



Original Article

Song adjustments by an open habitat bird to anthropogenic noise, urban structure, and vegetation

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Received 18 December 2015; revised 30 May 2016; accepted 31 May 2016; Advance Access publication 1 July 2016.

Urban environments challenge animals with 2 novel impediments to communication: low-frequency anthropogenic noise, which masks vocalizations, and large sound-reflecting structures, which contribute to reverberation. We studied spectral and temporal traits of trill songs of chipping sparrows (*Spizella passerina*), a species historically found in open grassland habitat, to understand how noise, urban structure, and vegetation affected song traits. On the basis of the song features, males clustered into 2 groups. Males with songs that had lower minimum frequencies and broader bandwidths increased minimum frequency and decreased bandwidths with increasing noise, urban structure, and vegetation. Males with songs that had higher minimum frequencies and narrower bandwidths decreased minimum frequency and increased bandwidth with increasing vegetation but made no adjustments to noise or urban structure. To maintain high vocal performance of trill songs, males should increase trill rates to compensate for decreases in bandwidth, but they did not change this trait. As a result, vocal performance declined across all males with increasing noise and urban structure. Finally, peak frequency decreased with increasing urban structure, suggesting males put more energy into lower frequencies of their songs, possibly to improve sound transmission in human-built environments. Overall, both noise and structure influenced spectral features of songs with limited effects of song timing. Sound reflections from urban structures may have a strong, and underappreciated, influence on animal communication, which may compound the challenges of singing in noise.

Keywords: acoustic adaptation, anthropogenic noise, bird song, chipping sparrows, urban structure, vegetation.

INTRODUCTION

The natural environment has profoundly influenced the evolution of animal signals. Closed environments, such as forests, have tiers of surfaces that reflect and scatter sound, resulting in reverberation (i.e., the persistence of sound after signaling has ceased) and frequency-dependent attenuation (Morton 1975; Marten and Marler 1977; Richards and Wiley 1980; Boncoraglio and Saino 2007). These effects intensify with increasing signal frequency, bandwidth, and duration and with decreasing time between successive notes (Naguib 2003). Consequently, animals inhabiting closed habitats tend to produce signals that are shorter, lower frequency, and more tonal than those given in open habitats (Morton 1975; Wiley 1991). Open habitats, such as grasslands, have fewer sound-reflecting

surfaces, but unpredictable and irregular fluctuations in temperature and wind occur over space and time. These conditions favor amplitude- and frequency-modulated signals, which maintain their temporal characteristics over space (Brown and Handford 2000; Naguib 2003; Derryberry 2009). Across environments, signals are also affected by vocalizations of other animals and geophysical processes (e.g., wind and rain), all of which combine to affect the distance over which receivers may detect and perceive signals (Brenowitz 1982; Dubois and Martens 1984; Douglas and Conner 1999; Slabbekoorn and Smith 2002).

Recent and rapid transformation of natural landscapes to human-dominated ecosystems has created evolutionarily novel communication environments. Urbanization in particular has resulted in environments with high levels of anthropogenic noise and large sound-reflecting surfaces. Anthropogenic noise is characterized as high-amplitude, low-frequency sound (typically <4 kHz; Brumm 2004; Gill et al. 2015), which masks animal signals that overlap these frequencies, reducing the active space for communication (Laiolo 2010). At the same time, high densities of large

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sound-reflecting surfaces, including paved substrates (e.g., roads and parking lots) and vertical structures (e.g., buildings), are problematic: Unlike vegetation, which may absorb considerable sound energy (Martens and Michelson 1981), built structures are highly reflective (Wong et al. 2010). As a result, reflections of signals off buildings retain more energy than reflections in forests, potentially exacerbating signal degradation (Warren et al. 2006). A challenge for species dwelling in cities is that these novel environmental factors may not only favor signal structure that is different from the environment in which the species evolved, but each may favor different solutions in the same trait. For example, as noise increases, species increase the minimum frequency of their signals to minimize masking by noise (e.g., Slabbekoorn and Ripmeester 2008; Halfwerk et al. 2011; Parris and McCarthy 2013). However, urban structure should select against higher-frequency signals, as these more readily reverberate and develop echoes (Naguib 2003; Warren et al. 2006; Slabbekoorn et al. 2007); lower-frequency signals, which bend around sound-reflecting surfaces, should be favored. For species living in urban environments, how are signals structured to simultaneously cope with the potentially opposing effects of noise and urban structure?

Limited evidence exists regarding how noise and urban structure affect animal signals (Dowling et al. 2012; see Kight and Swaddle 2015), in part because most research has taken place in seminatural sites within or near urban areas (e.g., Proppe et al. 2012; Narango and Rodewald 2016). Noise appears to have a greater influence than urban structure on minimum frequency in several species, as this trait increased with increasing noise regardless of structure (Dowling et al. 2012). Noise and urban structure interacted to influence other song traits, and increased urban structure was linked with changes in maximum frequency and bandwidth but only under low noise conditions in some species, whereas in others, minimum frequency increased with noise, but only in less urbanized areas (Dowling et al. 2012). At least some of the species studied to date produce multiple song types (Halkin and Linville 1999; Smith et al. 2011; Haggerty and Morton 2014), leaving open the possibility that the responses reflected differential song use (Bermúdez-Cuamatzin et al. 2009; Halfwerk and Slabbekoorn 2009) rather than adjustment of song structure per se. Moreover, whereas noise is predicted to strongly influence spectral traits, sound reflection and reverberation degrade the timing of signals by filling in the gaps between individual notes and songs (Naguib 2003), yet whether animals adjust temporal traits in relation to urban structure remains poorly understood (Kight and Swaddle 2015).

