Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization?

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A R T I C L E   I N F O

When animals colonize cities they often have to adapt their physiology, life history and behaviour to the novel environment. Songbirds rely on acoustic communication for reproduction, and recent studies indicate that songs vary between urban and nonurban habitats. In cities, birds sing louder or use higher frequencies compared to their conspecifics in forests. These habitat-specific differences in song have been interpreted as an adaptation of the city birds to mitigate acoustic masking by low-frequency traffic noise. We compared the songs of blackbirds, *Turdus merula*, from the city centre of Vienna and the Vienna Woods and found that forest birds sang at lower frequencies and with longer intervals between songs. This difference in song pitch might reflect an adaptation to urban ambient noise. However, the song divergence could also be the result of more intense vocal interaction in the more densely populated city areas or a side-effect of physiological adaptation to urban habitats. We emphasize the need for experimental studies in blackbirds, but also in other species, to clarify a possible causal link between urban acoustics and song characteristics of city birds.

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Songbirds, like many other animals, rely on acoustic communication to establish and defend territories, and to attract mating partners. Thus successful signal transmission is crucial and therefore the structure of songs can be adapted to the environmental acoustics to transmit particularly well in a given habitat (Catchpole & Slater 2008). Such habitat-dependent song variation has been demonstrated between species as well as between populations (e.g. Morton 1975; Hunter & Krebs 1979; Wiley 1991; Badyaev & Leaf 1997). By and large, forest birds sing at lower pitch and with a slower frequency or less amplitude modulation, while birds in open habitats often use broadband sounds with more rapid trills (Morton 1975; Richards & Wiley 1980; Wiley 1991). In forests, dense vegetation attenuates high frequencies and, depending on acoustic signal structure, reverberations can degrade (Wiley & Richards 1978) or enhance acoustic signals (Slabbekoorn et al. 2002; Nemeth et al. 2006). Open habitats lack such reverberation effects and also strong frequency-dependent attenuation, but here atmospheric turbulence can have a considerable impact on sound

transmission (Wiley & Richards 1978). However, adaptation to the environment does not necessarily mean a design for maximum transmission. Degradation and attenuation of signals is not always a disadvantage, since birds sometimes face a trade-off between targeted receivers and nontargeted eavesdroppers (McGregor & Dabelsteen 1996). For example, in the song of the white–browed warbler, *Basileuterus leucoblepharus*, species identity is encoded in sound structures that resist sound attenuation and degradation, while individual identity and perhaps motivation are found in acoustic parameters that degrade strongly during sound transmission (Aubin et al. 2004). But, even if there are several functions of birdsong that require different transmission distances or 'active spaces' (Mathevon et al. 2003), we can still assume that, at least in territorial birds, some parts of a song have evolved to be easily detected at a long range.

An important environmental constraint impeding signal detection is ambient noise, and it is thought that environmental noise plays an important role in the evolution of birdsong (Ryan & Brenowitz 1985; Brumm & Slabbekoorn 2005). Birds use a number of strategies to avoid signal masking by background noise, including adjustments in song timing, song structure and performance (Brumm & Slabbekoorn 2005). Nightingales, *Luscinia megarhynchos*, for instance, sing louder (Brumm & Todt 2002) in noisy conditions and dippers, *Cinclus cinclus*, use particularly high frequencies well

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above the noise of the fast-running streams in their habitat (Brumm & Slabbekoorn 2005). King penguins, *Aptenodytes patagonicus*, maintain communication in windy situations by producing more calls in a calling bout (Lengagne et al. 1999); a similar phenomenon has also been found in chaffinches, *Fringilla coelebs*, singing close to waterfalls and torrents (Brumm & Slater 2006). In urban habitats anthropogenic noise constrains avian communication; in particular, the effects of traffic noise on birdsong have raised considerable interest among researchers (Brumm 2006; Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2007). Recent studies have shown that birds can vary their songs with the amount of background noise: nightingales sing louder in the presence of traffic noise (Brumm 2004) and robins, *Erithacus rubecula*, evade acoustic masking by shifting their singing activity towards the night in areas that are noisy during daytime (Fuller et al. 2007). Several urban bird species use higher minimum frequencies in places with higher background noise levels (e.g. great tits, *Parus major*, in Europe: Slabbekoorn & Peet 2003; house finches, *Carpodacus mexicanus*, and song sparrows, *Melospiza melodia*, in North America: Fernandez-Juricic et al. 2005; Wood & Yezerinac 2006; Bermúdez-Cuamatzin et al., in press). In a comprehensive study, Slabbekoorn & Boer-Visser (2006) compared the songs of great tits from 10 European cities and forests nearby, and found that the urban birds consistently sang with higher minimum frequencies than their conspecifics in the forests. This shift to higher frequencies has been interpreted as an adaptation to the traffic noise in cities, as higher frequencies will suffer less masking in low-frequency noise. However, acoustic masking in great tits is comparatively low, because their high-pitched songs overlap little with traffic noise. Shifts in song structure should be much more crucial in species with lower-pitched song.

