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Urban-associated drivers of song variation along a rural–urban gradient

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Most studies demonstrating associations between avian song and urbanization have tested noise as the primary driver, but alternative explanations remain largely unexplored. In particular, urban-associated changes in vegetation, density of conspecifics, and morphology also may promote changes in song. In this study, we 1) identified relationships between urbanization and song characteristics and 2) evaluated the extent to which altered song was explained by variation in noise level, vegetation, social context, and morphology of individual birds. We monitored the territories and recorded songs of northern cardinals (*Cardinalis cardinalis*) within forest stands in central Ohio that varied with surrounding urbanization. As landscapes surrounding forests urbanized, songs were longer, sung at faster rates, and comprised of higher-frequency notes. Noise best predicted minimum song frequency, with individuals singing at higher frequencies in environments with higher levels of background noise. However, temporal attributes of song (e.g., syllable rate, length) were best explained by conspecific densities, which are substantially greater in urban than rural landscapes. Morphology and vegetation did not predict any song attributes tested. These findings show that although anthropogenic noise may shape urban-associated changes in song, other features of the urban environment may be more important contributors to patterns in song variation.

Key words: **acoustic adaptation, bird song, body morphology, conspecific densities, noise, northern cardinal, urbanization, vegetation.**

INTRODUCTION

Although the consequences of the human footprint on other organisms are most commonly measured in terms of demography or habitat preferences, anthropogenic pressures can prompt a wide variety of behavioral shifts and, in some cases, can lead to novel behavioral adaptations (Shochat et al. 2006; Alberti 2015). Variable urban systems are a great laboratory in which one can example behavioral responses to human activities, and within them, the structural attributes of bird song have been one of the most extensively studied behaviors. Vocal behavior is sensitive to a wide range of environmental conditions (Morton 1975; Slabbekoorn and Smith 2002a; Hansen et al. 2005; Kirschel et al. 2009), has strong fitness implications (Catchpole 1987; Buchanan and Catchpole 1997; Gil and Gahr 2002), and can be highly variable among populations and individuals (Catchpole and Slater 2003; Nelson and Poesel 2007). Because habitat attributes can impede or attenuate sound (Anderson and Conner 1985; Nelson and Marler

1994; Badyaev and Leaf 1997; Bradbury and Vehrencamp 1998; Slabbekoorn and Smith 2002b), there should be strong selective pressure for vocalizations that propagate efficiently in a given habitat (i.e., acoustic adaptation hypothesis; Morton 1975). Indeed, cities are different from natural areas in a myriad of ways, and accordingly, avian song behavior should be different as well.

The most commonly cited difference in bird song is a rise in minimum frequency in urban compared with nonurban settings (Slabbekoorn and den Boer-Visser 2006; Mockford and Marshall 2009; Gross et al. 2010; Seger et al. 2010; Dowling et al. 2012) and in noisier areas within developed areas (Fernández-Juricic et al. 2005; Bermudez-Cuamatzin et al. 2009). Songs of urban birds also may have different lengths and rates (Brumm and Slabbekoorn 2005; Nemeth and Brumm 2009), comprised of different song types (Halfwerk and Slabbekoorn 2009), reflect lower energy in low-frequency notes (Wood and Yezerinac 2006), and of louder song amplitude (Brumm 2004). Whether such urban-associated shifts reflect long-term selective environments for effective communication (Tobias et al. 2010) or short-term behavioral plasticity in the production of bird song (Gross et al. 2010; Verzijden et al. 2010; Bermúdez-Cuamatzin et al. 2010; Goodwin and Podos 2013), there are a number of attributes of cities that may be drivers. Change in the urban acoustic environment is the most frequently invoked explanation for song variation, in part because

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overlap with competing natural sounds can thwart effective communication and promote shifts in dominant frequencies and timing (Bradbury and Vehrencamp 1998). Environmental noise in urban habitats is composed primarily of sound energy in the lowest frequencies (<2 kHz) typical of traffic, construction, and other anthropogenic sources (Slabbekoorn and Peet 2003), which presumably could select for song characteristics that avoid a masking effect.

