits of a successful  
avian urban adapter, the noisy miner  
(*Manorina melanocephala*)**

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## Summary

Increasing urbanization means that wildlife must adjust to this altered environment or be excluded from it. Most species appear to be unable to adjust to the high disturbance levels and changes to habitats and resources that accompany urbanization, but a few thrive in this evolutionarily novel environment. To date research on urban colonization by wildlife has focused largely on resource-based (i.e. food and habitat) limitations to colonization. By contrast, much less attention has been given to behavioural traits that might facilitate urban habitation. The current study focused on the behaviour of an avian urban adapter, the noisy miner, *Manorina melanocephala*. Firstly, I compared the response of urban and rural noisy miners to a startling sound stimulus (a loud noise). Secondly, several calls of this species were compared between urban and rural conspecifics. Finally, the amplitude of noisy miner alarm calls was compared between areas with contrasting background noise levels (arterial roads and residential streets) in the urban environment. Urban noisy miners were less 'flighty' and more aggressive than rural individuals in response to loud noise playback. Focal birds in both areas usually remained at the playback site and visually surveyed the area, suggesting that noisy miners are inherently quite bold (i.e. have a relatively high disturbance-tolerance). Although urban noisy miners exhibited a shift in the minimum frequency (kHz) of some call-types relative to rural individuals, it was not sufficient to preclude vocal masking from low level, background, anthropogenic noise. However, several call components of this species appear to be naturally suited to being heard in noisy urban environments (i.e. they have high dominant and maximum frequencies [kHz]). As an additional and/or alternate vocal modification, noisy miners also exhibited the Lombard effect, calling more loudly on noisy arterial roads than on quieter residential streets in

urban Melbourne. Overall, the findings suggested that noisy miners are probably inherently well suited to inhabiting cities by virtue of having a relatively high disturbance-tolerance and calls with features that make them easy to detect in noisy environments. In addition, these birds appear to have the flexibility to adaptively modify their vocal behaviour through adjustments to the frequency (kHz) and amplitude of their calls in such a way as to retain broadcast efficiency in the noisy city environment.

## **Declaration**

I Helene Lowry declare the work presented in this thesis is my own and was undertaken during my PhD candidature, in the School of Biological Sciences, Monash University.

Wherever sources of information or the work of others has been used, I have acknowledged this in the text. This thesis has not been submitted for a higher degree to any other university or institution.

Helene Lowry

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## Introduction and Thesis Outline

Urban environments create many challenges for wildlife, such as high disturbance levels and the availability of novel resources (Reijnen et al. 1997; Fernández-Juricic & Telleria 2000). Although certain species seem unable to cope with these novel challenges, there are a suite of species, described as urban ‘adapters’ that are able to thrive in high disturbance urban habitats (McKinney 2006). To date, research has tended to focus on resource-based limitations on wildlife in urban environments. However, behaviour might also be important to a species’ (or individual’s) ultimate success, with more behaviourally ‘flexible’ or ‘bolder’ animals expected to do better under extreme conditions (Reale et al. 2007).

The noisy miner, *Manorina melanocephala*, is a large (length 26cm; mass 70-80g), communally-breeding colonial honeyeater (Meliphagidae), native to eastern and south-eastern Australia (Higgins et al. 2001). Noisy miners demonstrate complex social and aggressive behaviours that are easily observed and quantified making them ideal for field-based research (Dow 1977; Grey et al. 1997, 1998; Higgins et al. 2001; Hastings & Beattie 2006; Parsons et al. 2006). They typically inhabit open *Eucalyptus* woodlands and lightly timbered farmland (Grey et al. 1997) and appear to have benefited from human-mediated habitat degradation (Clarke & Oldland 2007). Accordingly, in more recent times, noisy miners have successfully colonized urban environments where they have reached high densities (Low 2002). This thesis investigates several behavioural traits of this very successful avian urban adapter that have probably been important in facilitating this colonization process.

The studies undertaken in this thesis involved the design of a new field methodology for measuring disturbance-tolerance in birds, in addition to the use of sound-recording equipment and sound analysis programs for vocal communication research. The results are used to expand knowledge on how the noisy miner is behaviourally responding to high disturbance urban environments. Comparison is made of the disturbance-tolerance and several call variables (i.e. call frequency (kHz) and amplitude) in both urban and rural habitats, to determine whether urban populations are diverging behaviourally from rural counterparts. The chapters are presented as individual manuscripts formatted to meet the specifications of different scientific journals to which they have been submitted for publication.

Chapter 1 is a comprehensive literature review on the behavioural responses of wildlife (vertebrates) to urbanization. This review provides a general overview of research investigating how various vertebrates occupying urban habitats adjust their behaviour in urban landscapes. Firstly, I discuss the major theoretical issues attributed as drivers of behavioural change in urban-dwelling vertebrates. Secondly, I review how wildlife in cities respond to altered environmental conditions, investigating changes in behaviour(s) associated with reproduction, foraging and using shelter. I finish by reviewing how urban wildlife has adapted to high disturbance levels in cities, incorporating research into human and sensory disturbances. I suggest that behavioural flexibility (or the ‘temperament’ of an animal) may play an important role in determining which species – or individuals – are ultimately able to inhabit high disturbance urban environments.

Chapter 2 investigated the disturbance-tolerance (or boldness) of noisy miners in urban and rural habitats. This was measured by comparing the tolerance of focal birds to a startling sound stimulus (a loud noise). This is the first field-based study to use a noise disturbance as a measure of boldness in birds. Urban noisy miners appear to be less flighty (or bolder), and exhibit significantly more aggressive behaviours in response to a startling sound stimulus than rural birds. This chapter is in press in *Ethology*.

In Chapter 3 several components of a range of different vocalizations (calls) were compared between urban and rural noisy miners to identify if urban individuals are adjusting their vocalizations to avoid vocal masking in noisy urban environments.

Although a small shift in minimum frequency was recorded for lower frequency calls, this shift was not large enough to prevent masking of these calls from urban noise. However, analysis of other call components suggested noisy miner calls may be naturally well suited to being heard in urban habitats (i.e. maximum and dominant frequencies above that of anthropogenic noise) and therefore may not require modification. This chapter is currently under revision for publication in *Behavioral Ecology & Sociobiology*.

Chapter 4 investigated another type of vocal adjustment in urban noisy miners: changes in sound signal amplitude (the Lombard effect). This was the first urban-based study to look into amplitude adjustments of bird 'calls' (as apposed to bird song). Comparison of several noisy miner alarm calls under contrasting noise conditions indicated that birds occupying noisier sites (arterial roads) had significantly louder alarm calls than individuals occupying quieter sites (residential streets). Thus noisy miners appear to be employing the Lombard

effect as a mechanism to improve sound signal transmission in urban noise. This chapter is currently under review for publication in *Plos One*.

The final summary and conclusions section (chapter 5) integrates the main findings of my thesis into a more general overview of noisy miner behaviour and how it might contribute to the ultimate success of this species in urban environments.

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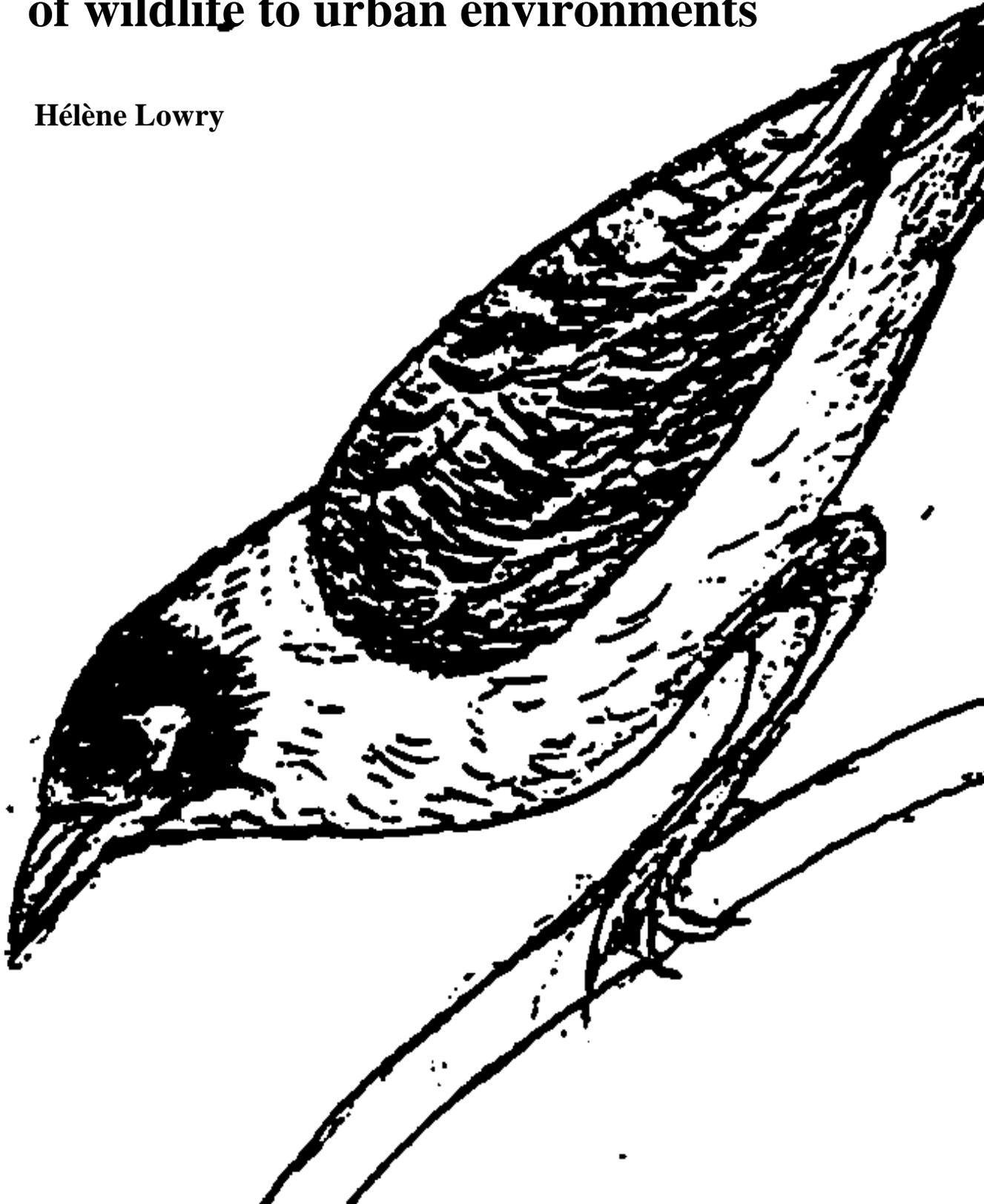
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# Chapter 1

## A review of the behavioural responses of wildlife to urban environments

Hélène Lowry



## **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 Fund 2007). This novel environment presents wildlife with a new set of challenges, in particular a loss of natural resources (i.e. habitat and food) and elevated (anthropogenic) disturbance levels (i.e. pedestrian traffic, vehicular traffic and industrial noise) (Reijnen et al. 1997; Fernández-Juricic & Telleria 2000). It is well documented that urbanization leads to an overall loss of biodiversity (or biotic homogenisation) (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 (Munyenyembe et al. 1989; Lim & Sodhi 2003; French et al. 2005; Garden 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 literature describing behavioural modifications in urban wildlife, with urban-based animals often demonstrating behaviours which differ from those of their rural counterparts (Cooke 1980; Traut & Hostetler 2003; Donaldson et al. 2007; Evans et al. 2010; Kitchen et al. 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.

Accordingly, several studies have demonstrated behavioural flexibility (or phenotypic plasticity) in urban adapter species (Lefebvre 1995; Seferta et al. 2001; Webster & Lefebvre 2001; Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006; Bouchard et al. 2007; Levey et al. 2009). There is also some suggestion that genetic differences may be involved in the changed behaviour(s) observed in urban populations (Partecke et al. 2004 & 2005). More recently, behavioural research has begun to recognize that vertebrates show individual differences in behaviour (or temperaments), which may have a genetic basis (Bolnick et al. 2003). Thus, some animals might be inherently better suited to inhabit urban environments in the first instance (i.e. be of 'bold' temperament).

This review comprises three parts. Initially I outline some major theoretical issues which are related to 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. I then 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. I do this by reviewing how the behaviour of wildlife is modified in response to urban conditions, particularly with respect to reproduction, foraging and the use of shelter. I then evaluate how some species are able to alter their behaviour(s) to withstand high disturbance levels in urban landscapes.

## **Major theoretical issues**

### *Modifying behaviour*

Urban environments are novel in that they usually present wildlife with a different set of selection pressures from 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). 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 often described as being behaviourally flexible (or phenotypic plasticity). 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 genetic adaptations is often unknown.

### *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 to proximally adjust its morphology and/or behaviour to best suit the conditions of its immediate environment and thus potentially increase its fitness (Thibert-Plante & Hendry 2011). 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 and genetic variance, and numerous studies have demonstrated altered behaviours in urban wildlife as individuals respond and adjust to new conditions (see Estes & Mannan 2003; Prange et al. 2004; Dowding et al. 2010 for examples of altered behaviours in urban populations).

Until recently, there was no evidence of evolutionary responses to urbanization that involved genetic adaptation. However, research on European blackbirds, *Turdus merula*, has begun to address this issue. Genetic adaptation has been found in the stress physiology of blackbirds in urban environments; hand-reared, city-born birds showed a lower acute (short-term) corticosterone stress response than forest-born birds (Partecke et al. 2006a). Conversely, research on an urban and a nearby rural population of blackbirds found no evidence of genetic differentiation between adult birds, but disparities in breeding density, daytime activity and flightiness suggest that there was phenotypic plasticity in urban individuals (Partecke et al. 2006b). 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. Further research is required to determine the extent of genetic adaptation in urban wildlife populations.

### *Communication in urban noise*

There are numerous studies demonstrating vocal modifications in songbirds in response to ubiquitous background (anthropogenic) noise in urban environments (Slabbekoorn and den Boer-Visser 2006; Wood & Yezerinac 2006; Nemeth & Brumm 2009). However, animals also experience background noise in natural environments to varying degrees. Thus Slabbekoorn & Ripmeester (2007) suggest modifications to birdsong in urban areas are likely to be phenotypic in nature and reflect the songbirds' need to cope with a wide variety of noises in natural habitats. Accordingly, adaptation to communicating in urban environments might involve either selection of individuals with specific genotypes within the overall population or exploiting existing phenotypic potential (Hunter 2007). Currently there are no studies demonstrating a genetic adaptation in the vocalizations of urban birds.

Whether modified behaviour(s) in urban individuals ultimately lead to genetic divergence between urban and rural populations is dependent on whether dispersal continues between urban and neighbouring rural populations. Changes to sexual traits such as song in birds and changes to timing of reproductive development enhance the likelihood of genetic divergence through populations becoming reproductively isolated (Slabbekoorn & Ripmeester 2007).

### *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 analogous situations. These individual differences are referred to as an animals' temperament, which describes behavioural differences that are repeatable 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 animals' temperament can have a direct bearing on how it responds to new (or 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).