Blackbirds, *Turdus merula*, are one such species that sings at lower frequencies. Similar to great tits, blackbirds are also successful colonizers of urban habitats. Blackbirds started to settle in European cities more than 150 years ago (Stephan 1999), and in urban areas the species has changed from a former shy woodland dweller to a rather tame city bird. The song of the blackbird seems typical for a forest bird: its far-reaching melodious motifs with a narrow bandwidth and rather long elements are well suited for long-range communication in a closed, echoic habitat (Dabelsteen et al. 1993).

We compared songs of blackbirds in the inner city of Vienna with songs from the Vienna Woods. Since these sites represent extremely different blackbird habitats they offer an ideal opportunity to search for possible differences in song structure related to environmental acoustics. In this study, we focused on frequency and temporal characteristics of song. We discuss our findings in the context of an adaptation to environmental acoustics as well as alternative explanations related to urbanization.

METHODS

In 2007 and 2008 we recorded the songs of 20 urban and 19 forest blackbirds in the inner city districts of Vienna (48°12′36″N and 16°21′21″E, 180 m above see level) and in forest areas of the Vienna Woods (48°14′25″N and 16°15′04″E, 350 m above see level). The nearest distance between two recorded individuals of the two habitats was 6.3 km. Each recording site was visited only once to avoid double recordings. The city habitats were varied with blackbirds singing on trees, on the rooftops of houses 20 m high close to parks or in small courtyards with trees. The Vienna Woods habitat was mainly mature deciduous forest. In the forest every recorded bird was at least 200 m from the nearest settlement or main road.

To document differences in environmental noise in the city and forest habitats we revisited 10 different forest and city territories between 21 and 27 March 2009 and measured the ambient noise characteristics. All measurements were taken in the morning between 0500 and 0700 hours. During measurement no blackbird was singing closer than approximately 100 m. Sound level was measured with a CEL 383 Integrating Impulse Sound Level Meter at 1.5 m height. We measured the equivalent continuous sound level (L_{eq}) for 1 min by using an A-weighting filter (L_{Aeq}) and a linear response setting (L_{Leq}). The frequency response of an A-filter is approximately flat from 1 to 8 kHz, which is about the frequency range of the blackbird song. In both filter settings the mean noise levels ±SD in the city were higher and more variable than in the forest (L_{Aeq}: city: 54.0 ± 7.1 dB; forest: 45.4 ± 1.8 dB; L_{Leq}: city: 71.3 ± 9.2 dB; forest: 60.0 ± 5.4 dB). At each location at least 1 min of environmental noise was recorded to quantify its spectral distribution (Fig. 1). The spectra in the city were dominated by low-frequency traffic noise while in the forests the songs of other species played a more important role.

Urban blackbirds were recorded between 7 and 24 April and forest blackbirds between 9 and 25 April. The observer was present at both sites prior to the dawn chorus. The city birds started to sing earlier ($\overline{X} \pm SD = 41 \pm 28$ min before sunrise, $N = 5$ days) than the forest birds (25 ± 21 min after sunrise, $N = 7$ days). Therefore songs of the city birds were, on average, recorded 69 min earlier. Taking this time difference into account, we recorded the birds in both habitats within similar time intervals after the start of the dawn chorus (in the city within 2 h 32 min, in the forest within 2 h 39 min).

