



Which birds adjust the frequency of vocalizations in urban noise?

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Urban environments present an opportunity to study the evolution of animal communication in acoustically novel habitats. Several species of birds raise the minimum frequency of vocalizations in urban noise, which is louder at lower frequencies. We recorded 12 species of birds in urban and nonurban environments, and tested whether the extent to which different species raise their minimum frequency is related to the frequency range they use. We found that raising the minimum frequency is common in urban birds and is not restricted to passerine song, but also occurs in other vocalizations of passerines and parrots. There was a strong curvilinear relation between the extent to which urban birds raise the minimum frequency and the typical minimum frequency of the species: species with intermediate minimum frequencies (around 1–1.5 kHz) raised the frequency more than species with either higher or lower minimum frequency. This suggests that high-frequency species, which are less affected by urban noise, do not need to adjust the frequency of vocalizations as much. It also suggests that for species with very low frequencies, in a frequency range where urban noise augments exponentially, increasing frequency may not overcome masking by noise efficiently, and these species may use different adaptations. This indicates that frequency differences between species influence the way in which they respond to the same communication problem (masking by low-frequency noise), and possibly also the subsequent evolution of acoustic signals.

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Acoustic communication plays a major role in the social life of many animals. Birds are one of the most vocal groups of animals, relying on acoustic signals to attract mates, defend territories, synchronize behaviours and warn of dangers (Marler 2004; Catchpole & Slater 2008). The use of these signals is affected by many environmental factors (Warren et al. 2006; Slabbekoorn et al. 2007). Ambient noise, in particular, masks vocal signals and reduces the distance over which they can be detected, that is, their active space (Brumm & Slabbekoorn 2005). Adaptation of bird vocalizations to habitats differing in noise levels or other acoustic properties is widespread (Brumm & Slabbekoorn 2005; Slabbekoorn & Ripmeester 2008). For example, some urban birds increase signal redundancy (Brumm & Slater 2006), vocalize louder (Brumm 2004), use more pure tones (Dubois & Martens 1984) or avoid times of more intense noise (Bergen & Abs 1997; Fuller et al. 2007).

Raising the minimum frequency of songs has been documented in various urban songbird species (reviewed in Slabbekoorn & Ripmeester 2008). This should alleviate acoustic masking by the characteristically strong ambient noise of urban environments, because urban noise is progressively louder at lower frequencies

(Wood & Yezerinac 2006), and therefore the lower frequencies of vocalizations suffer the most masking. Since raising the minimum frequency of vocalizations seems to be common in urban birds, the extent to which different species do this offers an opportunity to study the evolution of vocal signals in novel environments from a comparative perspective. For example, are most urban species modifying their vocal signals in similar ways or do species differ in how they respond to noise, and what explains those differences?

It has been suggested that, because urban noise is louder at lower frequencies, species that vocalize at lower frequencies are more affected by urban noise (Rheindt 2003; Parris & Schneider 2009). This hypothesis predicts that species vocalizing at lower frequencies should raise their frequency to a greater extent. It is also possible that raising the frequency of vocalizations is not an efficient way of overcoming masking by noise for all species. If at a certain frequency range noise levels are too loud for small adjustments in frequency to be efficient, other strategies for coping with noise may be used instead.

In this paper we test these hypotheses with a comparative study on the extent to which the frequency of avian vocalizations changes in urban habitats. We recorded 12 species in urban and nonurban environments, and tested both for frequency increases in urban environments and whether the extent of the increase in minimum frequency is explained by the average frequency of the various species.

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METHODS

Study Sites and Recordings

We recorded birds in 18 urban sites (parks and roadside vegetation within 5 km from the centre of Melbourne, Australia, or along a major road), and in 14 nonurban sites (farmland and nature reserves more than 18 km from the city centre and away from busy roads). Urban sites were at least 500 m apart, and nonurban sites at least 1 km. We did not record in coastal areas because of the noise of strong wind, or in dense forest because fewer species exist there that also live in cities.