An open question is whether individuals within a given population respond in similar ways to noise and structure or whether responses vary depending on song structure. Songs of individual males differ in complex ways (e.g., Borror 1961), influenced for example by differences in bill morphology, age, and condition (Huber and Podos 2006; Podos 2010; Giraudeau et al. 2014), but whether males with different song structures make the same adjustments in the same traits is unknown. For example, in noisy environments, males that produce songs with minimum frequency lower than average should increase this trait in noise to minimize masking, but males that sing with higher minimum frequencies that are less or not overlapped by noise may not need to adjust their song at all. Such intraspecific variation in song adjustments to noise and structure would suggest divergent solutions to these novel environmental features, possibly leading to local adaptation, but evidence so far is lacking (but see Leader et al. 2005).

In this study, we explored the influences of anthropogenic noise, urban structure, and vegetation on the trill songs of chipping sparrows (*Spizella passerina*). Chipping sparrows evolved in

open grassland habitat (Middleton 1998), and thus, both noise and structure present novel selection pressures on song. Trill songs transmit well in open habitat, but the temporal features of these songs degrade through reverberation in closed habitat (Richards and Wiley 1980; Brown and Handford 2000; Naguib 2003), an outcome that should be particularly pronounced in cities with large sound-reflecting surfaces (Richards and Wiley 1978). Within a population, chipping sparrows produce a range of song variants, but individual males sing only 1 song type (Marler and Isaac 1960; Borror 1961; Figure 1). Thus, we tested whether 1) chipping sparrows with different song variants adjust their songs differently to noise and structure; 2) noise and structure affect different features of chipping sparrow songs; and 3) vocal performance, which integrates both spectral and temporal aspects of trill song (Podos 1997), is affected by both noise and structure (see Luther et al. 2016).

We recorded songs from chipping sparrows along a rural–urban gradient in southwest Michigan, analyzed spectral and temporal song traits, and ran a cluster analysis to group males by their songs. Two groups of males were identified: Group 1 males produced songs that had lower minimum frequencies, higher maximum frequencies, broader bandwidths, and lower trill rates than group 2 males. We predicted that group 1 males would increase minimum frequency in noise to minimize masking and decrease maximum frequency in structure to minimize reverberation, but we did not expect changes in temporal traits. We predicted that group 2 males with higher trill rates would decrease trill rate with increasing structure, but no adjustments in response to noise would be detected. We also predicted that noise would have stronger effects on spectral traits but structure would have stronger effects on song timing, and these results would combine to decrease vocal performance in increasing noise and structure.

METHODS

Study species

Chipping sparrows produce a simple trill song consisting of serially repeated, frequency-modulated notes, and each male sings a single variant of this song (Figure 1). Males sing at high rates during the day when unpaired, but once paired, spontaneous daytime singing almost completely stops with males singing at unpredictable times (Liu and Kroodsma 2007). We were interested in effects of noise and structure on broadcast song to females, and therefore, we did not record males around the dawn chorus during which time males direct their songs at same-sex neighbors (Liu 2004; Liu and Kroodsma 2007).

Field recordings

We recorded males between 0700 and 1200 in April ($n = 29$) and May ($n = 24$) of 2011 ($n = 22$) and 2012 ($n = 31$) within Kalamazoo (42.290N, 85.586W) and Barry counties (42.600N, 85.317W), MI. The sites ($n = 26$) at which we recorded chipping sparrows varied from largely rural areas with low noise and few human-built structures, to sites with little structure near major roads and highways, and to highly urbanized locations that were noisy and had a high proportion of sound-reflecting surfaces (Supplementary Material). Sites were selected opportunistically, based on the presence of appropriate habitat for chipping sparrows, reportings on eBird, and our detections of singing males. We visited all sites except one only once and recorded 1–3 males per site; sites were separated by at least 0.5 km, larger than the maximum territory width of 75 m

maximum frequency (Hz), song duration (s), and time till next song (s). We calculated bandwidth (Hz) as the difference between maximum and minimum frequencies and trill rate as number of notes in each song divided by song duration (notes/s). We applied a finite impulse response filter and then power spectra generated for each song to quantify peak frequency (Hz) or the frequency with the highest amplitude. To assess vocal performance, we ran quantile regression of bandwidth and trill rate ($\tau = 0.9$) and calculated vocal deviation as the orthogonal distance between each male's song and the 90th percentile regression line (i.e., residuals, Wilson et al. 2014).

Manual measurements can introduce bias through cursor placement, an issue that is avoided when using sound analysis programs to automatically identify minimum and maximum frequencies using a set amplitude threshold relative to peak frequency (Zollinger et al. 2012). When signal-to-noise ratios are low, automatic measurements may be problematic (Verzijden et al. 2010; Cardoso and Atwell 2011), which was the case when we analyzed chipping sparrow songs using this approach (see [Supplementary Material](#)). We therefore manually placed cursors to measure minimum and maximum frequency. To ensure consistency in cursor placement, only one of us (J.R.J.) analyzed songs. Furthermore, we measured minimum and maximum frequency for each note within a song, then averaged these measures to produce a mean minimum and maximum frequency for each song, and finally averaged over all songs for a given male for analysis (see also [Narang and Rodewald 2016](#)).