In total 1015 songs with 6583 song elements were analysed. For both habitats, the number of analysed songs per individual was similar (range, mean ± SD: city: 4–61, 28.5 ± 19; forest: 4–71, 28.5 ± 19.3). Blackbirds sing with immediate variation and songs vary considerably (Dabelsteen 1984). The results could thus be biased by the low number of analysed songs in a few individuals. Therefore, we restricted our analysis of song variables to individuals with at least 10 analysed songs. Here we present the results of this reduced data set comprising 17 individuals from the city and 16 from the forest. Analysis of the more extensive data set produced similar results with the same conclusions.
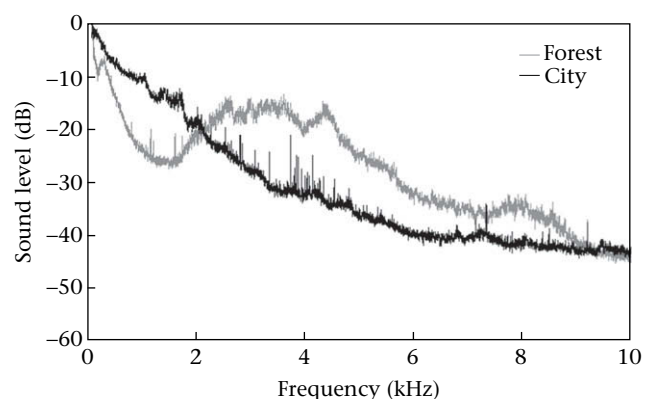

Figure 1. Typical environmental noise spectra from a city and a forest territory (FFT size = 32 768; window type: Hamming; high-pass filter at 70 Hz). The spectra are based on two 1 min recordings taken with an omnidirectional microphone with linear frequency response (AKG CK 62 ULS). The microphone was placed 1.5 m above the ground. No blackbird was singing in the territory during the sound recording. Both spectra are normalized to the same value. In the louder city territory the equivalent continuous sound level L_{Aeq} measured over 1 min was 58.8 dB, whereas in the forest L_{Aeq} was 47.1 dB. In the city, the high sound level at low frequencies was due to traffic noise; in the forest the rise of sound level above 2 kHz was due to distant vocalizations of other bird species (great tit, *Parus major*, blue tit, *Cyanistes caeruleus*, song thrush, *Turdus philomelos*, chaffinch, *Fringilla coelebs*, robin *Erithacus rubecula*, and great spotted woodpecker, *Picus major*).
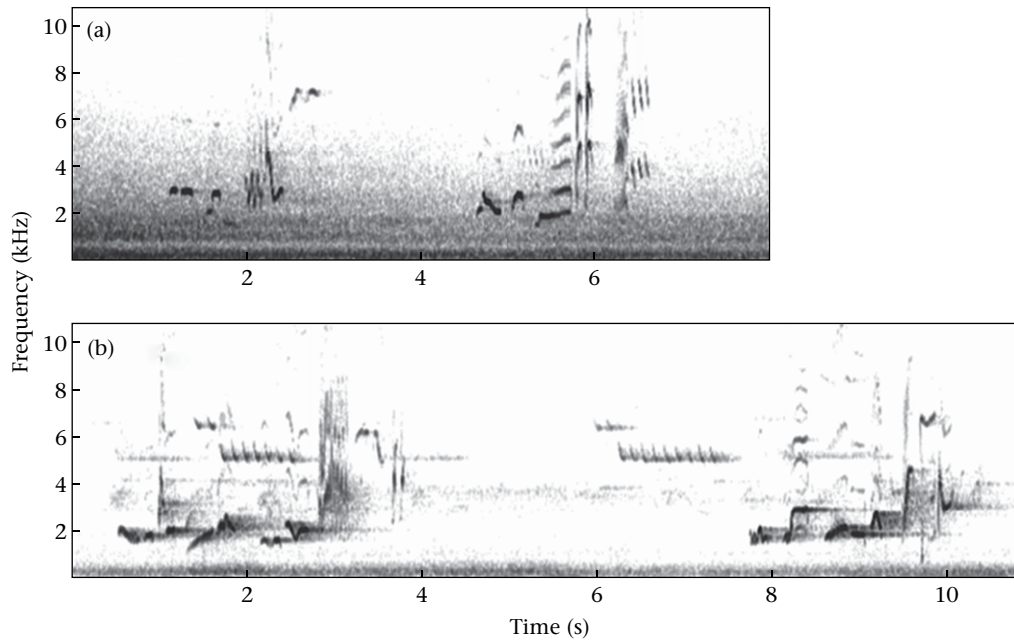
Figure 2. Examples of songs from male blackbirds recorded in (a) the city centre of Vienna and (b) the Vienna Woods. Note the low-frequency traffic noise in the urban habitat and the songs of other species in the background of the forest recording.

