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Predicting the Effect of Urban Noise on the Active Space of Avian Vocal Signals

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ABSTRACT: Urbanization changes the physical environment of nonhuman species but also markedly changes their acoustic environment. Urban noise interferes with acoustic communication in a range of animals, including birds, with potentially profound impacts on fitness. However, a mechanistic theory to predict which species of birds will be most affected by urban noise is lacking. We develop a mathematical model to predict the decrease in the active space of avian vocal signals after moving from quiet forest habitats to noisy urban habitats. We find that the magnitude of the decrease is largely a function of signal frequency. However, this relationship is not monotonic. A metaregression of observed increases in the frequency of birdsong in urban noise supports the model's predictions for signals with frequencies between 1.5 and 4 kHz. Using results of the metaregression and the model described above, we show that the expected gain in active space following observed frequency shifts is up to 12% and greatest for birds with signals at the lower end of this frequency range. Our generally applicable model, along with three predictions regarding the behavioral and population-level responses of birds to urban noise, represents an important step toward a theory of acoustic communication in urban habitats.

Keywords: acoustic communication, behavioral ecology, bioacoustics, masking, metaregression, traffic noise, urban ecology.

Introduction

Communication is the basis of all social interactions between animals. Birds communicate using acoustic signals (songs and calls) for a variety of social purposes, such as attracting mates, maintaining a pair bond, defending territories from rivals, begging for food, and warning of danger from potential predators (Collins 2004; Marler 2004). There are many constraints on acoustic communication in natural habitats, and an individual will benefit from signaling only if the signal is successfully transmitted to the targeted receiver or receivers (Brenowitz 1986).

The active space of an acoustic signal (i.e., the distance over which it can be detected by a conspecific animal) depends on a range of variables, including the amplitude of the signal, its spectral and temporal properties (e.g., frequency, bandwidth, frequency and amplitude modulation, note-repetition rate), the positions of the sender and the receiver, the structure of the habitat through which the signal travels, the amplitude and spectral composition of ambient noise, prevailing weather conditions, and the ability of the receiver to extract information from the transmitted sound (Marten and Marler 1977; Wiley and Richards 1978; Forrest 1994; Blumenrath and Dabelsteen 2004; Brumm and Naguib 2009). Thus, successful transmission of a signal depends on three groups of potentially interacting variables—those related to the sender and its signal, those related to the environment through which the signal travels, and those related to the receiver. Successful reception of a signal depends on it being detected and correctly interpreted by the receiver: it must be loud enough to be heard and its original structure sufficiently intact to be recognizable (Lohr et al. 2003).

Acoustic interference or masking occurs when background noise reduces the maximum distance over which a signal can be detected (Marten and Marler 1977). Birds use a number of strategies to optimize the active space of their signals against a background of natural noise (Brumm and Slabbekoorn 2005). These include using signals that transmit well through a given habitat, choosing singing locations to improve signal transmission, and making short-term changes to signal characteristics to reduce the masking effect of noise. For a given signal amplitude, simple signals that are concentrated in a narrow frequency band are likely to transmit farther than complex signals, such as those that include multiple syllables, harmonics, trills (rapidly repeated elements), and/or frequency modulation (e.g., Dabelsteen et al. 1993; Lohr et al. 2003; Naguib et al. 2008).

The acoustic adaptation hypothesis (Morton 1975, 1986) proposes that the acoustic properties of a given habitat will exert selection pressure on the vocal signals of

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animals in that habitat. In the case of signals designed for long-distance communication, such as certain types of birdsong, selection should favor the use of signals that confer the greatest broadcast area (Morton 1975). Therefore, populations and species occupying acoustically different habitats will adapt their vocalizations to broadcast with greater efficiency in each. For example, animals in closed (densely vegetated) habitats such as forests are predicted to use longer, slower vocal signals with a lower acoustic frequency, a narrower frequency range, and fewer trills than animals in open habitats such as meadows (Ey and Fischer 2009). Signals with these characteristics are expected to transmit further and experience less degradation in the highly reverberative conditions of a forest. A recent meta-analysis of data from 26 studies (including intra- and interspecific comparisons) concluded that birds in closed habitats sang at a lower frequency and in a narrower frequency range than birds in open habitats, although evidence for an effect of habitat on the time between song elements was equivocal (Boncoraglio and Saino 2007).

Two particular properties of urban habitats are likely to constrain acoustic communication in cities. First, urban habitats often experience high levels of anthropogenic noise such as road-traffic noise, much of which occurs in the lower-frequency bands below 2 kHz (Patricelli and Blickley 2006; Warren et al. 2006). Thus, both the total amplitude and the spectral shape of background noise tend to differ between urban and rural habitats. Second, the structural complexity of urban landscapes—which may include streets lined with tall, reflective buildings that form “urban canyons,” neighborhoods of low-rise buildings, and areas of undeveloped green space such as parkland—presents animals with a highly variable acoustic environment. Reverberation of signals is likely to be pronounced in urban canyons, while parks and gardens may attenuate sound in a similar way to natural forests and woodlands (Warren et al. 2006; Nemeth and Brumm 2010). Interestingly, the reflective nature of urban canyons may reduce the attenuation of signals below that observed in natural habitats, potentially increasing their active space, although the attenuation of urban noise may be similarly reduced (Iu and Li 2002; Warren et al. 2006). On the basis of the acoustic adaptation hypothesis, we would expect urban birds to adapt their long-range vocal signals to reduce both the masking effect of urban noise and the rate of signal degradation in the particular part of the urban landscape that they inhabit. Changes to signals that could improve detectability in noise include singing/calling at a higher frequency and in a narrower frequency range, and reducing frequency modulation (Lohr et al. 2003; Patricelli and Blickley 2006). Using simpler, more tonal signals with fewer trills and vocalizing more slowly may improve detectability in highly reverberative parts of the city landscape such as urban canyons (Wiley and Richards 1982; Warren et al. 2006).