### *Boldness and urban life*

Several studies have demonstrated a link between boldness and dispersal in animals. A study comparing behavioural traits of an invading *Gambusia* fish species and non-invading species found that invasive fish 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*, whereby bolder (or faster/more explorative) individuals dispersed further than more timid (or slower) individuals (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 melanocephala*, in response to a sound stimulus (loud noise) (Lowry et al. in press; Chapter 2). Although we can only speculate that boldness may predispose an animal to successfully inhabiting urban environments, the hypothesis warrants further investigation.

## **Behavioural modifications in response to altered environmental conditions**

### ***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 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 behaviour(s) 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 birds. 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 & Henson 2006).

It is unclear to what extent changes in the timing and duration of breeding in urban individuals is 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 secretion 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.

### ***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 impact on animals foraging efficiency 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; Tigase et al. 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 such 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 to avoid roads and were more active after midnight when human and vehicular traffic was 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 less active and showed avoidance of more developed areas during daylight hours (Tigase et al. 2002). At the same time, more urbanized individuals 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 et al. 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 of individuals to only enter urban areas 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 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 increased 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 coopers 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, which demonstrated high juvenile feeding rates in urban environments, urban European starlings, *Sturnus vulgaris*, had a low food provisioning rate of nestlings and correspondingly poor nestling success rates (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 et al. 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 than specialist species to the urban environment (Chace & Walsh 2006) and highlights the importance of incorporating behavioural assays, such as food innovations into urban wildlife research.

#### *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 tibicens*, 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 an urban bird, the great tit,

found that food-supplemented male songbirds changed the timing of their dawn chorus until after sunrise, whereas unsupplemented males did not (Saggese et al. 2010). 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. 2010).

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 the aforementioned studies, focal animals fed on natural resources when supplemented foods 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, which are 'scavengers', 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 et al. 2009). Whether the former survive due to other advantages obtained in urban environments (e.g. reduced competition for food) is 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 adapter species in both field and laboratory studies (Lefebvre 1995; Seferta et al. 2001; Webster & Lefebvre 2001; Martin & Fitzgerald 2005; Echeverria et al. 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 et al. 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 Modifying behaviour).

### *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.

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 & Hazel 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 both urban and rural crows might help resolve this issue.

### *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 for den sites in urban habitats rather than natural sites. 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 usage 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).

Man-made 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 successfully occupy urban areas, has been observed exploiting artificial structures as shelter sites in cities (Koenig et al. 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 substrates (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 ex-urban 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 Reproduction and Foraging sections for other examples of behavioural flexibility in urban adapters).

## **Behavioural adjustments to disturbance**

### *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, surpassing even habitat loss (Schlesinger et al. 2008). Accordingly, understanding why some species adjust well to the presence of humans and others do not has become a fundamental question in urban ecology (Levey et al. 2009). 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 (Fernandez-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 (Fernandez-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 by the geese (rate of feeding) (Gill et al. 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 (hereafter FID), the distance between an animal and an approaching human when the animal flees (Fernandez-Juricic et al. 2001). Body size (Cooke 1980; Fernandez-Juricic 2001; Blumstein et al. 2005; Blumstein 2006), age of first reproduction (Blumstein 2006) and availability of escape options (Fernandez-Juricic 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 to it (Mirza et al. 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; Evans et al. 2010; Kitchen et al. 2010; Lowry et al. in press; Chapter 2). Whether this disparity is wholly explained by habituation to humans in urban individuals is contentious. A review by Frid and 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 (Rodríguez-Prieto et al. 2009; Lowry et al. in press; Chapter 2).

Rodríguez-Prieto et al. (2009) put forward the 'risk allocation' hypothesis which postulates that an animal will decrease its anti-predator effort in response to increasingly frequent high-risk situations. To test this, Rodríguez-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 bigger 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 birds were more wary of human approach (i.e.

flushed at larger distances) than those occupying less urbanized landscapes (Valcarcel & Fernandez-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 & Fernandez-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 and Nilon (2008) investigated the inter-relationship between population density, intraspecific aggression, and reduced fear of humans in urban populations of gray 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 et al. 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; Martin & Reale 2008). Individuals may habituate 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 sensitised 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 which 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 Boldness and urban habitation). 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 thus 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. 2006a). 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 et al. 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 weights than rural individuals (Ruiz et al. 2002). Due to the limited research available on stress responses in urban wildlife, it is difficult to know how stressed urban animals typically are, and if they are, what might cause this stress (i.e. temperament versus resource-related stress). Future studies might investigate whether there are associated differences in stress levels, boldness, and body condition in urban adapters and their rural counterparts.

Aggression is a behaviour 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; gray squirrel: Parker & Nilon 2008; noisy miner: Lowry et al. in press; Chapter 2). Warren 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. Whether these animals become more aggressive as a result of becoming urbanized or are inherently aggressive is less clear.

Two very successful avian urban adapter 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 et al. 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 & Neelson 2003; noisy miner: Lowry et al. in press; Chapter 2). The research on Australian magpies looked at aggression toward human intruders, whereas noisy miner research found that miners responded aggressively to a single application of 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 in nature. A study by Warne and 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 mocking birds, *Mimus polyglottos*, to nest approach by humans and found that individuals very quickly learnt to identify particular humans as potential threats (Level et al. 2009). It was suggested that this level of perception and rapid learning (or behavioural flexibility) might predispose mockingbirds and other species to successfully exploit urban environments.

Research seems to suggest that two main factors might drive the observed differences in behavioural responses to human disturbance in urban wildlife. Firstly, behavioural flexibility appears to allow some animals to habituate or become desensitised to frequent, novel threats in urban environments more readily than others (see *Modifying behaviour & Phenotypic Plasticity versus Genetic Adaptation*). Secondly, 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 *Boldness and urban habitation*).

### *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 which can negatively affect species diversity and richness (Stone 2000; Rheindt 2003; Francis et al. 2009). In particular, constant background noise in urban environments can affect communication through vocal masking. In this part of the review, I will 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 (i.e. signals used in mate attraction, territory defence, antipredator behaviour, and parent-offspring communication; Slabbekoorn 2004) 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 1-2kHz; see Slabbekoorn & Peet 2003). There are numerous studies demonstrating such frequency shifts in the songs of urban birds. For example, urban great tits (Slabbekoorn and 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; Slabberkoorn et al. 2007; Hu & Cardoso 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 their 'calls' in urban environments (Parris et al. 2009; Hu & Cardoso 2010; Potvin et al. 2011; Lowry et al. in review; Chapter 3). Whereas songs are learned, calls 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 (Lowry et al., in review; Chapter 3), 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 which 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 and 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, *Colluricincla harmonica*, was sung at a higher dominant frequency in the presence of traffic noise. In 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 et al. 2010). A study by Hu and Cardoso (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 ex-urban species. Katti and 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 be able 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 and Baptista (2010) conducted the first long-term study of urban bird song in this context. They investigated three adjacent dialects in white-

crowned sparrow, *Zonotrichia leucophrys*, song 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 to identify to what extent the described shifts in signal frequency in urban birds are leading to vocally distinct urban and rural populations. 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 et al. 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 et al. in review; Chapter 4).

Nemeth and 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 from 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 than 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 et al. 2007) have also been shown in urban animals. The latter does not require animals to alter the structure of their vocalizations and has been demonstrated in anurans inhabiting a pond in central Thailand (Sun & Narins 2005). The authors found that individuals of three species (*Microhyla butleri*, *Rana nigrovittata* and *Kaloula pulchra*) significantly reduced their calling rate during playback of motorbike and airplane flyby noise (Sun & Narins 2005). However, one species, *Rana taipehensis*, increased its calling rate throughout periods of elevated noise. The authors suggested that the reduction in calling rates in the other cohabiting species actually stimulated calling in *Rana taipehensis*, a secondary effect of anthropogenic acoustic interference on anuran communication (Sun & Narins 2005).

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*; interference effects on song at noisy compressor sites had a significant negative impact on male breeding success (Habib et al. 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 make better predictions about which species will ultimately be better equipped to inhabit noisy urban environments.

## **Conclusions**

Research into behavioural responses employed by wildlife occupying cities demonstrates the remarkable adaptability of some animals to urbanization. These behavioural responses are diverse, ranging from changes to food and den preferences to adjustments to the structure of vocalizations. Research suggests that behavioural flexibility (or phenotypic plasticity) may be an important characteristic for a species to succeed in this novel environment. There is also the possibility that some species might be naturally well suited (or pre-adapted) to occupying cities through possessing behavioural traits, such as a high level of disturbance-tolerance (a bold temperament) and/or vocalizations lying outside the main sound frequency range of constant anthropogenic noise. This suggests that members of species which are less 'plastic' or naturally timid in temperament are likely disadvantaged in changing, high disturbance environments and consequently likely to be precluded from colonizing urban environments.

Despite substantial research focused on the behaviour(s) of urban wildlife, there are noticeable gaps in knowledge that need to be addressed. Although we know that urban animals often differ from rural conspecifics in aspects of their behaviour, to what extent are

these differences leading to behaviourally distinct urban and rural populations? Several authors have postulated that selection pressures exerted on urban wildlife differ so much from those operating in natural habitats that selection for traits suitable for urban occupation could lead to the emergence of an urban phenotype(s) (Slabbekoorn & Ripmeester 2007). Expanding research on whether these disparities in behaviour have a genetic basis would help to address this issue. Additionally, temperament and the role it might play in allowing urban habitation by a species warrants more attention. If urban environments do, indeed, favour bolder (and more aggressive) individuals, this might have significant implications for wildlife management in cities. Research on the effects of noise disturbance on urban wildlife would also profit from more studies on animal calls (of birds and other taxa), because research in this area is currently disproportionately orientated towards bird song. By furthering research into the behaviour(s) of urban wildlife we will gain a better understanding of which species will be able to successfully colonize cities and towns and which will ultimately be excluded from them (Sutherland 1998; Warren et al. 2006).

### **Argument and critical background**

In light of the issues discussed above, two areas of research on urban wildlife warrant further examination (a) the temperament of urban adapted species (i.e. disturbance-tolerance) and (b) the signals of successful urban adapters, encompassing both the components of the signals as well as signal amplitude. Although there is a growing body of scientific literature describing behavioural modifications in urban wildlife, to date, this research has tended to focus on particular behaviours within a species, rather than a

combination of behaviours. Therefore investigating multiple traits (i.e. temperament and vocal adjustments) within a single species, would help identify if these described behaviours occur in combination or independently.

### *Temperament*

Research on urban adapters suggests that temperament may be important to the success of some species. In particular, an individual inhabiting high disturbance urban habitat might require a high disturbance-tolerance (i.e. a bold temperament) due to the excessive costs of continuously fleeing from frequent disturbances (i.e. stress and time taken away from resource acquisition). Although there are only a relatively small number of studies that have experimentally measured disturbance-tolerance in both urban and rural individuals (namely birds), these studies did find urban birds were less 'flighty' (or bolder) than their rural counterparts (Cooke 1980; Traut & Hostetler 2003; Donaldson et al. 2007; Evans et al. 2010; Kitchen et al. 2010). However, in all cases, 'Flight Initiation Distance' in response to an approaching human was used as a measure of disturbance-tolerance. This could be confounded with habituation to humans in urban individuals. Therefore, research into an avian urban adapter using a measure of disturbance-tolerance not directly associated with humans (i.e. measuring an animals' response to a startling sound stimulus) would provide a more generalized measure of boldness and offer a worthwhile addition to behavioural research on urban adapters.

### *Vocal modifications*

Urban adapters need to be able to successfully communicate (avoid vocal masking) in noisy urban environments. This might occur either by an individual having signals naturally well suited to being heard in urban noise or through vocal adjustments. Research suggests that some avian urban adapters can make vocal adjustments that may prevent masking of their signals by anthropogenic noise (Slabbekoorn & Peet 2003; Brumm 2004; Wood & Yezzinac 2006; Hu & Cardoso 2009). However, these studies have investigated adjustments to either the components of a species' signals or signal amplitude, but not both. Accordingly, investigation of both types of vocal adjustments in an avian urban adapter would extend research in this area. What's more, there is currently only a single study measuring amplitude adjustments in an avian urban adapter species (Brumm 2004), and comparison at the intra-urban level remains largely unexplored. This is important because if an animal can make adjustments to suit different noise levels within urban landscapes this would allow it to occupy more urban habitats. Thus research on a vocal modification in an avian urban adapter at the intra-urban level could proffer a more detailed examination of adaptability (or behavioural flexibility).

Vocal research on avian urban wildlife is currently disproportionately orientated toward song (as apposed to calls). Whereas songs are learned, calls are usually innate and therefore expected to show limited plasticity. This begs the question can an avian urban adapter that uses calls make the same types of vocal adjustments identified in other avian urban adapters that use song? It might be that amplitude adjustments offer an alternate temporal mechanism to avoid masking in urban inhabiting species with limited vocal plasticity (i.e.

calling animals). Consequently, research in this area would profit from studies investigating an avian urban adapter that uses calls.

### ***Research outline***

The noisy miner is an ideal model species for a detailed behavioural study on an avian urban adapter due to its extraordinary success in urban environments (Higgins et al. 2001; Low 2002). Additionally, it is well known for its gregarious behaviour and conspicuous calls in both urban and rural habitats (Jurisevic and Sanderson 1994; Higgins et al. 2001). By investigating the behaviours of multiple urban and rural populations of noisy miners, I aimed to identify if miners were inherently bold (as a measure of disturbance-tolerance) (see Chapter 2) and/or had vocal components outside the main frequency range of anthropogenic noise (see Chapter 3), thus predisposing this species behaviourally to inhabit urban environments. Alternatively, if urban miners contrasted in these behaviours from rural counterparts it would suggest at a behavioural flexibility (or plasticity) (i.e. through habituation to frequent disturbances and vocal adjustments) in this species, a trait that has been identified as being critical in adjusting to city-living in other urban adapters. As an additional measure of behavioural flexibility in noisy miners, I measured signal amplitude in multiple urban-based populations experiencing different levels of noise disturbance (see Chapter 4). This study also provided an investigation of behaviour in an urban adapter at the intra-urban level.