However, human development simultaneously affects several ecological attributes that may influence song behaviors in similar ways. For example, variation in vegetation can favor efficient transmission of different vocalizations in different habitat types (Morton 1975; Bradbury and Vehrencamp 1998), forest stands (Anderson and Conner 1985) or strata (Nemeth et al. 2001). Similarly, urban landscapes are composed of dense exotic vegetation (Borgmann and Rodewald 2005), younger trees, or buildings (Warren et al. 2006) that may inhibit acoustic transmission. In addition, because song occurs within particular social contexts, changes in avian densities within cities (Bakermans et al. 2006; Shochat et al. 2006; Rodewald and Shustack 2008b) may drive song variation by altering competition for resources and territorial interactions between neighbors (Brumm 2004; Ritschard et al. 2011), exaggerating traits in response to increased aggression (Searcy and Beecher 2009; Linhart et al. 2013), or mediating testosterone (Ketterson et al. 1992; Ritschard et al. 2011). Lastly, song variation may be a function of interspecific body or bill size (Ryan and Brenowitz 1985; Gil and Gahr 2002; Badyaev et al. 2008; Derryberry 2009). Although differences may be due to patterns of individual song use then morphological constraint per se (Handford and Lougheed 1991). As suggested by Slabbekoorn et al. (2007), song changes observed in cities may reflect morphological differences observed in rural and urban individuals that settle in urban territories (Rodewald and Shustack 2008a; Liker et al. 2008); however, to our knowledge, this remains untested.

In order to determine the proximate causes of urban-associated behavioral changes, ecologists should strive for a mechanistic approach (Shochat et al. 2006). Our understanding of the processes that shape song structure in urban habitats remains incomplete and largely focused on noise as the primary cause. This study simultaneously evaluated the evidence for 4 non-mutually exclusive hypotheses explaining urban-associated song variation. Specifically, we proposed that song could vary in response to increased urbanization because of 4 non-mutually exclusive predictions: 1) *noise:* loud anthropogenic noise elicits upward shifts in frequencies and longer songs because urban ambient noise masks sound in the lowest frequencies and redundancy increases the likelihood of being heard; 2) *conspecific densities*: higher densities of conspecifics promote faster and longer songs due to changes in motivational states, and higher frequencies because of increased aggressive encounters; 3) *vegetation:* higher densities of understory plant stems favor songs that are lower frequencies and at faster syllable repetition because these sounds suffer reduced degradation from scattering effects; and 4) *body morphology:* smaller body sizes are related to increases in frequency and faster rates because of morphological limitations in song production and modulation and/or individual quality in song performance.

METHODS
Study area

This study was conducted between March and August in 2011 in 9 mature riparian forest stands along 3 rivers (Olentangy, Darby, and Alum Creek) in and around Columbus, OH. Digital orthophotos

were used to quantify landscape composition (buildings, impermeable surface, agriculture, forest, shrubland, wetland, and open water) within a 1-km radius from the site, and these metrics were used in a Principal component analysis (PCA) to create an index of urbanization for each site (see Rodewald and Shustack 2008a for more details). Sites were separated by at least 2 km and were composed of contiguous linear riparian habitat with similar forest widths and sizes (~4–6 Ha). Dominant tree species included maple (*Acer* spp.), sycamore (*Plantanus occidentalis*), elm (*Ulmus* spp.), and cottonwood (*Populus deltoids*). Dominant understory shrubs were amur honeysuckle (*Lonicera* spp.), multiflora rose (*Rosa multiflora*), Ohio buckeye (*Aesculus glabra*), and box elder (*Acer negundo*).

Study species

We used the northern cardinal (hereafter "cardinal") to investigate variation in song characteristics. Cardinals are a synanthropic species that breed in a variety of habitats in both rural and urban landscapes. Cardinals have a long nesting season (early-April to late-August in this region) and sing from territorial perches throughout season. Song appears to be used in both male–male competition and female attraction (Halkin and Linville 1999).

Data collection

We visited sites weekly ($n = 10$ visits) to spot-map densities of breeding cardinals. Observers systematically walked a 2-ha gridded area for at least 1 h and noted observations of singing, calling, and parental behavior of birds. At the end of the season, we delineated territories for each individual to determine number of breeding pairs per site using 3 observations as a minimum for territory inclusion (Bibby et al. 2000) as well as territorial mapping of color-banded cardinal pairs and nesting attempts.

We captured cardinals at each site using mist-nets and fitted with a steel USGS band and a unique combination of 3 color bands ($n = 45$). On capture, we measured tarsus and wing to quantify body size and bill length, width, and depth for bill size. We collected additional song and territory information from 45 color-banded males across the 9 sites. Males that were unable to be captured were included in analyses if they were paired with a banded female ($n = 5$) and/or exhibited reliable territory boundaries and song perches as determined by our spot-mapping efforts and behavioral observations ($n = 4$).

To assess stem densities within the territory for each focal male, we sampled vegetation surrounding 1 early and 1 late nest (i.e., 2 nest attempts per male) as well as a randomly located plot within the territory, in order to capture within-season variation. An "early-season" nest was defined as the first nest active in April–May, whereas the first nest active between June and July was considered a "late-season" nest. Within the circle, we identified and assigned trees and large woody shrubs to one of 4 size classes (3–8, 8–26, 26–38, and 38+ diameter at breast height [dbh]) within an 11.3-m radius sampling circle centered on the nest (Martin and Conway 1994). For each quadrant of the circle, we also estimated percent shrub cover of the most abundant 3 shrubs (including exotic honeysuckle). Lastly, we averaged measurements from the 3 plots to get a vegetation density per territory.