Many species of songbirds are known to vocalize differently in noisy urban habitats, including singing or calling at a higher frequency (a frequency shift; e.g., Slabbekoorn and Peet 2003; Wood and Yezerinac 2006; Parris and Schneider 2009; Potvin et al. 2011), singing more loudly (an amplitude shift, also known as the Lombard effect; Lombard 1911; Brumm 2004; Leonard and Horn 2005), and changing diurnal singing patterns to avoid the noisiest times of day (a temporal shift; Warren et al. 2006; Fuller et al. 2007). The common blackbird *Turdus merula* was observed to sing at both a higher frequency and higher amplitude in urban areas than in forest habitats (Nemeth et al. 2013). In this study, city birds tended to use higher-frequency song elements that can be produced at a higher amplitude than lower-frequency elements (Nemeth et al. 2013).

A number of studies have shown that songbirds can change the frequency of their song in response to changes in background noise over very short time frames (Bermúdez-Cuamatzin et al. 2009; Halfwerk and Slabbekoorn 2009; Gross et al. 2010; Verzijden et al. 2010). Potvin (2012) recently found that the silvereye *Zosterops lateralis* can make real-time changes to the frequency of its contact calls in response to changes in the frequency of background noise—the first time this has been observed for an unlearned vocal signal. However, most studies of vocal behavior in urban habitats are correlational; birds have been observed to sing or call differently in urban noise, but a clear causal relationship between noise and vocal behavior has not been established (e.g., Slabbekoorn and Peet 2003; Slabbekoorn and den Boer-Visser 2006; Fuller et al. 2007; Parris and Schneider 2009; Potvin et al. 2011). Throughout this article, we will use the term “shift” to describe an observed change in the frequency, amplitude, or timing of songs in urban noise without implying direct causation.

While other features of a vocal signal, such as its complexity, duration, and syllable rate, may affect propagation and detectability in built environments, there is little information about how birds alter these features to compensate for the acoustic properties of urban landscapes. In a study of silvereyes in eastern Australia, urban populations sang slower songs (fewer syllables per second) and fewer syllables per song than rural populations (Potvin et al. 2011), while the songs of urban silvereyes covered a broader frequency range than the songs of their rural counterparts (Potvin and Parris 2012). Habitat type (urban or rural) was also an important predictor of repertoire composition, independent of geographic location (Potvin and Parris 2012). Nemeth and Brumm (2009) found that common blackbirds sang shorter songs with fewer notes per song in the city of Vienna than in a nearby forest. Cardoso and Atwell (2011) compared the repertoire of one urban and one rural population of dark-eyed juncos (*Junco hyemalis*) and concluded that only half the frequency shift observed in the urban population could be explained by modification of existing memes. This suggests selection for certain memes or creation of new memes in urban habitats.

Currently, there is no general mechanistic theory to predict which bird species are likely to experience the greatest acoustic interference (i.e., the greatest reduction in the active space of their vocal signals) in urban noise. Because noise in frequency bands close to an acoustic signal contributes more to the masking of that signal than noise in other frequency bands (Egan and Hake 1950), low-frequency signals (or signal components) may be expected to suffer more acoustic interference from urban noise than high-frequency signals. However, the range of frequencies that contribute to masking (and, thus, the level of masking) tends to increase with signal frequency, so higher-frequency signals need to be louder (of a higher amplitude) to be detected in broadband noise (Klump 1996). In general, higher-frequency signals or signal components also attenuate faster than low-frequency signals as they travel through the environment (Marten and Marler 1977; Brenowitz 1986; Dabelsteen et al. 1993). Another trade-off exists between signal frequency and the amplitude at which a bird can vocalize, and this trade-off is strongly mediated by body size. In general, larger birds call or sing at a lower frequency but a higher amplitude than smaller birds (Wallschlager 1980; Calder 1990; Hu and Cardoso 2009). These complexities obscure the expected impact of urban noise on the active space of a signal.

Here we synthesize available knowledge to develop a mathematical model that predicts the active space of avian vocal signals in forest noise and urban noise. We use the model to examine the effect of signal frequency and amplitude on the decrease in communication distance experienced by different bird species after moving from natural, forested habitats to urban habitats if their vocal signals remain unchanged. We then test the predictions of the model with a metaregression of observed frequency shifts in urban noise in eight species of songbirds and assess the expected gain in communication distance conferred by shifting the frequency of song. The benefit birds obtain from frequency shifts in urban noise has been the subject of recent debate (Nemeth and Brumm 2010; Nemeth et al. 2012; Slabbekoorn et al. 2012). Finally, we present a series of predictions, arising from our general model, that together with the model represent an important step toward a theory of acoustic communication in urban noise.

Methods

Acoustic Communication in Noise

All else being equal, the active space of an acoustic signal increases with amplitude. As a sound propagates, its energy spreads over a greater sphere of disturbance. The inverse-square law predicts that the amplitude of a sound (measured as pressure or intensity) will decrease by 6 dB for each doubling of distance from the source (Forrest 1994). In natural habitats, sound generally attenuates at a faster rate than expected from the inverse-square law, due to processes such as atmospheric absorption, scattering, and/or boundary interference (excess attenuation). Background noise reduces the active space of a signal by increasing the hearing threshold of the receiver; that is, the signal must be louder to be detected in noise than in quiet. This masked threshold can be more than 25 dB higher than the threshold in quiet conditions, dramatically reducing the distance over which a signal can be detected (Klump 1996; Lohr et al. 2003). In the auditory system of terrestrial vertebrates, a series of auditory filters are arranged along the basilar membrane of the inner ear, allowing for frequency selectivity and discrimination between different sounds. The bandwidth of an auditory filter (the critical bandwidth; Fletcher 1940) is the band of frequencies that are passed by the filter. When a signal is presented in masking noise, the frequencies falling within the critical bandwidth contribute most to the masking of the signal. In general, the larger the critical bandwidth, the more a signal is masked in broadband noise.