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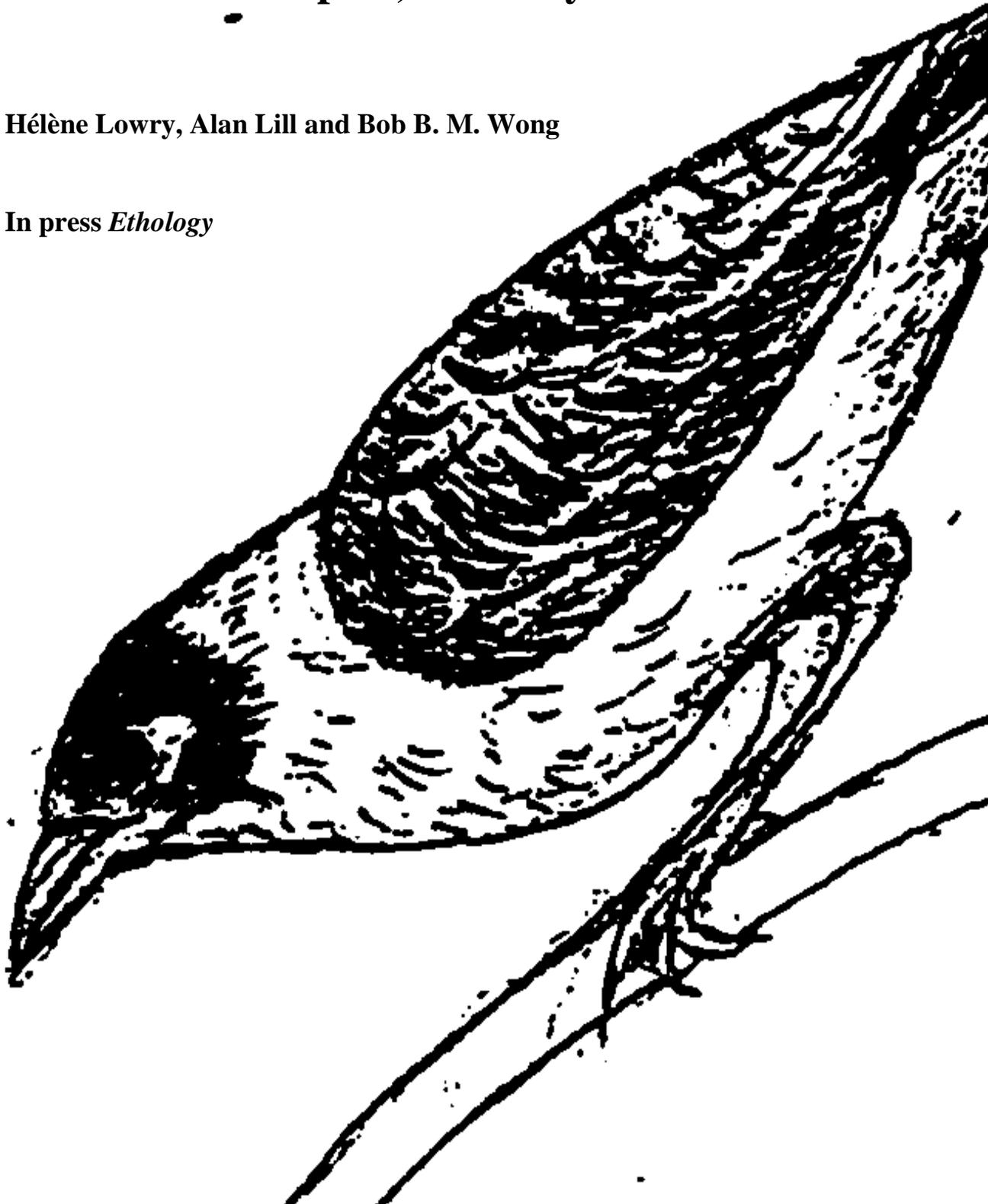
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## Chapter 2

# Tolerance of auditory disturbance by an avian urban adapter, the noisy miner

Hélène Lowry, Alan Lill and Bob B. M. Wong

In press *Ethology*



## **Abstract**

Urbanization creates challenges for wildlife, most notably through changes in resource availability and the frequent occurrence of sensory disturbance. Some native species, however, have been able to exploit and thrive in urban environments. Research, in this regard, has mostly focused on the ecological conditions that have allowed such species to prosper. In contrast, less attention has been devoted to evaluating how they cope with human proximity and disturbance. In a field experiment on a successful Australian ‘urban adapter’, the noisy miner, *Manorina melanocephala*, we compared tolerance of a loud, startling sound stimulus by urban and rural individuals. We found group size differences between birds occupying urban and rural sites: more urban birds came into the testing area in response to the initial alarm call playback compared to rural birds. Urban and rural birds also differed significantly in their behavioural response profile to the test sound stimulus. Nearly half (47.5%) of the rural, but only 22.5% of the urban birds took flight and of those that did, only 1 of 9 urban individuals retreated >5m, compared with 13 of 19 rural birds. About one third of urban, but only 5% of rural individuals responded to the sound stimulus with aggressive displays. The most frequent response to the stimulus, irrespective of habitat type, was to remain near the sound source and engage in visual surveillance. The high frequency of this response in both urban and rural individuals suggested that most noisy miners were quite ‘bold’, a temperament trait that is likely to be important in successful urban colonization by birds.

*Key words:* human disturbance; urban adapter; noisy miner; startling stimulus; aggressive displays; boldness

## **Introduction**

Urbanization presents many challenges for wildlife, including changes in the availability of vital resources, such as food and shelter, and frequent sensory disturbances, such as industrial and vehicular noise and pedestrian traffic (Reijnen et al. 1997; Fernández-Juricic & Telleria 2000). However, some native species, often termed ‘urban adapters’, seem to be ‘pre-adapted’ to exploit urban conditions and thrive in these highly modified environments (Blair 2004; McKinney 2006; Parsons et al. 2006). Insights into why such species are able to prosper in cities whilst others fail are important for understanding the capacity of organisms to exploit changing environments (McKinney 2002; Blair 2004; Faeth et al. 2005) and in devising effective management strategies for urban wildlife (Lunney & Burgin 2004; Chace & Walsh 2006; Baker & Harris 2007; Lunney et al. 2008; Chamberlain et al. 2009). Studies of urban adapters have mostly focused on how cities provide their ecological requirements (Chace & Walsh 2006; Lowry & Lill 2007; Croci et al. 2008), with less attention being given to evaluating how such species are able to cope with human disturbance.

In urban areas, anthropogenic disturbance is usually persistent and frequent (Fuller et al. 2007). For individuals of any species, the cost of ignoring a potentially threatening disturbance must be balanced against the cost of responding, which takes time and energy away from other vital activities and can also be physiologically stressful (Nudds & Bryant 2000; Frid & Dill 2002; Cooper & Frederick 2007; Price 2008). Temperament is likely to be important in enabling species to accommodate to a range of urban stressors (Fraser et al. 2001; Dingemanse et al. 2003). In particular, we might expect members of urban populations to be ‘bolder’ (defined by Coleman and Wilson (1998) p.927 as “the

willingness of an individual to take risks, especially in novel situations”) and tolerate human disturbance more readily than rural conspecifics who come into contact with humans less often (McDougall et al. 2006). For example, some European and Australian birds that have successfully colonized urban areas have been shown to be less wary of approach by humans than rural conspecifics (Cooke 1980; Rollinson 2003; Møller 2008; Kitchen et al. 2010).

The noisy miner, *Manorina melanocephala*, is a large (length 26cm; mass 70-80g), communally-breeding honeyeater (Meliphagidae), native to eastern and south-eastern Australia (Higgins et al. 2001). Noisy miners exhibit complex, but well-documented, social and aggressive behaviours that are easily observed and quantified (Dow 1977; Grey et al. 1997, 1998; Higgins et al. 2001; Hastings & Beattie 2006; Parsons et al. 2006). They typically inhabit open, grassy woodlands that have often been fragmented and degraded by human activity. However, they have also relatively recently occupied many cities and towns throughout their range, where they exploit natural and human-subsidized food resources and have reached high densities (Low 2002). The aim of the present study was to experimentally investigate whether urban noisy miners had a higher tolerance of, and exhibited ‘bolder’ behaviour towards, a startling sound stimulus (a loud noise) than rural conspecifics. To our knowledge, this is the first field based study to use a noise disturbance as a measure of boldness in birds. We wanted a more generalized measure of boldness, rather than one directly associated with humans, such as measuring Flight Initiation Distance in response to an approaching human, which we felt could be confounded with habituation to humans in urban birds.

## Methods

### *Study sites and location of Noisy miner colonies*

Although noisy miners can breed at any time of year (Higgins et al. 2001), experimental work was conducted in April-June during the main non-breeding season. A colony was defined as a group of three or more individuals at least one km away from any other group of conspecifics. Colonies were found by playing back noisy miner alarm calls previously recorded at urban and rural sites (cut-and-pasted into a coherent sequence using Raven Pro Interactive Sound Analysis Software) through a hand-held speaker, as described by Clarke and Oldland (2007). All recordings used for the study were in an uncompressed (i.e. wav) format. The use of uncompressed sound files is important in vocal playback studies to ensure that focal individuals do not perceive the compressed signals differently. Forty urban and forty rural colonies were tested. Urban colony sites were located in metropolitan Melbourne, Australia ( $37^{\circ}50'S$ ,  $145^{\circ}00'E$ ) and included sports fields, playgrounds and public spaces containing a mixture of native and exotic vegetation. Rural sites were in the Central Victorian Goldfields near Maryborough ( $37^{\circ}00'S$ ,  $143^{\circ}44'E$ ) and Bendigo ( $36^{\circ}40'S$ ,  $144^{\circ}15'E$ ), about 150-165 km north of Melbourne, and incorporated roadside *Eucalyptus* corridors and open *Eucalyptus* woodland in National and State parks.

### *Experimental procedure*

We conducted a playback experiment to test the response of noisy miners to a sudden noise disturbance. This was achieved using a speaker attached to the top of an adjustable

tripod (set at 1 m height), linked to an Mp3 player via a 10 m connector lead. The tripod was wrapped in army camouflage fabric to reduce its visibility and was positioned centrally to where a colony had previously been located. A sound-level meter (Radio-shack Db 33-4050) was used to ensure that playback amplitude was set at a predetermined level of 80dB, which is >15dB above the background sound amplitude averages found in studies measuring urban noise (Brumm 2004; Fuller et al. 2007). When any trial had to be terminated due to inclement weather, passing pedestrians or vehicles, the colony was re-tested a minimum of 2 days after the initial attempt.

To minimize any effects of observer presence, playback and behavioural observations were carried out remotely (observer minimally 10 m from the speaker) using the handheld Mp3 player and a pair of binoculars. Dark-coloured clothing was worn at all times. Trials began with playing-back the alarm calls of noisy miners to attract birds to the speaker using the same recording employed during the initial detection of colonies. The alarm calls were played for 40-s, or until at least three noisy miners were perching within 5m of the speaker. The number of birds that came into the testing area in response to the initial alarm call playback was recorded as a measure of group size. A focal bird was then selected using a systematic spatial rule (i.e. the second bird in from the left margin of the group). After a 3-s pause, the observer broadcast a recording of either the test sound or a silent control. The former comprised a loud, hollow-sounding ‘bang’ made by a large, industrial pressing machine. The behaviour of the focal bird was recorded (as frequencies of occurrence) at the start and conclusion of the 3-s pause to determine if there were any changes in behaviour prior to presentation of the stimulus or control ‘sound’ (silence). Observed behaviours shown in response to the sound stimulus

or control silence were grouped into several categories (M. Clarke pers. comm.) described in Table 1. Behaviours (4) (a-e) appeared to be similarly motivated and as such we grouped them together into a single category.

#### *Ethical note*

Noisy miners commonly alarm call in response to a wide variety of threats under natural conditions (Jurisevic & Sanderson 1994) and similar alarm-calling assays have been used before on this species with no adverse effects (Clarke & Oldland 2007). Initial field trials showed that birds returned to 'relaxed' behaviours <10-s after testing. The study received ethics approval from The Biological Sciences Animal Ethics Committee of Monash University.

#### *Statistical analyses*

A Fisher's exact probability test was used to examine if there were any significant differences in behavioural response profiles between urban and rural noisy miners. Two-way Fisher's exact tests were also employed to determine which particular behavioural responses contributed to significant differences between urban and rural colonies. Statistical analyses were conducted with R version 2.2.0 (The R Foundation for Statistical Computing).

## Results

Group sizes of attracted birds (total number of birds present during testing) varied significantly between urban and rural sites ( $p=0.001$ ,  $n=40$  urban and 40 rural sites, Fisher's exact test). Only 5% of rural birds occurred in groups of  $>10$ , compared with 35% of urban birds. Rural birds occurred equally often in the two smaller group size categories recorded ( $<5$  and 5-10, both 47.5%), whereas urban birds only occurred in groups of  $<5$  on 22.5% of occasions.

There was a significant difference between urban and rural noisy miners in their behavioural response profile to the 'startle' stimulus ( $p=0.003$ , Fisher's exact test) (Table 2). Nearly half the rural, but only ~20% of the urban birds took flight ( $p=0.034$ , Fisher's exact test). Flight distance also varied ( $p=0.013$ , Fisher's exact test), with only one of nine urban birds fleeing  $>5\text{m}$  in response to the 'startle' stimulus, compared with 13 of 19 rural individuals. Aggressive/defensive displays also occurred more frequently in urban than rural individuals; nearly a third of urban, but only 5% of rural individuals exhibited such behaviours ( $p=0.006$ , Fisher's exact test). The other two response types ('visual surveying' and 'jump-startle') (Table 1) did not differ ( $p>0.05$ ) between rural and urban individuals.

'Controls', which measured the percentage of focal birds that changed their behaviour from pre-to-post-'silence', were conducted for both urban and rural sites. There was a difference in response behaviours between 'control' and 'startle' tests in both urban and rural populations ( $p<0.0001$  in both cases, Fisher's exact test). Only 7.5% (rural) and 15% (urban) of tests involved a change in behaviour between the beginning and end of

the 3-s presentation of ‘control’ silence, whereas 87.5% (rural) and 92.5% (urban) of tests involving broadcasting of the ‘startle’ stimulus evoked behaviour change.

## **Discussion**

### *Fleeing from the sound stimulus*

One key result was that urban noisy miners were less likely to take flight and exhibited shorter retreat distances than rural conspecifics in response to the startling sound stimulus. Of the focal birds that took flight in urban areas, only one moved from the tree that it occupied at time of testing, whereas the majority of rural birds that took flight relocated to a different tree, indicating that urban birds did not flee just because a ‘safe haven’ was closer. This finding needs to be tested for other cities colonized by this species, but is consistent with the results of several studies comparing flight initiation distance (FID) in conspecific birds inhabiting high- and low-level disturbance environments (Cooke 1980; Keller 1989; Rollinson 2003; Walker et al. 2006; Møller 2008; Kitchen et al. 2010). A high level of disturbance-tolerance is likely to be important in successful urban colonization by birds. If urban noisy miners did not, to some extent, decrease their response to the high levels of human activity and noise in cities, the costs in time deducted from other fitness-enhancing activities (such as feeding) and energy spent on vigilance and fleeing from disturbances would probably be unsustainable (Frid & Dill 2002).

However, the reduced flightiness and shorter retreat distances observed in urban noisy miners may not necessarily have reflected greater tolerance of the startling sound

stimulus. Urban noisy miners were not only found to be generally less ‘flighty’ (or bolder), but on average significantly more urban than rural individuals approached the sound source in response to the initial alarm call playback. Although group size at the time of testing was obviously not an accurate population density measure, we suggest that it probably reflected a trend toward larger colonies in urban than rural habitats. Higher population densities and smaller territories have been correlated with relatively shorter retreat distances from threatening stimuli in urban than rural conspecifics in other bird species (Møller 2008). Long-distance retreat from perceived threats might therefore be avoided because it would frequently result in conflict with neighbouring colonies through territorial incursions. Additionally, urban birds may have been less likely to flee due to perceived ‘safety in numbers’. Risk-taking behaviour, for example, has been shown to vary with social context in great tit, *Parus major*, with certain individuals becoming bolder in the presence of a companion (Van Oers et al. 2005).

