

# Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas?

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Urban environments have become an increasingly important part of the world's ecosystems, and the characteristics that enable animals to live there are not fully understood. A typical urban characteristic is the high level of ambient noise, which presents difficulties for animals that use vocal communication. Urban noise is most intense at lower frequencies, and, therefore, species vocalizing at higher frequencies may be less affected and thus better able to inhabit urban environments. We tested this hypothesis with within-genera comparisons of the vocalization frequency of 529 bird species from 103 genera. We found that species occurring in urban environments generally vocalize at higher dominant frequency than strictly nonurban congeneric species, without differing in body size or in the vegetation density of their natural habitats. In most passerine genera with low-frequency songs, which are more subject to masking by noise, minimum song frequency was also higher for urban species. These results suggest that species using high frequencies are preadapted to inhabit urban environments and that reducing noise pollution in urban areas may contribute to restore more diverse avian communities. *Key words*: anthropogenic noise, song, urban bird communities, vocalizations. [*Behav Ecol* 20:1268–1273 (2009)]

Human-modified habitats, and in particular urban environments, have spread rapidly across the globe and become an important part of the world's ecosystems. Large cities arose very recently and contain many novel characteristics such as intense anthropogenic activity and noise. Although most animals are unable to persist in urban environments, some species thrive there. These species are expected to differ from nonurban species in ways that make them adaptable to urbanization (McKinney 2006). For example, birds that inhabit cities have broader environmental tolerance than their congeneric species, suggesting that they can withstand human-induced habitat changes better (Bonier, Martin, and Wingfield 2007). Also, successful city colonization in birds is influenced by factors such as a diversified diet and the ability to nest in urbanized areas (McKinney 2006). However, the characteristics that allow some species to persist in human-disturbed habitats are not fully known.

Birds rely heavily on acoustic signals, such as songs and calls, to attract mates, defend territories, synchronize behaviors, and warn of dangers (Catchpole and Slater 2008), and this may have implications for which species can inhabit cities. A typical urban feature is its ambient noise. Urban noise, notably traffic noise, is ubiquitous, louder than most natural sources of noise, and stronger at lower frequencies (Klump 1996; Brumm and Slabbekoorn 2005; Warren et al. 2006). Noise can therefore mask vocal signals, especially at lower frequencies, reducing the active space for acoustic communication (Klump 1996; Brumm and Slabbekoorn 2005). This may entail fitness costs to the birds, and it was hypothesized that noise can drive species out of urban areas even when other habitat requirements are adequate (Slabbekoorn and Ripmeester 2008).

Birds are known to make vocal adjustments in response to interference by urban noise. Some species sing louder when

anthropogenic noise is louder (Cynx et al. 1998; Brumm 2004), which to some extent is energetically costly (Oberweger and Goller 2001; Thomas 2002; Ward et al. 2003), or sing at times when urban noise is less severe (Fuller et al. 2007). Several species sing at higher frequencies in cities and near loud anthropogenic noise sources, thus reducing the amount of signal masking by noise (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Wood and Yezzerinac 2006; Slabbekoorn et al. 2007; Parris and Schneider 2009). These behaviors show that urban noise interferes with avian vocal communication. In addition, many studies reported that avian species diversity and breeding densities are lower in developed areas, which are typically noisy (reviewed in Slabbekoorn and Ripmeester 2008). In some cases, this decline was shown to be directly related to noise levels (Stone 2000; Habib et al. 2007).

These detrimental effects of noise, together with the fact that urban noise intensity decreases with increasing frequency, suggest that species with higher frequency vocalizations are better able to inhabit urban environments as their vocal signals are less susceptible to interference by urban noise (Rheindt 2003; Slabbekoorn and Ripmeester 2008; Parris and Schneider 2009). This hypothesis predicts that bird species occurring in urban areas have higher frequency vocalizations than strictly nonurban species, a prediction that has not yet been tested.

Here, we test this prediction with within-genera comparisons of the frequency of vocalizations across a large sample of European, North American, and Australian avian genera. By conducting comparisons within genera, we minimize variation in many factors that may contribute toward urban living, such as feeding guild or nesting type (McKinney 2006), and also control for phylogenetic effects (e.g., Bonier, Martin, and Wingfield 2007).

We studied both passerines and nonpasserines. They differ in that the songs of most passerines are generally more complex and longer range signals than the vocalizations of nonpasserines (Marler 2004; Catchpole and Slater 2008). In passerines, we measured and compared the frequency of songs because this is the most important vocal signal across

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the group, whereas in nonpasserines we measured the frequency of all their vocalizations. Because of these differences, we analyzed passerines and nonpasserines separately.