The critical bandwidth at a particular frequency can be estimated from the ratio of the masked threshold of a tone of that frequency in broadband noise to the spectrum level of the noise. This is known as the critical ratio or signal-to-noise ratio (Langemann et al. 1995; Klump 1996). In a laboratory experiment, Langemann et al. (1995) observed that critical ratios in the European starling *Sturnus vulgaris* increased with signal frequency, from 21.8 dB at 1 kHz to 26.9 dB at 6.3 kHz. Thus, a 1-kHz tone needed to be 21.8 dB louder than the background noise to be detected, while a 6.3-kHz tone needed to be 26.9 dB louder. Klump (1996) analyzed data on critical ratios in 10 bird species and found the average pattern to be similar to that reported for starlings. Therefore, in broadband noise, the masking of acoustic signals in birds generally increases with signal frequency. However, urban noise is not distributed evenly across all frequencies, with much of the acoustical energy concentrated below 2 kHz. So when determining the masking effect of urban noise on signals or signal components of different frequency, one must consider both the critical ratio (higher for high-frequency signals) and the acoustical energy of the noise at the relevant frequency (higher at low frequencies; Lohr et al. 2003).

The masked threshold of the receiver equals the spectrum level of noise at the frequency of the signal plus the critical ratio of a signal of that frequency.

Description of the General Model

We constructed a general model to predict the change in the active space of a bird's song or call after moving from a rural, deciduous forest to a city park with deciduous trees as a function of the amplitude and frequency of the signal, the excess attenuation of sound in deciduous forest, the frequency spectrum of noise in forested and urban habitats, and the masked threshold of the receiver in the two types of noise. Both the sender and the receiver were assumed to be perched 2 m above the ground to minimize the absorption of the signal by soft ground and to exclude the effects of relative position on signal propagation (Wiley and Richards 1978; Dabelsteen et al. 1993; Holland et al. 1998).

We began by considering the amplitude and the frequency of the signal created by the sender. Empirical observations of the amplitude of vocal signals in birds are available for only a limited number of species (Calder 1990; Brumm 2004). However, these data are sufficient to demonstrate that, on an interspecific level, signal power scales with the body mass of a species (Calder 1990; Gillooly and Ophir 2010). We modeled the scaling relationship between signal power P (mW) and body mass m (g) as

$$P = Am^{B}, \tag{1}$$

with the parameters A and B estimated from linear regression of log-transformed values for P and m using data on 35 species (Brackenbury 1979; Calder 1990; Brumm 2004, 2009; Patricelli et al. 2007). We converted power to sound pressure level (SPL) using the following equation, derived from the reference value of 0.03 W = 97 dB SPL (Brackenbury 1978):

$$L = 82 + 10\log_{10}(P), \tag{2}$$

where L is the sound pressure level of the signal in dB at 1 m from the signaler. We investigated the sensitivity of our model to uncertainty in the relationship between signal power and body mass by multiplying and dividing the predicted relationship by a factor of 10. However, this did not change the qualitative results (data not shown).

The acoustic frequency of bird vocalizations also correlates with body mass (Wallschlager 1980; Gillooly and Ophir 2010). The scaling relationship between the dominant frequency of a signal F (kHz) and body mass m was

$$F = am^{-b}, \tag{3}$$

with the parameters a and b estimated using data on 526 species of birds (the data set of Hu and Cardoso [2009] with two potential errors removed: the mute swan *Cygnus olor* and Allen's hummingbird *Selasphorus sasin*). A similar relationship can be estimated for the minimum frequency of a signal and body mass. Combining equations (1)–(3), the SPL of the signal at 1 m (L) as a function of the dominant frequency of the signal is

$$L = 82 + 10\log_{10}A + \left(\frac{10B}{b}\right)\log_{10}a - \left(\frac{10B}{b}\right)\log_{10}F. \tag{4}$$

The estimates for the parameters a, b, A, and B are given in table 1.

Beyond this relationship with amplitude (eq. [4]), the frequency of an acoustic signal or signal component influences its active space in noise in three ways. First, the rate of excess attenuation of a signal varies with frequency (Marten and Marler 1977). Second, in most real-world situations, background noise is not evenly distributed across the frequency spectrum, so the level of noise varies with frequency. And third, the critical ratio of a signal increases with signal frequency (Klump 1996). As outlined above, the masked threshold of the receiver in noise equals the sum of the spectrum level of noise at the frequency of the signal plus the critical ratio of a signal of that frequency.

We modeled the excess attenuation (E) of signals of different frequencies in dB/m with piecewise linear regression, using data on attenuation at a height of 2 m in deciduous forest with leaves (Marten and Marler 1977; fig. 1). The attenuation of bioacoustic signals in complex urban environments is poorly understood (Warren et al. 2006; Nemeth and Brumm 2010). We considered that excess attenuation in urban parks with deciduous trees would be similar to that observed in rural deciduous forests. However, we also formulated our model using Nemeth and Brumm's (2010) estimate of attenuation in urban habitats (8 dB per doubling of distance, plus atmospheric attenuation per the international standard ISO 9613–1) to investigate the sensitivity of the model to the choice of attenuation function. Using this second approximation of

Table 1: Parameter estimates for scaling relationships between signal power at 1 m and body mass (A and B; eq. [1]) and signal frequency and body mass (a and b; eq. [3]) obtained from linear regression of log-transformed variables

Parameter	Mean	SD	2.5%	97.5%
A	−3.11	.41	−3.89	−2.32
B	1.14	.087	.97	1.30
a	2.16	.038	2.08	2.24
b	−.61	.027	−.67	−.55

Note: Results are presented as mean and standard deviation of posterior distributions and 2.5th and 97.5th percentiles.

