Original Article

Comparative effects of urban development and anthropogenic noise on bird songs

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Many avian species live, breed, and communicate in urban areas. To survive and reproduce in these areas, birds must transmit their signals to intended receivers. As an arena for acoustic communication, 2 salient features of the urban environment are an abundance of reflective surfaces and a high level of low-frequency anthropogenic noise. Each presents unique communication challenges, with hard surfaces reflecting and distorting high frequencies and noise masking low-frequency song components. Based on this, we predicted that noise level would affect minimum song frequency and urban development (percentage of impervious surface) would affect maximum frequency and frequency range. We compared the effects of urban development and noise on songs of 6 bird species at 28 sites along an urban to rural gradient, across a broad range of noise levels. We found that minimum song frequency increased as noise level increased for 2 of 6 species, with 5 of 6 species showing a strong trend in the predicted direction. Species with lower frequency songs were more affected by noise. Maximum frequency and frequency range decreased for 2 of 6 species as urban development increased, and this effect was stronger for species with higher frequency songs. For some species, minimum frequency only increased with noise at less urban sites and similarly, maximum frequency and frequency range only decreased with urbanization at quiet sites, suggesting a trade-off between different vocal adjustments. Ours is the first study to investigate how noise and urban development affect song frequency characteristics of multiple bird species. *Key words:* acoustic adjustment, acoustic interference, anthropogenic noise, bird song, signal transmission, urbanization. *[Behav Ecol 23:201–209 (2012)]*

INTRODUCTION

With human population growth, landscapes become increasingly developed and habitats important to wildlife become permanently altered (Marzluff 2001). Anthropogenic modification of habitats can have a particularly strong effect on acoustic communication in animals because their vocalizations are specifically adapted to both the structural and the acoustic characteristics of their local environment (Orejuela and Morton 1975; Wiley and Richards 1978; Hunter and Krebs 1979; Rabin and Greene 2002; Warren et al. 2006).

The impervious surfaces of developed areas affect animal signals by scattering sound waves and creating multiple reverberations that can cancel and distort portions of the signal (Truax 1978; Slabbekoorn et al. 2007). These effects depend on the frequency of the signal. Scattering, reverberation, and atmospheric and vegetative absorption are stronger for high-frequency than for low-frequency signals (Wiley and Richards 1982; Boncoraglio and Saino 2007). Reverberations of high frequencies create many overlapping echoes that decay randomly, whereas low frequency sounds often form one discrete echo (Richards and Wiley 1980). Multiple overlapping echoes with unpredictable arrival times can mask, cancel, or distort structural features of the signal (Richards and Wiley 1980; Slabbekoorn et al. 2007). This effect is especially strong for

broad bandwidth signals (Boncoraglio and Saino 2007). In addition, large barriers in urban habitat (such as buildings) absorb and reflect high-frequency sounds, whereas low-frequency sounds are diffracted around barrier edges and continue to propagate (Truax 1978; Rossing and Fletcher 2004).

An additional effect of increased human population density and continued urban development is an increasing level of anthropogenic noise. Background noise presents a challenge for animal communication because it increases the masked hearing threshold (threshold of audibility for a specified sound in the presence of another sound) of receivers (Yost 2000; Barber et al. 2010) and thereby limits the signal's active space (distance over which a sound can be heard). Most anthropogenic noise (including air and road traffic noise) occupies a frequency range below 2000 Hz (Slabbekoorn and Peet 2003). This low-frequency noise disrupts the transmission of low-frequency signal components by masking that region, which changes the frequency range that the receiver hears and interferes with the receiver's ability to hear the signal's original content (Lohr et al. 2003; Brumm and Slabbekoorn 2005; Halfwerk et al. 2011).

Animals use acoustic signals for functions like species recognition, mate attraction, and territory defense, making them central to their reproductive success and survival (Kroodsma and Byers 1991; Brumm and Slabbekoorn 2005). A signal must be well matched to the acoustic environment in order to reach the receiver and maintain information content. In highly reverberant structural environments, we would expect low-frequency songs with narrow frequency ranges to be

favored, whereas we would expect songs with a high minimum frequency bound to be favored in areas where anthropogenic noise is present. Because different bird species have different song frequency and structural characteristics, we would also expect the effects of noise and urbanization on song to differ by species. Specifically, in highly reverberant urban environments, we would expect species with high-frequency broad bandwidth songs to be more impacted by reverberation and we expect them to adjust songs more in response. We would expect species whose songs have a lower minimum frequency bound to be more impacted by masking in areas with high noise levels and we expect them to adjust songs more in response. Numerous observational and experimental studies have shown that several bird species sing with a higher minimum frequency when low-frequency ambient noise is present (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Wood and Yezerinac 2006; Nemeth and Brumm 2009; Bermúdez-Caumatzin et al. 2010). To our knowledge, no studies have investigated how both urban development and noise level affect bird song in more than one species.

In this study, we investigated how the frequency characteristics of the songs of 6 bird species vary with urban development and with the decibel level of the background noise. Based on both sound transmission and masking theory outlined above, we made the following predictions: 1) The minimum frequency of bird songs will be affected by background noise level and this affect will be stronger for species with lower frequency songs. We expect urban development will have little or no effect on minimum frequency. 2) The maximum frequency of bird songs will be affected by the amount of urban development and this affect will be stronger for species with higher frequency songs. We expect noise level will have little or no effect on maximum frequency. 3) The frequency range of bird songs will be affected by the amount of urban development and this affect will be stronger for species with higher frequency songs. We expect noise level will have little or no effect on frequency range.

MATERIALS AND METHODS

Research was conducted at 28 study sites across an urban to rural land-use gradient in the greater Washington, DC and Baltimore metropolitan areas. Study sites were part of the Smithsonian Neighborhood Nestwatch citizen science project (http://nationalzoo.si.edu/ConservationAndScience/MigratoryBirds/Research/Neighborhood_Nestwatch). In this project, participating citizens volunteer their private property for use as study sites and can also participate in data collection for some projects.