#### *Responding aggressively to the sound stimulus*

A second key observation was the common occurrence of an aggressive response to the startling sound stimulus by noisy miners. Studies of other successful avian urban colonisers have also reported the occurrence of aggressive responses to a repeatedly presented, visually perceived threat at the nest (Jones 2008; Levey et al. 2009). However, the present investigation showed that a single, threatening (or alarming) sound stimulus encountered away from the nest was sufficient to elicit an aggressive response in noisy miners. Moreover, urban individuals exhibited aggressive behaviour significantly more often than rural conspecifics in response to the presentation of this stimulus. This seemed

to indicate a propensity for bold behaviour in these urban birds, especially given that (a) the stimulus did not provide much information that would allow a bird to effectively assess its severity as a threat from a distance and (b) it was not obviously associated with humans, repeated exposure to whom might be expected to lead to habituation in the urban environment. It is not possible to entirely dismiss habituation to loud noise events in the urban environment as the cause of the bolder behaviour shown in response to the test-sound-stimulus by urban noisy miners. However rural birds (including those tested in the current study) often inhabit roadside vegetation and, as a result, may experience exposure to passing trucks and other vehicular traffic, which create sporadic loud noise events. Habituation also requires frequent exposure to the stimulus (Evans et al. 2010), in this case a directed ‘loud’ noise (*sensu* Wiley & Richards 1978), which even in the urban environment seems unlikely for the kind of sound stimulus that we presented. Additionally, habituation cannot account for the more frequent occurrence of aggressive responses observed in urban birds.

#### *The origin of boldness in urban noisy miners*

If, as our study suggests, suburbia contained bolder noisy miners than the nearby rural environment, there are two ways in which this might have occurred. First, individuals that initially colonized Melbourne may have been inherently bolder than those that did not. These birds would therefore naturally have been better equipped to persist and thrive in the disturbance-rich urban environment, with further selection then possibly enhancing this boldness. Second, learning may also have been important, with birds habituating to a new set of potentially threatening stimuli within the urban environment. Research on a

single urban and a nearby rural population of European blackbirds, *Turdus merula*, in Germany found no evidence of genetic differentiation between adult urban and rural individuals, but disparities in breeding density, length of the daytime activity period and ‘tameness’ suggested that there was sufficient phenotypic (behavioural) plasticity in this species to facilitate urban colonization (Partecke et al. 2006a). However, other comparative studies with European blackbirds suggest that differences between populations may be subject to some level of genetic control (Partecke et al. 2006b; Partecke & Gwinner 2007). More recently, a study by Møller (2008) demonstrated that variation in relative FID of urban populations of successful urban adapter bird species in Europe was predicted by the estimated number of generations since urbanization, suggesting that genetic adaptation had occurred. A recent study investigating behavioural traits in urban and rural populations of male song sparrows, *Melospiza melodia*, identified a correlation between boldness and territorial aggression; urban birds were bolder and more territorial than rural conspecifics, suggesting that urban boldness may be part of a behavioural syndrome (Evans et al. 2010). Heritable differences in risk-taking and exploratory behaviour demonstrated in hand-reared great tits also seem to suggest the existence of avian ‘personalities’ (Van Oers et al. 2004). To determine what process is driving the divergence between urban and rural noisy miners’ responses to a startling sound stimulus, future studies might investigate whether there is genetic differentiation between city and country birds, and if there is any evidence of a behavioural syndrome in this species manifested in stable, correlated differences (Sih et al. 2004) in boldness and aggression among individuals.

### *Responding with visual surveillance to the sound stimulus*

The third key finding in the present study was that ‘visual surveying’, in which a noisy miner visually monitored its surroundings whilst remaining in the immediate vicinity of the sound stimulus’ origin (Table 1), was the most common response by urban individuals and very common in rural birds. Of all the responses observed, it should have been the most cost-effective if it was adaptive, because of its presumed relatively small energy expenditure. The frequent occurrence of this response in both urban and rural individuals seemed to indicate that most noisy miners in the study had a ‘bold’ temperament. Sirot (2007) described a ‘bold’ bird as being alert for some time when disturbed and only taking flight if the threat actually proved to be a predatory attack. Our finding may therefore indicate that there is a behavioural pre-disposition to inhabit urban environments in the noisy miner, stemming from a naturally high tolerance of sensory disturbance (i.e. boldness), although a comparison of the relative frequency of the visual surveillance or similar responses to this kind of sound stimulus in other urban adapters and avoiders (McKinney 2002) would be required to reach this conclusion unequivocally. Another apparent manifestation of boldness in noisy miners is their tendency to react aggressively to a wide range of bird species and some mammals (e.g. domestic dogs) that do not appear to pose a competitive or predatory threat (Dow 1977) and even to their own mirror image (A. Lill, unpublished data). If boldness is inherent in noisy miners, an intriguing, unanswered question is what the adaptive value of this trait might have been in the species’ original natural habitat.

## **Acknowledgements**

This study complies with all the relevant State and Federal legislation of Australia.

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**Table 1** Categorization of behaviours exhibited by noisy miners on presentation of the startling sound stimulus

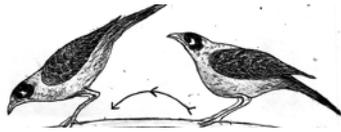
Response categories	Behaviour	Description
<b>(1) Take flight:</b>		
a) >5m		Focal bird left the immediate area, landing a minimum of 5m away from its original perching position
b) <5m		Departing focal bird landed within 5m of its original perching position
<b>(2) Jump-startle:</b>		
		Focal bird took flight in a jump-like manoeuvre directly upwards from its original perching position and landed either back in the original perching position or on the branch <1m directly above it
		
<b>(3) Visual surveying:</b>		
		Focal bird remained in its original perching position whilst observing its immediate surroundings by turning its head from side-to-side
		
<b>(4) Aggressive/defensive:</b>		
a) Posturing/Alarm-calling		Focal bird assumed a 'pointed' stance, with the neck stretched out toward the target, the bill held closed, or open if alarm-calling (described by Higgins et al. (2001) as a strong threat behaviour)
		

b) Wing-wave/bill-gape/  
Yammer-call



Focal bird flexed its wings at the carpal joints, with the wings held out in a rigidly-waving stance accompanied by open bill-gaping and a yammering call (described by Higgins et al. (2001) as a threat display)

c) Forward branch hop



Focal bird took a forward movement along the branch towards the source of the threat in a hop-like movement, with its body in a crouch-like, pointing stance

d) Agitated flight

Focal bird flew in a direct horizontal line above the speaker set-up. This is an aggressive, inward flight, not a form of retreat behaviour

e) Swoop

Focal bird made a direct inward flight low over the speaker set-up in a dive-bomb type manoeuvre

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**Table 2** Proportional and actual occurrence of various behaviours in response to presentation of the starling sound stimulus in focal noisy miners in urban and rural colonies n=40 birds in each environment.

<b>Colony location</b>	<b>Percentage (actual frequency) of response behaviour</b>			
	<b>Take flight</b>	<b>Jump startle</b>	<b>Visual Surveying</b>	<b>Aggressive/defensive</b>
<b>Urban</b>	22.5 (9)	15 (6)	32.5 (13)	30 (12)
<b>Rural</b>	47.5 (19)	5 (2)	42.5 (17)	5 (2)

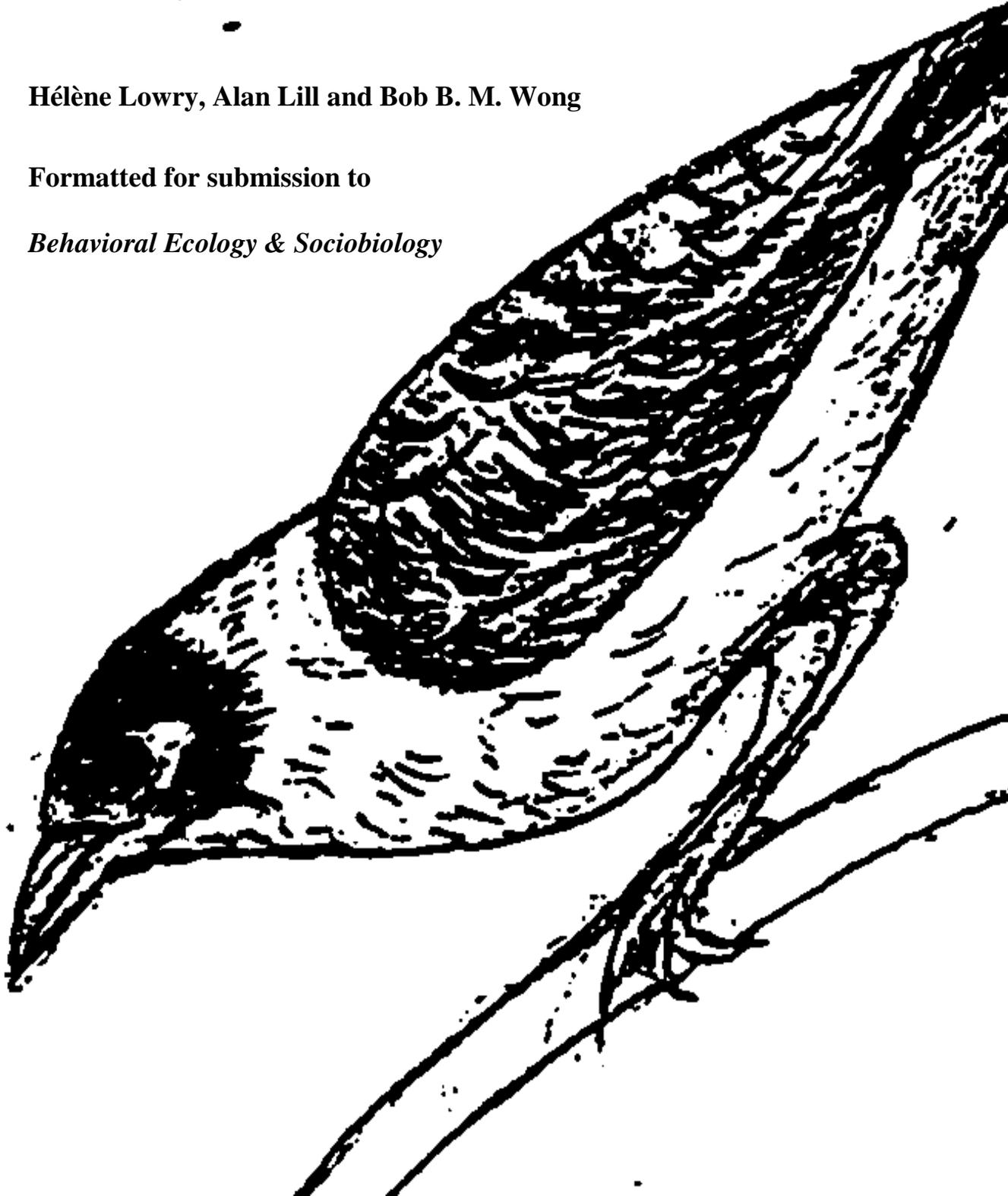
## Chapter 3

# The effect of anthropogenic noise on vocal communication in an avian urban ‘adaptee’, the noisy miner

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## Abstract

Urban environments are characteristically noisy, which can pose a challenge for animals that communicate acoustically. Although evidence suggests that some birds can make acoustic adjustments that preclude masking of their signals in high disturbance environments such as cities, studies to date have tended to focus on acoustic signals important in mate attraction (e.g. songs). Far less attention has been given to the impact of urban noise on other kinds of calls. To redress this, we compared a range of different vocalizations (encompassing alarm calls, begging calls and parent response calls) among urban and rural individuals of a successful Australian ‘urban adapter’, the noisy miner, *Manorina melanocephala*. We found that urban miners had significantly higher minimum frequencies for calls with low base-frequencies (< 2kHz); however, calls with base-frequencies ‘naturally’ above the main frequency range of urban noise (> 2kHz) had the same minimum frequency in urban and rural birds. Maximum frequency was significantly higher in urban miners for all call types, whilst dominant frequency and call duration did not differ between urban and rural individuals. Although urban noisy miners exhibited differences from rural individuals in the minimum frequency of calls, this shift was not large enough to avoid masking from low-frequency anthropogenic noise. Nevertheless, our findings suggest that the calls of noisy miners may be ‘naturally’ well suited to being heard in noisy urban environments by virtue of having (a) high maximum frequencies, (b) dominant frequencies above that of low-level anthropogenic noise and (c) several important call-types with frequencies that are higher than the main frequency range associated with urban noise.

**Key words:** acoustic signals; anthropogenic noise; call adjustments; noisy miner; urban adapter.

## **Introduction**

Anthropogenic noise is a common feature of urban environments and has the capacity to mask the vocal signals of animals that rely on acoustic communication. In this regard, recent observations suggest that anthropogenic noise may potentially exclude certain species from urban areas (Hu and Cardoso 2009). Yet, despite frequent sensory disturbance, some animals including many that rely on acoustic communication not only are able to cope with a noisy environment but appear highly adept at exploiting the conditions afforded by urbanization (Blair 2004; McKinney 2006; Parsons et al. 2006). Termed ‘urban adapters’ (McKinney 2006), such species provide us with a unique opportunity to understand why some species are able to prosper under human-altered conditions whilst others languish (McKinney 2002; Blair 2004).

With the exception of sudden, loud noises, anthropogenic noise is most prevalent at lower sound frequencies (1-2 kHz) (Slabbekoorn and Peet 2003). Short periods of elevated environmental noise levels can be mitigated by a short-term behavioural response, such as temporarily halting vocalizing (Lengagne 2008). By contrast, ubiquitous, low-level noise poses a greater challenge in terms of vocal masking (Slabbekoorn and Ripmeester 2007). This is especially true for many birds that rely heavily on acoustic signals in social interactions, mate attraction, territory defense, antipredator behaviour, and parent-offspring communication (Slabbekoorn 2004). Some evidence suggests that birds in noisy urban environments make vocal changes, such as alterations to frequency (kHz),

timing, duration, and/or amplitude of songs. For example, urban European robins, *Erithacus rubecula* reduced sound interference by singing at night in areas that were noisiest during the day (Fuller et al. 2007), whilst the common nightingale, *Luscinia megarhynchos* increased the amplitude of its signals in the presence of fluctuating and chronically elevated noise levels (Brumm 2004). Other research has found that urban song sparrows, *Melospiza melodia*, (Wood and Yezerinac 2006) and great tits, *Parus major* (Slabbekoorn and den Boer-Visser 2006) increased the minimum frequency of song notes and, in so doing, effectively reduced vocal masking in urban environments (see also: Nemeth and Brumm 2009; Parris and Schneider 2009; Potvin et al. 2011 for examples of frequency adjustments). Despite substantial research into facultative shifts in the vocalizations of urban birds, most studies have tended to focus on vocalizations important in mate attraction (e.g. songs). Surprisingly, far less attention has been given to calls that are produced in other important social contexts, such as alarm signalling and parent-offspring communication (Hu and Cardoso 2009; Potvin et al. 2011).