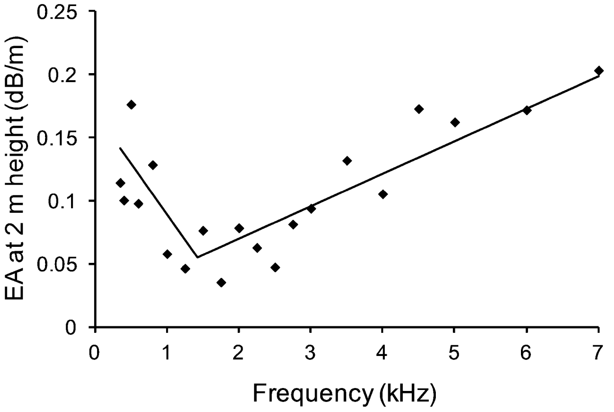

Figure 1: Excess attenuation (EA) of a signal (dB/m) at 2-m height in deciduous forest with leaves as a function of signal frequency (kHz); piecewise linear regression (line) using data from Marten and Marler (1977; diamonds).

signal attenuation in urban habitats did not change the qualitative results of the model (data not shown).

We used the average noise spectrum in dB/Hz (spectrum level) recorded at 10 sites in a deciduous forest (Vienna Woods, Austria) and the average noise spectrum plus 1 SD recorded at 10 sites in central Vienna, Austria, to represent the spectrum of noise in forested and urban habitats, respectively (from fig. 2 of Nemeth and Brumm 2010; fig. 2*A*, lower and upper curves, respectively). The urban noise spectrum had an equivalent continuous sound level (L_{Aeq}) of 61.1 dB(A), which is toward the upper end of sound levels observed in 15 territories of the nightingale in Berlin, Germany (Brumm 2004), and 26 neighborhood parks in Phoenix, Arizona (K. M. Parris, unpublished data). The forest noise spectrum had an equivalent continuous sound level of 45.4 dB(A). We added the average critical ratios observed in 10 bird species (Klump 1996) to the spectrum level of noise to estimate the masked thresholds of signals of different frequencies in each habitat (fig. 2*B*).

The active space of the signal, or maximum communication distance (d_{mc}), in each habitat was calculated by solving the following implicit equation for d_{mc} (adapted from Lohr et al. 2003 and Nemeth and Brumm 2010):

$$D = 20\log_{10}\left(\frac{d_{\mathrm{mc}}}{d_0}\right) + E(d_{\mathrm{mc}} - d_0), \qquad (5)$$

where D is the difference between the amplitude of the signal at d_0 (L) and the masked threshold of the receiver (in dB SPL), that is, the amount by which the signal can attenuate while still remaining detectable by the receiver. The parameter d_0 is the distance from the sender at which the amplitude of the signal is measured (1 m, in our case). The first term on the right-hand side of the equation represents attenuation due to spherical spreading, and the second term represents excess attenuation, with E being excess attenuation in dB/m. The sound pressure level of the signal (L) may be used directly if known for a particular species, or estimated via relationships with body mass and signal frequency (eqq. [1]–[4]). Note that the maximum communication distance represents the distance over which a signal can be detected by a conspecific bird; this is likely to be greater than the distance over which the signal can be discriminated and its information interpreted by a receiver (Lohr at al. 2003).

Combining the equations and data described above, we modeled the maximum communication distance of signals with frequencies ranging from 0.8 to 6.4 kHz in forested and urban habitats. We then calculated the change in maximum communication distance when a bird moves between the two habitats (or when a forested habitat is urbanized) as a function of signal power and frequency, assuming no change to these signal characteristics. Un-

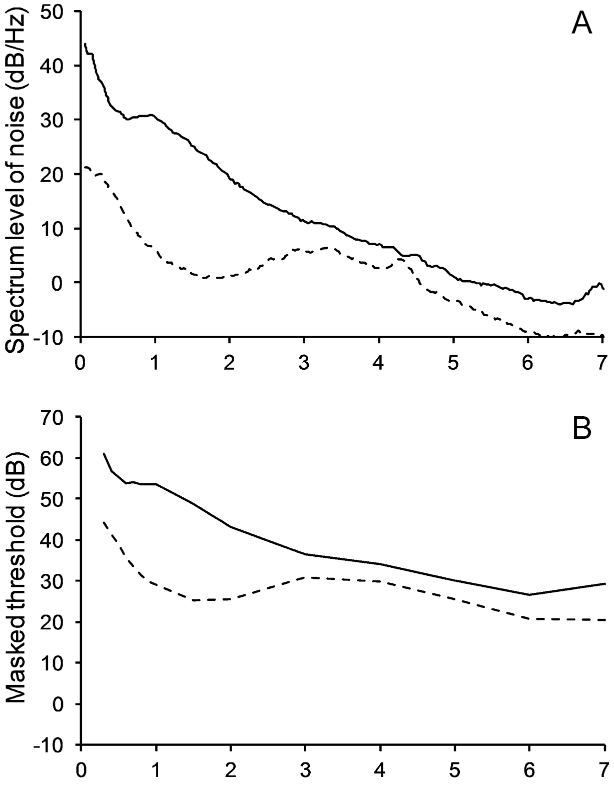

Figure 2: Spectrum level of noise (dB/Hz; *A*) and masked threshold of signals (dB; *B*) in forested and urban habitats (dashed and solid lines, respectively) as functions of frequency (kHz); data from Klump (1996), Nemeth and Brumm (2010, their fig. 1).

certainty in the coefficients shown in equations (1)–(4) was propagated to the predictions by fitting the model to data using WinBUGS 1.4, a program for Bayesian Markov chain Monte Carlo (MCMC) data analysis (Spiegelhalter et al. 2003). To ensure that WinBUGS was sampling from the stationary distribution, we discarded the first 100,000 samples as a burn-in before taking 500,000 samples from the posterior distribution to estimate parameters, thinned to 1 in 10 samples. The implicit equation (5) was solved by exporting the MCMC samples from WinBUGS to Mathematica (Wolfram Research 2010; supplementary code files available online).[1] We calculated the mean and standard deviation of the posterior distributions of the model parameters and predictions, along with the 2.5th and 97.5th percentiles to represent the 95% credible interval (CI) around the predicted relationship.