Songs were recorded with a Tascam DAP1 Portable DAT Recorder or a Marantz PMD 660 digital recorder with a sampling rate of 44.1 kHz. Both recorders were connected to a Telinga stereo microphone mounted in a Telinga parabola with a diameter of 56 cm. Parabolas amplify and focus the sound, which was necessary to record birds in sufficient quality in both the noisy city environment and the forest where the songs of other species can interfere with blackbird song (Fig. 2). The distance of the microphone to the singing birds varied from 5 m to approximately 20 m. Songs were digitally transferred to a computer and analysed with the software AVISOFT SAS LabPro 4.4 (R. Specht, Berlin, Germany). Spectral parameters were measured with a frequency resolution of 22 Hz (Hamming window; FFT length = 1024). Temporal parameters were measured separately with a resolution of 2.9 ms (Hamming window; FFT length = 128).

Following previous categorizations of the blackbird song into a motif and twitter part (Todt 1970; Dabelsteen 1981), we classified all song elements as either motif or twitter elements (Fig. 3). The motif elements are at the beginning of the song; they are lower pitched (below 3.5 kHz) and produced with higher amplitude. The twitter elements consist of softer elements with higher maximum frequencies and a broader frequency range. Song elements are separated by more than 50 ms and the pauses between songs last from 0.5 to 3.5 s (Dabelsteen 1984).
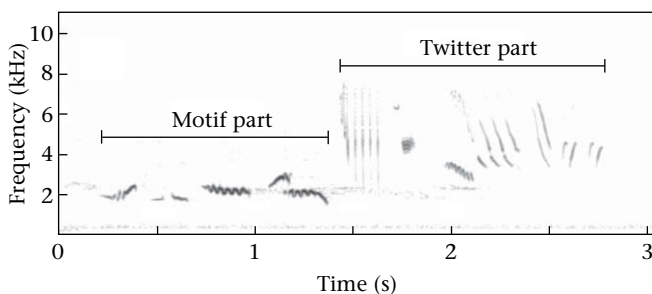

Figure 3. Spectrogram of a typical blackbird song comprising a motif part of low-pitched whistle-like elements and a twitter part of higher-pitched broadband elements.

The motif and twitter elements were the basic units of analysis, and for each male we calculated the average value of the following temporal and frequency variables: length of element, loudest frequency of a song element (i.e. the frequency at the maximum amplitude in the spectrum), minimum and maximum frequencies (i.e. the lowest and highest frequency below 15 dB of the peak amplitude). Minimum and maximum frequencies of motif and twitter elements were very highly positively correlated with the loudest frequency (Pearson correlations of the average values for 39 individuals: motif elements: $r_{\text{PeakFreq, MinFreq}} = 0.84$, $r_{\text{PeakFreq, MaxFreq}} = 0.94$; twitter elements: $r_{\text{PeakFreq, MinFreq}} = 0.84$, $r_{\text{PeakFreq, MaxFreq}} = 0.93$; all $P < 0.001$). Therefore we decided to reduce our variable set and used the loudest frequency as a representative measure for all spectral characteristics of song elements. A second, possibly even more important reason to use only the loudest frequency as the spectral measure was the difficulty in measuring low frequencies. Minimum frequencies were not always easy to estimate in the presence of low-frequency background noise. Considering these uncertainties, we also omitted the bandwidth of

Table 1
Differences in blackbird song structure between forest and city birds compared with two-tailed Mann–Whitney U tests

Variable	City N=16	Forest N=17	Z	P
Whole song				
Duration of song (s)	**1.83±0.299**	**2.28±0.390**	**−3.03**	**0.002**
Duration of intersong intervals (s)	2.98±0.933	3.66±1.26	−1.69	0.094
Duration of interelement intervals (ms)	112±21	111±16	−1.44	0.86
Number of elements per song	5.4±1.65	6.4±1.66	−2.11	0.034
Motif part				
Loudest frequency motif elements (Hz)	**2334±90.0**	**2132±71.4**	**−4.50**	**<0.001**
Length of motif elements (ms)	173±20.1	173±141.0	−0.43	0.68
Twitter part				
Loudest frequency twitter elements (Hz)	3979±506.4	3640±499.1	−1.95	0.05
Length of twitter elements (ms)	242±69.2	242±64.6	−0.0	1