At each study site, a center point was established at the front left corner of the central structure of the property (typically a house). This center point was used for land cover measurements and ambient noise measurements. All birds were recorded within 400 m of this point. We measured ambient noise level using an Extech 407730 sound level meter. Measurements were C weighted and taken for 5 min total in 4 cardinal directions, and the highest readings (that were not the result of wind or abrupt noises) from each direction were recorded and averaged. We took readings between 6:30 AM and 9:00 AM (active time of day for singing for all 6 species) on the same day that birds were recorded at that location. To determine the level of urban development, the percentage of impervious surface within a 400 m radius around the site center was measured for each site. We chose a radius size of 400 m because bird communities are significantly affected by traffic noise up to a distance of about 400 m (Reijnen and Foppen 1997; Weiserbs and Jacob 2001; Reijnen and Foppen 2006). Percentage of impervious surface was determined using 30m–resolution National Land Cover Data 2001 (Homer et al. 2004) in ArcGIS 9.2 (Environmental Systems Research Institute 1999–2006).

We recorded songs using a Sony TCM-5000EV tape recorder (Sony, New York, NY), Maxell UR type 1 90-min tapes (Maxell, Atlanta, GA), and a Sennheiser ME 66 shotgun microphone (Sennheiser, Old Lyme, CT). Songs from the following species were recorded: American Robin (*Turdus migratorius*), Carolina Wren (*Thryothorus ludovicianus*), Gray Catbird (*Dumetella carolinensis*), House Wren (*Troglodytes aedon*), Northern Cardinal (*Cardinalis cardinalis*), and Song Sparrow (*Melospiza melodia*). We chose these species because they are present in rural, suburban, and urban areas and can be readily recorded at all sites. All 6 species vocalize at frequencies low enough to be masked by low-frequency anthropogenic noise (Cimprich and Moore 1995; Haggerty and Morton 1995; Johnson 1998; Halkin and Linville 1999; Sallabanks and James 1999; Arcese et al. 2002) and at frequencies high enough to be attenuated and distorted in reverberant environments (Morton 1975).

We recorded a total of 145 individual birds (7 American Robins, 33 Carolina Wrens, 8 Gray Catbirds, 16 House Wrens, 45 Northern Cardinals, and 36 Song Sparrows). Each individual bird was recorded once, and an average of 6 birds were recorded per site. The observer approached the singing bird as close as possible during recordings (I attempted to maintain a maximum recording distance of 10 horizontal meters). When more than one individual of the same species was recorded at a site, a minimum distance of 50 m between individuals was assured. Number of songs recorded from each individual bird ranged from 2 to 20 (average 8.5 + 4.7 songs). We recorded birds between 30 May 2008 and 11 August 2008, which is during the breeding season for all species studied (Cimprich and Moore 1995; Haggerty and Morton 1995; Johnson 1998; Halkin and Linville 1999; Sallabanks and James 1999; Arcese et al. 2002). Birds were recorded between 6:30 AM and 11:30 AM, with most (75%) of the songs recorded before 10 AM. We collected information on weather at the time of each recording. Bird song playback from a separate project occasionally occurred at the same site where I was recording. This was true for recordings of only 4 individuals. We determined the effect of weather on the dependent variables in the study using a simple linear regression.

Recordings were digitized from tapes using sound recording program Wildspectra Live (http://www.unc.edu/~rhwiley/wildspectra/) at a sampling rate of 22 050 Hz, a frequency resolution of 344 Hz, and a temporal resolution of 2.9 ms. We used the sound analysis program Wildspectra to generate a chart of frequency and spectral intensity for each song analyzed. We used this chart to determine maximum frequency (the highest frequency on the chart), minimum frequency (the lowest frequency on the chart), and frequency range (maximum frequency minus minimum frequency). We analyzed songs at a frequency resolution of 344 Hz and a temporal resolution of 2.9 ms. Songs were normalized (a method of standardization that sets the largest amplitude in a sound equal to the maximal value and scales other amplitudes proportionately) and 2 songs from each individual were measured and the values averaged.

Before statistical analyses were performed, outliers were located in each analysis using the Fourth-Spread method (Hoaglin et al. 1991) and the outlying songs were examined for irregularities and all were reanalyzed to control for possible measurement error. One extreme outlier was removed from analysis, which had no effect on the results. To determine the effects of ambient noise level and urban development on the acoustic features of bird song, we used linear mixed-effect models (LMMs) for each species. The site where birds were recorded was set as a random effect. Minimum frequency, maximum frequency, and frequency range of recorded songs

were set as dependent variables and ambient noise level, percentage of impervious surface, and the interaction of noise level by impervious surface were set as independent variables. For each species, 1 model was run for each of the 3 dependent variables.

The residuals from each model were tested for normality using a Shapiro–Wilk W test. We determined the effect of collinearity of explanatory variables on the model estimates by calculating the variance inflation factor for each model. The statistical program JMP 9.0.0 was used for all statistical analyses. We corrected for multiple comparisons by calculating the false discovery rate (Benjamini and Hochberg 2000) based on 18 tests (1 model for each of 3 dependent variables for 6 species).

There was a significant interaction between ambient noise level and percentage of impervious surface for several of the models. We determined the nature and direction of the interaction in these models by grouping the data into discrete categories of one of the predictor variables (noise level or level of urban development). We then determined the relationship between the other predictor variable and the response variables within each grouped category. We grouped the data into 2 categories for noise level (high noise or low noise) and 3 categories for urban development (rural, suburban, or urban) using K-means clustering. We determined the direction of relationships at each level of the predictor using a simple linear regression.

To determine which species were more affected by noise and urbanization, based on their song frequency characteristics, we calculated the species-typical minimum and maximum frequency for each species. We did this by calculating the average minimum and maximum frequency of birds recorded at nonurban sites (sites binned at rural or suburban by K-means clustering). The strength of the effect of noise and urbanization on song characteristics was determined by the size of the P value (smaller P value, stronger effect).