Predicted Effect of Urban Noise on the Active Space of Individual Species

We also used equation (5) and the masked thresholds in forested and urban areas described above to estimate the change in the active space of song for six individual species of birds with known signal power at the dominant frequency of the signal (i.e., L was known and not estimated from signal frequency; Calder 1990; Hu and Cardoso 2009). These species—the willow warbler *Phylloscopus trochilus*, the chiffchaff *Phylloscopus collybita*, the common whitethroat *Sylvia communis*, the Eurasian blackcap *Sylvia atricapilla*, the song thrush *Turdus philomelos*, and the common blackbird *Turdus merula*—form three pairs of congeners, with the members of each pair having similar body masses (table A1). All are known to occur in both deciduous forests and urban parks and gardens in Europe (Hu and Cardoso 2009; Avibirds 2011). This analysis was designed to explore the level of masking experienced by individual bird species in urban noise and how this varies with song power and song frequency.

Metaregression of Published Data

We tested the predictions of our general model with a metaregression of published data on frequency shifts in urban noise observed in eight species of songbirds: the great tit *Parus major* (Slabbekoorn and Peet 2003; Slabbekoorn and den Boer-Visser 2006; Mockford and Marshall 2009), the house finch *Carpodacus mexicanus* (Fernández-Juricic et al. 2005), the song sparrow *Melospiza melodia* (Wood and Yezerinac 2006), the common blackbird (unpublished data from the study reported in Nemeth and Brumm 2009), the grey shrike-thrush *Colluricincla harmonica*, the grey fantail *Rhipidura fuliginosa* (Parris and Schneider 2009), the silvereye *Zosterops lateralis* (Potvin et al. 2011), and the reed bunting *Emberiza schoeniclus* (Gross et al. 2010). See table A2 for more details of these studies, including effect sizes and standard errors. Metaregression is a type of meta-analysis that is analogous to an analysis of covariance (Lajeunesse 2010). While a simple meta-analysis aims to estimate a single effect size by combining data from a number of studies, metaregression aims to relate the effect size observed in different studies to one or more covariates (Thompson and Higgins 2002).

In our metaregression, we estimated the effect of song frequency (the covariate) on the increase in the minimum frequency of each species' song in urban noise (the effect size) using Bayesian linear regression in WinBUGS 1.4 (Spiegelhalter et al. 2003; McCarthy 2007). The regression model included uninformative priors to reflect an absence of prior information and error terms to account separately for within-study error (based on the standard error reported for each study) and unexplained sources of variation between studies. Therefore, studies with less precise effect sizes had less influence on the metaregression, as recommended by Thompson and Higgins (2002). We calculated the mean and standard deviation of the posterior distributions of the model coefficients, along with the 2.5th and 97.5th percentiles to represent the 95% credible interval around the predicted relationship. We discarded the first 100,000 samples as a burn-in before taking 500,000 samples from the posterior distribution to estimate parameters. We checked stationarity by examining the history of samples obtained from WinBUGS.

Expected Gain in Active Space with Frequency Shifts in Urban Noise

Using the general model and the results of the metaregression described above, we assessed the expected gain in active space with predicted frequency shifts in urban noise for songs with a minimum frequency of 1.5–4.5 kHz. We reran the general model in WinBUGS and Mathematica using values for minimum frequencies following the predicted frequency shift. To ensure that WinBUGS was sampling from the stationary distribution, we discarded the first 20,000 samples as a burn-in. We then took 100,000 samples from the posterior distribution to estimate parameters, thinned to 1 in 10 samples. We expressed the increase in active space following the frequency shift as a percentage to allow the benefit of this behavioral strategy to be easily assessed.

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[1] Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

Results

Our general model predicts that the decrease in communication distance experienced by birds after moving from natural to urban habitats is largely a function of signal frequency. This is not unexpected, given our current understanding of acoustic communication in noise. However, the relationship between the magnitude of the decrease and the signal frequency is a complex one (fig. 3). Birds with vocal signals of around 1.5 kHz are predicted to experience, on average, the greatest reduction in the active space of their signals after moving from forested to urban habitats. The effect size decreases for signals lower than 1.5 kHz as well as for signals higher than 1.5 kHz until leveling off at around 3 kHz. The predicted reduction in active space is then reasonably constant until approximately 5 kHz, after which it increases gradually (fig. 3).

The estimated proportional reduction in active space ranges from 0.27 to 0.63 (95% CI: 0.26, 0.67) for vocal signals in the frequency window of 0.8–2.9 kHz, with those between 1.1 and 1.6 kHz predicted to suffer a proportional reduction greater than 0.6. For example, a bird singing at 1.5 kHz and an amplitude of 101 dB SPL at 1 m has a predicted maximum communication distance of approximately 415 m in a rural, deciduous forest and 160 m in an urban park with deciduous trees—a proportional reduction of 0.63. In contrast, the maximum communication distance of a bird singing at 4 kHz and an amplitude of 82.8 dB SPL at 1 m is 105 m in deciduous forest and 88 m in an urban park—a proportional reduction of just under 0.2. The window of maximum decline in communication distance occurs in the area of the frequency spectrum that experiences the greatest change in background noise levels after moving from a rural, deciduous forest to an urban park (fig. 2). While this frequency window is beneficial for communication in the forest due to relatively low levels of background noise and a low rate of excess attenuation, it becomes detrimental for communication in urban areas because it coincides with high levels of background noise.

