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Urban habitats impact the song and reproductive success of a migratory bird,
the gray catbird (*Dumetella carolinensis*)

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A thesis submitted to the Graduate Faculty of

JAMES MADISON UNIVERSITY

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Abstract

Urban environments are relatively recent on an evolutionary timescale, and, as such, they create novel selection pressures that may influence fitness and mate choice. Many ecologically significant factors change with increasing levels of urbanization, such as increasing anthropogenic noise, increasing impervious surface, and decreasing forest cover. There is growing empirical evidence that anthropogenic noise affects features of birdsong and, separately, that avian nesting success varies across an urban gradient, but rarely do studies examine both – a necessary step to elucidate the evolutionary potential of these novel pressures. I investigated song features, body morphometrics, and reproductive success in male gray catbirds across an urban gradient. Noise was included in best-fit models as a predictor for minimum and peak frequencies, with increases in noise level associated with increases in frequencies, which likely improves signal transmission in noisy habitats. For minimum frequency, male body size was also included in the best-fit model such that larger-bodied males sang with significantly lower minimum frequencies. Models of maximum frequency and frequency bandwidth both showed significant increases with increasing impervious surface and canopy cover. Nests were significantly more likely to fledge in areas of higher impervious surface, lower canopy cover, and less noise. Surprisingly, nests of males with slower song phrase rates were significantly more likely to fledge and contain more nestlings. Additionally, models revealed interactions between frequency measures and nesting success. In urban habitats, males that sang higher minimum frequencies were more likely to have successful nests, while males in suburban and rural habitats were more likely to fledge nests if they sang at lower minimum frequencies. Similarly, males in urban habitats had significantly more

nestlings per nest as maximum frequency increased while their suburban and rural counterparts showed the inverse relationship. These results indicate urbanization not only influences song features, but also the nesting success of gray catbirds with certain song features, indicating a potential shift in selection occurring in urban environments. Future research should further expand this connection between sexual selection, reproductive success, and variation across an urban gradient to aid in urban development plans that will minimize negative impacts on migratory songbirds.

Introduction

As human populations steadily increase, urban environments worldwide are expanding at a rapid rate, which has considerable impacts on wildlife populations (Grimm et al., 2008). Urban habitats are highly modified compared to undisturbed or less developed areas. The interspersed buildings, roads, and green space found in cities creates a unique patchwork of fragmented habitats. An increase in habitat heterogeneity affects habitat suitability, food availability, the presence of native or novel predators or competitors, and can limit animal movement (Corrêa et al., 2018; Davison et al., 2009; Riley, 2006). Changes in the physical landscape may be the most conspicuous difference between rural and urban habitats, but pollution, including added noise and light at night, has significant impacts on wildlife as well (Swaddle et al., 2015).

Light pollution has been shown to impact species' presence, behavior, and physiology in urban and disturbed habitats. The occurrence of novel predators in conjunction with anthropogenic (human-generated) light pollution changes existing predator-prey dynamics (Balogh et al., 2011; Swaddle et al., 2015). Artificial light causes some bird species to sing earlier in the day and begin breeding earlier in the year (Kempenaers et al., 2010) and low levels of constant light suppresses immune system response in wild hamsters (Bedrosian et al., 2011). Additionally, studies report induced stress responses, potentially because of interrupted sleep, for both light (Japanese monkeys *Macaca fuscata fuscata*; Nozaki et al., 1990) and noise pollution (greater sage-grouse *Centrocercus urophasianus*; Blickley et al., 2012)

Anthropogenic noise produced by traffic and machinery is generally low frequency (<2000 Hz) and high amplitude. Noise pollution in urban environments has

negative impacts on animals that rely on acoustic communication (Francis & Barber, 2013; Shannon et al., 2016; Slabbekoorn & Ripmeester, 2008). Ware et al. (2015) reported forest songbird diversity was lower in the presence of noise, and individual birds exposed to noise had lower body condition. These unique characteristics of urban environments are relatively new on an evolutionary timescale, and as such they create novel selection pressures that have the potential to influence fitness and mate choice. It is important to determine whether these environmental factors are actually driving evolutionary changes in urban populations, a crucial aspect to the ecology of species impacted by urbanization that remains understudied in vertebrates (Swaddle et al., 2015).

Multiple studies have investigated the effects of noise pollution on acoustic signaling in animals (Slabbekoorn & Peet, 2003). When background noise overlaps the frequency range of acoustic signals in wildlife species it causes “signal masking,” which disrupts communication between sender and receiver (Slabbekoorn & Ripmeester, 2008). In species of frogs, insects, birds, and whales, acoustic signals in the presence of low-frequency noise differ from signals in less noisy areas in predictable ways that avoid the masking effects of anthropogenic noise (Kunc & Schmidt, 2019). Specifically, there is accumulating evidence for multiple species of birds that populations in urban areas sing at higher minimum frequencies than their counterparts inhabiting more rural areas (Slabbekoorn & Peet, 2003; Walters et al., 2019). Since birds rely heavily on acoustic communication for survival and reproduction and are ubiquitous in urban environments, they are an ideal taxonomic group for the study of anthropogenic noise and its effects on wildlife.

Birdsong functions primarily in mate attraction and territory defense and is therefore subject to sexual selection. For example, female mate choice studies in great tits (*Parus major*) and canaries (*Serinus canaria*) demonstrate a preference for lower frequency song (Halfwerk, Bot, et al., 2011; Pasteau et al., 2007). This presents a problem because urban environments generate significant amounts of low-frequency noise that could mask low-frequency song and thus make transmission less effective. Huet de Aunay and colleagues (2014) found that female canaries exposed to noise exhibited significantly reduced responses to low-frequency song, while their response to high-frequency song remained the same as compared to controls without noise exposure. When female great tits were tested for response to low- and high-frequency songs, either in the presence or absence of noise, females were more likely to respond to high-frequency songs during noise treatments. This contrasts with the finding that they prefer lower frequency songs under normal conditions (Halfwerk et al., 2011). Both of these studies suggest that female preference for low-frequency song disappears in the presence of urban noise, which begs the question of whether song traits in urban populations will change via the intersection of natural and sexual selection.