We recorded spontaneous bird vocalizations with an Audio Technica ATR-55 directional microphone and an M-Audio Micro Track 2 solid state recorder. We alternated visits to urban and nonurban sites from early August to early October 2008 (late winter to spring), on days with no strong wind or rain, and recorded birds between 0600 and 1000 hours. To avoid recording the same bird twice, at each site we recorded along a single transect line (lengths from 2 to 6 km). When walking back along the transect line we sometimes made additional recordings, but only for species that had not been recorded previously on that transect. Also, birds of the same species were only considered to be different individuals when recordings were made more than 100 m apart along the transect line. Measurements in recordings of the same individual were averaged and counted as a single data point. If birds vocalized in a group, we considered the data as from a single individual, as it was not possible to assign the vocalizations to the various birds. Some recordings were discarded because they had low signal to noise ratios that made frequency measurements difficult, the songs were atypically short or different species were vocalizing simultaneously.

We recorded all species that vocalized and analysed those for which we obtained good-quality recordings for a minimum of nine individuals in both urban and nonurban sites. Twelve species fitted this criterion, comprising both passerines and nonpasserines (Table 1). For these species, on average we recorded 25 individuals (minimum 10) at urban sites and 27 at nonurban sites (minimum nine; Table 1). The number of songs or vocalizations recorded from each individual ranged from one to more than 20, depending mostly on the vocal behaviour of the species. Throughout we use individuals, rather the songs or vocalizations, as the statistical units.

Noise and Frequency Measurements

We measured the amplitude of ambient noise of each site at approximately 0800 hours using a Lutron SL-4001 sound level meter. The locations of noise measurements within the site were random (wherever we happened to be at 0800 hours). We measured maximum amplitude holding the sound level meter vertically for approximately 10 s (setting: maximum hold, range 50–100 dB, A weighting). We repeated this four times and averaged the measurements. Measurements were replaced if disrupted by a gust of wind or a loud bird call close by that triggered a reading not representative of the site. In 29 sites, also at approximately 0800 hours, we recorded background noise for 60 s pointing the directional microphone upwards and always using the same recording level. We generated an average amplitude spectrum (in mV) for each of the background noise recordings with the software Avisoft-SASLab Pro v.4.40 (Avisoft Bioacoustics, Berlin, Germany), and then converted Volts into decibels, using the same arbitrary reference for all spectra.

We measured the dominant and minimum frequencies of bird vocalizations. Dominant frequency was measured as the frequency of maximum amplitude in the power spectrum, using an automatic

tool of Avisoft (peak frequency tool). Minimum frequency was measured by placing the cursor at the lower edge of the lowest note of the vocalization on the spectrogram (FFT length of 512 on 22 050 Hz files, corresponding to a frequency resolution of 43 Hz). We used this method because, especially in the urban sites, noise in the lower-frequency range prevents the use of automatic measurements (e.g. Wood & Yezerinac 2006; Slabbekoorn et al. 2007).

For five of the passerine species we studied, the main long-range vocal signal was the song. Therefore, we only compared songs for these species. We selected and measured every song separately. Two other passerine species (*Manorina melanophrys*, *Grallina cyanoleuca*), did not have songs but had a dominant call type, which we analysed instead. A single measurement was taken for groups of vocalizations separated by less than 1 s, because bursts of calls close together could be difficult to distinguish. Different measurements were taken and then averaged if separated by more than 1 s. The two nonpasserine species (*Trichoglossus haematodus*, *Platycercus eximius*) and three other passerines (*Anthochaera carunculata*, *Manorina melanocephala*, *Acridotheres tristis*) used a variety of long-range calls without a particularly dominant call type. For these we analysed all calls. As before, separate measurements were taken and averaged when calls were more than 1 s apart. In all cases, multiple measurements on the same individual were averaged.

Analyses

Within species

For each species, we tested whether urban birds have higher-frequency vocalizations than nonurban birds, using independent-sample *t* tests. As this hypothesis makes a unidirectional prediction, we used one-tailed tests.