Quantification of noise, urban structure, and vegetative structure

To determine whether noise influenced song traits, we sampled sound pressure levels (decibels, dB) directly from recordings 1 s prior to each randomly selected song (AviSoft calculates unweighted dB). We first calibrated recording systems inside an anechoic chamber by recording a 1 kHz sine wave at 55 dB played through a JBL D315 speaker (Harmon-Kardon Industries, Inc.) set at 1 m from the microphone. We repeated this for each gain setting on the Marantz, creating unique.wav files for each setting. On the basis of the gain setting used during field recording, we opened the corresponding.wav file within AviSoft and then used the Calibration window to calibrate the program to this reference sound. Next, we set a finite impulse response filter to measure noise between 1 and 4 kHz only ($\bar{X} \pm SE = 54.3 \pm 1.3$ dB; range = 36–66; $n = 53$); this includes frequency ranges (1–2 kHz) typically considered as noise (e.g., [Warren et al. 2006](#)) and frequencies that overlap chipping sparrow song, and excludes noise at low frequencies (<1 kHz) over which songbirds hear relatively poorly ([Okanoya and Dooling 1987](#)). We measured sound pressure levels from samples that either did not contain song from other species or, if songs were present, they added ≤ 3 dB to calculated levels (<5% of songs). To assess the effect of songs on sound pressure levels, we used the erase tool to remove the song from waveform and compared dB levels with and without the song. If sound pressure levels differed by >3 dB, we excluded the focal song and randomly selected another for analysis. If the difference was <3 dB, we used the dB reading including background song for analysis. Noise measurements across songs of each male were log averaged for analyses.

To determine the influence of urban structure or vegetative structure on song traits, we calculated the proportion of area around males occupied by human-built structures (hereafter urban structure) and tree canopy cover (hereafter vegetative structure). We measured structure in circular buffers with increasing

radii of 25, 50, and 100 m ([Supplementary Material](#)), treating the song perch of each male as the center of its territory and extending radii from that point. Radii lengths corresponded to the mean area of chipping sparrow territories: The 25-m radius reflects the approximate edge of a typical male's territory, the 50-m radius corresponds to the center of the nearest neighbor's territory (Job JR, unpublished data), and the 100-m distance class reflects the next nearest neighboring male and approaches the limit over which chipping sparrow song transmits under noisy condition (Gill SA, unpublished data).

We overlaid GPS coordinates of each singing perch onto aerial photographs (0.3-m resolution) in ArcGIS v. 10.2 (Microsoft Digital Globe, [ESRI 2013](#)) and drew polygons over urban structures and tree canopy cover within 100 m of each male's location. We used photos from 2009 for built structure and photos from 2014 for vegetation. We distinguished between horizontal (e.g., roads and parking lots) and vertical (e.g., buildings) urban structures, as both types of surfaces may reflect sound. However, a large percentage of our sites contained no vertical structure within buffers: 66.0%, 43.4%, and 32.1% of sites had no buildings within 100, 50, and 25 m of perches, respectively. To avoid large numbers of zeros in analysis, we therefore combined vertical and horizontal structure, which was absent from far fewer sites (1.9%, 3.8%, and 11.3% of sites had no horizontal structure within 100, 50, and 25 m, respectively). This resulted in an urban structure variable that contained fewer zeros (100 m: 1.9%, 50 m: 3.8%, and 25 m: 11.3%). We subtracted the proportion of urban and vegetative structure within the 25- and 50-m circular buffers from the 50- and 100-m buffers, respectively, to improve data independence. Thus, structure variables represent the proportion of urban or vegetative structure in concentric rings within 0–25, 25–50, and 50–100 m from song perches. Finally, the area occupied by urban and vegetative structure was divided by the total surface area of each ring, yielding the proportion of each male's territory covered by urban and vegetative structure at each of 3 spatial scales.

Statistical analyses

We conducted a cluster analysis using the *k*-means method to group males by their mean song traits. A plot of the within-groups sum of squares by number of clusters revealed 2 primary groups, which we retained in analyses. We refer to these clusters as group 1 ($n = 45$ males) and group 2 ($n = 8$) males.

We analyzed song traits in relation to noise, urban structure, and vegetative structure using multiple linear regression. Quantitative explanatory variables (i.e., noise and all structure variables) were centered for analyses. We first examined whether it was appropriate to fit models containing both male song groups by including group, all quantitative variables, and interactions between group and the quantitative variables. If none of the interactions were significant, we fit a model containing group and all quantitative variables. We then sequentially removed variables using likelihood ratio tests and comparison of Akaike's information criterion corrected for small sample sizes (AICc) values. Models that differed in AICc values by <2 were considered indistinguishable ([Burnham and Anderson 2002](#)), and we used the model with the fewest parameters as the best subset model. We then used likelihood ratio tests and comparison of AICc values to determine if first-order interactions among the quantitative variables in the best subset model should be included in the final model. Finally, we confirmed that slopes did not differ between song groups in the final model by testing whether interactions between song

group and quantitative variables were significant. We verified that final models satisfied regression model assumptions by examining residual plots and performing a correlation test for normal probability plots (Looney and Gullede 1985) and the Brown–Forsythe test for constancy of error variance (Kutner et al. 2005). Trill rate was log-transformed to satisfy model assumptions; no other transformations were needed.

Significant interactions between song group and minimum frequency and bandwidth occurred; therefore, we performed separate analyses for each song group for these traits and present these results separately from the other song traits. For group 1, we fit a model containing noise and all structure variables, and then proceeded as described above. Due to the small sample size of group 2 males ($n = 8$), we could not fit models containing all possible quantitative variables. Consequently, we first examined correlations between a given song trait and the quantitative variables to select a subset of potential predictors to include in the initial model. Model simplification then proceeded as described above. To assess the adequacy of these models, we plotted residuals against potential individual and first-order interaction terms that were omitted from the models; no clear patterns existed for any of the response variables. For all models, variance inflation factors were <3 , suggesting that multicollinearity should not strongly affect parameter estimates. We performed all analysis using R v. 3.2.3. (R Development Core Team 2015) and provided results of the model testing procedure in the [Supplementary Material](#).