Another song trait driven by sexual selection and influenced by anthropogenic noise is vocal performance in the Passerellidae (New World sparrows). Vocal performance describes the ability to execute a physically challenging song. One example is maximizing trill rate and frequency bandwidth – two traits known to trade off (Podos, 2001; Podos et al., 2009). Vocal performance functions in both male-male competition and female mate choice (Ballentine et al., 2004; Caro et al., 2010; Moseley et al., 2013; Phillips & Derryberry, 2017). An analysis of white-crowned sparrow (*Zonotrichia*

leucophrys) song from territories with varying levels of anthropogenic noise found males on noisier territories produced songs with reduced bandwidth and lower vocal performance (Luther et al., 2016). A study conducted in the same region showed male white-crowned sparrows on noisy territories respond more aggressively to songs with a wider frequency bandwidth compared to narrower ones indicating that changes in song to adapt to noise may have consequences when it comes to territory defense (Phillips & Derryberry, 2018). Another song trait that is also likely difficult to produce, song complexity, differs in urban noise for both white-crowned sparrows and song thrushes (*Turdus philomelos*): songs produced by urban populations were more complex than those produced by rural ones (Deoniziak & Osiejuk, 2019; Moseley et al., 2019). The results from these studies document how urbanization affects birdsong characteristics other than minimum frequency. Given that myriad song traits differ in urban areas, it is an open question how, or if, these differences relate to male body quality and fitness potential. There is still very little empirical work that has looked at both changes in song features due to urbanization and the effects these changes have on fitness (reviewed in Slabbekoorn, 2013).

Certain song features may honestly indicate male quality, and theory predicts song features that are difficult to produce and/or energetically demanding are constrained such that only high-quality males are able to produce them (Andersson 1994). To examine if signals are honest, researchers investigate if components of birdsong correlate with both male quality, such as body size or condition, and measures of reproductive success. An investigation of swamp sparrows (*Melospiza georgiana*) found that vocal performance is positively correlated with male age and size (Ballentine, 2009).

Additionally, Halfwerk and colleagues (2011) found correlations between males singing low-frequency songs and increased reproductive success in great tits. In another study, a positive relationship was observed between song-phrase rate and male parental quality in gray catbirds (*Dumetella carolinensis*; Dolby et al., 2005). However, little research has been done to determine if these types of correlations differ across the rural to urban gradient within a species, even though urbanization has clear impacts on both sexual signals (Huet des Aunay et al., 2014; Luther et al., 2016; Walters et al., 2019) and reproductive fitness in birds (Borgmann & Rodewald, 2004; Francis et al., 2009; Kight et al., 2012).

Regarding reproductive fitness, there is growing evidence that birds breeding in urban environments have greater success at the nest stage compared to their rural counterparts. Harvey et al. (2021) reported urban small ground finches (*Geospiza fuliginosa*) had higher nesting success than nonurban finches. Similarly, Kosiński (2001) found a higher percentage of nest survival in greenfinches (*Carduelis chloris*) in urban sites compared to rural sites and Ryder and colleagues (2010) reported the same for gray catbirds (*Dumetella carolinensis*). These findings may be explained by differences in predator pressures on nests across the urban gradient, as evidenced by researchers that reported predation on artificial nests declined with increasing intensity of urbanization (Gering and Blair 1999).

Nesting success is important for conservation of bird species and migratory species are some of the most threatened. Migratory birds are of special interest because they may only come into urban areas to breed. If we only assess habitat based on bird surveys that document presence, then we may be misinterpreting habitat quality. A study

in Oregon found spotted towhees (*Pipilo maculatus*) preferred nesting nearer residential edges. However, the individuals that nested nearer residential areas had a significantly lower rate of fledgling survival than those nesting farther away, revealing an “ecological trap” in which animals are attracted to an area that ultimately produces a negative population growth rate (Shipley et al., 2013). Similarly, a study in two densely populated suburban areas determined them to be ecological traps for gray catbirds due to low fledgling survival (Balogh et al., 2011). It is important for the objectives of conservation to parse out which environmental factors are the best predictors of nesting success. Further, there may be species-specific patterns rather than one-size-fits-most models to better inform land developers.

In summary, there is much research on the effects of urbanization on birdsong and separately, on how reproductive success varies across an urban gradient. However, there is no empirical work published that explores relationships across all three: urbanization, birdsong, and reproductive success. A review on the effects of urbanization on sexual selection published in 2022 stated, “we lack a good understanding of whether reported changes in traits [across an urban gradient] result in adaptive benefits (Cronin et al., 2022).” Therefore, there is a clear gap in the knowledge that needs to be filled. It is known that birdsong is important in mate choice and is affected by the urban gradient. However, for catbirds, it is unknown what song parameters are important in female choice and how these song features in conjunction with reproductive success vary across the urban gradient.

My research questions fall at the intersection of sexual selection and urban ecology to ask if song traits in the gray catbird honestly indicate male quality, and if this

varies across the urban gradient. In addition, I assessed how urbanization impacts nesting success in gray catbirds, as their prevalence in any given area does not necessarily mean that the habitat is suitable or high quality. One must determine reproductive success of a species to accurately evaluate habitat quality, as some suburban and urban habitats may actually be population sinks. Research that assesses productivity can help inform urban planners on best practices for optimal biodiversity as cities continue to grow.

The gray catbird is an appropriate species for which to investigate the impacts of urbanization on song traits and reproductive success because it is a migratory songbird that commonly breeds across the urban to rural gradient. Catbirds form pairs during the breeding season and males contribute to the success of nests by acquiring and defending a quality territory; as well as, helping to feed the young at both the nestling and fledgling stage. If a nest fails due to predation or weather, then pairs will attempt to nest again. Catbird pairs will attempt two to three broods per breeding season. Male gray catbirds are vocal mimics; they mimic other birds through imitation and also invent and improvise new songs (Kroodsma et al., 1997). Most research on birdsong and urbanization up to this date has focused on birds that sing short, stereotyped songs: catbirds are unique in that they sing long, complex songs. Recent work has shown that males in this species, like in other species, sing with a higher minimum frequency in more urban environments with greater anthropogenic noise (Rhodes et al. *unpub. data*). Importantly, few studies have been published on catbird song in general and on which song traits are influenced by selection, such that any song patterns I document will add to the general knowledge of song in this species.

Current study

Specifically, the purpose of my study is to investigate the connection between male song quality, male body size, and fitness via nesting success while examining how these features are impacted by an urban gradient. For catbirds, some song traits that may reveal quality include song-phrase rate, minimum frequency, and frequency bandwidth, as these traits have been shown to function in sexual selection in other songbirds (Catchpole and Slater, 1995). Classical body morphometrics in birds include beak measurements, wing length, tail length, and mass. To quantify fitness and male reproductive success I will use number of nestlings and nest fate (fledged or failed). These reproductive success metrics were selected because a better-quality male will hypothetically maintain a territory with good food availability which can support more nestlings and more protected nest sites which would influence nest failure due to weather or predators.