## MATERIALS AND METHODS

### Habitat classification

We gathered habitat information for all species for which we obtained recordings (recording sources in the next section). For each species, we classified its habitat use based on the habitat descriptions in Poole (2005) for North American species, the *Birds of the Western Palearctic* series for European species (Cramp 1977, 1980, 1983, 1985, 1988; Cramp and Brooks 1992; Cramp et al. 1993; Cramp and Perrins 1994a, 1994b), and for the Australian species, the *Handbook of Australian, New Zealand and Antarctic Birds* (Marchant and Higgins 1990, 1993; Higgins and Davies 1996; Higgins 1999; Higgins et al. 2001, 2006; Higgins and Peter 2002). When habitats for the breeding and nonbreeding season differ, only the description for the breeding season was used.

A species was classified as occurring in urban environments when its habitat description mentioned any human-built structures or human-altered environments except for the following: 1) agriculture and orchards, 2) parkland, 3) artificial water bodies (e.g., dams and sewage farms), 4) small aircraft structures (airfields and airstrips), 5) low-density settlements (settlements, villages, farm houses, and ski resorts), 6) roads and railways, 7) docks and wharves, and 8) mines and power stations. These were considered insufficient to classify a species as urban because although some are associated with noise production (e.g., railways and airstrips), they are often away from urban centers, and the noise they imply could be very occasional. Examples of common words describing urban habitats include towns, suburbs, streets, buildings, industrial, airports, and parks or gardens. When such words are associated with a term that is nonurban, such as “gardens in rural areas,” the habitat was considered nonurban. Thus, classifying a species as occurring in urban environments (hereafter abbreviated to “urban species”) does not mean that it is an urban specialist but simply that it occurs in those environments. The habitat description of some species included references to urban environments but with qualifiers denoting uncommonness. Examples of such words include sometimes, occasionally, and rarely. We considered these descriptions ambiguous and excluded those species from the analysis. All the remaining species were classified as nonurban. Only the genera containing both urban and nonurban species were used in the subsequent analysis.

Classifying species as occurring in urban environments based on habitat descriptions may be influenced by the detail

of these descriptions, which differs to some extent among species. Nevertheless, we relied on these descriptions (references above) because they are the most authoritative and provide the best cue available for occurrence in urban areas for this large data set. Also, differences in the detail of descriptions should be random in relation to the hypothesis tested and thus only make the analysis conservative.

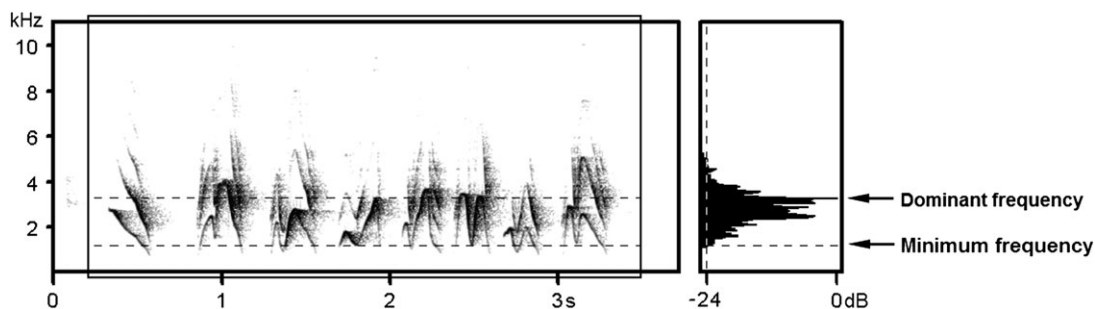
### Frequency measurements

We obtained recordings from commercially available sources: Perrins (1998) for European species, Cornell Laboratory of Ornithology (1990, 1992) for North American species, and Stewart (1999, 2000, 2001, 2002, 2003, 2004, 2005) for Australian species. These sources contained representative recordings of nearly 60% of the bird species in these continents. Based on the written information accompanying the recordings and on our screening of their background noise, these were rarely made in urban environments.