RESULTS

The ambient noise level across study sites varied from 60.7 to 74.3 dB (65.4 + 4.04 dB, $N = 28$). Air, road and rail traffic, and construction machinery and appliances such as pool pumps and air conditioning units were the primary sources of background noise at our study sites. Background noise at all sites, including those that were rural, could be attributed to anthropogenic sources. Weather had no effect on maximum frequency (analysis of variance [ANOVA]: $N = 145$, $R^2 = 0.02$, $F = 3.06$, $P = 0.083$), minimum frequency (ANOVA: $N = 145$, $R^2 = 0.02$, $F = 3.52$, $P = 0.063$), or frequency range (ANOVA: $N = 145$, $R^2 = 0.01$, $F = 2.20$, $P = 0.141$).

The species-typical song range in our study for American Robin was 1808 Hz (average minimum frequency) to 3729 Hz (average maximum frequency), 1671–5260 Hz for Carolina Wren, 1377–7398 Hz for Gray Catbird, 1892–7195 Hz for House Wren, 1450–4666 Hz for Northern Cardinal, and 2114–7828 Hz for Song Sparrow (see spectrograms—Figure 1).

The residuals for each LMM were normally distributed, with the exception of the model for frequency range for Northern Cardinal, which became normally distributed after log transformation, and the maximum frequency models for Carolina Wren and House Wren, which also became normally distributed after transformation. Ambient noise levels increased significantly as the percentage of impervious surface increased (pairwise correlation: $N = 145$, $r = 0.57$, $P \leq 0.0001$), but this collinearity had a negligible effect on model variance (the variance inflation factor for all models was below 2.8).

Minimum song frequency increased as ambient noise level increased for 2 of 6 species, with 5 of 6 species showing a strong increasing trend (Figures 2 and 3), whereas urban development had no effect on minimum song frequency. American Robin (LMM: $F_1 = 2.29$, $R^2 = 0.67$, $P = 0.0837$, $N = 7$), Gray Catbird (ANOVA: $F_1 = 70.32$, $R^2 = 0.97$, $P = 0.0011$, $N = 8$), Northern Cardinal (ANOVA: $F_1 = 3.98$, $R^2 = 0.23$, $P = 0.053$, $N = 45$), and House Wren (LMM: $F_1 = 2.47$, $R^2 = 0.19$, $P = 0.14$, $N = 16$). For Carolina Wren, there was a significant effect of the interaction between percentage of impervious surface and ambient noise level (LMM: impervious × ambient: $F_1 = 5.1$, $R^2 = 0.30$, $P = 0.0315$, $N = 33$, Figure 3). When this interaction was further investigated, lowest frequency increased with ambient noise at rural sites, but there was no effect at suburban or urban sites (Figure 4).

Maximum frequency decreased with percentage of impervious surface for 2 of 6 species (Figures 5 and 6), Northern Cardinal (LMM: $F_1 = 4.24$, $R^2 = 0.24$, $P = 0.047$, $N = 45$) and Gray Catbird. For Gray Catbird, there was a significant effect of the interaction between percentage of impervious surface and ambient noise level (LMM: impervious × ambient: $F_1 = 8.75$, $R^2 = 0.74$, $P = 0.042$, $N = 8$). There was also a significant effect of the interaction between percentage of impervious surface and ambient noise level for Northern Cardinal (LMM: impervious × ambient: $F_1 = 5.32$, $R^2 = 0.24$, $P = 0.0274$, $N = 45$), but this effect became only marginally significant after controlling for multiple comparisons. When the interaction between percentage of impervious surface and ambient noise level for Northern Cardinal and Gray Catbird was further investigated, maximum frequency decreased with impervious surface at low noise sites, but there was no effect at high noise sites. For American Robin, we found the opposite pattern, maximum frequency increased with impervious surface (LMM: impervious: $F_1 = 18.35$, $R^2 = 0.84$, $P = 0.0013$, $N = 7$).

Frequency range decreased with percentage of impervious surface for 2 of 6 species (Figure 7), Northern Cardinal (LMM: $F_1 = 4.2$, $R^2 = 0.20$, $P = 0.048$, $N = 45$) and Gray Catbird. For Gray Catbird, there was a significant effect of the interaction between percentage of impervious surface and ambient noise level (LMM: impervious × ambient: $F_1 = 8.97$, $R^2 = 0.71$, $P = 0.0401$, $N = 7$). There was also a significant effect of the interaction between percentage of impervious surface and ambient noise level for Northern Cardinal (LMM: impervious × ambient: $F_1 = 4.44$, $R^2 = 0.198$, $P = 0.0426$, $N = 33$), but this effect became only marginally significant after controlling for multiple comparisons. When the interaction between percentage of impervious surface and ambient noise level for Northern Cardinal and Gray Catbird was further investigated, frequency range decreased with impervious surface at low noise sites, but there was no effect at high noise sites. For American Robin, we found the opposite pattern, frequency range increased with impervious surface (LMM: impervious: $F_1 = 26.3$, $R^2 = 0.87$, $P = 0.0068$, $N = 7$).

For Song Sparrow, neither percentage of impervious surface nor ambient noise level affected minimum frequency (LMM: noise: $F_1 = 1.09$, $R^2 = 0.49$, $P = 0.322$, $N = 36$; impervious: $F_1 = 2.44$, $R^2 = 0.49$, $P = 0.14$, $N = 36$), frequency range (LMM: noise: $F_1 = 0.14$, $R^2 = 0.64$, $P = 0.721$, $N = 36$; impervious: $F_1 = 2.9$, $R^2 = 0.64$, $P = 0.12$, $N = 36$), or maximum frequency (LMM: noise: $F_1 = 0.03$, $R^2 = 0.56$, $P = 0.87$, $N = 36$; impervious: $F_1 = 1.54$, $R^2 = 0.56$, $P = 0.23$, $N = 36$).