I predict males with larger body size and beak size will have greater reproductive success and sing at lower minimum frequencies. Ryder et al. (2012) reported larger-bodied catbirds had greater reproductive success and other research has shown correlations between body and beak size and song frequencies (Ballentine, 2009; J. Podos, 2001). I predict song phrase rate will positively correlate with male body size. In addition, I predict a difference in the correlations across the urban gradient with regard to minimum frequency and fitness: males of high reproductive success in rural environments will have lower minimum frequencies than males with high reproductive success in the more urban environments. In regard to fitness and urbanization, I predict

nesting success will increase with increasing amounts of impervious surfaces and reduced amounts of canopy cover.

Methods

General methods

Study species

The gray catbird is a migratory songbird that breeds across southern Canada and much of the United States east of the Rocky Mountains where habitat is suitable. It is a medium-sized bird that favors habitats dominated by shrubs and vines which, makes it a common resident of forest edges, old fields in transition to forest, and backyards from rural to urban environments. Gray catbirds are in the Mimidae family, named as such due to these birds' ability and habit of mimicking songs of other birds and sounds in their environment. Gray catbirds are socially monogamous but do participate in extra pair copulations (EPC), especially in populations that have a higher breeding density (Ryder et al., 2012). Males and females look alike, but when multiple body measurements are taken together, males are slightly larger; for example, males have slightly longer wings, with males ranging from 85-97mm and females ranging from 81-95mm (Pyle, 1997).

Study sites

Study sites ranged from restoration projects on rural farms to suburban parks to urban parks and were located in western Virginia and the greater Washington, D.C., metro region (Table 1, Figure 1). Field teams directed by Dr. Moseley from James Madison University and the Smithsonian Migratory Bird Center collected data during the

summer breeding seasons from late April to the end of July from 2017 to 2021. I

contributed to data collected in summers 2020 and 2021.

Table 1. Study site locations and descriptions. Habitat categories and the order sites are listed in, are based upon level of urbanization PC1 scores from Table 2.

Site	Code	Habitat Type	State	Description
Bells Lane, Staunton, VA	BEL	Rural	VA	Rural farm with restored habitat, surrounded by farmland
Crusher Run Farm, Port Republic, VA	CRU	Rural	VA	Rural farm with restored habitat, surrounded by farmland
Wheaton Regional Park, Wheaton, MD	WHE	Rural	MD	Botanical gardens surrounded by regional forest & suburbs
Opal Daniels Park, Takoma Park, MD	OPA	Suburban	MD	Neighborhood park in suburban matrix
James Madison University Edith J. Carrier Arboretum	JMU	Suburban	VA	Arboretum surrounded by urban/suburban matrix
Westover Park, Harrisonburg, VA	WES	Suburban	VA	Neighborhood park in suburban matrix
Dumbarton Oaks Park, Rock Creek Park, D.C.	DUM	Urban	DC	Neighborhood park in suburban matrix
Smithsonian National Zoological Park, D.C.	SIZ	Urban	DC	Urban park in urban/suburban matrix
Smithsonian Castle, National Mall, D.C.	SMI	Urban	DC	Urban park along the National Mall



Level of urbanization

To determine the level of urbanization at each site, three components were assessed: ambient noise, percent impervious surface, and percent canopy cover. Noise measurements were taken between 5:00 and 11:00am, from multiple locations, at each site throughout the 2021 breeding season using a Larson Davis Sound Level Meter, Model 831C. Following methods from Phillips & Derryberry (2018), each measurement had a standardized duration (4 min) with the meter facing in each cardinal direction (1 min each). The average LAeq and LA90 from all measurements taken at a site were used to equate ambient noise level at that site (Appendix, Table S1). LAeq represents the noise level collected over a period of time as a single number using A-weighting while LA90 is the noise level that is exceeded for 90% of the measurement time.

I downloaded land cover data from the Chesapeake Conservancy website from aerial and satellite imagery from 2013 and 2014 with a 1m resolution. To determine level of urbanization at both the individual nest and site levels, I used percent canopy cover and percent impervious surface as these measures have been used by others to equate level of urbanization specifically in relation to avian species (Evans et al., 2018; Minor & Urban, 2010; Ryder et al., 2010). I used ArcGISPro to reclassify land cover into two new layers: canopy cover and impervious surfaces. Water was set to “NODATA” during reclassification so that it would be excluded from calculations of percent cover class in a given area. Site centers were determined by finding the centroid location of catbird nests at each site. I calculated percent impervious surface and canopy cover within a 500m and 1000m radius of each site centroid using ArcGISPro (Appendix, Table S1). For my nesting success analysis, instead of using the site centroid I calculated canopy cover and

impervious surface within 100m of each nest. These buffers were selected because they have been previously shown to predict gray catbird abundance (100m, Evans et al., 2018), adult survival (500m, Evans et al., 2015), and nesting success (1000m, Ryder et al., 2010).

Finally, to categorize sites into general habitat types, I performed a principal components analysis to decompose variables including impervious surface at 500m and 1000m buffers, canopy cover at 500m and 1000m, and noise level including both LAeq and LA90, and generated a PC1 value for urbanization level (eigenvalue = 3.58, explaining 59.6% of variation, Table 2). All variables loaded positively on the PC1, but impervious surface cover and noise variables had larger (~0.50) loading values (Pearson's R), while the loading values for canopy cover were close to zero. Therefore, a site with a high PC1 (0.62 – 3.00) is more urban and a site with a low PC1 value (-2.8 – -0.34) is more rural. The range of PC1 values for suburban sites was -0.31 – 0.44. Each site was categorized as urban (PC1 0.62 – 3.00), suburban (PC1 -0.31 – 0.44), or rural (PC1 -2.8 – -0.34) based upon its PC1 score (Table 1 and Appendix, Table S1).

Table 2. Loadings for habitat principal components analysis.

Variable	Habitat PC1 loadings
500m Impervious surface	0.477
1000m Impervious surface	0.504
500m Canopy cover	0.089
1000m Canopy cover	0.033
Noise - LAeq	0.503
Noise - LA90	0.507
Eigenvalues	3.578
Percent variance	59.63

Male morphometrics

Birds were captured using mist nets and potter's traps and banded with one aluminum USGS band and three colored bands, so that individuals could be identified after release. All capture and handling procedures used were approved by the James Madison University IACUC and the USGS Federal Bird Banding Lab (USGS-BBL Permit #23407, JMU IACUC Protocol #20-16530). For each bird banded, the following data were taken: age, sex, mass (g), and various morphometrics including wing, tail, tarsus, and beak lengths (mm). Tail and wing length were measured to nearest 1 mm using a wing chord ruler. Tarsus length and four beak dimensions were measured to the nearest 0.01 mm using digital calipers. Beak length to nares was measured from tip of the upper mandible to the end of anterior end of the nostril. Beak width and depth were both measured at the posterior edge of the nostrils.