We recorded song between 15 min and 5 h after sunrise on weekdays between March and June of the breeding season. We conducted weekly focal watches for 30 min on each territory in order to record song behavior and measure noise on each male over multiple occasions within the breeding season. Territory visits were alternated in order to capture variation in noise and song over time of day.

Vocalizations were digitally recorded when a male was observed singing using a Marantz PMD 670 digital recorder and a Seinheiser directional microphone. Songs were sampled at 44.1 kHz with a bit rate of 768 kbps and saved as uncompressed mono.wav files. The male's identity was confirmed by visual identification of color bands (45 males, most observations) and/or associations with known females or nesting attempts during the recording, or immediately thereafter.

After each weekly recording, noise decibel (dB) levels were measured using a sound pressure level meter (American Recorder Technologies, 0.1 dB resolution) on A/low weighting calibrated to 94 dB using IEC651 Type II standards and slow response time weighting to capture the dB value of the background noise level. The A weighting was chosen because it best measures the frequency bandwidth of sound that comprises the range of cardinal song (700–8000 Hz; Halkin and Linville 1999). At the approximate song perch, a noise measurement was taken in each direction every 15 s for a total of 4 measurements per sound recording. All weekly noise measurements were pooled and averaged over each individual's territory.

Song analysis

Digital spectrograms were created using Raven 1.4 Pro (Cornell Lab of Ornithology, see Supplementary Material). All variables were measured using the manual cursor and by the same observer (D.L.N.). Although frequency measurements can also be measured by power spectra (Zollinger et al. 2012), visual measurement can provide a valid measurement of frequency and is not prone to large measurement error when the signal to noise ratio is small in the presence of background noise (Verzijden et al. 2010; Cardoso and Atwell 2011, 2012) as in the case of urban habitats. To preserve high measurement resolution, we measured time elements of songs using a discrete Fourier transform of 256 and 1024 for frequency elements. For each song sample, we measured minimum and maximum frequency as the position of the lowest and highest frequencies on the spectrum and frequency bandwidth as the difference between these measurements. Peak frequency was calculated in Raven as the frequency with the highest power relative to other frequencies within the song. For time measurements, we recorded song length (seconds), number of syllables, number of syllable types, and syllable rate (syllables/second). Mean measures of song characteristics per male were used in analyses to minimize any subjectivity.

Songs were included in subsequent analyses only if they were 1) composed of 3 or more syllables, 2) clean recordings with minimal reverberations, 3) free of significant overlap with other biological or ambient sounds, and 4) able to be assigned to a territory based on color band combinations or associations with color-banded females. Because there is more variation among than within song types and identical song types in a bout are inherently similar and non-independent, we selected the highest quality recording of each song type during the sampling period for digital analysis. Song types were defined according to Lemon (1965) such that a type was specified as a unique "utterance" of 1 or more syllable types where the time between syllables (<1 s) was less than the time between songs (>1 s). Different combinations of syllable types were considered different song types. As some song features may be used more often than others, identical song types sung on subsequent observation periods were included as unique measurements.

Statistical analysis

We used a series of linked approaches to determine which alternative hypotheses best predicted urban song variation. First, we tested for variable redundancy using a Pearson's correlation matrix. Second, we conducted PCA on both song and vegetation variables separately to extract components that best explained variation. To examine changes in song characteristics as surrounding landscapes became more urban, we used the principal components of song in a linear regression with the urban index values. Pearson's correlations were used to describe associations between our variables of interest (i.e., noise, vegetation, density, and morphology) and urbanization. Finally, we used Akaike's information criteria (AICc) corrected for small sample sizes to test our alternate hypotheses explaining song variation.

Prior to analysis, we tested variables for equal variance (Levene's test for homogeneity of variance) and normality (normal quantile plot, Shapiro–Wilks Test), but no variables required transformation. We screened for possible multicollinearity with Pearson's correlation tests, and in cases where a pair of variables was highly correlated ($r > 0.7$), we excluded 1 member from analysis. Average high frequency and average frequency bandwidth were highly correlated ($r = 0.99$), as were song length and number of syllables ($r = 0.80$). We chose to remove frequency bandwidth as a redundant variable because maximum frequency was largely driving this relationship. We also chose to retain number of syllables and removed song length.