Recordings were downsampled to 22 050 Hz for measurements. We measured dominant and minimum frequency using the automatic measurement tools of the software Avisoft-SASLab Pro v.4.40 (Avisoft Bioacoustics, Berlin, Germany). Dominant frequency is the frequency with the highest sound amplitude measured over the selected vocalization (see Figure 1). Minimum frequency was measured as the frequency at which sound amplitude drops below  $-24$  dB relatively to maximum amplitude (e.g., Rheindt 2003; see Figure 1). Where necessary, we removed background noise from the recordings using digital filters, taking care that the filter was only applied to frequencies below the vocalization's, as seen in the spectrogram (Figure 1). A few recordings ( $<5$  out of ca. 600 recordings) had to be discarded because of poor sound quality that prevented using the  $-24$  dB threshold, but in most cases alternative recordings for those species existed; only one species was discarded for this reason.

For passerines, we measured dominant and minimum frequencies of each song in the recordings. Songs are generally louder and more complex than the other types of vocalizations and were identified based on the written information accompanying the recordings. We averaged the measurements of all songs for each species. For nonpasserines, we selected all the vocalizations in each recording and took a single measurement of dominant and minimum frequencies. For species with more than one recording (e.g., species occurring in more than one continent), we averaged across the different recordings.

Some passerine species, mostly Australian, did not have long-range songs in the recordings and were not used in the analysis. As a result, 16 genera were excluded because the species that remained were either all urban or all nonurban. The final data set comprises 103 genera (61 passerines and 42 nonpasserines) and 529 species (204 urban and 325 nonurban). Each genus



**Figure 1** Spectrogram (left panel) and power spectrum (right panel) of a white-breasted whistler (*Pachycephala lanioides*) song, illustrating the measurements of frequency. Broken lines indicate the frequency traits and the  $-24$ -dB threshold used to measure minimum frequency.

contained an average of 5.1 species (standard error [SE] = 3.8). The list of species and the frequency measurements are provided in the Supplementary material.

### Body mass and vegetation density

We also obtained data on the body mass and the vegetation density of the natural nonurban habitats of these species, as these are 2 likely factors influencing the frequency of avian vocalizations (Ryan and Brenowitz 1985; Boncoraglio and Saino 2007). If species colonizing cities differ in body mass or in the vegetation density of their natural habitats, differences in their frequency of vocalizations could be related to these factors rather than to urban living.

We obtained data on body mass from Dunning (2008). When different values were given for each sex, the male body mass was used. For 3 species that were not included in Dunning (2008), we used the mean of the range of male body masses given in the *Birds of the Western Palearctic* series or the *Handbook of Australian, New Zealand and Antarctic Birds* (references above).

Using the same habitat descriptions as above and ignoring the description of urban spaces, we classified the vegetation density of the breeding habitat of each species as 1—open (e.g., desert with sparse vegetation, prairie, cultivated fields, and rocky habitat), 2—semiclosed with low vegetation (e.g., dense brush, chaparral, marsh, and riverine vegetation), 3—semiclosed with high vegetation (e.g., open forest, forest edge and clearings, tall shrubland, and desert yucca or cactuses), and 4—closed (forest). Intermediate scores were used when breeding was described in more than one category (see Supplementary material).

### Data analysis

Within each genus, we took the average of frequency measurements, body masses, and scores of vegetation density for all species classified as occurring in urban environments and the same for all species classified as nonurban. For the frequency traits and scores of vegetation density, these averages were approximately normally distributed in every group (passerines, nonpasserines, urban, and nonurban; Kolmogorov–Smirnov tests, all  $Z$ 's < 1.27, all  $P$ 's > 0.08). Body mass data were positively skewed, and we corrected these with logarithmic transformations, after which the data were approximately normally distributed (Kolmogorov–Smirnov tests, all  $Z$ 's < 0.97, all  $P$ 's > 0.31).

We compared the urban and nonurban within-genus averages with 2-tailed paired sample  $t$ -tests, separately for passerines and for nonpasserines. Because urban noise is louder at lower frequencies, we might expect that differences in frequency between urban and nonurban species are larger in genera that vocalize at lower frequencies, in which case the regression slope of urban on nonurban frequencies would be lower than 1. Therefore, we tested if the regression slopes of urban on nonurban within-genus average frequencies differed from unity. When the slopes were lower than 1, we also tested for a difference between urban and nonurban species in the 50% of genera that vocalize at lower frequencies, also with paired  $t$ -tests. All statistical tests were conducted in SPSS v. 15.0.