To assess outliers from body and beak measurements, first I used R (version 4.0.3) to create a summary of all measurements taken from all male catbirds captured across the study sites (n=304 birds) to get a representation of the data ranges (Appendix, Tables S2 and S3). I then produced a list of males that were considered outliers for each measurement within the full set of 304 males. An outlier was defined as any measurement above the 75th or below the 25th percentile by a factor of 1.5 times the interquartile range. Next I produced a list of outliers that were calculated using the subset of males for which I have song and/or nesting data (n=112). If a males' measurement was an outlier when calculated from the subset of 112 males but was not an outlier when calculated within the greater set of 304 males, then the measurement was retained in the data set. If the measurement was considered an outlier in both the complete data set and

subset, then it was further considered. Six males had one outlier measurement each. Five of those outliers were retained because they were believed to be accurate measurements. One was deemed to have been a possible mistake in measuring or data entry and was excluded from data analysis.

I replaced missing measurements (“NAs”), with the mean for that measurement for the male’s capture site based on the complete data set of 304 males. If a male was missing more than one body or beak measurement, the NAs were retained. Males missing multiple measurements were omitted from the associated analyses (i.e., if a male had two missing beak measurements, he was excluded from all analyses including beak).

I conducted a principal components analysis (PCA) to decompose multiple measures of male body quality: one for body measurements (wing, tail, tarsus, and mass; Table 3) and one for beak measurements (width, depth, and length to nares; Table 3). The beak PCA resulted in only one principal component (PC) with an eigenvalue greater than 1.0 (eigenvalue = 1.43). Beak size PC1 explains 48% of variation in beak measurements, and all measurements load positively; so, a larger beak size PC1 corresponds with a larger beak (Table 3). The body PCA resulted in two PCs with eigenvalues greater than 1.0. Body size PC1 (eigenvalue = 1.55, explaining 38.8% of variation) has all measurements loading positively, so a larger body size PC1 corresponds with a larger overall body size. The body shape PC2 (eigenvalue = 1.41, explaining 35.3% of variation) loads positively for mass and tarsus and negatively for wing and tail measurements, so a larger body shape PC2 corresponds with a heavier, longer-legged bird with shorter wing and tail feathers (Table 3).

Table 3. Principal components analysis (PCA) outputs used for beak and body. Loadings indicate the magnitude and directionality of each biometric within the PCA. Percent variance represents how much variation in the metrics is represented by the PCA.

Variable	Beak size PC1 loadings	Body size PC1 loadings	Body shape PC2 loadings
Bill length	0.675	-	-
Bill width	0.487	-	-
Bill depth	0.554	-	-
Tarsus	-	0.329	0.589
Mass	-	0.444	0.517
Wing	-	0.691	-0.220
Tail	-	0.467	-0.581
Eigenvalues	1.435	1.552	1.413
Percent variance	47.83	38.81	35.32

Song analysis methods

Field recordings of vocalizations

Gray catbird songs were recorded from May to July each year of the study. Males were identified using their unique combination of colored leg bands. Recordings were created using Marantz Professional PMD561 digital recorders and Sennheiser ME 66 microphones. Some, but not all, recordings were made with the assistance of a parabolic reflector. The parabolic reflector was used for sites where excessive background noise necessitated its use to produce more usable recordings. Song recordings were made at a sampling rate of 44.1 kHz and saved as uncompressed WAV files.

Song processing

Songs were measured and analyzed using RavenPro software (version 1.6).

Recordings were first filtered to 1000 – 9500 Hz to eliminate sound that falls outside of the catbirds vocal range. After filtering, only recordings with a good signal to noise ratio (i.e., catbird song was sufficiently louder than environmental noise; evidenced from the waveform) were selected for processing.

Table 4. Sample size from each site for song analyses.

Site - habitat	Song n Males
BEL - rural	8
CRU - rural	8
WHE - rural	12
OPA - suburban	8
JMU - suburban	11
WES - suburban	4
DUM - urban	5
SIZ - urban	9
SMI - urban	8
Total	73

Catbird song is composed of long bouts of multiple notes or elements. I, along with members of the Moseley Lab, processed recordings by finding continuous stretches ('bouts') of catbird song and using the selection tool to place a box around each utterance or element for which Raven generates various measurements of time and frequency. When a period of silence was noted between notes within a song as seen on the spectrogram, those notes were considered individual elements. A bout is defined as four or more consecutive elements without a minimum of 1-second silent break between them.

Using RavenPro and R I calculated peak frequency, minimum frequency, maximum frequency, bandwidth, and phrase rate for each male. Peak frequency is the frequency at which the maximum power or energy occurred within a given selection or element. I calculated average peak frequency per male by taking the mean of all peak frequency measures from each male's elements. In order to measure the minimum and maximum frequencies of each element selected, I used the Peak Frequency Contour (PFC) measurement in RavenPro. The PFC measurement divides each selection into time bins and measures the peak frequency for each time bin creating a contour of peak frequencies for each selection. Thus PFC minimum frequency is the lowest peak frequency from all the time bins of a given element, and PFC maximum is the highest peak frequency. I selected the 10% lowest minimum PFC elements and the 10% highest maximum PFC elements and took their means to get average minimum and maximum frequency measures. Frequency bandwidth for each male was calculated by subtracting average minimum frequency from average maximum frequency.

Duration 90 is a measurement in Raven that records the time in seconds that 90% of energy was produced across a selection. This measure of time was used to calculate phrase rate because it removes variation in how tight individuals box elements and whether elements were lumped or split. To calculate phrase rate per bout, I divided time singing (sum of duration 90 for all elements within a bout) by the duration of the entire bout. Duration of bout was determined by finding the difference between beginning time of first element and ending time of last element within a bout. I then calculated the mean phrase rate across all bouts per male.

Song statistical analysis

I used stepwise model selection in R to determine what male features (body size and beak size) and/or measures of urbanization (landcover and noise) best predict song traits including bandwidth, phrase rate, minimum frequency, maximum frequency, and peak frequency. For each song trait as the response variable, the initial model included the following as predictor variables: Noise (LA90), beak size PC1, body size PC1, body shape PC2, impervious surface, and canopy cover within a 1000m buffer. Final models were selected based upon Akaike Information Criterion (AIC) value. I used the stepAIC (package MASS) and boot.stepAIC (package bootStepAIC) functions in R which uses bootstrapping and backward stepwise regression to determine the best fit model. I conducted model selection separately for each of the five song traits. All song traits were normally distributed except for phrase rate, which was log transformed to normalize distribution. All predictor variables were checked for collinearity (function vifstep, package usdm) and scaled for their Z score before inclusion in the model.