A similar approach was used to reduce the number of vegetation variables. Because numbers of 3–8 cm dbh honeysuckle stems were strongly correlated with total number of small stems (3–8 cm dbh; $r = 0.99$) and percent honeysuckle shrubs (<3 dbh) was correlated with total percent shrub density was correlated with ($r = 0.96$), we excluded specific honeysuckle measurements in favor of broader structural measurements.

In order to initially identify which song features changed with increasing urbanization, we performed a linear regression between the song components and landscape index. Each site had a unique urban index; therefore, site was not included as a separate variable in the models. Because our aim was to only include song variables that may be functionally different in our subsequent models, and we expected song features to be more strongly related to local variables rather than urbanization per se, we considered an alpha <0.1 to indicate significant relationships.

To examine the association between song variation and ecological factors associated with urbanization, we used an information theoretic approach for multiple models using Akaike's information criteria (AICc) corrected for small sample sizes (Burnham and Anderson 1998). We chose 5 a priori variables that represented alternative hypotheses to explain song variation: noise levels (noise), vegetation composition (understory density, large and small trees), conspecific density, body size, and a global model containing all variables. In addition, we considered a null model where the predictive variable was a constant to account for the possibility that none of our a priori models explained the variation in the data. The model with the lowest ΔAICc value indicated the model with the best fit while minimizing the number of parameters. All models were generalized linear models using song characteristic as the dependent variable and each environmental hypothesis as an independent variable using Gaussian distribution and identity function (Zurr et al. 2007). Missing data points were included in the models by filling in mean values for the variable because this imputation method does not affect the sample mean for the variable and thus does not introduce bias (Zurr et al. 2007). All statistics were performed using program R 3.1.1 for Windows (R Development Core Team 2014).

RESULTS

Recorded males

In 2011, 66 males were recorded over the season. Using our criteria for song inclusion and excluding males not recorded in the focal area, we measured 610 songs with 8.28 ± 4.55 song types from each male ($n = 54$, 27 from rural and 27 from urban). Minimum low frequency of cardinal song was 1047.87 and maximum high frequency was 8694.15 Hz, which overlaps with the range of typical low-frequency ambient noise (<2 Hz, Slabbekoorn and Peet 2003).

Principal components analysis

Using song averages for each male, we reduced the variables, number of syllables, minimum frequency, maximum frequency, peak frequency, and song rate into 3 latent variables (eigenvalues > 1) using a PCA that explained 80.8% of the variation in song (Zurr et al. 2007). The first principal component (PC1) described songs becoming slower and shorter and ranged from -3.18 to 2.60, which represented a difference of 18.22–6.17 average syllables and 5.67–2.41 average syllables per second. The second principal component (PC2) increased with peak frequency and high frequency, reflecting a range of average peak frequency from 2045.65 to 3560.13 Hz and average high frequency Hz from 3549.41 to 8131.40. The third principal component (PC3) was negatively related to minimum frequency such that increases in PC3 described decreases in minimum frequency, and it represented a difference between 1047.87 and 1749.68 in average minimum frequency Hz. Hereafter, we call these variables as temporal components (PC1), peak/high frequency (PC2), and minimum frequency (PC3).

A PCA of the variables, trees in 4 size classes (3–8, 8–23, 23–38, and 38+ dbh), and percent shrub cover showed that 3 components explained 73.5% of the variance. The first principal component (PC1) had factors that loaded positively toward high shrub densities and saplings (Table 1). The second principal component (PC2) had factors that loaded positively toward small and medium trees (Table 1). The third principal component (PC3) had factors that loaded negatively toward only large trees, therefore higher values contained low numbers of larger trees (Table 1). We described the latent variables as understory density (PC1), small trees (PC2), and large trees (PC3).

Urban-associated changes in song

The temporal principal component of song was negatively associated with urbanization (β: -0.31 ± 0.16, $F_{1,52} = 3.45$, $P = 0.07$; Figure 1) meaning urban songs were longer and faster. The component that represented minimum frequencies also decreased over the gradient (β: -0.28 ± 0.12, $F_{1,52} = 5.10$, $P = 0.03$; Figure 1) such that minimum frequencies rose as sites became more urban (Figure 2). The component for peak and high frequency increased over the rural–urban gradient (β: 0.30 ± 0.14, $F_{1,52} = 4.95$, $P = 0.03$; Figure 1) as well, such that urban songs had higher peak and maximum frequencies.

Evidence for alternative mechanisms

As expected, as landscapes surrounding forests urbanized, the environment changed in ways that might affect bird song. As urbanization increased, site-level noise ($r = 0.81$), conspecific densities ($r = 0.89$), large trees ($r = 0.92$), and shrub densities ($r = 0.94$) (influenced by presence of exotic honeysuckle) increased, whereas body sizes decreased ($r = -0.79$) (Table 2). Numbers of small trees had no relationship with urbanization ($r = -0.28$).