Table 1

Anthropogenic noise and the proportion of urban and vegetative structure around singing perches varied among male chipping sparrows

	Range	$\bar{X} \pm SE$
Anthropogenic noise (dB) ^a	36.1–65.8	54.3 \pm 1.3
Urban structure ^b		
0–25 m	0.00–0.77	0.31 \pm 0.029
25–50 m	0.00–0.80	0.35 \pm 0.026
50–100 m	0.00–0.52	0.27 \pm 0.021
Vegetative structure ^b		
0–25 m	0.00–0.78	0.30 \pm 0.029
25–50 m	0.00–0.78	0.24 \pm 0.026
50–100 m	0.011–0.51	0.19 \pm 0.018

^aAnthropogenic noise was measured as the sound pressure levels (dB) in 1–4kHz frequency bands.

^bData are the proportions of urban or vegetative structure within concentric rings centered on male singing location with radii ranging from 25 to 100 m.

Table 2

A k-means cluster analysis identified 2 groups of male chipping sparrows based on song traits

	Group		$t_{(df)}^a$	<i>P</i>
	1 (<i>N</i> = 45)	2 (<i>N</i> = 8)		
Minimum frequency (Hz)	3334.1 \pm 52.2 ^b	3965.2 \pm 299.6	–2.075 _(7.43)	0.074
Maximum frequency (Hz)	8637.8 \pm 68.8	7198.6 \pm 259.9	5.35 _(8.008)	0.001
Peak frequency (Hz)	5665.6 \pm 67.9	5848.0 \pm 138.1	–1.19 _(10.69)	0.26
Bandwidth (Hz)	5303.7 \pm 88.7	3233.3 \pm 235.9	8.22 _(9.088)	0.01
Song length (s)	2.48 \pm 0.06	2.38 \pm 0.1	0.79 _(11.41)	0.44
Time to next song (s)	7.16 \pm 0.3	6.15 \pm 0.4	2.11 _(13.34)	0.054
Trill rate (notes/s)	12.4 \pm 0.6	20.3 \pm 2.2	–3.41 _(7.89)	0.01

^aResults of independent *t*-tests comparing the song traits of the 2 groups of males.

^bData are presented as $\bar{X} \pm SE$.

RESULTS

Noise and structure

Noise levels and the proportion of urban and vegetative structure around males ($n = 53$) varied considerably (Table 1). Mean noise levels, measured between 1 and 4kHz, ranged from ~ 36 dB for males at relatively undisturbed natural sites to more than 65 dB at urban sites and by roads. The areas around males also varied in the proportion of urban and vegetative structure, with some males at natural sites having territories with no urban structure (0%) and considerable tree cover (78%) to those in urban areas in which almost 80% of the territory contained urban structures but no vegetative structure (0%). Noise levels were not correlated with urban structure (Pearson correlations, 50–100 m: $r = -0.02$, $P > 0.9$; 25–50 m: $r = 0.02$, $P > 0.8$; 0–25 m: $r = 0.01$, $P > 0.9$) or vegetative structure (50–100 m: $r = -0.16$, $P > 0.2$; 25–50 m: $r = -0.16$, $P > 0.2$; 0–25 m: $r = -0.11$, $P > 0.4$).

Males cluster by song characteristics

Male chipping sparrows clustered in 2 groups based on differences in most song traits (Table 2; Figure 1). Males in group 1 ($n = 45$) produced songs with significantly higher maximum frequencies and broader bandwidths, and significantly slower trill rates than males in group 2 ($n = 8$). Group 1 males also tended to give songs with lower minimum frequency and longer gaps between successive songs than group 2 males. The 2 groups differed in minimum and maximum frequencies by more than 600 and 1400 Hz, respectively (see Table 2), whereas the difference between groups in peak frequencies was slight (~ 180 Hz). Song duration was also similar between the groups.

Group-specific song responses to noise and structure

Only 2 traits, minimum frequency and bandwidth, showed group-specific responses to noise and structure (Table 3). For group 1 males, minimum frequency of songs increased with increasing noise level ($t_{(41)} = 3.48$; $P < 0.01$; Figure 2a), urban structure within 25 m of perches ($t_{(41)} = 3.38$; $P < 0.01$; Figure 2c), and vegetative structure within the 50- to 100-m buffer ($t_{(41)} = 3.38$; $P < 0.01$; Figure 2e). Without a concomitant increase in maximum frequency (Table 3), bandwidth decreased with increasing noise ($t_{(41)} = -2.28$; $P < 0.05$; Figure 2b), urban structure within 25 m of perches ($t_{(41)} = -2.82$; $P < 0.01$; Figure 2d), and vegetative structure within the 25- to 50-m buffer ($t_{(41)} = -2.19$; $P < 0.05$; Figure 2f).

Group 2 males adjusted minimum frequency and bandwidth differently. Minimum frequency decreased with increasing vegetative

Table 3
Song adjustments by chipping sparrows in response to anthropogenic noise, urban structure, and vegetative structure