Nesting success methods

Nest data collection

Catbird nests were located by observing adult behaviors, such as carrying nesting material or food. Nests were monitored to determine number of eggs, number of nestlings, and nest fate (fledge/fail). Social parents of nests were determined through observation of banded individuals incubating or making feeding trips to the nest.

Nesting success analyses

Due to the nature of field work, some males were never captured and therefore lacked morphometric measurements or were never recorded for their songs, which excluded them from analyses examining male body size or male song, respectively. In order to use as much data collected as possible and still account for missing data, I ran separate models for assessing whether urbanization, body size characteristics, or song characteristics predicted nesting success as these models contained different sample sizes (Table 5). For example, the model created with urbanization metrics as predictor variables and nest fate as the response used data from 193 nests, while the model with song metrics as predictors and nest fate as the response used data from 106 nests. There were 15 nests for which we had nest fate data, but there was uncertainty about number of nestlings. These nests were removed from analyses using number of nestlings as the response variable.

Table 5. Samples size of nests and males used for each model selection with nest fate or number of nestlings as the response variable. Number of nests from each site (n Nests) and number of unique males for which there are nests, for each site (n Males).

Predictor variables	Nesting success (fledge/fail)						Number of nestlings					
	Urbanization metrics		Males biometrics		Song features		Urbanization metrics		Males biometrics		Song features	
	n nests	n males	n nests	n males	n nests	n males	n nests	n males	n nests	n males	n nests	n males
Site - habitat												
BEL - rural	14	13	8	7	8	7	11	11	6	6	6	6
CRU - rural	18	14	12	8	10	6	16	12	11	7	9	5
WHE - rural	49	29	45	25	20	10	43	26	40	23	19	10
OPA - suburban	9	6	8	5	8	5	8	6	7	5	7	5
JMU - suburban	30	18	21	9	21	9	28	18	19	9	19	9
WES - suburban	13	8	11	6	9	4	13	8	11	6	9	4
DUM - urban	10	7	9	6	7	4	10	7	9	6	7	4
SIZ - urban	20	13	17	10	10	5	20	13	17	10	10	5
SMI - urban	30	21	25	16	13	7	29	21	25	17	12	7
Total	193	129	156	92	106	57	178	122	145	89	97	55

I used R to conduct model selection with backward stepwise regression to determine what characteristics, if any, best explain variation in reproductive success. I ran separate model selections for my two response variables that represent reproductive success: nest fate (fledge/fail) and number of nestlings. I used the glmer function (package lme4) to run generalized linear mixed models (GLMM) for each response variable. I chose to use a mixed model so I could add male ID as a random effect to account for males with multiple nests. If final models showed no variance due to male ID as a random effect, I then reran these models using a generalized linear model (glm

function). R does not have a stepwise function for GLMM, so I ran it manually by starting with the full model including all possible predictor variables and then removing the variable with the highest p value at each step. I selected the model with the lowest AIC value as the final model. I selected the glmer and glm functions because they inform the model of the response variables' distribution. Nesting success of fledged versus failed was a logistic regression with a binomial distribution while the number of nestlings had a Poisson distribution. Predictor variables for all model selection were checked for collinearity and scaled for their Z score before inclusion in the model.

For the models created to determine what body morphometrics or song characteristics predict nesting success, I added the habitat categorical variable (rural, suburban, urban) as an interaction for any potential final predictor variables to see if their correlations varied with level of urbanization. If including the habitat variable as a predictor improved the model fit, then it became part of the final model.

Results

Song Analyses

The best fit model using backward stepwise regression and AIC values to predict each song characteristic from 73 banded males (Table 6, Table 4) are as follows. The best model for predicting minimum frequency included noise (average LA90) and Body size PC1 ($F = 5.122$, $P = 0.008$, Table 6, Figure 2A, 2B). Males with larger body sizes had significantly lower minimum frequencies ($T = -2.329$, $\beta \pm SE = -21.24 \pm 9.119$, $P = 0.023$). Louder noise was associated with higher minimum frequencies, but though included in the best fit model and significantly correlated in simple linear regression ($r^2 = 0.06$, $p =$

0.04, $\beta = 3.18$), louder noise was not statistically significant within the model ($T = 1.811$, $\beta \pm SE = 16.51 \pm 9.119$, $P = 0.075$, Figure 2D). Peak frequency significantly increased with louder noise ($T = 3.808$, $\beta \pm SE = 109.1 \pm 28.64$, $P < 0.001$, Figure 2D), and the best fit model also included beak size PC1 such that higher peak frequencies were associated with smaller beak sizes, but this variable was not statistically significant on its own within the model ($T = -1.448$, $\beta \pm SE = -41.48 \pm 28.64$, $P = 0.152$; full model $F = 7.266$, $P = 0.001$). The best fit models for both maximum frequency and bandwidth included beak size PC1, body shape PC2, impervious surface, and canopy cover ($F = 4.013$, $P < 0.01$; $F = 3.424$, $P = 0.013$). Maximum frequency and bandwidth were positively correlated with amount of impervious surface (Figure 2C) and canopy cover, negatively correlated with beak size, and was positively but not significantly related to body shape (PC2). The final model for phrase rate included impervious surface, canopy cover, and Body shape PC2 ($F = 5.728$, $P = 0.001$) as predictor variables. Phrase rate significantly increased with an increase in canopy cover ($T = 3.799$, $\beta \pm SE = 0.029 \pm 0.008$, $P < 0.001$). Phrase rate also increased with an increase in impervious surface but was not significant ($T = 1.900$, $\beta \pm SE = 0.015 \pm 0.008$, $P = 0.062$). Phrase rate decreased with an increase in Body shape PC2, but not significantly ($T = -1.497$, $\beta \pm SE = -0.011 \pm 0.008$, $P = 0.139$).

All full models remain statistically significant using a standard Bonferroni correction of $\alpha = 0.05/5 \text{ tests} = 0.01$ except for frequency bandwidth ($p = 0.013$); however, frequency bandwidth remains statistically significant when using a sequential Bonferroni correction.

Table 6. Best fit models for each song characteristic as a response variable. Predictor variables in initial models were Body size PC1, Body shape PC2, Beak size PC1, Noise, Impervious surface and canopy cover. Impervious surface and canopy cover are for a 1000m buffer around site centroids. Significance indicated by bold values following sequential Bonferroni correction.