Model selection for song variation

When considering alternative mechanisms to explain urban-associated changes in temporal PC1, the top model was number of conspecific territories at the site level (Table 2; $w = 0.93$) meaning songs were longer and faster as sites conspecific density increased ($\beta = -0.22 \pm 0.06$, 95% confidence interval [CI]: -0.35, -0.10, $F = 12.53$, $P < 0.001$; Figure 2). Minimum frequency PC3 was best explained by and negatively related to noise levels at the territory site (Table 3, Figure 3; $w = 0.90$; $\beta = -0.13 \pm 0.02$, 95% CI: -0.18, -0.09, $F = 29.92$, $P < 0.001$) meaning that minimum frequencies were higher in noisier territories. Peak/high frequency PC2 of song was not well explained by any model, as the null model was included within the top model set (ΔAICc < 2; Table 4).

Table 1

Factor loadings and eigenvalues for the PCA of vegetation and song variables of male northern cardinals in central Ohio, 2011

| Variable | Components | | | | |
	1	2	3	4	5
Vegetation					
Eigenvalues	1.18	1.13	0.98	0.94	0.70
Saplings	0.77	0.15	−0.24	0.43	0.38
Small trees	−0.05	0.69	−0.32	−0.62	0.21
Medium trees	−0.13	0.81	−0.07	0.46	−0.33
Large trees	0.28	0.34	0.88	−0.11	0.10
% Shrub cover	0.84	−0.08	−0.11	−0.32	−0.42
Component interpretation	Increasing shrub density	Increasing small trees	Increasing large trees	—	—
Song					
Eigenvalues	1.31	1.09	1.00	0.87	0.58
Minimum frequency	−0.32	−0.04	−0.92	−0.17	0.13
Maximum frequency	0.26	0.73	−0.25	0.58	−0.07
Peak frequency	−0.16	0.79	0.12	−0.58	−0.05
Number of syllables	−0.84	0.17	0.27	0.23	0.38
Syllable rate	−0.90	−0.07	−0.02	0.13	−0.41
Component interpretation	Slower, shorter songs	Increasing peak/high frequency	Decreasing low frequency	—	—
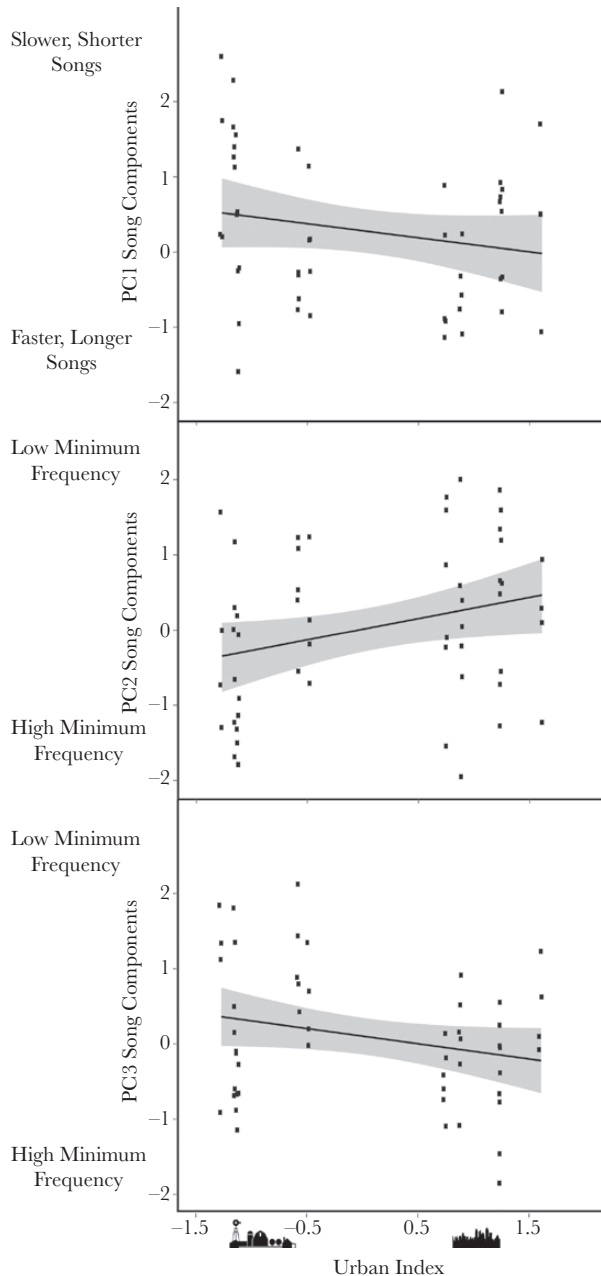
Figure 1

Temporal song components (PC1), peak/high frequency song components (PC2), and minimum frequency song components (PC3) across a range of urbanization. As urbanization increased, males sang songs that were longer and faster (PC1) and had higher peak, maximum (PC2), and minimum frequencies (PC3).