Song trait	Group	Variables	Estimate ± SE	$t_{(df)}$	<i>P</i>
Minimum frequency	1	Noise	19.3 ± 5.6	3.48 ₍₄₁₎	<0.01
		Urban structure 0–25 m	649.6 ± 192.1	3.38 ₍₄₁₎	<0.01
		Vegetation 50–100 m	1078.3 ± 319.4	3.38 ₍₄₁₎	<0.01
Bandwidth	2	Vegetation 0–25	−3116.0 ± 1065.0	−2.93 ₍₆₎	<0.05
		Noise	−24.9 ± 11.0	−2.28 ₍₄₁₎	<0.05
		Urban structure 0–25 m	−1074.2 ± 381.4	−2.82 ₍₄₁₎	<0.01
Maximum frequency	2	Vegetation 25–50 m	−969.5 ± 442.3	−2.19 ₍₄₁₎	<0.05
		Vegetation 50–100 m	3544.1 ± 1431.9	2.48 ₍₆₎	<0.05
		Group	−1439.3 ± 194.8	−7.39 ₍₅₁₎	<0.001
Peak frequency	2	Urban structure 50–100 m	−944.6 ± 383.8	−2.46 ₍₅₀₎	<0.05
		Group	182.5 ± 163.6	1.12 ₍₅₀₎	0.27
Song length		Noise	−0.008 ± 0.007	−1.078 ₍₅₁₎	0.29
Time to next song	2	Urban structure 50–100 m	2.8 ± 1.4	1.93 ₍₅₀₎	0.059
		Group	−1.009 ± 0.6	−1.64 ₍₅₀₎	0.11
Trill rate		Group	0.5 ± 0.1	4.24 ₍₅₁₎	<0.001
Vocal deviation	2	Noise	−18.8 ± 7.8	−2.10 ₍₄₉₎	<0.05
		Urban structure 0–25 m	−693.7 ± 253.8	−2.73 ₍₄₉₎	<0.01
		Group	−893.8 ± 153.6	−5.82 ₍₄₉₎	<0.001

Slopes for minimum frequency and bandwidth differed between the 2 male groups and were analyzed separately; for all other traits, groups were analyzed within single model. Variables shown for each trait are those from the best-fit models explaining variation in song traits identified using Akaike's information criterion corrected for small sample size (see [Supplementary Material](#) for model fitting results).

structure within 25 m of perches ($t_{(6)} = -2.93$; $P < 0.05$; [Figure 3a](#)) and bandwidth increased with increasing vegetative structure within the 50- to 100-m buffer ($t_{(6)} = 2.48$; $P < 0.05$; [Figure 3b](#)). Neither noise nor urban structure was included in the best-fit model (see [Supplementary Material](#)).

Effects of noise and structure on song across males

The remaining traits did not show group-specific responses. Across males, peak frequency decreased ($t_{(50)} = -2.46$; $P < 0.05$; [Figure 4](#)) and the time between songs tended to increase with increasing urban structure within the 50- to 100-m buffer ($t_{(50)} = 2.78$; $P = 0.059$). Vocal deviation became increasingly negative with increasing noise ($t_{(49)} = -2.10$; $P < 0.05$; [Figure 4a](#)) and urban structure within 25 m of perches ($t_{(49)} = -2.73$; $P < 0.01$; [Figure 4b](#)), with males in group 2 showing larger deviations than group 1 males ($t_{(49)} = -5.82$; $P < 0.001$; [Table 3](#)). Noise and structure did not explain variation in song length among males ([Table 3](#)). Mirroring results of *t*-tests comparing groups ([Table 2](#)), group was a significant predictor of song traits for maximum frequency ($t_{(51)} = -7.39$; $P < 0.001$) and trill rate ($t_{(51)} = 4.24$; $P < 0.001$), but neither noise nor structure variables were included in best-fit models for these song traits.

DISCUSSION

We explored how male chipping sparrows, with song adapted for transmission in open habitat, adjusted their songs when confronted by varying degrees of anthropogenic noise, urban structure, and vegetation. The proportion of urban and vegetative structures quantified over ecologically relevant distances influenced several spectral traits in chipping sparrows. Only minimum frequency and bandwidth changed with noise, and these adjustments occurred only in group 1 males with songs more overlapped by noise. Without adjustments in trill rate, this meant that vocal performance was poorer in noise, particularly for group 2 males. Thus, we found that anthropogenic noise, urban structure, and vegetation each influenced the structure of chipping sparrow song.

Individual chipping sparrows produce a single variant of their species-specific song, but songs varied considerably among males and a cluster analysis identified 2 groups based on differences in several spectral and temporal traits ([Table 2](#); [Figure 1](#)). Two traits, peak frequency and song duration, were similar between groups, but males in group 1 produced broader bandwidth songs with relatively lower minimum frequencies, higher maximum frequencies, and lower trill rates, whereas males in group 2 produced narrower bandwidth songs with higher minimum and lower maximum frequencies and higher trill rates. These combinations of traits are typical of trill song across sparrow species ([Podos 1997](#)), although high trill rate, narrow bandwidth songs, which are challenging to produce ([Podos 1996](#)), appear less common within and across species ([Podos 1997](#); [Luther et al. 2016](#); but see [Sockman 2009](#)). This pattern holds among males within our study population, contributing to uneven numbers of males in the clusters: More males produced broader bandwidth, lower trill rate songs ($n = 45$) than narrower bandwidth, higher trill rate songs ($n = 8$).

Given song differences, the challenges that noise and structure pose to males in each group differ and we predicted that males in the 2 groups would adjust their songs in different ways. To avoid masking by noise, animals across taxa increase minimum frequency of vocalizations with increasing noise (e.g., [Slabbekoorn and Peet 2003](#); reviewed in [Brumm 2013](#)), possibly via amplitude adjustments ([Nemeth et al. 2013](#)), and this pattern emerged for males in group 1. Males in group 2 did not change minimum frequency with increasing noise, but the average minimum frequency of their song was nearly 4 kHz and already 600 Hz greater than the average for group 1 males. Thus, males most at risk of experiencing song masking by noise shifted minimum frequency with increasing noise, whereas males with higher-frequency songs did not. Unexpectedly, group 2 males decreased minimum frequency with increasing vegetation around their song perches and group 1 males showed higher minimum frequencies with increasing urban structure within 25 m of perches as well as more distant vegetation (50–100 m). Noise was not correlated with either urban or vegetative structure, which suggests that the latter outcome was not the result of more structured