Variable	F	DF	R ²	Estimate ($\beta \pm SE$)	T	P value
Min frequency	5.122	2, 70	0.1027			0.008
Intercept				1367 \pm 8.949	152.8	<0.001
Noise				16.51 \pm 9.119	1.810	0.075
Body size PC1				-21.24 \pm 9.119	-2.329	0.023
Peak frequency	7.266	2, 70	0.1483			0.001
Intercept				3693 \pm 26.81	137.7	<0.001
Noise				109.1 \pm 28.64	3.808	<0.001
Beak size PC1				-41.48 \pm 28.64	-1.448	0.152
Max frequency	4.013	4, 68	0.1434			0.006
Intercept				7924 \pm 49.68	159.5	<0.001
1000m_Imp				172.0 \pm 53.74	3.200	0.002
1000m_Can				160.9 \pm 55.19	2.916	0.005
Beak size PC1				-118.9 \pm 56.81	-2.093	0.040
Body shape PC2				72.35 \pm 52.21	1.386	0.170
Bandwidth	3.424	4, 68	0.1187			0.013
Intercept				6557 \pm 49.90	131.4	<0.001
1000m_Imp				149.6 \pm 53.98	2.771	0.007
1000m_Can				156.05 \pm 55.44	2.815	0.006
Beak size PC1				-109.7 \pm 57.07	-1.923	0.059
Body shape PC2				73.19 \pm 52.44	1.396	0.167
Phrase rate	5.728	3, 69	0.1646			0.001
Intercept				-0.536 \pm 0.007	-72.02	<0.001
1000m_Imp				0.015 \pm 0.008	1.900	0.062
1000m_Can				0.029 \pm 0.008	3.799	<0.001
Body shape PC2				-0.011 \pm 0.008	-1.497	0.139

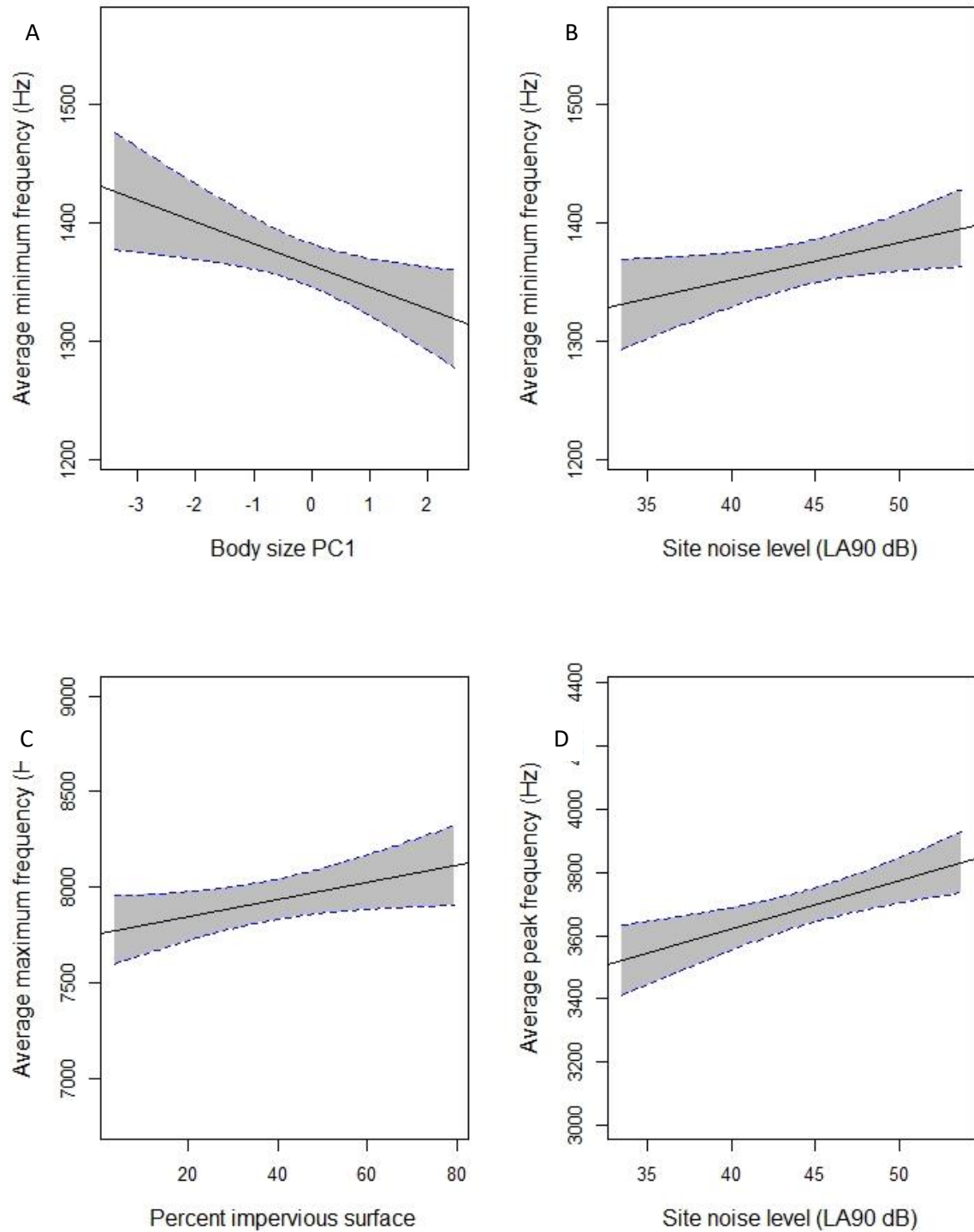


Figure 2. Predictor variables included in statistically significant best fit models with song features as the response variable. Graphs depict linear regression with 95% confidence intervals displaying relationships between song features, body morphometrics, and urbanization metrics (Table 6).

Nesting success

The best fit models using backward stepwise regression and AIC values to predict the likelihood a nest will successfully fledge are as follows (Table 7; Table 5 for sample sizes). An analysis using all nests for which we had nest fate ($n = 193$) produced two models with the same AIC value – a model with impervious surface cover and noise and a model with canopy cover alone. Nesting success significantly increased with increasing amounts of impervious surface and decreased with increases in noise level ($Z = 3.508$, $\beta = 0.742 \pm 0.211$, $P < 0.001$; $Z = -2.957$, $\beta = -0.624 \pm 0.211$, $P = 0.003$; Figure 3). Nesting success significantly decreased with increases in canopy cover ($Z = -3.376$, $\beta = -0.550 \pm 0.163$, $P < 0.001$; Figure 4).

For a subset of nests for which males were successfully caught and body morphometrics were assessed ($n = 156$ nests, 92 males), no significant models were produced in model selection (P values > 0.05). Thus, there was no correlations found between nesting success and the predictor variables tested: beak size PC1, body size PC1, and body shape PC2.