The noisy miner is a large (length 26 cm; mass 70-80 g), communally-breeding honeyeater (Meliphagidae), native to eastern and south-eastern Australia (Higgins et al. 2001). In recent times, this species has successfully colonized and reached high population densities in urban environments (Low 2002). Noisy miners are easily identified by their distinct and persistent loud calls (Jurisevic and Sanderson 1994) making them an ideal species for a field-based acoustic study. The aim of this study was to compare the pitch and frequency of calls produced by urban and rural noisy miners. A variety of call types was investigated (i.e. alarm calls, begging calls, parent-offspring calls) to determine whether urban birds have diverged vocally from their rural

counterparts. In particular, we were interested in determining whether such differences (if any) reduce masking by anthropogenic noise and/or, alternatively, if noisy miner vocalizations are inherently produced at higher frequencies than low-frequency, anthropogenic noise typical of the urban environment.

## **Methods**

Recording work was conducted during the main breeding season from August to December 2008. A colony was defined as a minimum of 3 noisy miners separated by at least 1 km from any other group of noisy miners. Colonies were located by playing back a noisy miner alarm call (in uncompressed wav file format) broadcast through a hand-held speaker, as described by Clarke and Oldland (2007). The alarm call was recorded using a hand-held directional Sennheiser RF-condenser microphone (MKH816TU) with a basket windshield (to reduce wind noise), connected to an M-audio micro-track 24/96 mobile digital recorder; the recording level was set at medium (specific gain setting) and the sampling rate at 44 kHz. Recordings of urban and rural noisy miner alarm calls were obtained by entering areas known to be occupied by noisy miners, with birds alarm calling in response to the observer's presence. Recordings of the most frequently heard alarm calls from multiple urban and rural sites were then cut-and-pasted into a coherent sequence using Raven Pro Interactive Sound Analysis Software (Charif et al. 2007). This was undertaken to ensure focal birds from both habitat types were responding to a recording that was not biased toward urban or rural sites lest there were differences in alarm calls between site types. Recordings were obtained from 140 colonies. These were equally divided between Metropolitan Melbourne, Victoria (37°50'S, 145° 00'E) (70

urban sites), and the Central Victorian Goldfields (70 rural sites), encompassing the Maryborough (37°00'S, 143° 44'E (165-km NW of Melbourne)) and Bendigo regions (36°40'S, 144° 15'E (151-km NNW of Melbourne)). Urban sites were located within parkland (multi-purpose sites comprising a combination of sporting fields, playgrounds and public space, with varying degrees of native and exotic vegetation); rural sites incorporated National and State parks (open *Eucalyptus* woodland), as well as roadside habitat (*Eucalyptus* 'corridors').

### Call sampling

Recording of noisy miner calls was conducted during the most vocally-active period of the day (0500-1000h) when birds are known to be 'vocally active' (Hochachka et al. 2009). Recordings were only made during dry, still conditions. Calls were recorded using the same recording equipment as that used to record alarm calls (see above). The recording level was set at 'medium' and the sampling rate at 44 kHz for both habitat types. On arriving at an occupied site, the observer located the closest out-of-nest juvenile, identified visually and by its distinctive begging call. The hand-held microphone was positioned so that clear air-space separated the microphone and the vocalizing bird, thus limiting interference from background noise. All calls of juvenile(s) and associated adults were recorded for a period of 8 min. During a recording session, we identified the type of call and whether the bird was perching or flying. In instances where more than one juvenile was present during recording, each was given a number (spoken onto a digital recorder at the time of recording), so that individual begging calls could be identified later. A recording session was terminated if no vocalizations other than the

begging call were obtained in 5 min or if weather conditions became unfavourable (i.e. wind velocity increased) or the focal juvenile(s) left the immediate area. In instances where a recording session was terminated before the 8 min limit, the site was revisited for a second session at least 10 days after the first visit.

#### Ambient noise sampling

To identify differences in ambient noise between urban and rural sites, ambient noise levels were recorded immediately after completion of call recordings, using the same equipment and settings as those used for recording bird calls. Ambient noise was recorded from the same location as the vocal recording. The observer first directed the hand-held microphone at the perching location of the calling bird and took a 1 min recording, then turned 90-degrees to record for a further minute etc., until a total of four 1 min recordings had been obtained.

#### Analysis of call recordings

Calls were digitised at a 44 kHz sampling rate and 16 bit encoding using the M-audio micro-track 24/96 mobile digital recorder and were downloaded directly into Raven-pro 1.3 Beta Version Software, in which spectrograms (Hamming type) were produced. Eight minute recordings of calls were divided into 1 min sections. Random numbers were then generated to identify the 1 min section of the recording which would be analysed for a particular call type. We recorded and compared 5 different call types between urban and rural birds: the juvenile begging call, adult-to-juvenile post-feeding call and three different kinds of adult alarm calls (see Fig 1. for call classifications and spectrograms).

Only one recording of each call type was analysed per study site. All call types analysed comprised a single, repeated note, with the exception of the post-feed call which comprised two distinct call notes. The first clear note of the selected call type was identified visually for analysis based on the clarity of the call spectrogram; a pre-determined number of repeats (further renditions of the same note) of that call was also selected for analysis (begging call=4-repeats, 3 alarm calls=3-repeats, post-feed-call=single (note-1) single (note-2)). The selected call notes were then cut-and-pasted into a composite file. Visual analysis was conducted from spectrograms on all replicates in cut-and-pasted files; measured manually by drawing a selection around the selected call note, where the top boundary is the highest frequency of the sound and the bottom boundary is the lowest frequency of the sound (Charif et al. 2007). The following vocal components were measured: minimum frequency (kHz), maximum frequency (kHz), frequency bandwidth (kHz) (highest minus lowest frequency), delta time (s) (call length) and dominant frequency (kHz) (the frequency with the most energy). For each field site, measurements of the repeats of each vocal component for each call type were then pooled and mean values were calculated.

#### Analysis of ambient noise recordings

Ambient noise recordings were digitised at the same settings as described for call recordings (see above) and downloaded into Raven-pro software. For each 1 min recording (four  $\times$  1 min per site), four 2 s sections were randomly selected and cut-and-pasted into files. All noise events were included within this initial analysis, including vocalizations of heterospecific birds. A total of sixteen 2 s sections were obtained from

each site, from which a site ambient noise mean value was calculated. For each section the following features were analysed: start time (s), end time (s), frequency range (kHz) and peak power (dB). A second analysis of frequency range which excluded sudden, loud noises was also undertaken, as it was thought that constant noise would be the greater challenge for birds in terms of call masking (Slabbekoorn and Ripmeester 2007). A single measure of the frequency range was obtained using the selection bar (see Charif et al. 2007 for details on creating range selections in Raven-pro) to visually identify the frequency band, which remained constant throughout the entire 1 min recording. The four maximum frequency values for each site were pooled and a site ambient noise mean value was calculated. Recordings of both noisy miner calls and ambient noise were analysed 'blind' as to the source of the recording (i.e. urban versus rural) to avoid any potential observer bias.

### Statistical analyses

All data were checked for normality and homogeneity of variances, but transformation was deemed unnecessary. Two sample t-tests were used to compare the calls of urban and rural noisy miners, as well as the ambient noise levels between urban and rural sites, with the results being presented as mean  $\pm$  SE and alpha was set at = 0.05. All analyses were performed using R version 2.2.0 (The R Foundation for Statistical Computing).

Ethics approval for our study was granted by The Biological Sciences Animal Ethics Committee of Monash University (protocol no.: BSCI/2008/05).

## Results

### Call features

The Minimum frequency of calls was not significantly different between urban and rural noisy miners for higher base-frequency (>2kHz) calls (Begging call and Alarm call (1); Fig. 2a). However, calls with low base-frequencies (<2kHz) had a significantly higher minimum frequency ( $p<0.03$ ) in urban than rural individuals (Alarm calls (2) and (3) and Post-feed-call notes; Fig. 2a). Maximum frequency, and consequently frequency bandwidth, was significantly greater in urban miners for all five call types (Fig. 2b & c). Conversely, dominant frequency did not differ significantly between urban and rural individuals for any call type (Fig. 2d) Call duration did not differ significantly between urban and rural birds with the exception of the second note of the post-feed-call, which was significantly longer in rural noisy miners (Fig. 2e).

### Ambient noise

Overall, urban study sites had significantly higher maximum ambient noise frequencies (and consequently a broader frequency range) than rural sites. This was true irrespective of whether short-term, loud noises (defined as lasting <10 s) were included or excluded from the analyses (with short-term noises events included: means urban =  $4.100\pm 1.193$ kHz, rural =  $2.519\pm 1.251$ kHz,  $t=-7.549$ ,  $p<0.001$ ; excluded: means urban =  $2.153\pm 0.551$ kHz, rural =  $0.956\pm 0.623$ kHz,  $t=-11.972$ ,  $p<0.001$ ,  $n_{\text{urban}}=n_{\text{rural}}=70$  in both analyses). The amplitude of ambient noise was also significantly higher in urban than

rural sites (means: urban =  $72.5 \pm 3.5$  dB, rural =  $63.5 \pm 3.5$  dB,  $t = -14.917$ ,  $p < 0.001$ ,  $n_{\text{urban}} = n_{\text{rural}} = 70$ ).

## **Discussion**

### **Comparison of call features in urban and rural habitats**

#### Minimum frequency

We found significant differences in the minimum frequency of relatively low frequency (kHz) call-types (<2 kHz) between urban and rural noisy miners. By contrast, we found that noisy miner calls with base-frequencies naturally above the main frequency range of urban noise (>2 kHz) as measured in this (see results: Ambient noise) and other urban studies (see Slabbekoorn and Peet 2003), had the same minimum frequency in urban and rural miners. In other words, there was no difference in calls that would be somewhat robust against vocal masking. However, urban noise often extends beyond the described main frequency band of 2 kHz and thus the possibility that the higher frequency noisy miner calls still overlapped spectrally with background urban noise cannot be discounted. Facultative shifts in minimum frequency of songs have been identified in several songbirds (Fernandez-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Wood and Yererinac 2006; Slabbekoorn et al. 2007; Nemeth and Brumm 2009; Potvin et al, 2011) and, more recently, in calls in urban environments (Hu and Cardoso 2010; Potvin et al. 2011). In these studies, birds were found to increase the lower frequency of signals above the main frequency band of anthropogenic noise and, in so doing, avoid vocal masking. Interestingly, the higher minimum frequency of the relatively low frequency

call-types observed in the present study, although statistically significant, was not sufficiently large to prevent masking of calls from background noise in urban habitats (Fig. 2a). A recent study of 12 species of urban birds encompassing both songs and calls found that species with intermediate minimum frequencies (1-1.5 kHz) raised the minimum frequency more than species with either higher or lower minimum frequencies (Hu and Cardoso 2010). Of the three noisy miner calls that had a higher minimum frequency among urban than rural individuals, two had minimum frequencies within the intermediate range described by Hu and Cardoso (2010). Interestingly, these authors found no difference between urban and rural noisy miner calls in their study, but given that they combined all call-types together in a single analysis, it is possible that they simply were unable to detect the differences that we detected by analysing different call types separately.

A possible explanation for the small shifts in minimum frequency observed in the current study (given the recent large-scale urban colonization by this species: Higgins et al. 2001) is that vocal adaptation to noisy urban habitats may still be in its early stages and may continue to evolve. Interestingly, small frequency shifts have also been observed in frogs inhabiting noisy environments. However, unlike songbirds, frogs do not learn their calls from conspecifics, and may therefore be expected to show a much slower population-level shift in call frequency (kHz) (Parris et al. 2009). Alternatively, it has been suggested that an increase in song pitch might not be an adaptation that reduces sound masking by anthropogenic noise, but rather a physiological side-effect of birds signalling at higher amplitudes in urban environments (Nemeth and Brumm 2010). Hence the shifts in

minimum frequency of calls observed in this study might simply be a side-effect of urban birds calling more loudly.

#### Maximum frequency and frequency bandwidth

Urban noisy miners showed substantially higher maximum signal frequencies than rural conspecifics for all five call types recorded in the current study. In the begging calls of tree swallows, *Tachycineta bicolor*, increases in maximum frequency have been observed with increasing noise levels at the nest (Leonard and Horn 2005). However, to date, most research on urban songbirds has found that urban and rural individuals do not differ statistically in the maximum frequency of the signals they produced (Slabbekoorn and Peet 2003; Fernandez-Juricic et al. 2005; Wood and Yezarinac 2006). There are two possible explanations for the difference observed in the current study. By raising the maximum frequency of calls, and consequently increasing the frequency bandwidth of the call, urban noisy miner may reduce masking during periods of elevated environmental noise, which can extend to much higher frequencies. However, in their natural rural habitat, open-woodland birds such as noisy miners tend to use higher maximum frequencies than forest-dwelling birds. This is probably because attenuation of lower sound frequencies over distance is more pronounced in open habitats (Hunter and Krebs 1979; Shy 1983; Wiley 1991; Nicholls and Goldizen 2006). We cannot, however, rule out a further possibility, which is that maximum frequencies are inherently harder to decipher when one is visually analysing call spectrograms, which have a tendency to 'fade-out' at higher frequencies (Wiley 1991). Given that urban focal miners were typically closer to the microphone than rural individuals were during recording sessions, the observed

difference between urban and rural calls in maximum frequency may simply reflect a difference in the clarity of the upper spectrum in call recordings. Recording the calls of urban and rural individuals under more ‘controlled’ conditions could potentially clarify this possibility.

### Dominant frequency

There was no discernable difference between urban and rural noisy miners in dominant frequency for any of the calls measured. Shifts in dominant frequency have been identified in other birds (Wood and Yezerinac 2006; Parris and Schneider 2009; Hu and Cardoso 2010) and frogs (Parris et al. 2009) inhabiting noisy environments. These shifts are generally interpreted as a mechanism that reduces masking by low-frequency anthropogenic noise. However, raising the minimum, rather than the dominant, frequency of signals appears to be more common in urban environments, despite the dominant frequency being the more important channel for acoustic communication. This suggests that modifications to the dominant frequency may be more costly to the signaller (Hu and Cardoso 2010). Species with inherently high dominant frequencies might therefore be expected to have a natural advantage in noisy urban environments. Research on 520 bird species’ vocalizations, encompassing ‘songs’ and ‘calls’, identified that species that are common in urban habitats generally vocalize at a higher dominant frequency than ex-urban, con-generic species (Hu and Cardoso 2009). A similar pattern has been shown for birds occupying roadside habitats; the songs of species that are more abundant near roads (indicating greater tolerance of noise) had significantly higher dominant frequencies than those of species that were less abundant near roads (Rheindt 2003). In the current study,

the dominant frequency of all five noisy miner calls was above the main frequency range of anthropogenic urban noise measured in this study (see results: Ambient noise), indicating that the calls are inherently audible in urban habitats. As with the differences observed in maximum frequency, the high dominant frequency of calls probably reflects natural selection for higher frequency signals in open woodland birds (see maximum frequency and frequency bandwidth). Thus Australian open-woodland birds may be vocally ‘pre-adapted’ to inhabit urban environments, which may partly explain why open-woodland birds are such common residents of Australian cities (Bayly and Blumstein 2001; Rollinson 2003; Shukuroglou and McCarthy 2006; Lowry and Lill 2007).