The strength of the effects of noise and urbanization on bird song differed by species. For species with a low species-typical minimum frequency (Gray Catbird, Northern Cardinal, and Carolina Wren, Figure 2) noise level had a strong effect on minimum frequency (P values, 0.011, 0.053, and 0.032, respectively). For species with a high species-typical minimum frequency (American Robin, House Wren, and Song Sparrow), noise level had little or no effect (P values, 0.084, 0.14, and
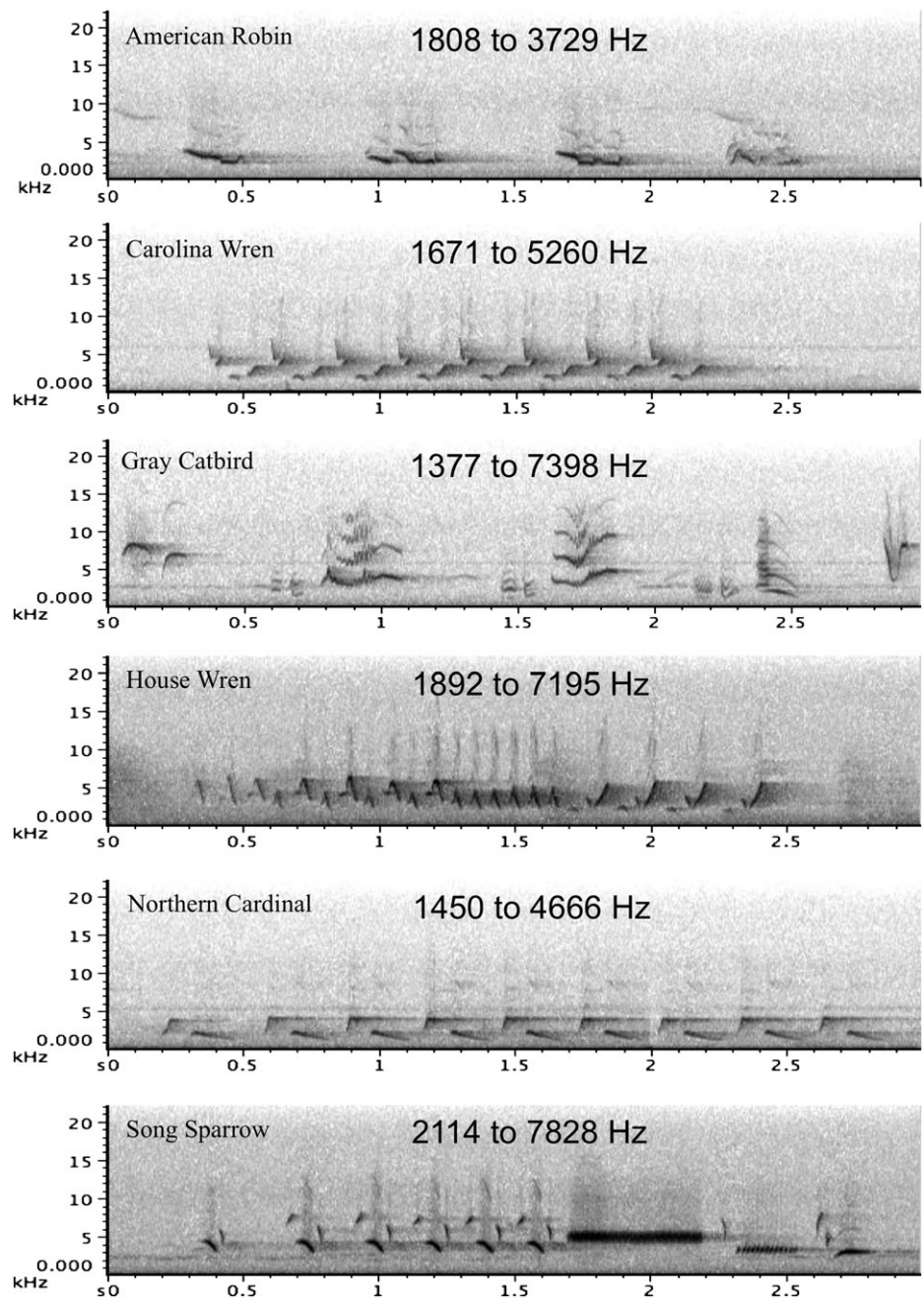
Figure 1
Spectrograms for 6 study species with species-typical frequency range (average minimum frequency to average maximum frequency for each species, calculated from individuals recorded at nonurban sites).

0.322, respectively). The effect of noise increased as the species-typical minimum frequencies became lower. Gray Catbird, the species with the lowest minimum frequency, showed the strongest effect.

For the species with the highest species-typical maximum frequency (Gray Catbird), urban development had the strongest effect on maximum frequency (Figure 5) and frequency range (Figure 6), whereas there was little or no effect of urbanization for species with a lower maximum frequency (Carolina Wren and American Robin). Although, this pattern was not consistent for all species, there was a strong effect of urbanization for Northern Cardinal, a species with a low maximum frequency and there was no effect of urbanization for House Wren, a species with a high maximum frequency. For American Robin, the species with the lowest maximum frequency and bandwidth, the maximum frequency and bandwidth

increased with urbanization (which is opposite to the pattern for Gray Catbird and Northern Cardinal).

DISCUSSION

We found that 2 salient features of the urban environment, abundant impervious surfaces and anthropogenic noise, both affect song characteristics and do so in different ways. As ambient noise level increased, minimum frequency of bird songs increased, whereas urban development had no effect, supporting our first hypothesis. As urban development increased, maximum frequency and bandwidth of songs decreased, whereas noise had no effect, supporting our second and third hypotheses. Support for these hypotheses indicates that these species make the adjustments we would expect for optimal transmission in loud reverberant urban environments. Although numerous