The reduction in communication distance calculated for the six individual bird species falls close to that predicted by the general model, which represents the effect averaged over all bird species (fig. 3). Within each of the three pairs of species, it is clear that the species with the greater signal power has the greater communication distance in both habitats (table A1). But it is also clear that the reduction in communication distance expected in urban noise is largely explained by the dominant frequency of the signal and that signal power has a minor effect at best (e.g., see *Turdus philomelos* and *Turdus merula*). Note that this analysis calculates the change in communication distance between the two habitats when both signal power and frequency are held constant.

Based on the general model described above, we would expect birds with important signal components in the frequency window of 0.8–2.9 kHz to change their signals in

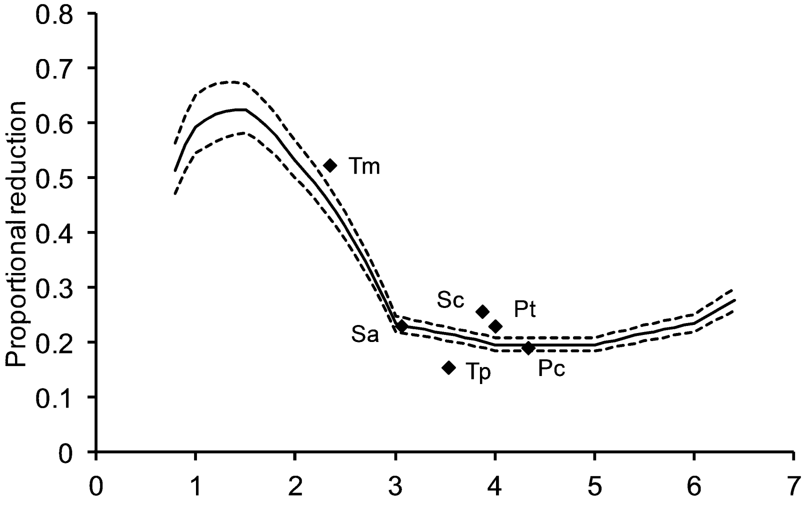

Figure 3: Results of general model: proportional reduction in active space of a signal (and maximum communication distance of signaler) after moving from a deciduous forest with leaves to an urban park with deciduous trees as a function of signal frequency (kHz). Solid line shows predicted relationship and dashed lines 95% credible intervals. Diamonds show reduction in communication distance calculated for six individual bird species; Pt = *Phylloscopus trochilus*, Pc = *P. collybita*, Sc = *Sylvia communis*, Sa = *S. atricapilla*, Tp = *Turdus philomelos*, and Tm = *T. merula*.

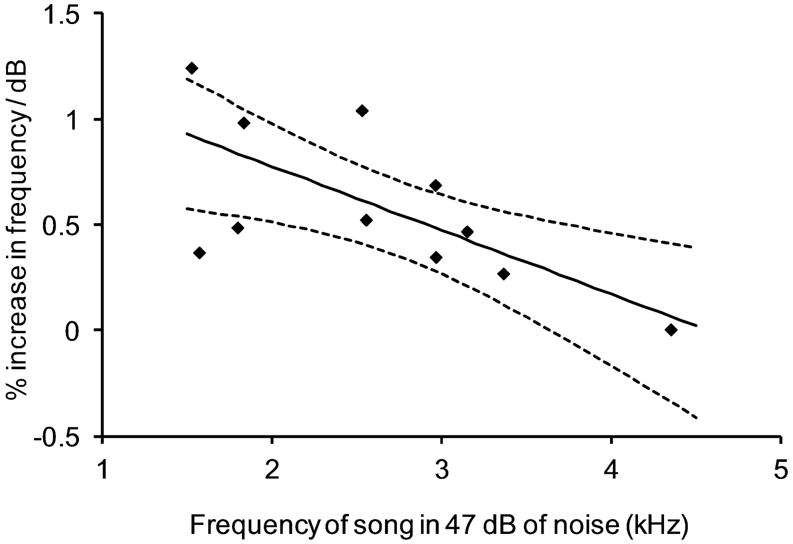

Figure 4: Metaregression of observed frequency shifts in urban noise (% increase in minimum frequency/dB of noise) as a function of minimum song frequency in 47 dB of noise (kHz). Solid line shows predicted relationship, dashed lines 95% credible intervals, and diamonds observed data.

response to urban noise more than birds with signals outside the window. We would also expect that the size of this change would decrease monotonically for signals with important components in the frequency range between 1.5 and 4 kHz (fig. 3). This latter prediction is supported by our metaregression of frequency shifts in urban noise across eight species of songbirds (fig. 4), which shows that the size of the frequency shift decreases as signal frequency increases from 1.5 to 4.5 kHz, with an estimated reduction of 0.3% per dB per kHz (95% CI: −0.52, −0.11; table 2). For example, the frequency of a 1.5-kHz song is predicted to increase by 0.93% per dB of noise. Thus, if a species sings a song (or song component) at 1.5 kHz in a quiet, rural habitat with a background noise level of 47 dB, it would be expected to sing that component 21.3%, or approximately 320 Hz, higher in an urban habitat with a background noise level of 70 dB. In contrast, a bird with a 4.4-kHz song component is expected to demonstrate a frequency shift of only 1.2%, or 52 Hz, under the same circumstances. We included all suitable published data on frequency shifts in urban noise in our metaregression, but these data are limited to signal frequencies ≥1.5 kHz. Frequencies below 1.5 kHz are largely used by nonpasserine birds such as doves, owls, gulls, and waterfowl. While many of these species inhabit urban areas, possible changes in their vocal signals in response to urban noise have not been examined.