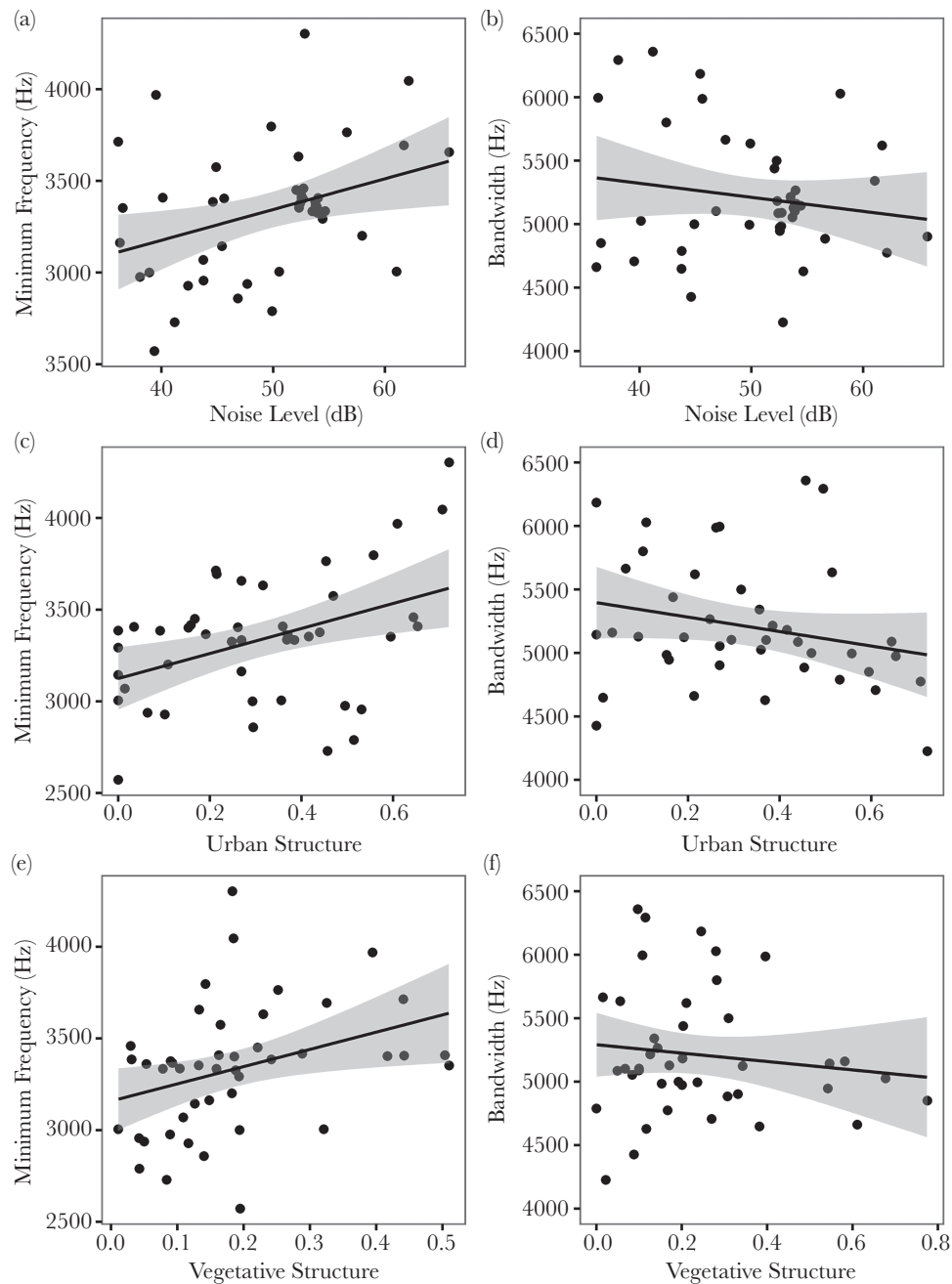


Figure 2

Among male chipping sparrows in group 1, minimum song frequency (Hz) increased in response to increasing (a) amplitude of anthropogenic noise, (c) urban structure within 25 m, and (e) vegetative structure between 50 and 100 m, whereas bandwidth (Hz) decreased in response to increasing (b) amplitude of anthropogenic noise, (d) urban structure within 25 m, and (f) vegetative structure between 50 and 100 m. Gray shaded areas represent 95% SE confidence regions.

habitat being noisier. These results provide evidence for intraspecific differences in spectral adjustments to anthropogenic noise and structure based on variation in signal attributes of individual males.

Temporal features of trill songs are highly vulnerable to degradation through reverberation, and we expected group differences in song adjustments in these traits in relation to structure. Despite group differences in temporal traits, unique adjustments in song timing were not detected. This result was most surprising for trill rate, which was almost doubled in group 2 compared with group 1 males (Table 2), but males in neither group

adjusted how quickly they produced the individual notes of their song in relation to urban structure. As sound reflects off large sound-reflecting surfaces, silent gaps in between the individual notes may be filled by the reflected sound, adding energy “tails” between notes (Naguib 2003; Slabbekoorn et al. 2007), thereby eroding a critical feature of trill song. Evidence for degradation of trill song due to reverberation comes from studies in forested environments (e.g., Naguib 2003; Slabbekoorn et al. 2007), and whether sound reflection from human-built structure affects trill songs in a similar manner is unknown and merits further study.