#### Call duration

Increasing the duration of signals has been shown to improve the detectability of sounds in white noise (Patricelli and Blickley 2006) and several studies have found facultative shifts in call duration in birds living in noisy conditions in urban habitats (Slabbekoorn and den Boer-Visser 2006; Nemeth and Brumm 2009). In contrast, research on urban song sparrows (Wood and Yezerinac 2006) and dark-eyed juncos, *Junco hyemalis* (Slabbekoorn et al. 2007), found that individuals did not change trill duration where both species showed adjustments to the frequency (kHz) of songs under noisy conditions. We found no differences in call duration between urban and rural noisy miners, apart from the second note of the post-feeding-call. Conceivably noisy miners lack the vocal plasticity to adjust the duration of call-notes. Alternatively, they may not need to adjust the duration of calls in urban environments because of ‘pre-adapted’ vocal traits, such as

the high maximum-frequency of their calls and having dominant frequencies above urban anthropogenic noise averages (see maximum frequency and frequency bandwidth and dominant frequency).

## Conclusions

Urban noisy miners exhibited differences in their calls from rural individuals that could reduce masking by low-level anthropogenic noise, but the shift in minimum frequency was not large enough to entirely avoid such masking. Call adjustments in this species may be at an early stage of adaptive tuning to urban conditions, a process which may be slower for calls than for learned songs. Our findings also suggest that the calls of noisy miners may be naturally well-suited to being heard in noisy urban environments, by virtue of having (a) high maximum-frequencies, (b) dominant frequencies above that of low-level anthropogenic noise and (c) several important call-types that are at higher frequencies than the main frequency range of urban noise. A detailed comparison of calls of other conspecific urban adapters and avoiders would be required to establish this conclusion unequivocally. Temporal adjustments in calls and associated behaviours, which are more 'plastic' and have been shown to improve signal transmission in noise (e.g. shifts in vocal amplitude (Brumm and Todt 2002; Brumm 2004)), and an increase in perching height during vocalizing (Kirschel et al. 2009) could also profitably be investigated as additional (or alternative) mechanisms employed by noisy miners to mitigate urban noise effects.

## **Acknowledgments**

This study complies with all the relevant State and Federal legislation of Australia.

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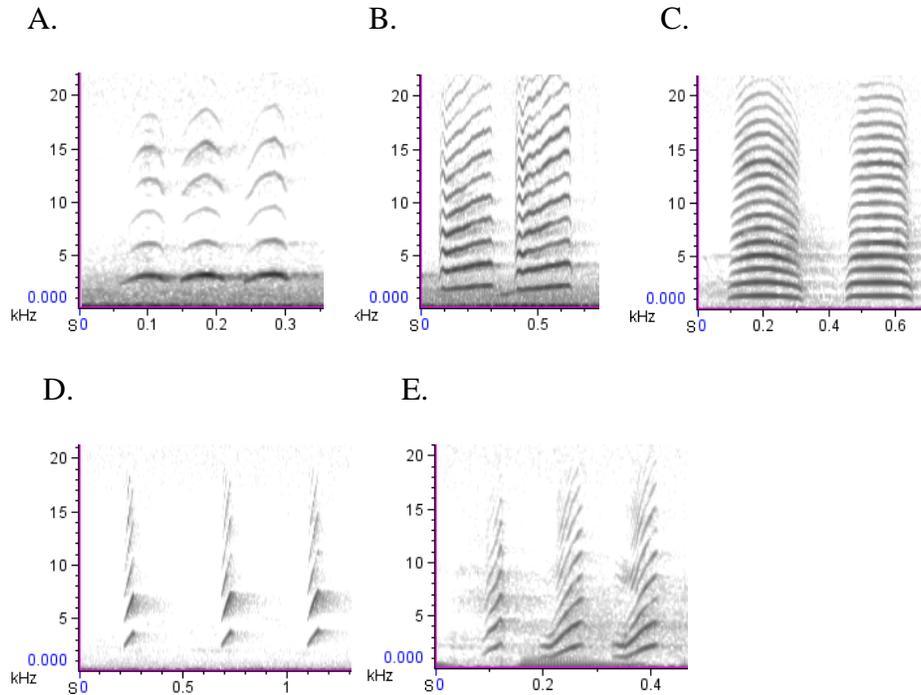
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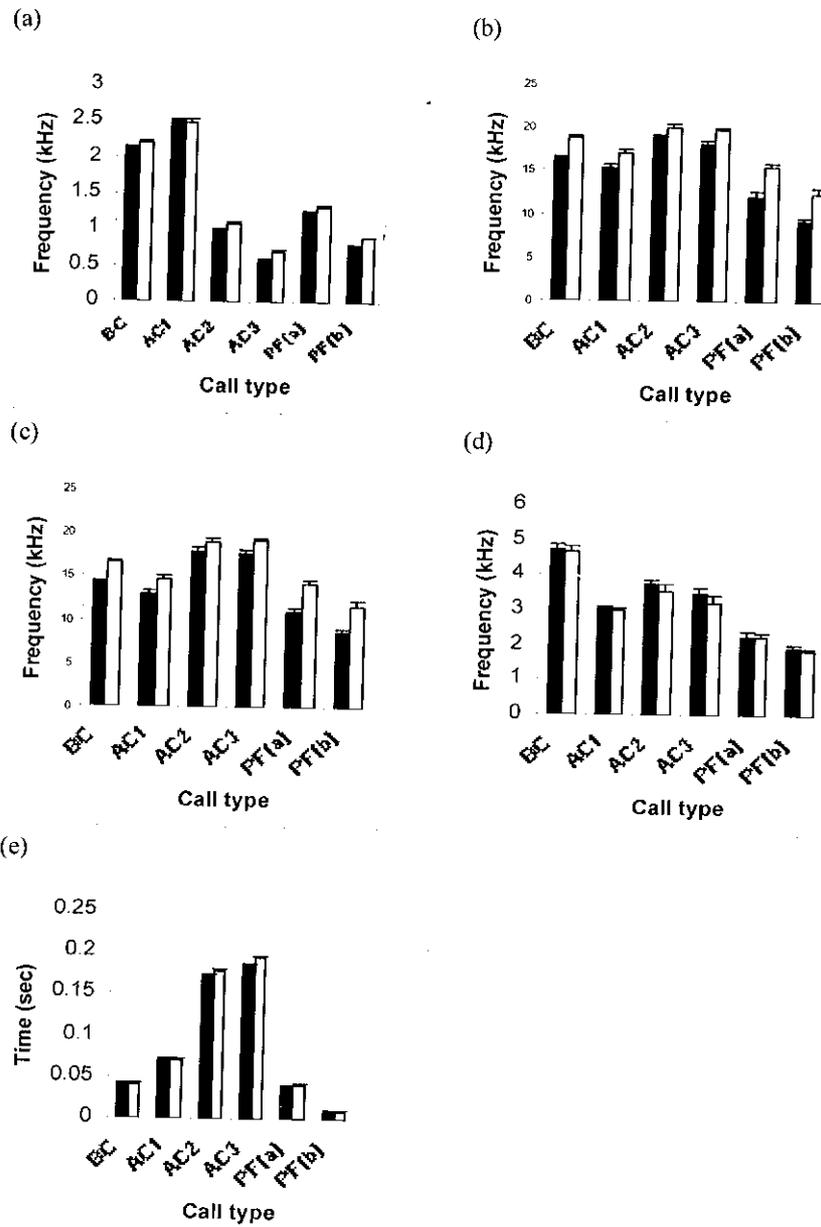
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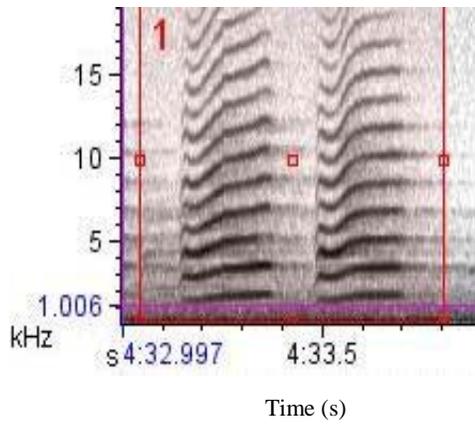


**Fig. 1** Spectrograms of all five noisy miner calls. (A) Alarm call (1) (AC1) repeated single note high-pitch whistle alarm call (associated with aerial predators and mobbing), (B) Alarm call (2) (AC2) loud repeated single note alarm call (associated with ground predators and mobbing), (C) Alarm call (3) (AC3) husky repeated single note alarm call (associated with ground predators and mobbing), (D) Begging call (BC) repeated single note chip call of fledglings, (E) Post-feed-call (PF) harmonic call of male to fledgling consisting of a single high intensity note followed by a series of ascending notes ranging 2 to 7 repeats.

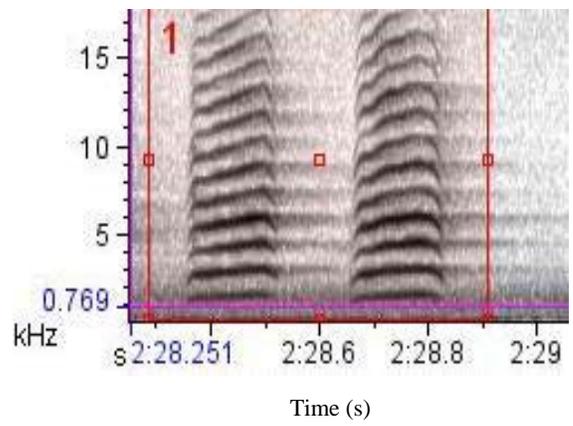


**Fig. 2** Comparison of five noisy miner call features: (a) minimum frequency, (b) maximum frequency, (c) frequency bandwidth, (d) dominant frequency and (e) call duration. Mean  $\pm$  SE are given for five call types ((BG) Begging call, (AC1) Alarm call (1), (AC2) Alarm call (2), (AC3) Alarm call (3), (PF) Post-feed-call (a) and (b)) among rural (black bars) and urban (white bars) populations

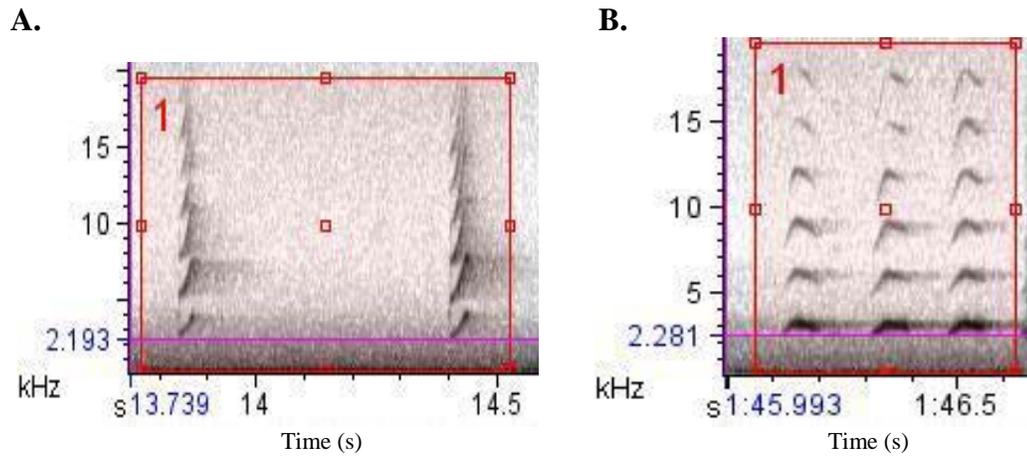
**A.**



**B.**



**Fig. 3** Spectrograms of the minimum frequency (marked by the pink line) of one of the lower frequency noisy miner alarm calls (AC2) show a small difference between (A) urban birds and (B) rural birds



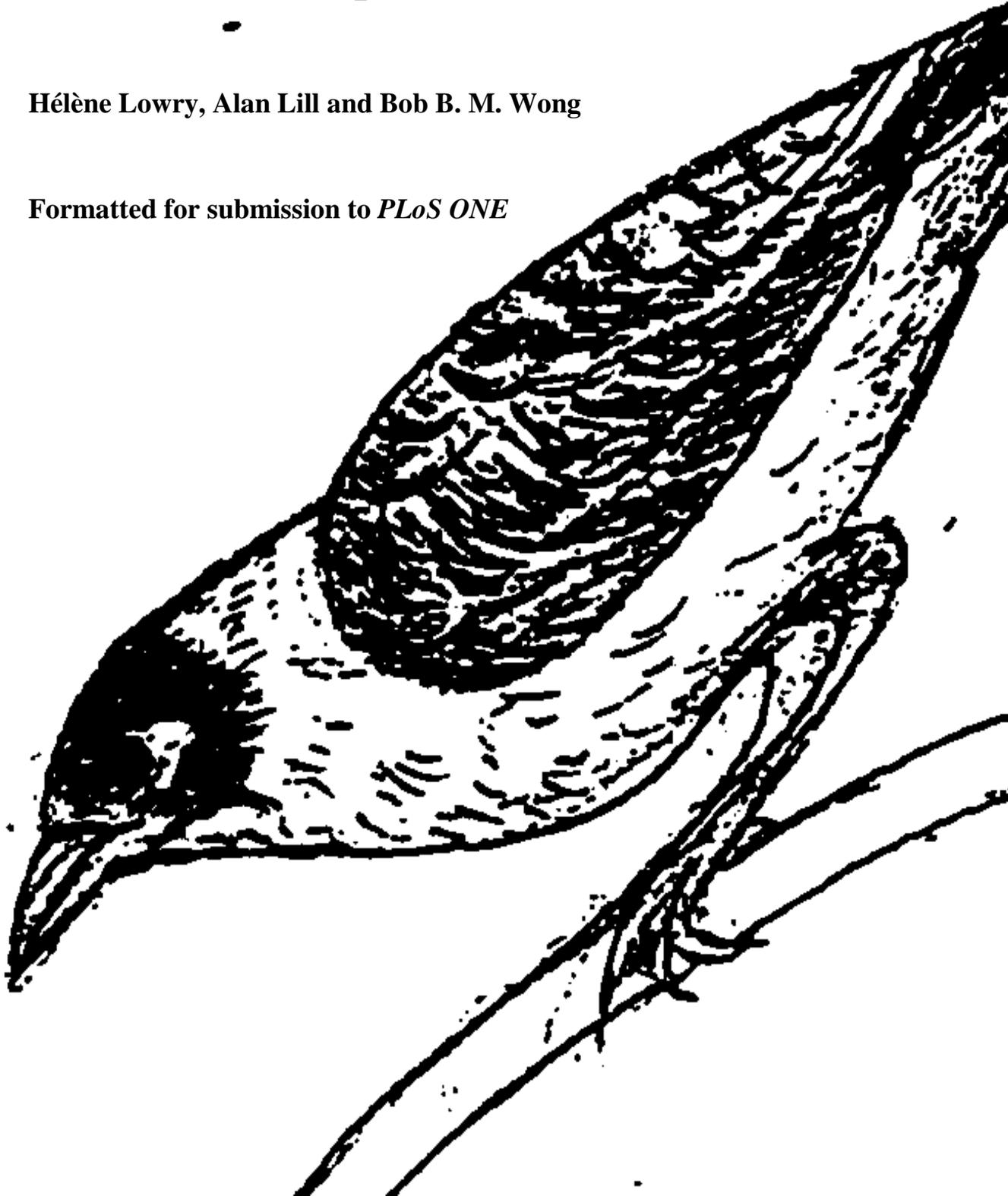
**Fig. 4** The minimum frequency (marked by the pink line) and all other call components ‘naturally’ avoid low-level anthropogenic noise (1-2kHz), as shown in spectrograms of noisy miner call recordings for (A) juvenile begging call (BC) and (B) adult high-pitch alarm call (AC1)

## Chapter 4

# How noisy does a noisy miner have to be? Amplitude adjustments of alarm calls in an avian urban ‘adapter’

Hélène Lowry, Alan Lill and Bob B. M. Wong

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## **Abstract**

**Background:** Urban environments generate constant loud noise, which creates a formidable challenge for many animals relying on acoustic communication. Some birds make vocal adjustments that reduce auditory masking by altering, for example, the frequency (kHz) or timing of vocalizations. Another adjustment, well documented for birds under laboratory but not field conditions, is a noise level-dependent change in sound signal amplitude (the Lombard effect). To date, however, field research on amplitude adjustments in birds has focused exclusively on song.