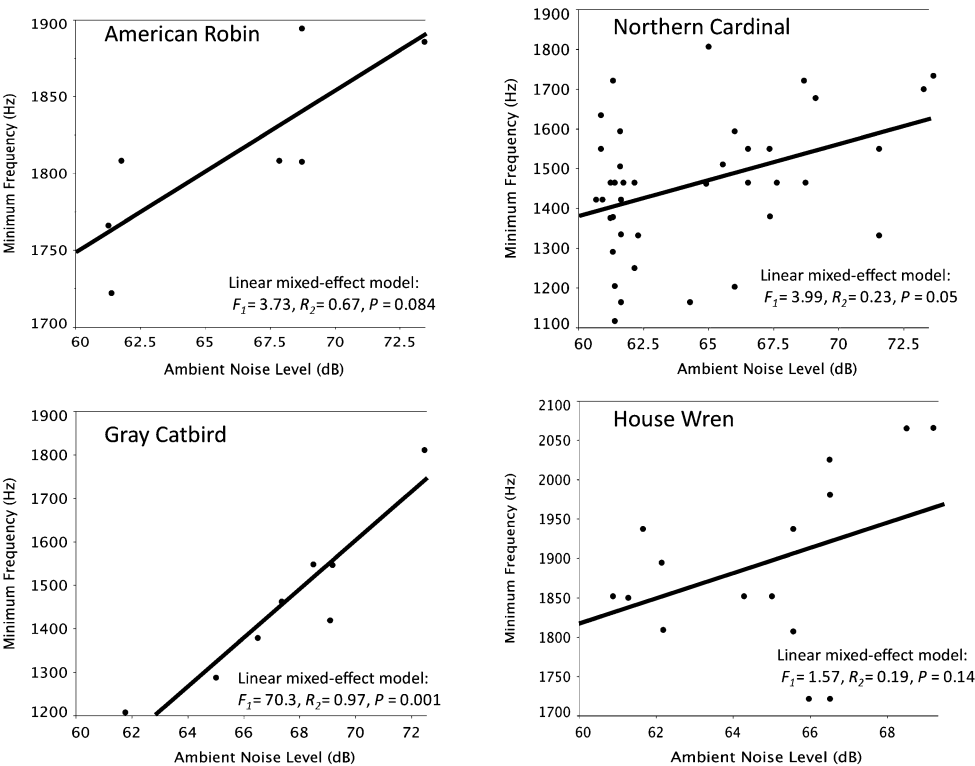| Species-typical minimum song frequency	Species	Predictor variable	P value	Support hypothesis prediction?
Highest	SOSP (N=36)	Noise level	0.3221	---
	HOWR (N=16)	Noise level	0.14	Yes
	AMRO (N=7)	Noise level	0.0837	Yes
	CARW (N=33)	Noise level	0.6261	**Yes (at rural sites)**
		Imp. surf.*Noise	**0.0315**	
	NOCA (N=45)	Noise level	**0.0525**	**Yes**
Lowest	GRCA (N=8)	Noise level	**0.0011**	**Yes**

Figure 2
Results of LMM for the effect of noise level on minimum frequency. Table lists how the strength of the effect varied with species-typical minimum frequency and also whether results support hypothesis 1.

previous studies provide evidence that birds make vocal adjustments in response to noise, ours is the first to investigate the effects of reverberation and refraction from urban structures, which we expect to equally constrain communication.
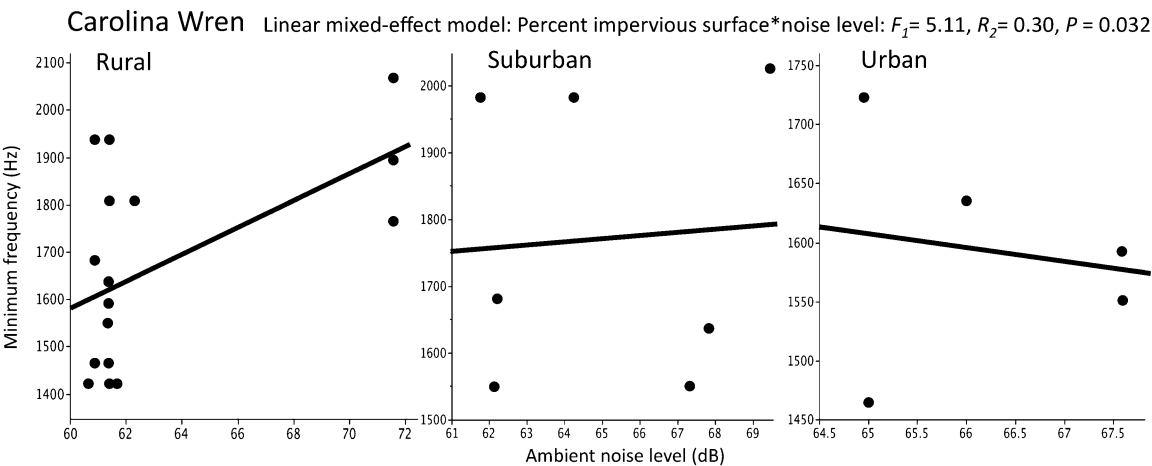
Species comparisons

Our study is also one of the very few urban song studies that include more than one bird species (but see Hu and Cardoso 2009, 2010). We included multiple species because birds with different song frequency characteristics are expected to require different degrees of adjustment for their songs to be well suited to urban environments. Indeed, we found that the strength of the effects of noise and urbanization on bird song differed by species. The lower the species-typical minimum frequency, the stronger the effect of noise level on minimum frequency. Similarly, the species with the highest maximum frequency was the species most affected by urbanization, whereas species with lower maximum frequencies were not affected by urbanization.

These results may indicate that species with songs that are more susceptible to the effects of urbanization and noise may be more likely to adjust their songs. Indeed, the above interpretation may explain the results for American Robin that

Figure 3
Results for minimum frequency. Simple linear regression of ambient noise level (dB) on minimum song frequency (Hz) for 4 species. Statistics listed are from LMM.