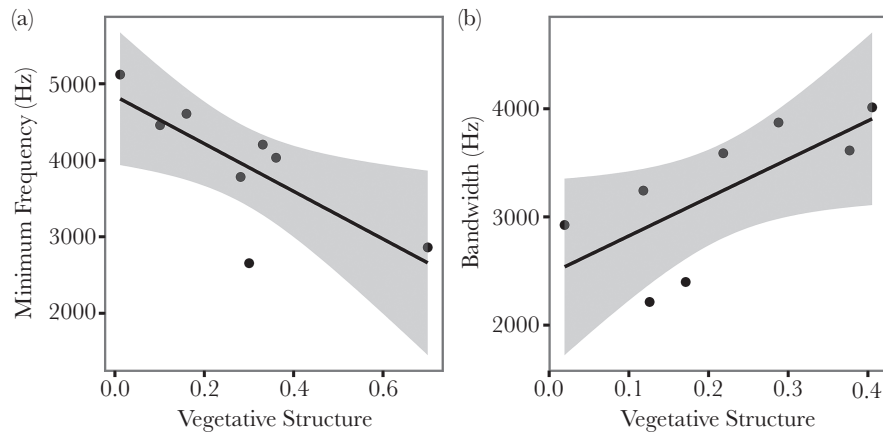


Figure 3

Among male chipping sparrows in group 2, minimum song frequency (Hz) decreased in response to increasing (a) amplitude of anthropogenic noise, whereas bandwidth (Hz) increased in response to increasing (b) vegetative structure at 100 m. Gray shaded areas represent 95% SE confidence regions.

Nevertheless, the absence of adjustments to trill rate suggests that males may be unable to change this trait, perhaps due to constraints imposed by bill size, female preference, and male–male competition, for example (constraints reviewed in Wilkins et al. 2013).

An alternative mechanism to decrease temporal degradation of songs is to sing shorter songs, which would minimize accumulation of reverberation over the song (Naguib 2003). Males might be expected to compensate for shorter songs by increasing song rate, that is, males sing shorter, slower songs more often. However, males increased the time between successive songs with increasing urban structure at larger spatial scales (50–100 m), but they did not change song duration. Thus, males sang less in territories with more urban structure, which contrasts with work in other species that males sing at higher rates in high-density urban populations (Ripmeester et al. 2010; Hamao et al. 2011; Narango and Rodewald 2016). As with trill rate, males may be constrained in song duration, as males sing shorter songs before responding aggressively to intruders (e.g., Nelson and Poesel 2011). Thus, changes to song duration could have negative fitness consequences, although whether such consequences exceed those that might accrue through song degradation is unknown.

Because no shifts in maximum frequency were detected but minimum frequency increased, group 1 males exhibited decreased bandwidth in relation to noise and nearby urban structure. Moreover, with no changes in trill rate, males also failed to compensate for reduced bandwidth by singing trills at a higher rate. Thus, vocal performance across males decreased in noise (see also Luther et al. 2016), and group 2 males performed more poorly than group 1 males. Assuming that female chipping sparrows prefer males with higher vocal performance songs (e.g., Ballentine et al. 2004; Caro et al. 2010), our results suggest that whereas all males perform less well in noise, group 2 males in particular could experience reduced mating success. Thus, we would expect selection against high trill rate, narrow bandwidth songs in noise, and selection for lower trill rate, broad bandwidth songs, possibly leading to an “urban dialect.” At present, we have no direct evidence that this is the case, but group 2 males were not sampled at high noise sites, but rather across a more narrow noise range (42.2–52.2 dB) than group 1 males (36.1–65.8 dB). We endeavored to record all singing males we encountered and thus do not think our opportunistic sampling was biased against group 2 males. However, more research is

needed, including a spatially balanced random sampling of males to confirm whether males with narrower bandwidth, high trill rate song avoid or are excluded from noisy habitat, as well as assessment of female preference for vocal performance in this species.

The 2 groups of males differed in most spectral traits, but peak frequency was similar across males. The difference in mean peak frequency between the groups was relatively minor (~180 Hz) compared with mean differences for minimum and maximum frequencies (>600 and >1400 Hz, respectively; Table 2). Peak frequency decreased with increasing urban structure (50–100 m), suggesting that males put more energy into lower frequencies of their song as distant urban structure increased. Such adjustments might influence transmission of peak frequency and minimize frequency-dependent reverberation in closed habitat. Thus, in addition to adjusting minimum frequency in noise, animals living in cities may adjust peak frequency to urban structure. A meta-analysis of studies exploring bird song features in relation to habitat structure found that peak frequency across species was higher in open than closed habitat species (Boncoraglio and Saino 2007); here, we show a similar pattern within a single species in relation to urban structure. Peak frequency may also vary with body size and may differ during spontaneous song versus song evoked by intruding males (e.g., Price et al. 2006; Hall et al. 2013; Geberzahn and Aubin 2014; but see Ripmeester et al. 2010; Benedict et al. 2012), which are 2 possibilities that merit further study in chipping sparrows.