The expected benefit to the signaler of frequency shifts in urban noise is relatively modest and declines with signal frequency (fig. 5). For signals with a baseline minimum frequency of 1.5 kHz, our analysis predicts an increase of approximately 12% in active space following the shift. This declines to approximately 4% for signals with a baseline minimum frequency of 2.0–2.8 kHz and to less than 1% for signals >2.9 kHz (fig. 5). For example, consider a bird singing at 1.5 kHz and 101 dB SPL at 1 m in an urban park with deciduous trees and a background noise level of 61.1 dB(A) SPL. If it does not shift the frequency of its song, the bird has a predicted maximum communication distance of 160 m; if it does, this communication distance increases by 19.5 m, to 179.5 m. And assuming that the bird is acting as an omnidirectional sound source, the area over which its song can be detected increases by approximately 26%, from 8 to 10.1 ha. While the resulting communication distance and area do not approach those expected in the rural forest with a background noise level of 45.4 dB(A) SPL (415 m and 54 ha, respectively), the increases expected with such a frequency shift are sufficiently large to be of potential benefit to the signaler.

Table 2: Coefficients of metaregression of observed frequency shifts in urban noise as a function of signal frequency (% increase in frequency/dB of noise/kHz)

Variable	Mean	SD	2.5%	97.5%
Constant	1.381	.324	.701	2.00
Signal frequency	−.302	.113	−.518	−.0626
SD (error)	.227	.126	.0247	.519

Note: SD (error) = standard deviation of error term estimating unexplained variation between studies.

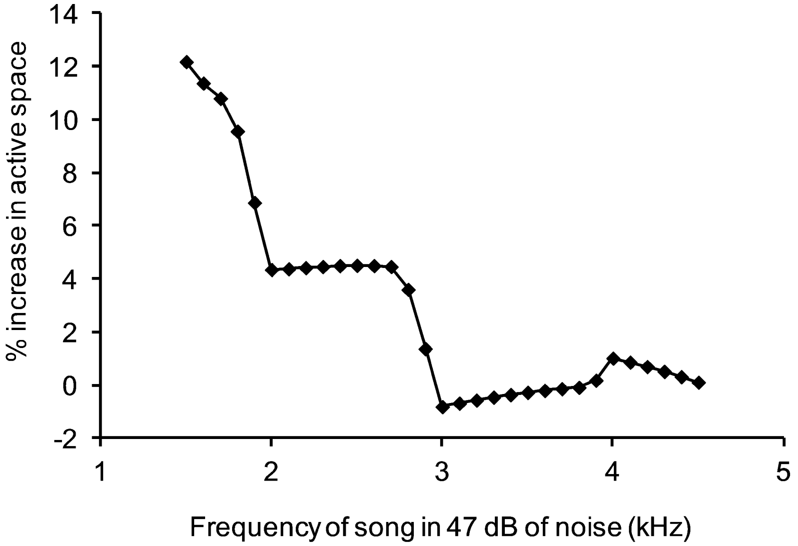

Figure 5: Expected benefit of frequency shifts in urban noise predicted by the metaregression: percentage increase in active space as a function of baseline minimum frequency of song in 47 dB of noise (kHz).

Discussion

A number of studies have investigated the impact of urban noise on acoustic communication in birds. However, this is the first study to formulate a general mechanistic model to identify which bird species are likely to experience the greatest reduction in their vocal signals' active space in urban noise. The model is applicable to bird communities globally and could be used to predict the impact of background noise on birds in both existing urban areas and future urban developments. Case studies of individual species with known signal amplitude confirm that signal frequency has a greater effect on the reduction in communication distance in urban noise than signal amplitude. While the active space of a signal in any habitat increases with amplitude, the proportional reduction in active space after moving from a rural to an urban habitat is greatest for signals in the frequency range of 0.8–2.9 kHz (but as noted above, we did not have sufficient data to estimate the effect on signals below 0.8 kHz).

Therefore, birds with songs or calls in this frequency window are likely to change the frequency, amplitude, or timing of their signals the most. This prediction is supported by our metaregression of observed frequency shifts in urban noise for signals ≥1.5 kHz, with lower-singing birds showing a greater frequency shift than higher-singing birds. However, data on frequency shifts in birds that sing or call below 1.5 kHz are needed to corroborate the model's predictions for the lower frequency range. We make two further predictions here. First, populations of birds with signals in the frequency window of 0.8–2.9 kHz will be more likely to suffer reduced breeding success in noisy urban habitats, if difficulty being heard translates into difficulty attracting and maintaining a mate and/or in reduced maternal investment in reproduction (e.g., Reijnen and Foppen 1994; Francis et al. 2009; Halfwerk et al. 2011). This is because the frequency shifts observed in the wild offer only a partial compensation for the active space of these signals that is lost in urban noise. Second, the size of a bird's territory or home range (as well as the amplitude and frequency of its acoustic signals) scales with body mass (Calder 1990); larger birds produce higher-amplitude signals with a greater active space, enabling them to defend larger territories. We therefore predict that larger birds will experience a greater proportional reduction in territory size in urban habitats than smaller birds.