**Methods:** We investigated amplitude regulation of alarm calls using, as our model, a successful urban ‘adapter’ species, the noisy miner, *Manorina melanocephala*. We compared several different alarm calls under contrasting noise conditions.

**Results:** Individuals at noisier locations (arterial roads) alarm called significantly more loudly than those at quieter locations (residential streets). Other mechanisms known to improve sound signal transmission in ‘noise’, namely use of higher perches and in-flight calling, did not differ between site types. Intriguingly, the observed preferential use of different alarm calls by noisy miners inhabiting arterial roads and residential streets was unlikely to have constituted a vocal modification made in response to sound-masking in the urban environment because the calls involved fell within the main frequency range of background anthropogenic noise.

**Conclusions:** The results of our study suggest that a species, which has the ability to adjust the amplitude of its signals, might have a ‘natural’ advantage in noisy urban environments.

**Keywords:** Lombard effect; amplitude adjustments; alarm calls; noisy miner; anthropogenic noise; urban adapter

## **Introduction**

Animals that rely on acoustic communication must ensure that their vocalizations are not masked by background noise. Individuals may therefore need to modify their signals under different sound conditions if they are to be discernible to conspecifics [1]. Whilst background noise is a ubiquitous feature of natural environments, the level of noise often associated with urban settings represents a particularly formidable challenge for individuals of many species that communicate acoustically [1-3]. A common feature of urban environments is constant, loud, anthropogenic noise. Insights gleaned from animals that are reliant on vocal communication, but are nevertheless able to succeed within the challenging acoustic environment posed by cities (described as urban ‘adapters’; [4]), can help us to understand the ability of species to cope with conditions altered by humans [5-7].

Some birds in urban environments have the capacity to make vocal adjustments. This is often achieved by altering, for example, the frequency (kHz) [8-13] and/or duration [9-10] of their signals in such a way as to avoid auditory masking by background noise. Another important form of vocal adjustment, which has been well documented for birds in laboratory studies [14-17] but has received surprisingly scant attention under more natural, field conditions, are noise-dependent changes to the amplitude of sound signals.

The Lombard effect, whereby animals maintain the broadcast area of their vocalizations by increasing vocal amplitude in response to an increase in background noise level [18], has been described for only one urban bird species, the common nightingale, *Luscinia megarhynchos*. In that species, birds inhabiting noisier locations sang more loudly than those living in quieter locations [19]. Interestingly, a study modelling the benefits of adjustments to vocal amplitude and frequency (kHz) in urban great tits, *Parus major*, and European blackbirds, *Turdus merula*, suggested that an increase in song amplitude was the more effective means of improving signal transmission in urban noise [20]. However, adjustments to vocal amplitude are energetically costly [21] and some species may simply lack the physiological capacity (e.g. through limitations of the communication system, such as low membrane tension of the trachea or bronchi; [22]) or vocal ‘plasticity’ to make such adjustments [1]. Given that many birds rely heavily on vocalizations to communicate [23], the ability to make amplitude adjustments in noisy environments could have a direct bearing on individual fitness and consequently influence which birds are able to inhabit urban environments.

To date, field research on amplitude adjustments in birds has focused almost exclusively on song, with very little (if any) attention being given to other types of vocalization. Additionally, most studies of urban adapters tend to only compare birds in urban and non-urban locations, but we know little about the differences that might occur within the urban environment. Accordingly, we conducted the first wholly urban field study comparing amplitude regulation of the alarm calls of a successful urban adapter species. Alarm calls differ functionally from songs in that they are used to communicate important information among conspecifics (and sometimes among heterospecifics) on

the appropriate response to a perceived threat (i.e. to assemble or flee) [22]. Masking of alarm signals by anthropogenic noise might therefore have a particularly strong impact on a species' success in urban environments.

The noisy miner is a large (length 26 cm; mass 70-80 g), native, Australian honeyeater (Meliphagidae) currently thriving in noisy, urban environments [24]. The species can be easily identified by its distinct and loud alarm calls [25]. The specific aim of the study was to determine whether noisy miners call in a manner consistent with the Lombard effect in urban environments. We did this by directly comparing the amplitude of their alarm calls in the immediate vicinity of roads with contrasting background noise levels. Additionally, associated behaviours known to improve signal transmission in birds (increases in perching height, use of in-flight calls and call selection; [9, 26, 27]) were investigated as other possible mechanisms employed by noisy miners that might mitigate the masking effect of urban noise.

## **Methods**

### Ethical note

From an ethical perspective, dogs are not novel stimuli to the focal species in urban environments, and the response elicited in noisy miners is short-lived and appears to have no adverse effects on the birds. Nonetheless, in this project a concerted effort was made to limit disturbance of the birds by visiting each site with the dog only once. Disturbance to birds caused by the dog's presence was also very brief (maximum of 3-min per focal individual) and the dog remained on the lead and was not allowed to approach within 5-m

of the perching bird. The dog appeared oblivious to the birds. The study was approved by The Biological Sciences Animal Ethics Committee of Monash University.

#### Study sites and locations of bird colonies

Although noisy miners can breed at any time of year [24], experimental work was conducted in February to April during the main non-breeding season. Noisy miners were located aurally (by their distinctive alarm calls) and visually whilst walking or driving along arterial roads and residential streets in metropolitan Melbourne, Australia (37°50'S, 145° 00'E), where the species is widely distributed. A colony was defined as a group of three or more noisy miners at least 500 m away from any other group of conspecifics. Eighty colonies were tested; these were equally divided between arterial road (>5000 vehicles per day) and residential street sites (<500 vehicles per day), which both contained a mixture of native and exotic roadside vegetation.

#### Experimental procedure

Recording of adult noisy miners' calls and observation of associated behaviours were undertaken on weekdays (Mon-Fri) during the peak morning vehicular traffic period (07:00-09:30 hrs; based on Vic Roads Traffic Volume Data [28]), which also coincides with the most vocally-active period of the day (05:00-10:00 hrs) when birds use much of their vocal repertoire [29]. Recordings were only made during dry, still conditions. We recorded alarm calls along a 400 m long transect next to the road. In order to elicit the actual alarm calls, an observer (H.L.) walked the length of the transect at a pace of 0.5 m/s with a domestic dog tethered on a short (1 m) lead. We used a dog to elicit alarm

calls because noisy miners frequently encounter dogs in urban environments and alarm call in response to their presence. On sighting an adult noisy miner within 5 m of the transect, the observer stopped, instructed the dog to sit beside her, and waited until the sighted individual vocalized. A hand-held Centre 322 Data Logger Sound level meter with a 1.3 cm Electret Condenser microphone was positioned so that there was a clear path between the microphone and the vocalizing bird, thus limiting interference from background noise. The time weighting on the meter was set on 'slow response' (1 s), the sampling range on 'auto' (measuring level range: 30-130 dB) and the frequency on A-weighting (used for general sound-level measurements) for all recordings. The recording continued until the bird had finished vocalizing, which sometimes comprised multiple call bouts. If the bird began vocalizing before the observer and her dog had approached within 5 m, the recording was made from the point where the observer was when the bird began vocalizing. For all recordings, the horizontal distance between the observer and the focal bird's perching location was paced out, and the perching height (m) of the focal bird was measured with a Haglof Electronic clinometer.

During a recording session, the focal bird's call choice (the type of alarm call it employed in response to the dog's presence; see Chapter 3 for alarm call classifications), any disturbance other than vehicular traffic within 5 m of the focal bird (e. g. pedestrian walking along footpath) and any other birds present (species, number of individuals and behaviour(s)) within that distance were also noted. Recordings were not conducted if a juvenile noisy miner was within 5 m of the transect, as adults would be expected to behave differently (i.e. be more aggressive) in the presence of juveniles. If the focal bird did not vocalize within 3 min or flew off, the observer moved on to a 'new' individual. If

the individual flew off after the observer had made a recording, binoculars were used to identify where it had gone to ensure that it was not re-sampled. In instances where no call recordings were obtained during an entire site visit, the site was revisited on another day at least 7 days later.

Ambient noise levels were recorded immediately after completion of alarm call recording, using the same equipment and settings. Ambient noise was recorded from the same point as the vocal recording. The observer first directed the hand-held sound-level meter at the bird's perching location and took a 10 s recording, subsequently turning 90° and repeating the process, until a total of four 10 s recordings had been obtained. We also documented, for each site, the number and type of all in-flight calls emitted by any noisy miners within 10 m either side of the transect line whilst the observer was walking the transect.

#### Acoustic analyses

The sound-level meter was directly connected to a PC and recordings were loaded into a data logger spreadsheet using Setup Testlink SE-322 (Sound Level Meter) – RS232 interface software program. For each data set, recording number, start and end time ( $\pm 1$  s), and sound amplitude level (minimum, maximum, and average in decibels (dB)) were noted.

Call recordings were taken at varying distances from the focal bird, so it was necessary to standardize all recordings to a set distance for analysis. Preliminary tests on the effect of distance on sound attenuation showed that there was a significant linear relationship

between the amplitude of a call and the ‘actual’ (or direct) distance between the focal bird and the observer. Therefore, we calculated the ‘actual’ distance from the horizontal and vertical distances using Pythagoras’ theorem and then converted all recordings to amplitude of the signal at 1 m from the vocalizing bird, as described in Brumm [19]. The signal-to-noise ratio of each recording was subsequently calculated from the standardized data according to the logarithmic computation procedures given in Leader et al. [30].

### Statistics

All data were checked for normality and homogeneity of variances. Two sample t-tests were used to compare call amplitude and corresponding background noise levels for noisy miners occupying arterial and residential roads, as well as perching height of focal birds in these two locations. An ordinary least squares linear regression was used to identify if there was a significant relationship between call amplitude and the background noise at sites. A Pearson’s Chi-squared goodness-of-fit test was used to compare the frequency of in-flight calls between arterial and residential road sites and a Fisher’s exact test to examine if there were any significant overall differences in type of alarm call used between noisy miners occupying the two types of site. Two-way Fisher’s exact tests were also employed to determine which particular call types contributed to significant differences between birds inhabiting arterial and residential sites. Unless indicated otherwise, all results are presented as mean±s.e. with alpha set at 0.05. Statistical analyses were conducted with R version 2.20 (The R Foundation for Statistical Computing).

## Results

There was a significant difference in background noise level between arterial and residential roads (mean amplitude: arterial =  $65.80 \pm 0.47$  dB, residential =  $50.83 \pm 0.50$  dB,  $t = 21.9069$ ,  $df = 96$ ,  $p < 0.001$ ). Alarm call amplitude of noisy miners was also greater at arterial than residential roads (mean amplitude (at 1 m distance from bird): arterial =  $88.60 \pm 0.59$  dB, residential =  $79.53 \pm 0.90$  dB,  $t = 8.713$ ,  $df = 95$ ,  $p < 0.001$ ). Overall, a significant relationship was found between the background noise level at a site and the amplitude of noisy miner alarm calls; individuals at noisier locations called more loudly than those at quieter locations (figure 1;  $r^2 = 0.552$ ,  $df = 95$ ,  $p < 0.001$ ), indicating that noisy miners were exhibiting the Lombard effect in urban Melbourne. The signal-to-noise ratio was significantly lower on arterial than residential roads ( $t = -11.132$ ,  $df = 95$ ,  $p < 0.001$ ).

Perching height (mean: arterial =  $6.8 \pm 0.52$  m, residential =  $6.6 \pm 0.73$  m,  $t = 0.2147$ ,  $df = 96$ ,  $p = 0.831$ ) and use of in-flight calling ( $\chi^2 = 2.0126$ ,  $df = 1$ ,  $p = 0.156$ ) were not significantly different between arterial and residential roads. However, call selection was significantly different between road types ( $p = 0.03$ , Fisher's exact test); birds on arterial roads were more frequently heard giving alarm call type 2 (70.4%) than residential road birds (54.6%), whilst the latter used alarm call type 3 (43.2%) more often than arterial road birds (20.4%) ( $p = 0.04$ , Fisher's exact test). Both these alarm calls are low-frequency in nature (Lowry et al. unpublished data), and so would not be expected to avoid masking by background noise. The high-pitched alarm call (alarm call 1), which would elude masking by low-frequency anthropogenic noise, was not significantly

different in occurrence between road types. It was only recorded on 5 occasions on arterial roads and once on residential roads ( $p=0.23$ , Fisher's exact test).

## Discussion

### Amplitude adjustments

Overall, our results indicate that noisy miners at noisier locations (busier arterial roads) were calling more loudly than individuals at quieter locations (residential streets). A similar pattern of amplitude adjustments in relation to background noise levels (the Lombard effect) has been shown in the song of another urban adapter, the common nightingale [19]. By increasing the amplitude of the signal, and thus increasing the signal-to-noise ratio (hereafter SNR), the 'active space' of the signal is maintained, so that conspecifics can detect a vocalization in noise [31]. Birds vary in their ability to hear in noise and thus the required SNR for an individual to communicate successfully with a conspecific in noise will differ among species [32]. There is some suggestion that passerines have poorer auditory sensitivity at lower sound frequencies [33], which correspond with the main frequency range of anthropogenic noise (see [34]).

Accordingly, passerines, such as noisy miners, may need to compensate for this in urban environments through amplitude adjustments compared to species that have more discriminating hearing at lower frequencies.

There are numerous laboratory-based studies demonstrating the Lombard effect for animal 'calls' (e.g. budgerigar, *Melopsittacus undulatus* [14]; common marmoset, *Callithrix jacchus* [18]; domestic fowl, *Gallus gallus domesticus* [35]). Interestingly, a

recent study by Nemeth and Brumm [20] suggests that amplitude adjustments are a more effective means of reducing sound attenuation in noisy conditions than frequency (kHz) adjustments (see also [8,9, 10,12, 36, 37] for examples of frequency adjustments in songbirds). This may help to explain why some bird species whose vocal signals fall within the main frequency range of anthropogenic noise (described as 1-2 kHz; [34]) and which lack the vocal flexibility to make frequency (kHz) adjustments (calls are expected to be less 'flexible' than learnt vocalizations such as song), are able to inhabit noisy urban environments.