Between species

We tested for a relation between species-typical minimum frequency and the adjustment in minimum frequency of urban relative to nonurban birds. We tested both for linear and curvilinear relations. For the linear test we regressed the urban versus nonurban difference in minimum frequency of each species on the species-typical minimum frequency, using a phylogenetic generalized least-squares (GLS) regression (Pagel 1999). The species-typical frequency is the mean of nonurban birds. For the curvilinear test we ran a GLS multiple regression of the urban versus nonurban difference on the species-typical frequency and its square. Since urban noise augments approximately exponentially with decreasing frequency (see below), we also ran these regressions using the logarithm of minimum frequency instead of its absolute value, as this may be a better predictor of the frequency adjustments.

We ran the GLS regressions with BayesTraits (M. Pagel & A. Meade, available from www.evolution.rdg.ac.uk), estimating the parameter λ to quantify the phylogenetic signal in the data and adjusting the phylogenetic correction accordingly (Freckleton et al. 2002). For this we compiled a phylogeny for our species based on Hackett et al. (2008) and Barker et al. (2002, 2004). Because we compiled information from different phylogenies we cannot use the original branch lengths. As an approximation, we set the depth of each node proportionally to the number of species in the clade minus 1 (e.g. Grafen 1989; Garland et al. 1992; Møller et al. 2008).

RESULTS

Noise was significantly louder in urban sites (mean \pm SE = 58.5 \pm 1.18 dB, $N = 18$) than in nonurban sites (50.0 \pm 0.92 dB, $N = 14$; *t* test: $t_{31} = 5.42$, $P < 0.001$), and was increasingly louder at lower frequencies, especially in urban environments (Fig. 1). The

Table 1
Dominant and minimum frequency of the 12 species studied: mean frequency, mean urban versus nonurban differences and its significance (*t* test)

Common name	Scientific name	Vocalization type	N (urban, nonurban)	Dominant frequency (kHz)			Minimum frequency (kHz)			<i>t</i> (<i>P</i>)
				Urban average (SE)	Nonurban average (SE)	Frequency difference (urban minus nonurban)	Urban average (SE)	Nonurban average (SE)	Frequency difference (urban minus nonurban)	
Rainbow lorikeet	<i>Trichoglossus haematodus</i>	Calls	(59, 44)	3.61 (0.06)	3.69 (0.09)	-0.079	1.40 (0.05)	1.27 (0.05)	0.140	2.00 (0.025)
Eastern rosella	<i>Platycercus eximius</i>	Calls	(10, 19)	2.53 (0.16)	2.39 (0.15)	0.142	1.36 (0.22)	0.88 (0.08)	0.488	2.07 (0.031)
Red wattlebird	<i>Anthochaera carunculata</i>	Calls	(33, 49)	1.62 (0.04)	1.61 (0.03)	0.012	0.82 (0.02)	0.77 (0.02)	0.042	1.70 (0.047)
Noisy miner	<i>Manorina melanocephala</i>	Calls	(29, 27)	3.55 (0.20)	3.32 (0.20)	0.234	1.39 (0.10)	1.24 (0.07)	0.151	1.29 (0.11)
Bell miner	<i>Manorina melanophrys</i>	Calls	(24, 31)	2.77 (0.01)	2.72 (0.01)	0.049	2.62 (0.01)	2.59 (0.01)	0.030	1.71 (0.047)
Pied currawong	<i>Strepera graculitha</i>	Song	(10, 17)	1.42 (0.05)	1.57 (0.05)	-0.148	0.55 (0.04)	0.55 (0.02)	0.006	0.02 (0.50)
Australian magpie	<i>Gymnorhina tibicen</i>	Song	(19, 56)	1.15 (0.03)	1.17 (0.02)	-0.025	0.63 (0.02)	0.61 (0.01)	0.020	1.09 (0.14)
Grey butcherbird	<i>Cracticus torquatus</i>	Song	(19, 21)	1.53 (0.04)	1.41 (0.04)	0.119	0.82 (0.04)	0.75 (0.02)	0.064	1.56 (0.075)
Magpie-lark	<i>Grallina cyanoleuca</i>	Call	(34, 23)	3.76 (0.10)	3.68 (0.14)	0.079	2.19 (0.05)	2.11 (0.06)	0.081	1.00 (0.16)
Willie wagtail	<i>Rhipidura leucophrys</i>	Song	(15, 9)	3.77 (0.12)	3.80 (0.17)	-0.031	2.12 (0.09)	2.04 (0.17)	0.079	0.46 (0.33)
Common myna	<i>Acridotheres tristis</i>	Calls	(32, 15)	2.84 (0.10)	2.85 (0.11)	-0.013	1.19 (0.05)	1.05 (0.11)	0.139	1.28 (0.11)
Common blackbird	<i>Turdus merula</i>	Song	(15, 11)	2.08 (0.04)	2.12 (0.06)	-0.047	1.36 (0.02)	1.25 (0.05)	0.117	2.45 (0.011)