DISCUSSION

Although loud acoustic environments are usually invoked to explain altered bird song in cities (Patricelli and Blickley 2006; Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Mockford and Marshall 2009), our findings indicate that other ecological changes associated with urbanization may contribute to differences. Whereas minimum song frequency was most related to the acoustic environment within territories, temporal changes in song structure (e.g., syllable rate) were best explained by high densities within
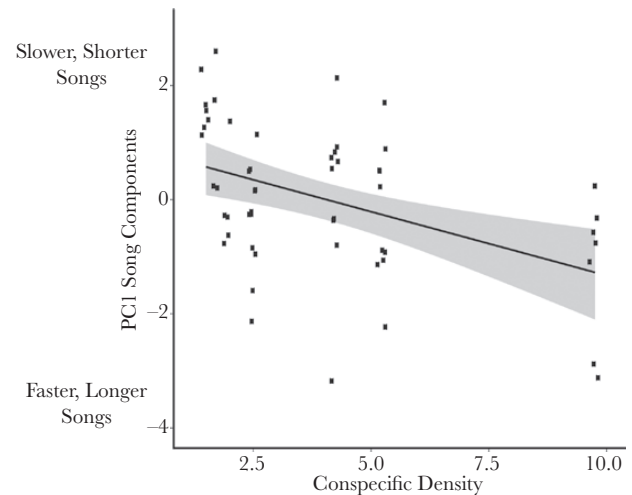

Figure 2

The relationship between temporal song characteristics and conspecific density. Males sing songs that are longer and faster (decreases in PC1) as sites have more cardinal territories per hectare.

urban habitats. Peak/high frequencies were not explained by any of our ecological models.

Changes in temporal characteristics, such as longer and faster songs, have been previously reported in studies of urban vocal behavior (Slabbekoorn and Den Boer-Visser 2006; Nemeth and Brumm 2009; Hamao et al. 2011; Potvin et al. 2011) contrary to predictions that slower songs should transmit better in the presence of urban noise (Slabbekoorn et al. 2007). Using an observational approach, temporal changes described by PC1 were best explained by increases in conspecific densities that accompany urbanization rather than anthropogenic noise. Like many resident generalist species, cardinals respond positively to urbanization and can be found at up to 4× higher densities at urban sites with dense understory vegetation (Leston and Rodewald 2006). Indeed, sites where honeysuckle had been experimentally removed had lower densities of cardinals (Rodewald AD, unpublished data).

The longer and faster songs of males from sites with high densities may be a behavioral consequence of increased territorial interactions between neighbors (Searcy and Beecher 2009). Our finding is consistent with other evidence from both urban (Ripmeester et al. 2010) and nonurban (Hunter and Krebs 1979) landscapes that temporal features increase with numbers of simultaneously singing males. In cardinals specifically, males sing at higher syllable rates and increase number of different syllable types in songs used in interactions with conspecifics (Ritchison 1988). Cardinals settling in habitats with dense urban bird populations may face increased aggression from other individuals, in addition to noise (Montague et al. 2013), which can manifest as behavioral shifts in song length and speed. Although familiarity with neighbors may decrease aggression (e.g., dear enemy effect, Fisher 1954), birds often increase or change vocal behavior when confronted with an unfamiliar floater male attempting to settle territories. Anecdotally, rogue banded and unbanded males were more often observed mid-season attempting to usurp territories in urban sites than in rural sites (Narango DL, personal observation). Increases in aggression may be a behavioral compensation to avoid sites becoming oversaturated with cardinal territories and conspecific density may be an important factor contributing to spatially variable song changes. Accordingly, a meta-analysis of studies comparing the relationship between habitat structure and

Table 2

Relative support for alternate models explaining temporal variation of northern cardinal ($n = 54$) song models using Akaike's information criterion corrected for small sample sizes (AICc)

Model	k	AICc	ΔAICc	AICc weight	Evidence ratio	β (SE)	P
Density	2	175.92	0	0.93	1	−0.22 (0.06)	<0.001
Noise	2	182.47	6.55	0.04	26.43		
Null	1	185.41	9.49	0.01	114.82		
Shrubs and saplings	2	185.58	9.65	0.01	124.82		
Body size	2	186.17	10.24	0.01	167.75		
Global	8	187.31	11.38	0	296.26		
Small trees	2	187.37	11.45	0	305.7		
Large trees	2	187.58	11.65	0	339.11		
All trees	3	189.63	13.71	0	946.46		
All vegetation variables	4	189.98	14.06	0	1129.69		

Models include variables that represent alternative hypotheses for song variation: density of conspecifics at the site level, noise levels (dBA) at the territory level, body size of the vocalizing male, vegetation at the territory level (tree classes and shrub densities), and a global and null model. SE, standard error.