The best model assessing male song parameters as predictors of nesting success ($n = 106$ nests, $n = 57$ males) included song phrase rate and an interaction between song minimum frequency and habitat type (urban, suburban, or rural) as significant. Nesting success significantly increased as phrase rate decreased ($Z = -2.404$, $\beta = -0.685 \pm 0.285$, $P = 0.016$). Nesting success significantly increased as minimum frequency increased using a baseline habitat type of urban ($Z = 2.531$, $\beta = 1.313 \pm 0.519$, $P = 0.011$). There were no significant differences between general habitat types – any combination of urban, suburban, or rural sites (P -values > 0.05). However, at suburban and rural sites, as minimum frequency decreased nesting success increased, and this slope was significantly different from the correlation found at urban sites in which nesting success significantly increased as minimum frequency increased (Table 7, Figure 5). All final models remained statistically significant using a standard Bonferroni correction of $\alpha = 0.05/3$ tests = 0.0167.

Table 7. Final best-fit models using generalized linear mixed models (GLMM) and generalized linear models (GLM) results for nesting success (fledge/fail). Impervious surface and canopy cover are for a 100m buffer around a nest. Significant effects indicated in bold, at $\alpha = 0.017$ following Bonferroni correction.

Variable predicting fledge/fail	N	Estimate ($\beta \pm SE$)	Z	P
I. a. Nesting success over urban gradient				
	193			
Intercept		0.186 \pm 0.156	1.189	0.235
Impervious surface		0.742 \pm 0.211	3.508	<0.001
Noise		-0.624 \pm 0.211	-2.957	0.003
Random effects		Variance	SD	
Male ID	129	0.093	0.306	
I. b. Nesting success over urban gradient				
	193			
Intercept		0.184 \pm 0.157	1.176	0.240
Canopy cover		-0.550 \pm 0.163	-3.376	<0.001
Random effects		Variance	SD	
Male ID	129	0.132	0.363	
II. Nesting success and male morphometrics				
	157	No sig. models		
III. Nesting success and male song features				
	106			
Intercept		0.725 \pm 0.490	1.480	0.139
Phrase rate		-0.685 \pm 0.285	-2.404	0.016
Min frequency at urban sites		1.313 \pm 0.519	2.531	0.011
Habitat_suburban vs urban		0.143 \pm 0.667	0.215	0.830
Habitat_rural vs urban		-0.915 \pm 0.618	-1.480	0.139
Min frequency * Habitat: suburban vs urban		-2.137 \pm 0.675	-3.166	0.002
Min frequency * Habitat: rural vs urban		-1.764 \pm 0.660	-2.675	0.007

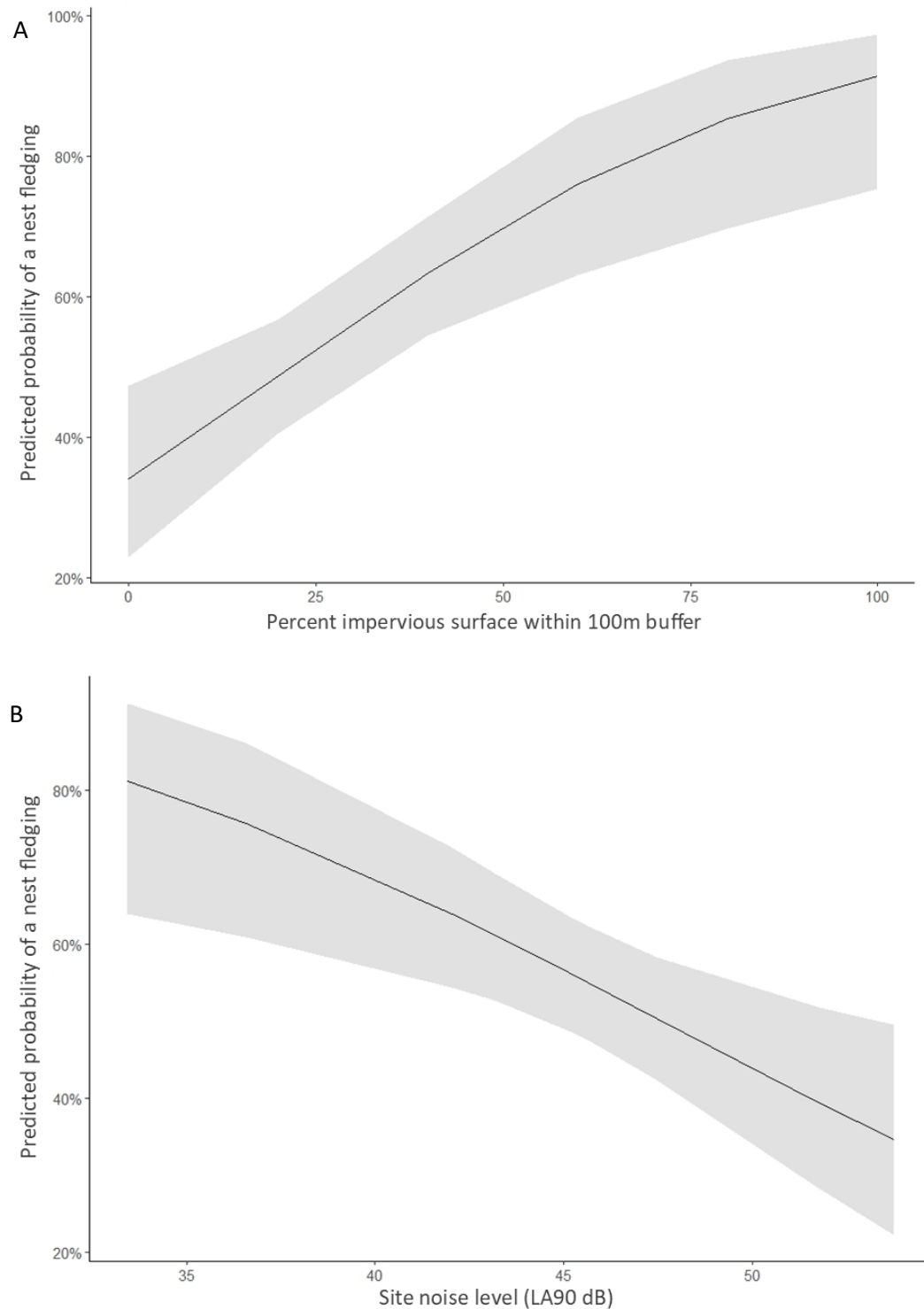


Figure 3. Predicted probability graphs for nesting success at all possible values of the predictor variables impervious surface (A) and noise (B) based upon the best fit generalized linear mixed model (Table 7). As impervious surface increased the predicted probability of a nest fledging significantly increased (A). As noise level increased the predicted probability of a nest fledging significantly decreased (B).