average minimum frequency of urban birds was higher than that of nonurban conspecifics in all species studied, and this difference was significant in five species, and marginally significant in two (Table 1). In two species, urban birds also had significantly higher dominant frequency (Table 1).

For the comparison between species we excluded *P. eximius* because its adjustment in minimum frequency was a clear outlier: the urban versus nonurban difference was 0.49 kHz, while for all the other species it was below 0.2 kHz. This extraordinary adjustment by *P. eximius* may be caused by urban and nonurban birds differing in the call types they use (personal observations). Among the remaining 11 species, both the species-typical minimum frequency and the frequency adjustment were approximately normally distributed (Kolmogorov–Smirnov tests: both $Z < 0.81$, both $P > 0.53$).

The phylogenetic signals of minimum frequency and of the frequency adjustments were very low: in the GLS regressions the estimated λ was zero, and so the results are identical to conventional nonphylogenetic regressions. The frequency adjustment was not linearly related to the species-typical minimum frequency (GLS regression: $R^2 = 0.01$, $N = 11$, $P = 0.73$; Fig. 2). There was a strong curvilinear relation between frequency adjustment and the minimum frequency of each species (GLS multiple regression: $R^2 = 0.84$, $N = 11$, $P = 0.001$), with species that had intermediate minimum frequencies (1–1.5 kHz) adjusting more than species that had higher or lower minimum frequencies (Fig. 2). When we used the logarithm of minimum frequency instead of the absolute value, results were qualitatively identical (linear relation: $R^2 = 0.10$, $P = 0.34$; curvilinear relation: $R^2 = 0.90$, $P < 0.001$).

DISCUSSION

Differences in minimum frequency between urban birds and nonurban conspecifics ranged from negligible to very large (0.5 kHz) in the species that we analysed, and significantly higher frequencies in urban birds were common (five of the 12 species studied). This agrees with the current view that raising the minimum frequency of vocalizations is a common avian adaptation to urban noise: except for one species (Parris & Schneider 2009), all the species that have been studied so far raised minimum song frequency when inhabiting environments with anthropogenic noise (reviewed in Slabbekoorn & Ripmeester 2008). This suggests that frequency changes in response to noise are common in passerines, but there may be publication bias in these data. The choice of the new species studied here was unbiased regarding whether they adjust the frequency of vocalizations to noise or not (birds were recorded opportunistically and the most abundant species were analysed), thus confirming that increasing the frequency of vocalizations is common in noisy urban environments.

All previous studies on this phenomenon have looked at oscine song. Oscine songs are behaviourally plastic because they are learned vocalizations (Catchpole & Slater 2008) and their frequency can also be modified by auditory feedback (Tumer & Brainard 2007). For these reasons, and since widespread urban noise is relatively recent in evolutionary time, it is thought that adjustments in urban oscine songs are a case of behavioural plasticity rather than genetic change (Patricelli & Blickley 2006). Such behavioural plasticity in the frequency of oscine songs has been shown in some species (Bermúdez-Cuamatzin et al. 2009; Halfwerk & Slabbekoorn 2009). We have for the first time also looked at the frequency of vocalizations other than song, in both passerines and nonpasserines. In each of these categories (song, calls, passerines, nonpasserines) we found cases of increased minimum frequency in the urban environment, indicating that the phenomenon is not restricted to oscine song. Behavioural plasticity is also known in the