## RESULTS

Within genera, urban birds generally sang or vocalized at higher dominant frequencies than nonurban species, both in passerines (mean paired difference  $\pm$  SE = 282  $\pm$  94 Hz,  $t$  = 2.98, degrees of freedom [df] = 60,  $P$  = 0.004; Figure 2A)

and nonpasserines (paired difference = 298  $\pm$  129 Hz,  $t$  = 2.32, df = 41,  $P$  = 0.026; Figure 2B). Urban species did not differ significantly from nonurban congeners in minimum frequency both for passerines (paired difference = 124  $\pm$  98 Hz,  $t$  = 1.26, df = 60,  $P$  = 0.21; Figure 2C) and nonpasserines (paired difference = -15  $\pm$  57 Hz,  $t$  = -0.27, df = 41,  $P$  = 0.79; Figure 2D). Body mass did not differ between urban and nonurban congeneric species in both passerines ( $t$  = 0.92, df = 59,  $P$  = 0.36) and nonpasserines ( $t$  = -0.05, df = 41,  $P$  = 0.96) nor did vegetation density of their native habitat (passerines:  $t$  = 0.56, df = 60,  $P$  = 0.58; nonpasserines:  $t$  = -0.74, df = 41,  $P$  = 0.46).

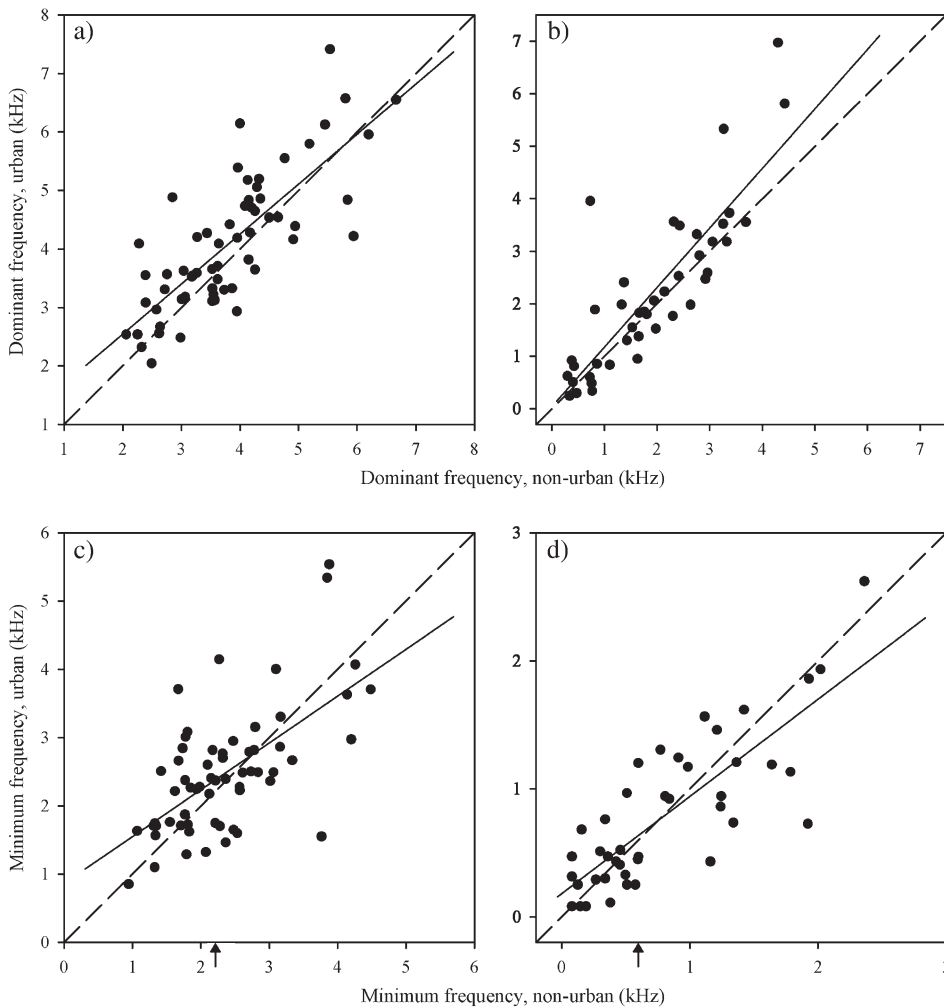
The regression slopes of urban on nonurban within-genus dominant frequency did not differ from unity (passerines:  $\beta$  = 0.86, 95% confidence interval [CI] = 0.68–1.03; nonpasserines:  $\beta$  = 1.13, 95% CI = 0.90–1.37; Figure 2A,B). The regression slope for minimum frequency was significantly lower than unity for passerines ( $\beta$  = 0.69, 95% CI = 0.46–0.91; Figure 2C), with urban species having higher minimum frequency than congeners in most of the 50% of genera that sing at lower frequencies (left half of the data points in Figure 2C; paired difference = 376  $\pm$  109 Hz,  $t$  = 3.47, df = 29,  $P$  = 0.002). For nonpasserines, the slope for minimum frequency was also lower than unity ( $\beta$  = 0.76, 95% CI = 0.58–0.94; Figure 2C), but in the 50% of genera that vocalize at lower frequencies, minimum frequencies did not differ significantly between urban and nonurban congeners (left half of the data points in Figure 2D; paired difference = 53  $\pm$  53 Hz,  $t$  = 0.99, df = 20,  $P$  = 0.33).