Carolina Wren Linear mixed-effect model: Percent impervious surface*noise level: F_1= 5.11, R_2= 0.30, P = 0.032
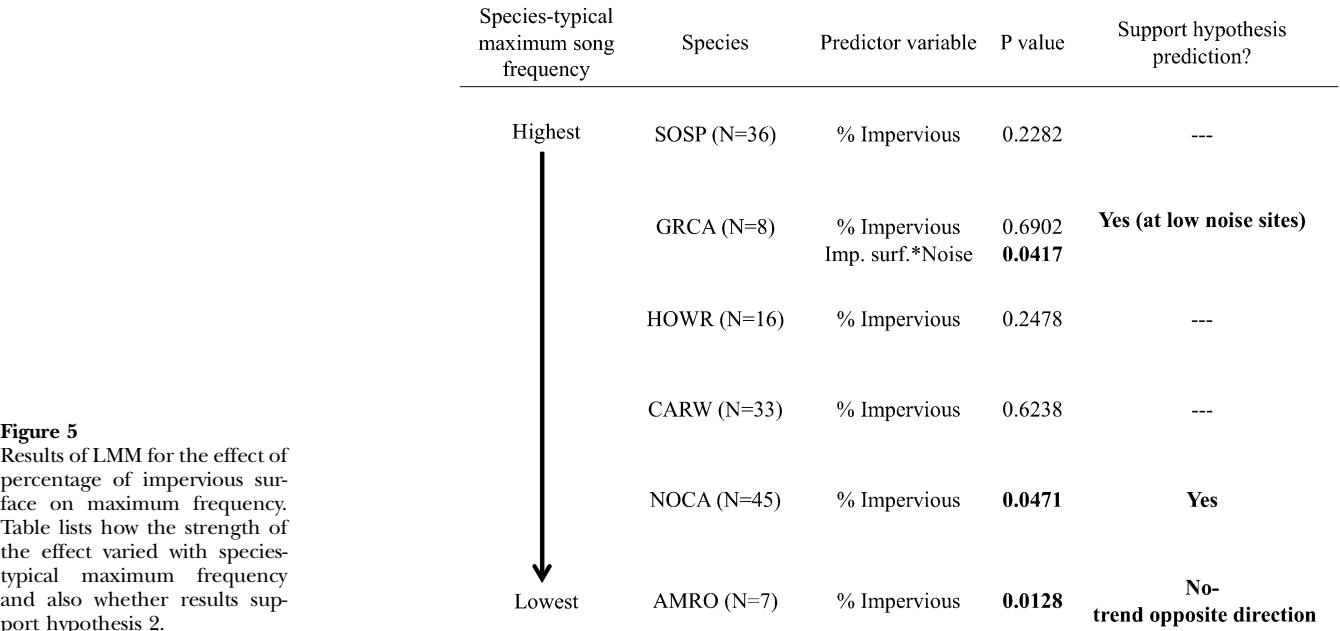
Figure 4
Results for minimum frequency for Carolina Wren. Simple linear regression of ambient noise level (dB) on minimum song frequency (Hz). Statistics listed are from LMM.
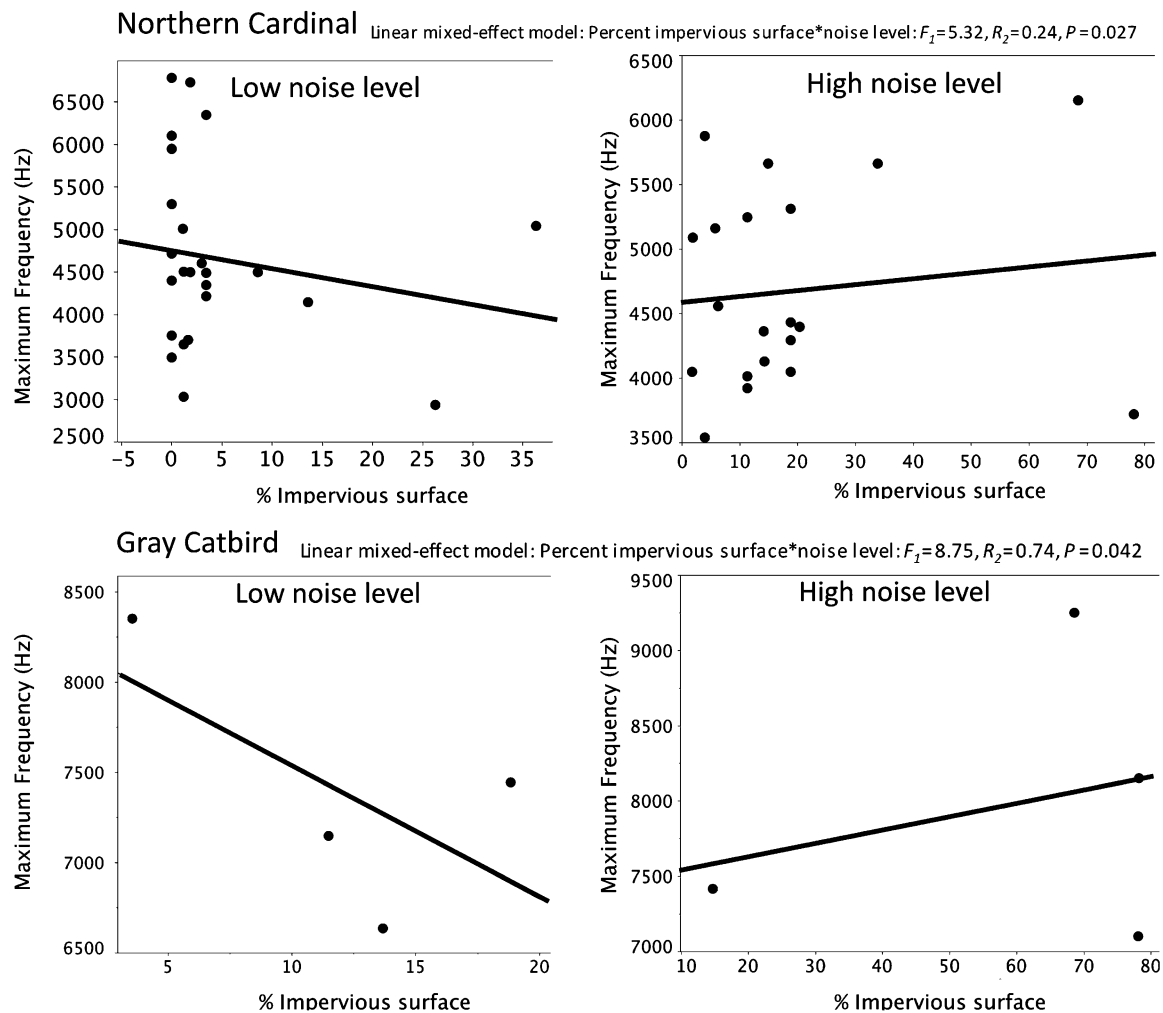
are inconsistent with other species. For American Robin, the maximum frequency and bandwidth increased with urbanization (the pattern was opposite for Gray Catbird and Northern Cardinal). American Robin has the lowest maximum frequency of all species studied (several thousand hertz lower), so their songs may be least susceptible to the effects of reverberation (which increase with frequency), and they may not be constrained to keep their maximum frequency low. Maximum frequency and bandwidth may increase with urbanization because noise in cities may pressure for an increase in minimum frequency, causing the entire song to shift up (which would be possible for American Robins, and not other species studied, because they have "room for adjustment").