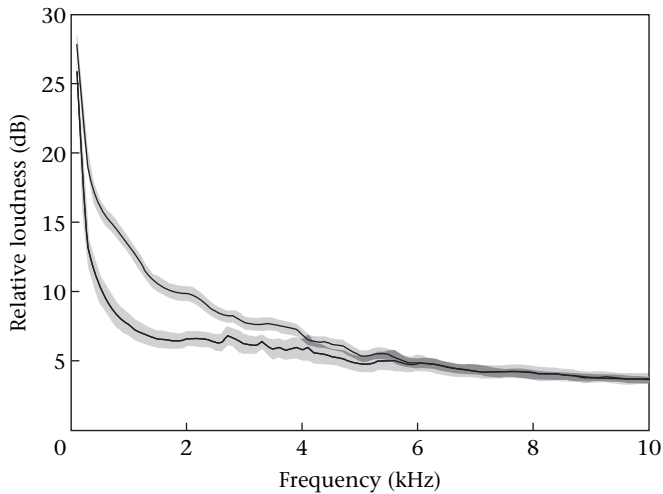


Figure 1. Average of amplitude spectra of background noise in urban sites (upper line, average of 18 sites) and nonurban sites (lower line, average of 11 sites). Shaded areas are ± 1 SE.

calls of passerines (e.g. [Mundinger 1970](#); [Nowicki 1989](#)) and the nonpasserine taxon that we studied (family Psittacidae; e.g. [Farabaugh et al. 1994](#); [Osmanski & Dooling 2009](#); [Scarl & Bradbury 2009](#)). Therefore, although we cannot with certainty interpret these differences as a result of behavioural plasticity, this is still the most likely explanation.

Unlike minimum frequency, the dominant frequency of vocalizations was not consistently higher in the urban environment, but it was significantly higher in two species. The dominant frequency should be the most important channel for acoustic communication and some species did raise it in the urban environment, but overall the results show that it is more common for birds to adjust the minimum frequency rather than the entire vocalization. As the loudness of urban noise decreases gradually towards higher frequencies ([Fig. 1](#)), dominant frequency is less masked than minimum frequency, and thus selection to raise it should be weaker. Additionally, there may be costs in adjusting the frequency of vocalizations. For example, raising the frequency would require greater muscle contraction at the syrinx ([Suthers et al. 1999](#)) and reduce the active space during silent periods

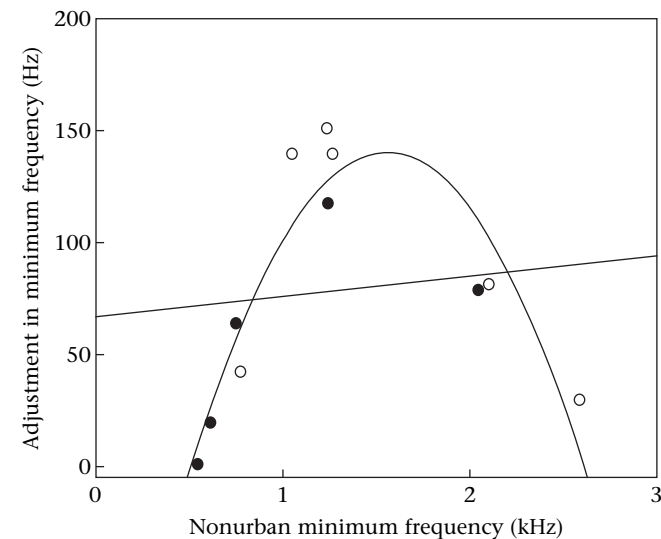


Figure 2. Scatterplot of the relation between urban versus nonurban differences in minimum frequency and the species-typical minimum frequency. The best-fit linear and curvilinear lines to these data are shown. Solid and empty dots indicate species with songs or calls studied, respectively.

as high-frequency sounds attenuate more rapidly ([Bradbury & Vehrencamp 1998](#)). These possible costs apply to changes in both minimum frequency and the entire vocalization, but should be more pronounced for the latter.