In the current study, signal amplitudes exceeded 90 dB in some instances, demonstrating that noisy miners have the vocal capacity to easily exceed the background sound amplitude averages recorded in this (see section 'Results') and other studies measuring urban noise (see [13,19]). Surprisingly, high-amplitude signal production is not limited to larger birds; Brackenbury [38] measured amplitudes ranging from 74-100 dB (at 1 m from vocalizing bird) in 17 European songbird species, some of which were <20 g in body weight. However, high-amplitude vocal output is energetically costly (i.e. involves an increased rate of oxygen consumption) [22] and, consequently, would be more costly to a small than a large bird, due to its higher mass-specific metabolic rate [22]. This is reflected in Brackenbury's [38] study, which found that generally the poorest performances (lower maximum total sound power) came from the smaller birds. Thus, smaller birds may experience particular difficulty in communicating vocally under continuously noisy conditions such as those encountered in cities. The ability to produce high-amplitude vocal signals over extended periods is likely to be an important pre-requisite for birds to successfully colonize noisy, urban environments, and a comparison

of the capacity to do this in other urban adapters and avoiders (*sensu* [5]) would be an interesting extension of the present study.

#### In-flight calls and perching height

Perching height adjustment and in-flight calling are both indirect mechanisms that can be employed by birds to improve signal broadcasting. By increasing its elevation, a bird can create a clearer transmission pathway for its signal (i.e. ground attenuation and wind and temperature ‘shadow zones’ have a greater impact at lower elevations *sensu* [39]) and thus improve its SNR [40], whilst use of in-flight calling allows the signaller to increase its vocal range to receivers on the ground [39]. This has been demonstrated for the European blackbird [41] and green hylia, *Hylia praxina* [26]. However, in the current study, we found that noisy miners showed no difference in perching height or the frequency of in-flight calls between arterial and residential roads. The similar average perching heights of vocalizing noisy miners in both road types may reflect similarities in the roadside vegetation (e.g. in tree height).

#### Call selection

Recently Luther and Baptister [27] found that white-crowned sparrows, *Zonotrichia leucophry*, favoured songs with the highest minimum frequencies over lower frequency songs in urban environments. We also found significant differences in alarm call selection between noisy miners inhabiting arterial and residential roads. However, the two alarm calls whose use differed between road types for the current study had low frequencies (< 2 kHz) (Lowry et al. unpublished data) that were within the frequency

range (1-2 kHz) of background anthropogenic noise (see [34]). Therefore use of either of these alarm calls would be unlikely to prevent masking by background noise in urban habitats. Theoretically this difference in alarm call selection could simply reflect a difference in response to the approaching observer during recording sessions; noisy miners at higher-disturbance sites (arterial roads) might experience pedestrians walking dogs less often than birds on residential roads and thus perceive the threat differently and select a different alarm call for that reason. However, research on noisy miner alarm calling has shown that these birds can alternate between all three of the described calls in response to the same threat, making the observed differences in the current study difficult to interpret [25].

## Conclusions

Urban noisy miners appear to exhibit the Lombard effect in avoiding masking of important vocal signals in noisy urban environments by amplitude adjustment. However, there was no evidence to suggest that other behavioural mechanisms known to improve signal transmission in noise in birds, such as increases in perching height and in-flight calling were being employed more commonly in noisier areas. Whilst we found significant differences in alarm call selection between noisy miners inhabiting arterial and residential roads, the low frequencies (kHz) of the calls selected fell within the main frequency range of anthropogenic urban noise (1-2 kHz) and thus use of these calls is unlikely to constitute a vocal modification made in response to sound-masking in the urban environment. Our findings, in conjunction with other research on signal amplitude adjustments in birds, seem to suggest that the type (i.e. call or song) and the frequency

(kHz) of the signals used may not necessarily limit a species' capacity to mitigate vocal masking by urban noise. A species, which has the ability to adjust the amplitude of its signals, might have a natural advantage in noisy urban environments.

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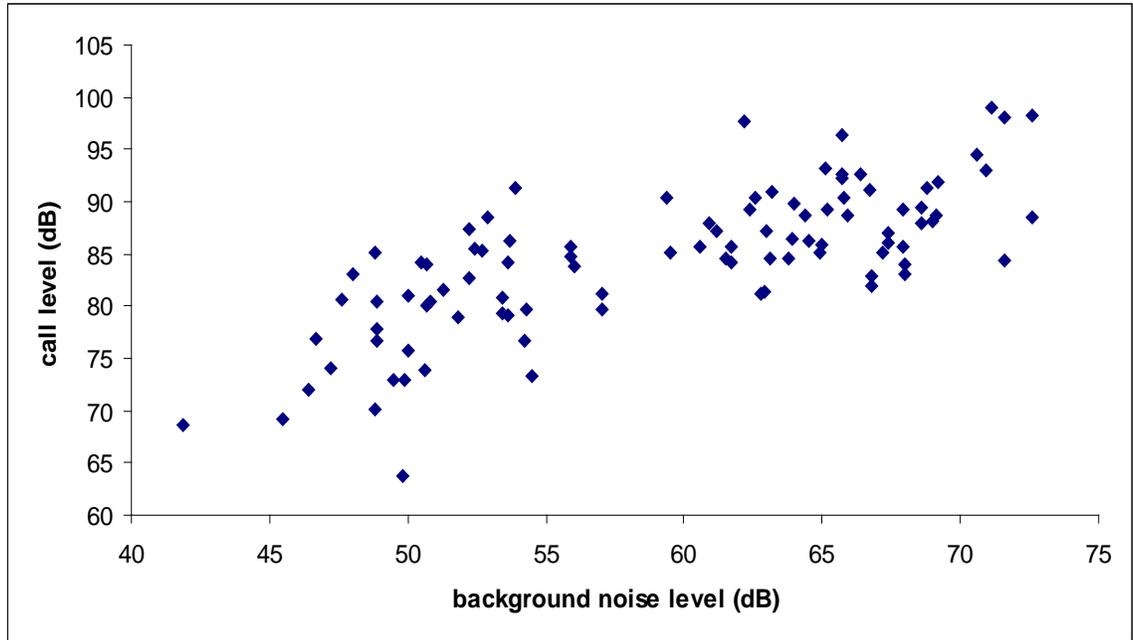
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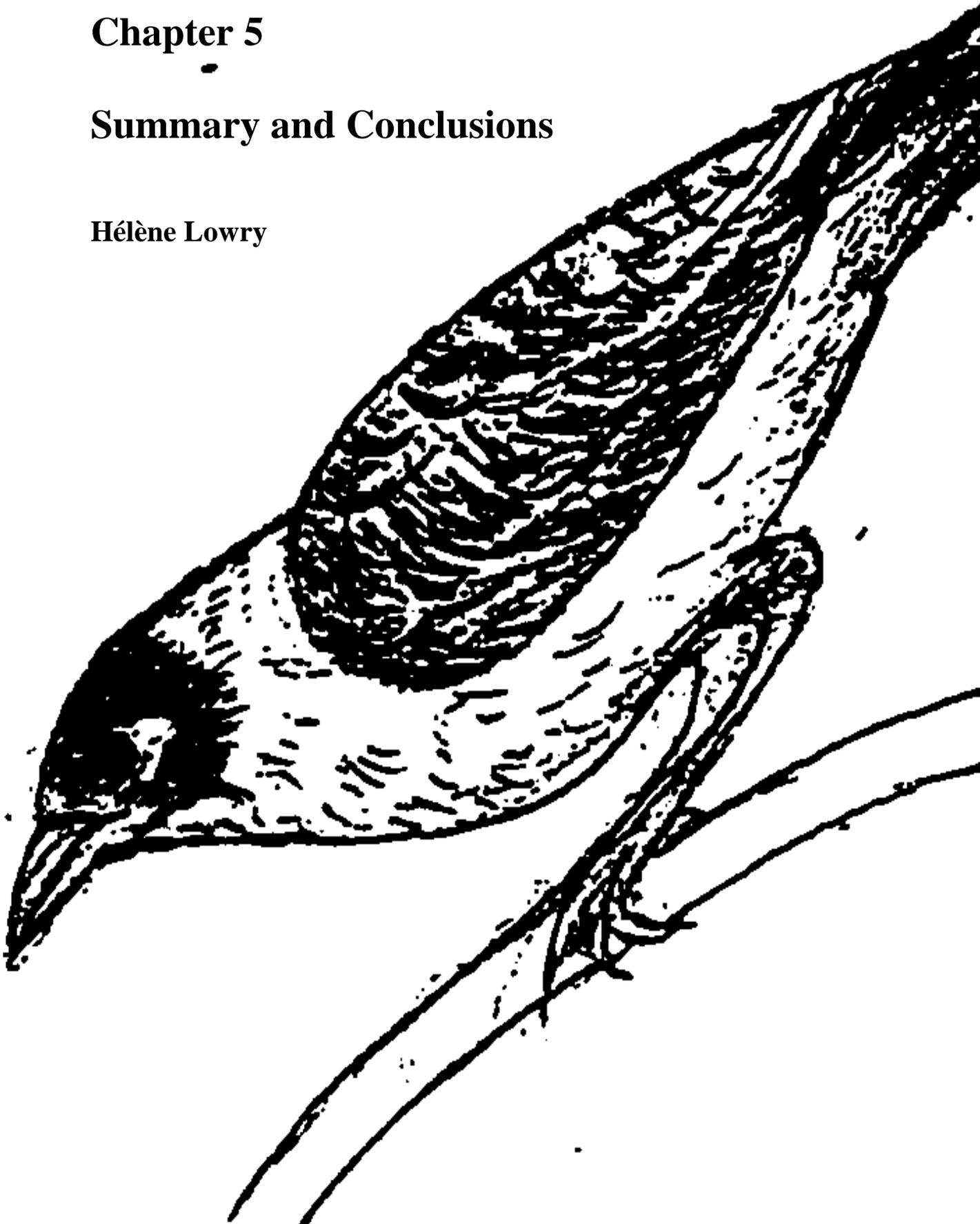


**Figure 1.** Relationship between environmental background noise level in urban habitat and the amplitude of urban noisy miner calls. Each datum represents the mean value (dB) for one noisy miner.

# Chapter 5

## Summary and Conclusions

Hélène Lowry



This study investigated several behavioural traits in a successful avian urban adapter, the noisy miner. The main aims of the research were to determine if urban birds had diverged from rural conspecifics in behaviours expected to assist urban habitation. In particular, I was interested in establishing if noisy miners (1) demonstrated a higher disturbance-tolerance (i.e. were bolder) in urban than rural environments and (2) if urban individuals adjusted their vocalizations in a manner that reduced masking by anthropogenic background noise through changes in frequency (kHz) and/or amplitude (the Lombard effect).

### **Tolerance of disturbance**

I hypothesised that for a bird to successfully inhabit high disturbance urban environments, it would need to have a high disturbance-threshold (i.e. a 'bold' temperament) given the energetic cost of responding to frequent disturbances would almost certainly be unsustainable in the long-term (Frid & Dill 2002). My study on the response of noisy miners to a startling sound stimulus demonstrated that urban individuals were less 'flighty' and exhibited more aggressive behaviours than rural birds. However, both urban and rural noisy miners most frequently responded to the stimulus by remaining in the immediate testing area and visually surveying their surroundings (Chapter 2). Whereas reduced flightiness has been demonstrated in other urban adapters (Cooke 1980; Møller 2008; Kitchen et al. 2010), this is the first study to show birds either not retreating or responding aggressively to a potential 'threat' stimulus. Although habituation to frequent disturbances in urban environments cannot be ruled out entirely

by this study, it cannot explain the higher rates of aggression recorded for urban noisy miners.

The frequent occurrence of both urban and rural focal miners staying in the testing area and visually surveying the area in response to the sound stimulus seems to suggest that most noisy miners had a relatively bold temperament, irrespective of whether they were inhabiting urban or rural areas. Whether particularly bold individuals (i.e. more aggressive birds) colonize urban habitats in the first instance, thus creating discrepancies in aggression and flightiness between urban and rural populations cannot be established from this kind of study. However, given the present findings, it would seem to warrant further investigation. For example, use of a sound stimulus to test disturbance-tolerance in other urban adapter species would help to identify if elevated aggression is more widespread among urban animals or if noisy miners are unique in this context.

Interestingly, the noisy miner has attracted considerable research interest for its highly aggressive behaviour toward cohabiting bird species in rural environments, lending support to the idea that this species may be inherently bold. Noisy miners may thus be temperamentally suited to colonizing high disturbance environments (see Dow 1977; Grey et al. 1997 & 1998; Hastings & Beattie 2006 for examples of noisy miners' effects on bird species assemblages in rural habitats).

### **Vocal modifications**

Although it is well established that some acoustically-communicating animals can adjust their vocalizations in urban environments (i.e. make frequency (kHz) and amplitude

adjustments), research to date has been disproportionately focused on birdsong. I wanted to redress this imbalance by determining if noisy miners could modify their 'calls' in urban environments or, alternatively, if their vocalizations are inherently produced at a frequency and/or amplitude that would naturally elude masking by anthropogenic noise. Although my results indicated that urban birds were adjusting the minimum frequency (kHz) of calls with low base-frequencies (i.e. calls that naturally fall within the main frequency range of urban anthropogenic noise of 1-2 kHz), these shifts were not large enough to prevent masking by urban noise (Chapter 3). Whether the observed frequency (kHz) adjustments represented an early stage of adaptive tuning to urban environments and will continue to evolve is unclear. A long-term study would be required to answer this question with any certainty. Alternatively, these shifts may be a consequence of signal amplitude adjustments (the Lombard effect), a vocal modification that noisy miners were clearly demonstrating in urban habitats. Specifically, my results showed that noisy miners inhabiting noisier arterial roads consistently called more loudly than individuals occupying quieter residential streets (Chapter 4).

The idea that frequency shifts might be a by-product of birds signalling more loudly was proposed by Nemeth and Brumm (2010) in a study modelling the benefits of adjustments to vocal amplitude and frequency (kHz) in urban birds. They found that an increase in song amplitude was the more effective means of improving signal transmission in noise. However, given that not all call-types measured in urban noisy miners had shifted in minimum frequency, it is difficult to decipher if the two vocal adjustments reported in this thesis (in minimum frequency and call amplitude) are linked. Future research should consider combining measurement of vocal amplitude and frequencies in the field to

identify if the two are associated (i.e. to ascertain if frequency adjustments are indeed a physiological side-effect of birds singing at higher amplitudes in urban environments).

If frequency shifts do improve sound signal transmission in urban noise, other call features measured in the present study suggest that noisy miners might be naturally well suited to being heard in noisy urban environments. In particular, their calls have high maximum and dominant frequencies and they possess several call-types that have minimum frequencies above the main frequency range of anthropogenic noise (Chapter 3).

### **Concluding remarks**

The main findings of my study suggest that noisy miners are inherently well suited to colonizing and inhabiting urban environments by virtue of having a high disturbance-threshold (or bold temperament) and vocalizations whose features make them likely to be clearly heard in noisy environments. There is also some indication that this species has the flexibility (or plasticity) to appropriately modify its behaviour (i.e. through sound frequency and amplitude adjustments) for urban conditions to some degree. These findings highlight the importance of incorporating behavioural assays into research on urban adapter species if we are to gain a better understanding of what allows some species, but not others, to inhabit urban environments successfully.

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