Table 3

Relative support for alternate models explaining minimum frequency variation of northern cardinal ($n = 54$) song models using Akaike's information criterion corrected for small sample sizes (AICc)

Model	k	AICc	ΔAICc	AICc weight	Evidence ratio	β (SE)	P
Noise	2	133.91	0	0.9	1	−0.13 (0.02)	<0.001
Global	8	138.39	4.48	0.1	9.37		
Density	2	154.41	20.5	0	28 275.1		
Small trees	2	156.2	22.29	0	69 255.8		
Null	1	156.28	22.37	0	71 993.4		
All trees	3	156.76	22.85	0	91 454.9		
Large trees	2	156.81	22.9	0	93 949.8		
Shrubs and saplings	2	158.33	24.42	0	200964		
Body size	2	158.43	24.52	0	210 700		
All vegetation variables	4	159	25.09	0	280 170		

Models include variables that represent alternative hypotheses for song variation: density of conspecifics at the site level, noise levels (dBA) at the territory level, body size of the vocalizing male, vegetation at the territory level (tree classes and shrub densities), and a global and null model. SE, standard error.
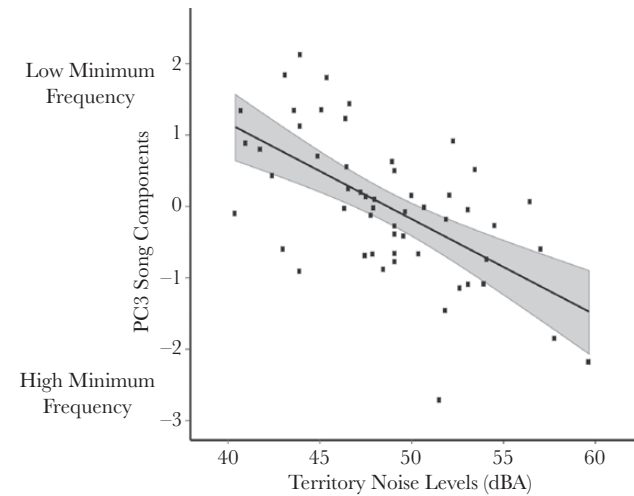

Figure 3

The relationship between minimum frequency and environmental noise. Males sing songs with higher minimum frequencies (decreases in PC3) as territories become louder.

song found weak support for strong acoustic adaptation in vocalizations (Boncoraglio and Saino 2007); however, most studies consider structural adaptation without social context.

On the other hand, temporal differences in song may be indicative of the quality of individuals settling in these habitats. For

example, plumage brightness, another indicator of quality in cardinals, declined with surrounding urbanization (Jones et al. 2010). In cardinals, song is also indicative of male quality such that shorter, slower songs indicated higher territory quality and reproductive success in birds in a nondeveloped landscape (Conner et al. 1986). Urban birds may be experiencing early developmental stress that reduces production of high-quality song (Buchanan et al. 2003). Large body size is also a quality measure in many species of birds (Kodric-Brown and Brown 1984) and may be associated with song (Gil and Gahr 2002). However, we did not find any support that morphology explained temporal attributes of song, although size was negatively associated with urbanization. Though we cannot completely discount effects of age and experience, all banded second-year birds were unable to retain territories, and most birds in this study were at least after-second year individuals.

Increases in certain song attributes, such as song length and rate, may result from plentiful food sources in areas with high densities. Song can be energetically expensive to develop and produce (Nowicki et al. 1998; Gil and Gahr 2002) and birds in lower quality habitat are known to have reduced song output (e.g., time spent singing; Van Oort et al. 2006). Likewise, birds with access to supplementary food sources exhibited sustained song production (Strain and Mumme 1988). In urban areas, generalist species have access to energetically rich foods year-round (e.g., bird seed). Although urban cardinals occur in higher densities, they appear to be matching population size with resource abundance and, therefore, are not experiencing reduced condition, survival, or reproductive

Table 4

Relative support for alternate models explaining peak/high frequency variation of northern cardinal (n = 54) song models using Akaike's information criterion corrected for small sample sizes (AICc)