The results revealed a large variation among species in the extent to which urban birds adjust the frequency of their vocalizations. There was a strong curvilinear relation between the extent to which urban birds raised minimum frequency and the typical minimum frequency of the species: species with intermediate minimum frequencies (around 1–1.5 kHz) adjusted frequency more than species with either higher or lower minimum frequency. On the one hand, this supports the hypothesis that species using higher frequencies are less affected by anthropogenic noise and thus do not need to adjust the frequency of vocalizations as much. Another study comparing two species inhabiting similar habitats also found evidence for this hypothesis, in that only the low-frequency species (range 1.5–4 kHz) covaried its minimum song frequency with traffic noise, but the high-frequency species (range 4–7.5 kHz) did not ([Parris & Schneider 2009](#)).

For species vocalizing at very low frequencies, however, this pattern did not stand. On the contrary, below 1 kHz the adjustment of minimum frequency decreased. These species with very low frequencies are the ones whose vocalizations are most masked by urban noise, which augments steeply in this range ([Fig. 1](#)), and thus we would expect that they would benefit the most from increasing minimum frequency. A possible explanation for these results is that in this frequency range, even if they increase the frequency of vocalizations (which is always a relatively small increase, [Table 1](#)), noise levels would still be too loud for the adjustment to have been an efficient adaptation. In such a situation, these species may have to adapt to noise using other strategies (e.g. vocalizing at a higher rate: [Slabbekoorn & den Boer-Visser 2006](#); vocalizing more loudly: [Brumm 2004](#); or avoiding periods of noise: [Bergen & Abs 1997](#); [Brumm 2006](#); [Fuller et al. 2007](#)), or may fail to adapt to urban noise. If increasing the minimum frequency is not an efficient adaptation for urban birds with very low frequencies, such species may then be more limited in how they can adapt to urban noise. Together with the higher level of masking to which their vocalizations are subject, this should make their lives difficult in urban environments. This should be generally true, since most species that tolerate urban environments have higher-frequency vocalizations than their strictly nonurban congeneric species ([Hu & Cardoso 2009](#)), suggesting that lower-frequency species are more affected by urban noise and less likely to colonize cities.

It is possible that other ecological factors, besides acoustics, also contributed to differences in the frequency of vocalizations between urban and nonurban birds. For example, it has been suggested that the frequency of blackbird, *Turdus merula*, songs in cities might be influenced by higher densities of birds, which could translate into more aroused singing during social interactions and an increase in the frequency of songs ([Nemeth & Brumm 2009](#)). We did not quantify individual densities or fine details of social behaviour, but social organization was qualitatively identical in and outside the city (i.e. species that flocked, were territorial or formed family groups in the city behaved similarly outside). Notwithstanding possible influences of other factors, acoustic differences are perhaps the most parsimonious explanation for these results, because correlations between the intensity of anthropogenic noise and minimum song frequency have been found in several species (reviewed in [Slabbekoorn & Ripmeester 2008](#)). Also, the relation between the frequency range that different species use and the extent to which they increased the minimum frequency of vocalizations points to acoustic factors (e.g. urban noise) still being the most probable cause for the observed frequency increases in urban areas.

Taken together, our results illustrate how, in a novel acoustic environment, different species may change their acoustic signals differently depending on the frequency range they use. These early stages of phenotypic divergence by urban birds are putatively due to behavioural plasticity, but this may, over time, be genetically assimilated (Price et al. 2003) and set different species into distinct evolutionary trajectories. We suggest that comparing how different species adapt to urban acoustics offers a potentially rich opportunity to study the microevolution of communication signals. As our knowledge of how different species adapt to urban noise improves, it will be possible to test how additional factors influence the evolution of acoustic signals.

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