Means are given ± SD. Differences significant after Bonferroni correction ($\alpha' = 0.00625$) are shown in bold.

songs. Furthermore, we measured the intervals between the elements, that is the time from the end of one element to the start of the next element and the intersong intervals as time from the end of one song to the start of the next one. Altogether we used eight variables for the analyses (Table 1).

Recordings in the two habitat types were not equally distributed between the years, but we found no significant difference in any of the eight frequency or temporal variables between the years within one habitat type (Mann–Whitney U tests: all $P > 0.15$). Therefore we pooled the data of both years for further analyses.

In the statistical analysis we first conducted Mann–Whitney U tests to compare song variables between the two groups. We chose nonparametric tests because a visual inspection of the data showed that they were not normally distributed. Variances between groups were not unequal (unequal variance t test for all eight variables: all $P > 0.1$) and thus the Mann–Whitney U test was appropriate to test group differences (Ruxton 2006). Then we performed a stepwise binary logistic regression to test how well these variables classify individuals as city and forest blackbirds. We chose logistic regression because it enables a multivariate comparison and it has less stringent assumptions on the distribution of the data than a discriminant analysis (Press & Wilson 1978; Tabachnick & Fidell 2001). To find the best predictor variables for city or forest birds, we used a forward stepwise logistic regression with a criterion value of < 0.10 for inclusion and > 0.15 for exclusion of a variable (Tabachnick & Fidell 2001). To avoid multicollinearity we excluded variables that were strongly correlated ($r > 0.4$). In our data set only duration of song and number of elements matched this criterion (Pearson correlation: $r_{37} = 0.80$, $P < 0.001$). Therefore we performed two stepwise logistic regressions, each with one of the two variables excluded. The results were similar, but here we only report the analysis of the data set that yielded the model with the highest effect size as measured by Nagelkerke's R^2 for explained variance (Tabachnick & Fidell 2001). This model includes the number of elements and excludes song duration. All statistical analyses were performed with SPSS 16.1 (SPSS Inc., Chicago, IL, U.S.A.). Statistical tests are two tailed.

RESULTS

The song structure of urban and forest blackbirds differed in both spectral and temporal characteristics. In the city habitats, the loudest frequencies of the motif elements were significantly higher than in the forest (Table 1). Urban birds also sang significantly shorter songs with fewer elements (Fig. 2).

The logistic regression model was highly significant (likelihood ratio test: $\chi^2_3 = 39.4$, $P < 0.001$). It had an overall Nagelkerke's $R^2 = 0.93$ and classified 97% of all individuals correctly. The main contributing variable was the loudest frequency of motif elements, but also the number of song elements and the different intersong intervals between city and forest birds were included and contributed to a significant improvement of the model fit (Table 2). Variables not in the final logistic model were loudest frequency of twitter elements, length of motif elements, length of twitter

Table 2
Likelihood ratio tests of individual model parameters of the logistic regression model

Effect	−2 Log likelihood of reduced model	χ^2	df	P
Intercept	27.864	25.291	1	<0.001
Loudest frequency motif elements (Hz)	36.846	34.046	1	<0.001
Duration of intersong intervals (ms)	12.285	5.966	1	0.015
Number of elements per song	14.915	8.596	1	0.003

$N_{forest} = 17$, $N_{city} = 16$. The chi-square statistic is the difference in −2 log likelihoods between the final model and a reduced model.

elements and duration of interelement intervals. Duration of song was excluded from the analysis to avoid collinearity (see Methods).