## DISCUSSION

This study provides the first comparison of the frequency of vocalizations between bird species occurring in urban environments and their nonurban congeneric species. It shows that urban species sing or vocalize with higher dominant frequency than their congeneric nonurban species and that in passerine genera that sing at lower frequencies urban species also have higher minimum song frequency than nonurban congeners. The frequency of bird vocalizations is generally related to the size of the species (e.g., Ryan and Brenowitz 1985; Wiley 1991) and to the vegetation density of their habitats (Boncoraglio and Saino 2007), but urban and nonurban species did not differ in body mass or in the vegetation density of their nonurban habitats. This indicates that the differences in frequency were not a correlated consequence of differences in size or in the type of habitat where urban species came from, suggesting that the sound frequency used by different species directly influences which species occur in urban environments.

Although several species increase frequency when living in urban environments (reviewed in Slabbekoorn and Ripmeester 2008), our results reflect differences among species rather than within-species adaptations to noise for 2 reasons. First, within-species variation in the frequency of vocalizations is typically less than differences among species. Second, urban adaptations usually remain geographically localized (e.g., Badyaev et al. 2008), especially adaptations to noise in songbirds that seem to be mostly due to behavioral plasticity (Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006), and thus, an unrealistic amount of gene flow or cultural spreading of urban adaptations toward nonurban areas would have been needed to influence our recordings and results.

It was hypothesized before that species with high-frequency vocalizations are less susceptible to interference by urban noise and may therefore inhabit cities more easily (Rheinhardt 2003; Slabbekoorn and Peet 2003; Parris and Schneider 2009). Indirect support for this came from within-species comparisons



**Figure 2**

Dominant (A, B) and minimum (C, D) frequencies of species occurring in urban environments and nonurban species for passerines (A, C) and nonpasserines (B, D). Each point plots the within-genus average of species occurring in urban environments against the average of nonurban congeneric species. For ease of comparison, a broken line depicts the 1:1 relation between urban and nonurban values. In panels (A) and (B), about two-thirds of genera fall above the 1:1 line. Solid lines are the best-fit linear regression lines, and arrows in the horizontal axis of panels (C) and (D) indicate the frequency that delimits the 50% of genera with lowest nonurban minimum frequency.

showing that birds sing at higher frequencies when faced with urban noise, which is typically more intense at lower frequencies (reviewed in Slabbekoorn and Ripmeester 2008). Raising the frequency of vocalizations in response to urban noise probably entails costs, for example, because it requires greater muscle contraction at the syrinx (Suthers et al. 1999) or it limits the expression of putatively sexually selected song traits (Slabbekoorn and Ripmeester 2008). Therefore, species that naturally sing or vocalize at high frequencies would suffer less of these costs.

Suggestive evidence that species using low frequencies are more sensitive to anthropogenic noise was first found in a comparison of 2 transects perpendicular to a noisy highway, where the abundance of species with low-frequency songs declined toward the road and a few species with high-frequency songs actually increased toward the road (Rheindt 2003). Recently, Parris and Schneider (2009) compared how a high-frequency (range = 4–7.5 kHz) and a low-frequency (range = 1.5–4 kHz) species adjust their songs to traffic noise and found that only the low-frequency species raised song frequency with increasing traffic volume and noise. This too suggests that species using lower frequencies are more sensitive to anthropogenic noise. Our finding that urban species tend to sing and vocalize at higher dominant frequencies than nonurban congeners corroborates these previous suggestions. It further suggests that the sound frequency that different species use contributed to shape the bird communities present in today's urban environments.