Our results for minimum frequency are consistent with those of Hu and Cardoso (2010). They found that species with intermediate species-typical minimum frequencies (1000–1500 Hz) adjusted songs more in response to noise than species with higher minimum frequencies. Our results additionally show that within those species that do make adjustments, the lower the minimum frequency, the stronger the adjustment.

Hu and Cardoso also found that species very susceptible to masking by noise (those with calls/songs below 1000 Hz) did not make adjustments, which may indicate that birds adjust more with increased masking only to a certain point. This has important implications for which species will be excluded from urban bird communities. If species whose songs are masked more by noise adjust their songs more in response (as our results suggest), then many species would have the capacity to adapt their songs for transmission in noise instead of being excluded from noisy areas (or relying on different kinds of adaptations).

Because our study did not include species with songs below 1000 Hz, we do not know if this is the case or if adjustment will continue only to a certain point (as Hu and Cardoso's results suggest). Future studies that investigate song adjustment across several species with widely varying song frequency characteristics (from below 1000 Hz to above 2500 Hz) would further inform this question. It is also important that future comparative studies include repertoire-singing species, like Great Tits, that may behaviorally respond to noise by switching

Figure 5
Results of LMM for the effect of percentage of impervious surface on maximum frequency. Table lists how the strength of the effect varied with species-typical maximum frequency and also whether results support hypothesis 2.

Species-typical maximum song frequency	Species	Predictor variable	P value	Support hypothesis prediction?
Highest	SOSP (N=36)	% Impervious	0.2282	---
	GRCA (N=8)	% Impervious Imp. surf.*Noise	0.6902 **0.0417**	**Yes (at low noise sites)**
	HOWR (N=16)	% Impervious	0.2478	---
	CARW (N=33)	% Impervious	0.6238	---
	NOCA (N=45)	% Impervious	**0.0471**	**Yes**
Lowest	AMRO (N=7)	% Impervious	**0.0128**	**No-trend opposite direction**

Northern Cardinal — Linear mixed-effect model: Percent impervious surface*noise level: $F_1 = 5.32$, $R_2 = 0.24$, $P = 0.027$

Gray Catbird — Linear mixed-effect model: Percent impervious surface*noise level: $F_1 = 8.75$, $R_2 = 0.74$, $P = 0.042$

Figure 6
Results for maximum frequency. Simple linear regression of percentage of impervious surface and maximum frequency (Hz) at 2 different noise levels for 2 species. Statistics listed are from LMM. Results for frequency range are not presented because the same patterns for the same species are shown in these maximum frequency plots.

to song types with different frequency characteristics (Halfwerk and Slabbekoorn 2009). This may represent an alternative mechanism for adapting song to urban environments but may be subject to similar limits of adjustment above and below certain frequencies.

We found no effect of noise or urban development on song for the Song Sparrow. This result differs from the results of Wood and Yezerinac (2006), who found that Song Sparrows in louder areas sang with higher frequency low notes. In our study, Song Sparrows have the highest species-typical minimum frequency of all species studied, so we predicted that they would be least affected by noise. The minimum frequencies of the Song Sparrows in our study were higher (between 1600 and 2800 Hz, average 2095 + 338 Hz) than those recorded in Wood and Yezerinac's study (between 1100 and 1900 Hz), even in rural areas. This may represent a geographic difference in dialects (Wood and Yezerinac's study was conducted in Oregon, ours in and around Washington, DC). Song Sparrows near Washington, DC may not have their songs masked by noise to the same extent as Western Song Sparrows and may not need to make adjustments.
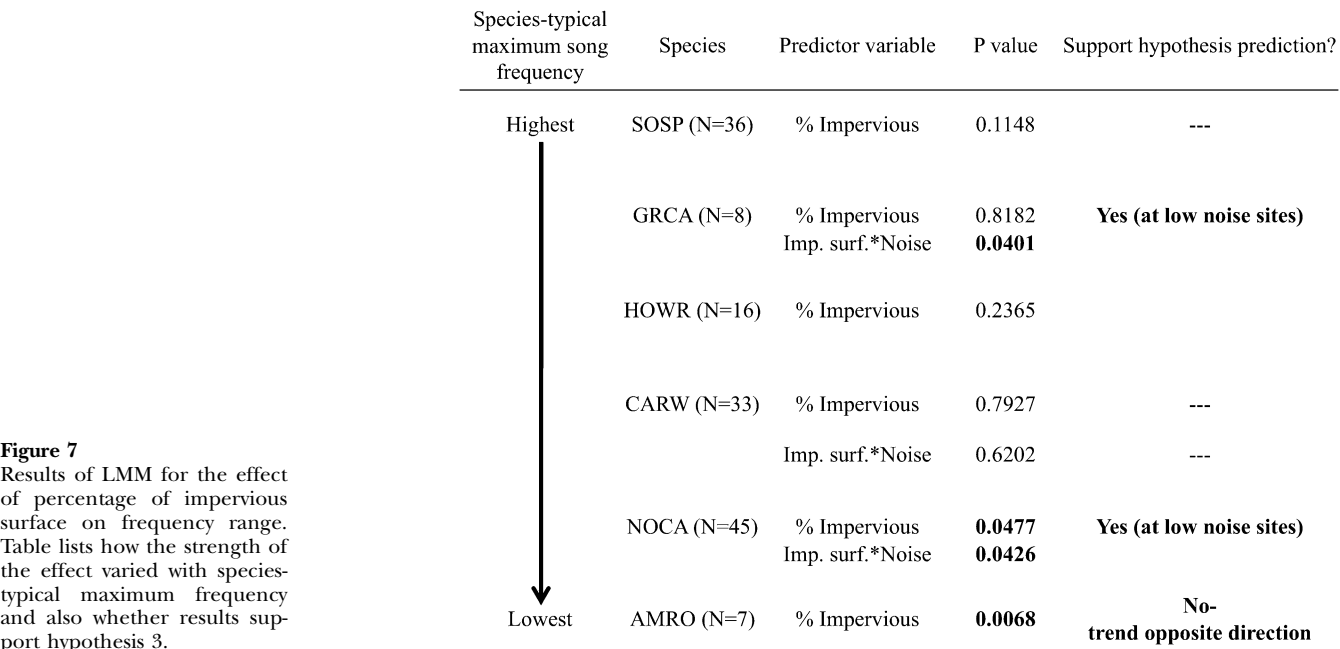
This could be an example of cultural evolution of dialects in response to urban noise. A recent study by Luther and Baptista (2010) found that White-crowned Sparrow dialects with higher minimum frequencies spread and replaced other dialects over the last 30 years in San Francisco, a period over which population levels and noise levels increased. A similar phenomenon may have occurred in the Washington, DC metropolitan area (the 9th most populous metropolitan statistical area, United States Census Bureau 2010) but may not have occurred in Portland (the 101st most populous metropolitan statistical area, United States Census Bureau 2010).