DISCUSSION

We found marked differences in spectral and temporal song characteristics of city and forest blackbirds. The use of higher frequencies in the motif song elements of urban blackbirds resembles the results found for great tits (Slabbekoorn & Boer-Visser 2006). Higher song frequencies in cities could be an adaptation to increased levels of anthropogenic low-frequency noise, as suggested for great tits (Slabbekoorn & Peet 2003), song sparrows (Wood & Yezerinac 2006) and house finches (Fernandez-Juricic et al. 2005; Bermúdez-Cuamatzin et al., in press). In these species, minimum song frequencies varied within cities and were positively correlated with the sound pressure level of ambient noise near the songpost. The higher frequency in the motif elements of the city blackbirds studied here could be caused by masking from traffic noise, too. However, lower-pitched song in the Vienna Woods could also indicate that the frequency shift in the city is a release from the constraints of sound transmission in forests, where birds sing at lower frequency to optimize their sound transmission in a more reverberating and frequency-absorbing environment (Morton 1975; Wiley & Richards 1978). In addition to the observed frequency shift, our urban blackbirds showed a nonsignificant trend to sing with shorter intersong intervals. Similar 'hurried songs' were also found in urban great tits in 10 European cities (Slabbekoorn & Boer-Visser 2006), such that shorter intersong intervals occurred together with shorter song elements. Slabbekoorn & Boer-Visser (2006) interpreted these shorter elements as an adaptation to a more open city habitat. In our blackbirds we found no temporal shift in the element length of city birds and thus no clear indication for such a putative adaptation to a more open habitat.

However, an adaptive response to the acoustic properties of the habitat is only one of several possible explanations for our results. In a state of higher arousal, blackbirds sing with higher frequencies and shorter song intervals (Dabelsteen 1984, 1985; Dabelsteen & Pedersen 1985; but see Ripmeester & Slabbekoorn 2007). Since it is exactly these features that we found in the songs of our city blackbirds, our results could be, at least partly, accounted for by differences in motivational state. A reason for higher arousal in city birds could be a higher bird density in urban areas. Higher densities could imply more intense social interaction with neighbours and therefore change the motivational state of a singer. Breeding density of blackbirds is generally higher in urban areas than in forests (Snow 1958), which was also true for our study sites (E. Nemeth, unpublished data).

An alternative explanation for differences in song is independent of signal transmission. Urbanization in blackbirds is related to changes in stress physiology (Partecke et al. 2006) and to timing of gonadal development and breeding (Partecke et al. 2004). Blackbirds from the city of Munich in southern Germany develop their gonads 3 weeks earlier than birds in a forest nearby and males in the city show on average higher amounts of luteinizing hormone throughout the season and lower amounts of plasma testosterone during gonadal development (Partecke 2005). A higher testosterone level leads to lower song frequencies in zebra finches, *Taeniopygia guttata* (Cynx et al. 2005), and it is possible that the same is true for blackbirds. Our recordings were made in April and if we expect a similar seasonal pattern in Vienna as in Germany there could be a difference in plasma testosterone between city and forest birds (Partecke 2005). However, since we have no endocrinological data from the Austrian population further investigations are necessary to prove such a relationship.

In conclusion, although our results are in concordance with an adaptation to the acoustic environment they could also be caused by other differences in urban life. Therefore, we hesitate to claim a causal connection between urban noise and a change in song features in blackbirds. In particular, the possible influence of breeding density on vocal communication seems to warrant further investigation. A higher density of breeding birds in cities in contrast to rural areas is a common phenomenon in many species, and it has been shown in 27 species that bird density increases with household density and decreases only in extremely densely populated areas (Tratalos et al. 2007). Higher bird densities could influence song transmission and song parameters in two ways. First, it could lead to increased male–male interactions and motivational changes in singing activity and song features (Goretskaia 2004). Second, it shortens the transmission paths between neighbouring males and should even ease acoustic communication since shorter transmission paths imply less attenuation and degradation of acoustic signals.

Considering the multitude of factors that change in an urban environment, it is not easy to pinpoint background noise as the crucial factor for changes in urban songs. The strongest evidence for adaptation of songs to traffic noise is a correlation between the amplitude of low-frequency background noise and the minimum frequency of song (Slabbekoorn & Peet 2003; Fernandez-Juricic et al. 2005; Wood & Yezerinac 2006; Bermúdez-Cuamatzin et al., in press). In blackbirds the lowest frequencies were difficult to measure in the presence of low-frequency noise, but even if that measurement problem could be resolved, we see these correlations only as a possible first step to prove an adaptation of avian communication to urban environments. Experimental studies are strongly needed to test and confirm the influence of urban noise and other factors on spectral and temporal features of birdsong.

Acknowledgments

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