Our study explored how chipping sparrows structure their signals given that anthropogenic noise and urban structure favor not only adjustments of different traits but may also favor opposite adjustments in the same trait. Chipping sparrows with lower minimum frequency songs (i.e., group 1 males) increased minimum frequency in response to not only noise as predicted but also nearby urban structure and distant vegetation. Noise and structure were not correlated; thus, responses to noise did not drive song adjustment to structure. Moreover, the estimate for the relationship between minimum frequency and noise was less than that for minimum frequency and structure (Table 3), suggesting that structure had a stronger influence on this trait. In addition, urban structure at a larger spatial scale (50–100 m) influenced peak frequency across all males, and vegetative structure at smaller spatial scales influenced minimum frequency and bandwidth for group 2 males. For chipping sparrows, therefore, urban structure appeared to have an overall greater influence on song structure than noise. Research on this

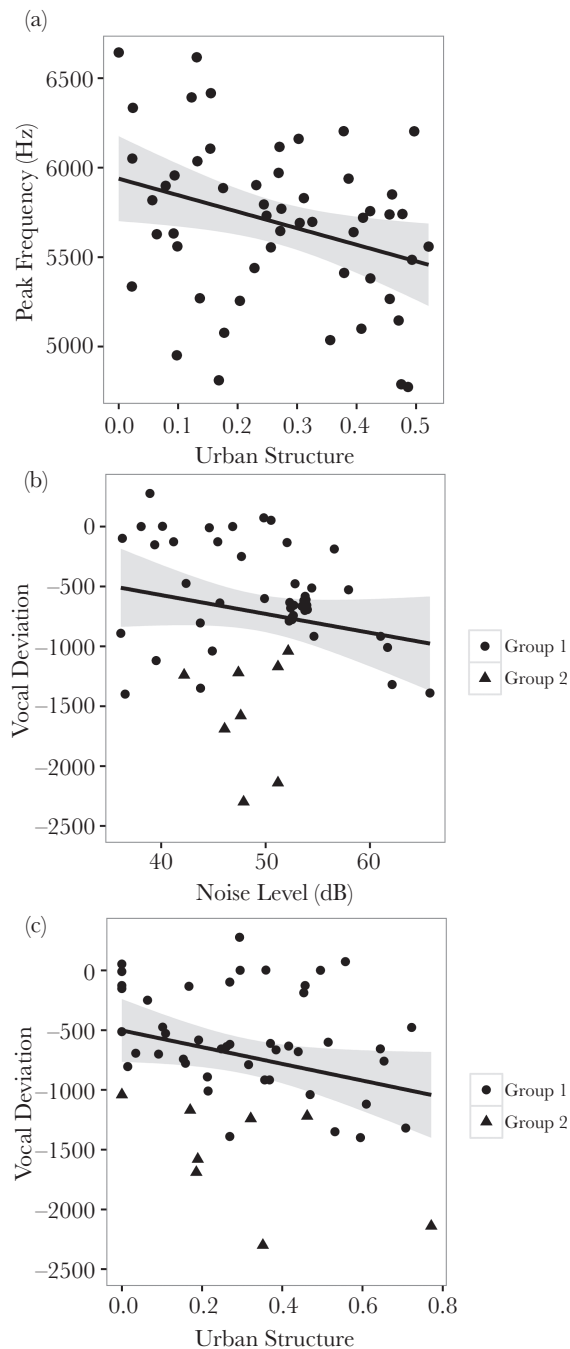


Figure 4 Across all male chipping sparrows, (a) peak frequency decreased in response to increasing urban structure between 50 and 100 m from song perches, and vocal deviation became increasingly larger and negative with (b) increasing urban structure within 25 m of song perches and (c) increasing noise. Gray shaded areas represent 95% SE confidence regions.

question is scant, but the relative importance of urban structure versus noise does not seem to hold in other species, as both features of urban habitat influenced song traits in several other species (Dowling et al. 2012; Proppe et al. 2012; Kight and Swaddle 2015; Narango and Rodewald 2016). Given the paucity of studies exploring both noise and structure, more work is needed to understand the influence of structure and reverberation versus noise and masking on animal communication.

Across animals, abundant evidence exists that anthropogenic noise influences the structures of signals, whereas how reverberations from large sound-reflecting structures, such as buildings, affect signals is poorly understood. Here, we show that noise and urban structure influenced variation in song traits in chipping sparrows, with the specific patterns of adjustment in 2 traits influenced by the specific song structure of males. No adjustments in trill rate or song duration occurred, which was unexpected as temporal traits should be strongly and negatively affected by reverberation. It may be that chipping sparrows cannot adjust these traits due to constraints imposed by female preference, a possibility that merits further study by exploring in part the extent to which individuals plastically adjust their song (see Montague et al. 2013). A largely unexplored alternative is that males benefit from sound reflections (see Slabbekoorn et al. 2002) and select signaling locations that optimize overlap between the signal and its reflections. That is, if reflected signals overlap actual signals, rather than occupying the gaps between notes, the amplitude of original signals and of the reflected sound would combine and thereby increase signal amplitude and improve song transmission in noise (Nemeth and Brumm 2009). Animals themselves increase signal amplitude under noisy conditions (Brumm 2004; Nemeth et al. 2013; Potvin and Mulder 2013), but the mechanism proposed here suggests a way for animals to increase signal amplitude without expending more energy. This mechanism might be unlikely for species with complex songs consisting of different note types, but chipping sparrows, with simple trill songs that repeat same element for the duration of the song, might benefit from signaling in structured environments.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

FUNDING

This work was supported by the American Ornithologists' Union Research Award and the WMU Graduate Student Research Fund to J.R.J.; a Faculty Research and Creative Arts Award (FRACAA) from WMU to S.A.G.; and a grant from the National Science Foundation to S.A.G. and K. Naghshineh (IOS-1257699).

We thank Bob Wong, M.J. Vohnhof, and 3 anonymous reviewers for comments that improved our manuscript; B. Stephens and K. Mulka for field assistance; K. Myers and K. Naghshineh for help with the calibration of recording units; and J. Glatz for technical guidance with ArcGIS. We are grateful to the Bird Banding Laboratory (Master permit no. 23665 to S.A.G.), Michigan Department of Natural Resources (permit SC 1394 to S.A.G.), and Western Michigan University's (WMU) Institutional Animal Care and Use Committee (nos. 10-11-01, 13-02-05) for permitting us to do this research.

Handling editor: Bob Wong

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