Our modeling demonstrates that the expected gain in active space following frequency shifts in urban noise is relatively modest. The greatest increase, 12%, is predicted for songs with a minimum frequency of 1.5 kHz, while smaller increases are predicted for songs of higher frequency. These results are similar to those of Nemeth and Brumm (2010), who estimated increases of 9%–13% in the active space of the songs of blackbirds and great tits with a 200-Hz shift in frequency. As the benefit conferred by shifting frequency is substantially smaller than that obtained by increasing the amplitude of a signal by 5.2 dB (as seen in urban nightingales; Brumm 2004), Nemeth and Brumm (2010) argued that frequency shifts in urban noise may not be adaptive unless the resulting increase in communication distance increases fitness. To date, no such increases in fitness have been demonstrated. There is good evidence that urban noise reduces both clutch sizes and the number of fledglings in great tits (Halfwerk et al. 2011), but there are no published data on the relative reproductive success of conspecific birds that sing lower- and higher-frequency songs in noisy urban environments. Furthermore, while the benefits of singing at a higher amplitude in urban noise may outweigh those of singing at a higher frequency, the relative costs of the two strategies are yet to be assessed (Patricelli and Blickley 2006; Slabbekoorn et al. 2012).

A number of signal features that were not included in our general model—such as bandwidth, signal length, syllable rate, and the use of complex elements such as trills—may all affect the degradation and the propagation of signals in urban habitats (Lohr et al. 2003; Patricelli and Blickley 2006; Warren et al. 2006). In future, the model could be adapted to include these signal features, if sufficient information were available on (1) how they affect signal degradation in the particular part of the urban landscape a given species inhabits and (2) the structure of that species' vocal signals. The model could also be modified to predict the distance over which a signal can be discriminated and the information it contains decoded. In their study of the budgerigar *Melopsittacus undulatus* and the zebra finch *Taeniopygia guttata*, Lohr et al. (2003) found an average difference of 3.29 dB between the birds' detection and discrimination thresholds in noise, translating to a discrimination distance that is 0.685 times the detection distance. Finally, the model could be used to assess the decrease in the active space of signals after moving from natural habitats other than forests (e.g., meadows or deserts) to cities by modifying the baseline (natural) noise spectrum and excess-attenuation function.

Some authors have argued that the discipline of ecology suffers from a lack of generally applicable theory (e.g., Peters 1991; Smallwood and Schonewald 1996; Lawton 1999). The development of theories that can be used to make quantitative—and therefore testable—predictions will help to advance the field. This may be especially true for the subdiscipline of urban ecology (Shochat et al. 2006; McCarthy 2009). Our mechanistic model combines information from a diversity of disciplines, including behavioral ecology, acoustics, physiology, and allometric scaling, to identify which birds will suffer the greatest reduction in the active space of their vocal signals in urban noise. We present it here, along with a series of predictions regarding the behavioral and population-level responses of certain groups of birds, as an important step in the development of a theory of acoustic communication in urban noise.

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APPENDIX

Table A1: Predicted decline in maximum communication distance (d_{mc}) of six species of songbird with known signal power, after moving from a rural, deciduous forest to an urban park with deciduous trees

Species	Common name	Body mass (g)[a]	Dom. freq. (kHz)[a]	Power (mW)[b]	SPL (dB)	*E* (dB/m)	Forest d_{mc} (m)	Urban d_{mc} (m)	Decline in d_{mc}
Phylloscopus collybita	Chiffchaff	8.3	4.33	.6	79.8	.130	94	76	.19
Phylloscopus trochilus	Willow warbler	8.7	4.00	.3	76.5	.121	78	60	.23
Sylvia atricapilla	Eurasian blackcap	16.7	3.06	4	88.0	.0955	147	113	.23
Sylvia communis	Common whitethroat	15.1	3.87	.15	73.9	.118	66	49	.26
Turdus philomelos	Song thrush	68.9	3.53	60	99.7	.109	212	179	.16
Turdus merula	Common blackbird	103	2.34	3	86.8	.0774	187	89	.52

Note: Dom. freq. is the dominant frequency of the species' song, power is song power at 1 m, SPL is the sound pressure level of song at 1 m, and *E* is excess attenuation.

[a] Data from Hu and Cardoso (2009).

[b] Data from Brackenbury (1979) and Calder (1990).

Table A2: Data used in metaregression of frequency shifts in urban noise (fig. 4), from left to right

Species	Common name	Reference	Freq. (kHz)	Effect size (%/dB)	SE
Melospiza melodia	Song sparrow	Wood and Yezerinac 2006, fig. 2	1.5238	1.2436	.2846
Colluricincla harmonica	Grey shrike-thrush	Parris and Schneider 2009, fig. 3; table 1	1.5693	.3702	.2747
Carpodacus mexicanus	House finch	Fernández-Juricic et al. 2005, fig. 3*a*	1.7948	.4881	.1996
Turdus merula	Common blackbird	E. Nemeth and H. Brumm, unpublished data	1.8310	.9844	.1603
Emberiza schoeniclus	Reed bunting (unpaired)	Gross et al. 2010, fig. 2*a*	2.5280	1.0423	.1669
Zosterops lateralis	Silvereye	Potvin et al. 2011, fig. 1*a*	2.5530	.5249	.3615
Parus major	Great tit	Mockford and Marshall 2009, fig. 3	2.9616	.6890	.1848
Emberiza schoeniclus	Reed bunting (paired)	Gross et al. 2010, fig. 2*a*	2.9645	.3483	.2335
P. major	Great tit	Slabbekoorn and Peet 2003, fig. 1*b*	3.1480	.4695	.2299
P. major	Great tit	Slabbekoorn and den Boer-Visser 2006, fig. 2*a*	3.3624	.2701	.0748
Rhipidura fuliginosa	Grey fantail	Parris and Schneider 2009, fig. 3; table 1	4.3500	.0061	.0965

Note: Freq. = minimum frequency of song in 47 dB of noise.

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Top, a silvereye (*Zosterops lateralis*), a small songbird that lives in rural and urban habitats in Australia, New Zealand, and a number of Pacific islands. Photograph by Jeremy Kruckel. *Bottom*, a silvereye on Lord Howe Island. Photograph by Jack Shick Photography.