Model	k	AICc	ΔAICc	AICc weight	Evidence ratio	β (SE)	P
Null	1	165.56	0	0.19	1	0.00 (0.14)	1.00
Body size	2	165.75	0.19	0.18	1.1	0.23 (0.17)	0.17
Shrubs and saplings	2	165.81	0.25	0.17	1.13	0.19 (0.14)	0.18
Noise	2	166.46	0.9	0.12	1.57	0.04 (0.03)	0.27
Density	2	166.86	1.3	0.1	1.91	0.05 (0.06)	0.36
Large trees	2	167.04	1.47	0.09	2.09	0.14 (0.17)	0.42
Small trees	2	167.45	1.89	0.08	2.57	−0.08 (0.15)	0.60
All trees	3	169.02	3.46	0.03	5.63		
All vegetation variables	4	169.42	3.86	0.03	6.9		
Global	8	175.96	10.4	0	180.96		

Models include variables that represent alternative hypotheses for song variation: density of conspecifics at the site level, noise levels (dBA) at the territory level, body size of the vocalizing male, vegetation at the territory level (tree classes and shrub densities), and a global and null model. SE, standard error.

Table 5

Correlation matrix (Pearson's r) between urbanization index and site-level ecological attributes (n = 9)

	Urban	Conspecific densities	Noise levels	Body size	Shrub/sapling density	Small trees	Large trees
Urban							
Conspecific densities	0.89**						
Noise levels	0.81*	0.96**					
Body size	−0.79*	−0.47	−0.31				
Shrub/sapling density	0.94**	0.96**	0.90**	−0.58			
Small trees	−0.28	−0.21	−0.33	0.23	−0.32		
Large trees	0.92**	0.64	0.54	−0.96**	0.74*	−0.26	

*$P < 0.05$, **$P < 0.01$.

performance compared with rural birds (Rodewald and Shustack 2008b). Adjustment of temporal attributes of song may indicate relaxed energetic constraints to song performance in areas with plentiful food resources.

To our knowledge, this study is one of the first to simultaneously test multiple competing hypotheses of urban-associated changes in song. Although true that a number of potential drivers of song changes (e.g., population densities, noise, vegetation, and morphology) may similarly change with urbanization (Table 5), our use of an AIC approach allowed us to rank models in terms of their relative ability to explain variation in song among birds. Our correlations should reduce, rather than improve, our ability to discriminate among potential drivers of song change, yet we still found evidence of strong relationships. Thus, because we explicitly tested several potential mechanisms, our study provides compelling evidence that noise is, indeed, driving changes in frequency but changes in density also contribute to shifts in temporal attributes of song.

Insights from this study are further supported by the fact that 1) the influence of habitat size and population dialects on behavior was minimized by using similarly sized forest fragments that differed primarily in landscape context within the same region and 2) territory-level features were considered in addition to landscape-scale phenomena. The latter is especially important given that frequency shifts could be a plastic behavioral response to a proximate acoustic environment (Bermúdez-Cuamatzin et al. 2010; Gross et al. 2010), an artifact of amplitude changes (Brumm 2004; Nemeth et al. 2013) and/or to avoid scattering by nearby objects such as buildings or impermeable surfaces (Warren et al. 2006; Dowling et al. 2012). We found that minimum frequency strongly increased with ambient noise, despite that noise variability within the site was

only 7.44 ± 3.20 dB. Although difficult to standardize across recording events, amplitude adjustment between territories might have explained changes in minimum frequency as upward frequency shifts is an artifact of singing louder (Zollinger et al. 2012). The lack of evidence for noise as the driver of peak/high variation suggests that there were other behavioral mechanisms unaccounted for in our study. Indeed, frequency changes may result from cultural or geographical drift of urban song dialects over time (Luther and Baptista 2010; Luther and Derryberry 2012) or use of different song types (Slabbekoorn and den Boer-Visser 2006; Halfwerk and Slabbekoorn 2009; Nemeth et al. 2013).

Our work shows that changes associated with urbanization, both ambient noise and population densities, can influence communication behavior within a population. Song adjustment driven by conspecifics may be a direct consequence of changes in motivational states of singers, food resources, or relaxing energetic constraints on song performance. We also demonstrate that when evaluating apparent "urban" differences in behavior, researchers should explicitly consider and test multiple proximate ecological drivers. Future studies should investigate whether alternative urban-associated changes also might impact communication in species that do not exhibit behavioral plasticity in vocal performance, as with non-oscines or suboscines (Ríos-Chelén et al. 2013). Moreover, because environmental and social heterogeneity may also influence signal reliability (Penteriani 2003; Cornwallis and Uller 2010), additional studies should consider whether there are fitness-related consequences to song variation for urban birds (Halfwerk and Slabbekoorn 2013), or if the informational content of urban song may have different relationships in natural systems as has been shown experimentally (Halfwerk et al. 2011).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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