Trade-off of adjustment to noise or reverberation

Several species seem unable to make song frequency adjustments in response to one pressure (either urbanization or noise) when the second is also present. For the Carolina Wren, birds recorded in loud environments had a higher minimum frequency if that environment was rural but not if that environment was urban or suburban. For Northern Cardinal and Gray Catbird, birds recorded in urban environments had a decreased maximum frequency and bandwidth if that environment was quiet but not if it was loud (although, for Northern Cardinal, this pattern was only marginally significant after multiple comparison correction).

We suggest that these results indicate a trade-off between 2 different types of song adjustment, decreasing the maximum

Species-typical maximum song frequency	Species	Predictor variable	P value	Support hypothesis prediction?
Highest	SOSP (N=36)	% Impervious	0.1148	---
	GRCA (N=8)	% Impervious	0.8182	**Yes (at low noise sites)**
		Imp. surf.*Noise	**0.0401**	
	HOWR (N=16)	% Impervious	0.2365	
	CARW (N=33)	% Impervious	0.7927	---
		Imp. surf.*Noise	0.6202	---
	NOCA (N=45)	% Impervious	**0.0477**	**Yes (at low noise sites)**
		Imp. surf.*Noise	**0.0426**	
Lowest	AMRO (N=7)	% Impervious	**0.0068**	**No- trend opposite direction**

Figure 7
Results of LMM for the effect of percentage of impervious surface on frequency range. Table lists how the strength of the effect varied with species-typical maximum frequency and also whether results support hypothesis 3.

frequency and increasing the minimum frequency, in response to 2 different environmental factors, urban structures and ambient noise. In other words, birds may decrease their maximum song frequency in response to an urban structural environment but may be less able to do so in the presence of noise. Similarly, birds may increase their minimum song frequency in response to noise but may be less able to do so when urban structures are present.

This may be the result of an environmental constraint. Birds singing in noisy environments would improve their song transmission by increasing their minimum song frequency, but when that environment is also urban, an increase in frequency would worsen transmission (due to higher sound reflection, absorption, and diffusion), thus constraining the minimum frequency adjustment. Similarly, birds in urban environments would improve their song transmission by decreasing their maximum song frequency and bandwidth, but when that environment is also loud, a decrease in frequency would worsen transmission (due to masking of low-frequency song portions), thus constraining the maximum frequency adjustment.

This result may indicate that noise and reverberation pressure for adjustments that are not simultaneously possible. This would prevent birds from optimally adjusting their songs and affect their ability to communicate in areas where both factors are present (like most urban areas). Although, if birds make shorter term real-time adjustments to song frequency and adjust their songs depending on the prevailing environmental pressure (noise level at the instant of singing, reverberation given the bird's singing position), then they would avoid this problem (at least in environments where noise is not constant). Indeed, Bermúdez-Caumatzin et al. (2010) found that birds made real-time adjustment of minimum song frequency when noise was experimentally presented. Because each bird in our study was only recorded once, instead of multiple times under different noise conditions and in different environmental conditions, and because noise and urbanization level at each site was considered fixed in our analyses, we were unable to fully investigate this possibility. Future studies are needed that investigate characteristics of urban bird songs on a finer scale, with repeated recordings of individuals and careful measurement of noise and environmental conditions at the moment of each recording, either in the field or under controlled laboratory conditions.

To date, ecology in urban areas has been largely understudied (Martin et al 2010) and although many recent studies have described the effect of urbanization on bird song, all consider only one urban feature, noise. Future research should consider urban habitat as a sound transmission environment (with both an acoustic and structural component). The landscape worldwide is being rapidly developed and as a result, habitats are fragmented, ambient noise levels are increased, and reverberant surfaces and barriers are introduced. This in turn affects animal communication by restructuring the spacing of individuals and disrupting the transmission of signals through reverberation and masking. We urge researchers to further investigate how a modified communication environment affects wildlife. An important next step would be to investigate whether species with certain signal characteristics are excluded from urban areas and if those species that remain to breed in these areas (such as urban adapted species) show a reduction in fitness.

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