The dominant frequency is the most representative measurement of a species' vocalizations frequency and should indicate the most important frequency for detection of conspecific calls. Because the loudness of urban noise decreases progressively toward higher frequencies, the higher dominant frequency of most urban species relatively to their nonurban congeners indicates that their vocalizations have a wider active space in urban environments. The slope of urban on nonurban dominant frequencies did not differ significantly from unity, indicating that the urban versus nonurban differences are not more pronounced for species that vocalize at low frequencies. Anthropogenic urban noise is louder at lower frequencies, but it affects the entire frequency range used by the birds (Klump 1996; Warren et al. 2006; Slabbekoorn and Ripmeester 2008). Therefore, this result suggests that even a moderate level of interference at the higher frequencies can contribute to the sorting of species in urban environments. This is not unexpected because natural sources of noise that are softer than the typical anthropogenic urban noise have been found to also interfere with avian vocal signals (Slabbekoorn and Smith 2002; Brumm and Slater 2006; Dingle et al. 2008).

Whereas we detected a stronger difference between urban and nonurban species in dominant frequency, previous studies found that songbirds inhabiting urban environments raise the minimum rather than the dominant frequency (reviewed in Slabbekoorn and Ripmeester 2008). This difference may be because we compared species, whereas the previous studies

examined within-species differences, which are more likely due to behavioral plasticity (Tumer and Brainard 2007; Slabbekoorn and Ripmeester 2008; Bermúdez-Cuamatzin et al. 2009). It might be easier for individual birds to adjust their minimum frequency as this is a more subtle adjustment than changing the main frequency of vocalizations. And because urban noise is louder at lower frequencies, this may explain why songbirds adjust primarily their minimum frequency. Although minimum frequency did not differ between urban and nonurban species for the entire sample we studied, the slope of urban on nonurban minimum frequencies was significantly lower than unity. Furthermore, in the passerine genera that sing at lower frequencies, urban species had higher minimum frequency than congeners. This indicates that, for passerine song, minimum frequency also influences the success of species as urban dwellers but mostly in taxa that sing at lower frequencies, for which masking by urban noise is a more severe problem.

Previous work on the relation between urban noise and the frequency of avian vocal signals used only passerine songs, and it is difficult to extrapolate how the conclusions would apply to nonpasserines. On one hand, nonpasserines are generally larger and use lower frequencies than passerines. They also generally lack the learning abilities present in most passerines (Catchpole and Slater 2008) and thus may lack the phenotypic plasticity to adjust the frequency of their vocalizations to noise (Slabbekoorn and Ripmeester 2008). For these reasons, nonpasserines could be more sensitive to interference by anthropogenic noise. On the other hand, unlike typical passerine songs, many nonpasserine vocalizations are not long-range signals (Marler 2004), and this could make them more resilient to interference by noise. These are opposing predictions and very general ones that overlook much of the diversity in vocal communication across species. It is therefore difficult to predict whether nonpasserines would be more or less sensitive to anthropogenic noise than passerines. We obtained identical results when analyzing passerine and nonpasserine dominant frequency, suggesting that, as a whole, both groups are affected by urban noise. However, for passerine song, we additionally found that in genera that sing at lower frequencies, urban species also have higher minimum song frequency. This additional result may reflect the higher reliance of passerines in long-range vocal communication.

There is much variation in noise levels within urban environments that we overlooked in this large-scale survey, and it would be interesting to address this level of variation in the future. For example, it would be interesting to know if avian communities differ between urban areas with more or less noise exposure but otherwise ecologically similar. Also, ubiquitous noise has only been prevalent in urban areas since the vulgarization of motor vehicles, and it would be interesting to know if historical records point to a withdrawal of low-frequency species from cities around that time.

Many factors likely determine whether a species can become an urban dweller. In birds, both physiological factors, such as adjusted stress responses, and ecological factors, such as feeding guild, nesting type, or environmental tolerance, have been identified as contributing toward urban living (McKinney 2006; Partecke et al. 2006; Bonier, Martin, Sheldon, et al. 2007; Bonier, Martin, and Wingfield 2007). Our results indicate that the frequency of vocalizations is an additional factor influencing whether species can successfully inhabit urban environments. This does not imply that other factors are less important. Although in most genera urban species vocalize at higher frequencies than nonurban species, about one-third of genera run counter to this pattern (Figure 2A,B), indicating that other ecological and life-history traits play important roles determining which species are able to live in urban

environments. In conclusion, our results indicate that the frequency of birdsongs and calls is one factor determining whether bird species can inhabit urban environments, lending support to the suggestion that mitigating noise pollution in urban areas may contribute to restore more diverse avian communities (Slabbekoorn and Ripmeester 2008).

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