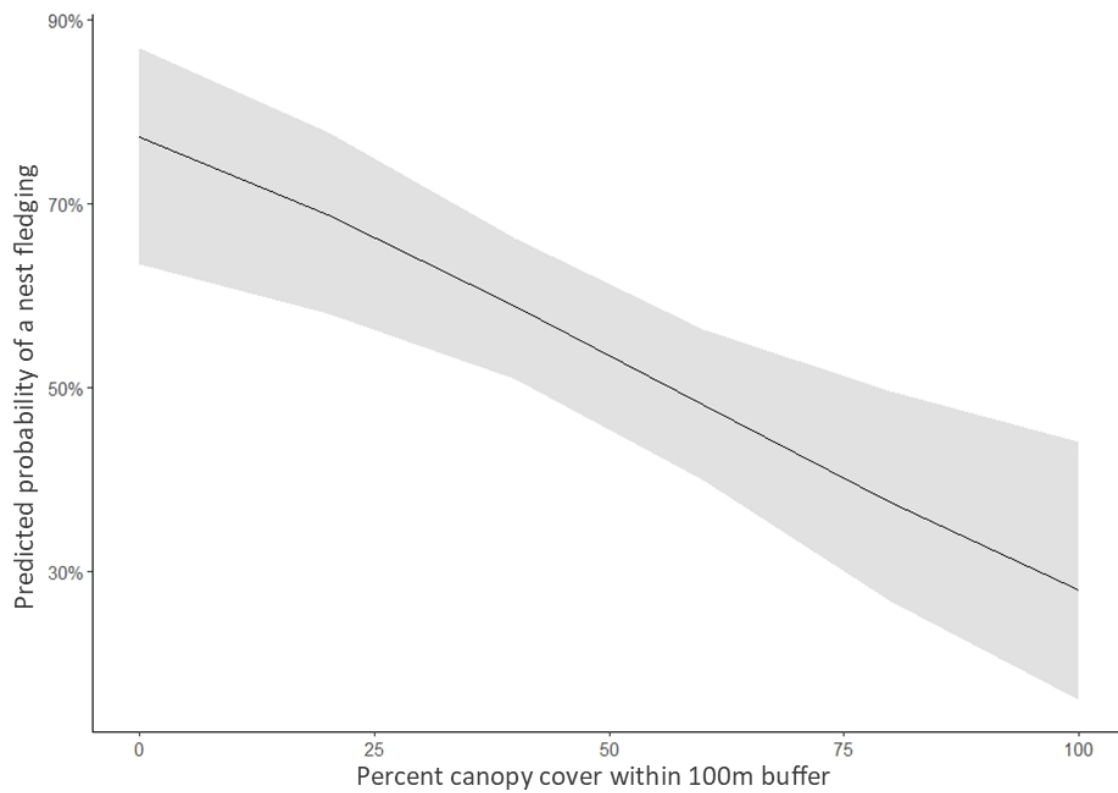


Figure 4. Predicted probability for nesting success at all possible values of percent canopy cover based upon the generalized linear mixed model (Table 7). As canopy cover increased the predicted probability of a nest fledging significantly decreased.

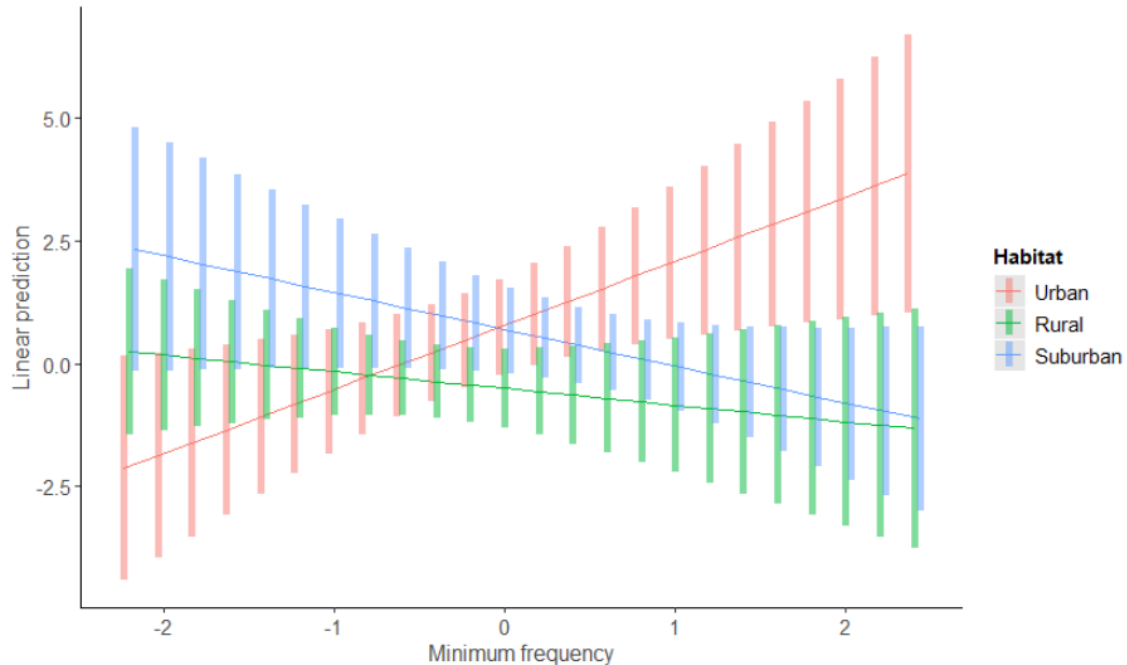


Figure 5. The interaction between minimum frequency and habitat for the final model predicting nesting success (Fledge / Fail). The model also included phrase rate as a predictor variable (Table 7). In urban habitats (red), the probability of a nest fledging significantly increased as minimum frequency increased. At suburban (blue) and rural (green) sites, as minimum frequency increased nesting success decreased, and this slope was significantly different from the correlation found at urban sites.

Number of nestlings

The best fit models using backward stepwise regression and AIC values to predict the number of nestlings in a nest are as follows (Table 8, Table 5 for sample sizes). Using all nests for which we had number of nestlings recorded ($n = 178$) produced a model with impervious surface and noise. Number of nestlings significantly increased with increases in impervious surface and decreased with increases in noise level ($Z = 2.927$, $\beta = 0.251 \pm 0.086$, $P = 0.003$; $Z = -2.577$, $\beta = -0.215 \pm 0.083$, $P = 0.010$).

For a subset of nests for which male morphometrics were assessed ($n = 145$ nests, $n = 89$), no significant models were produced in model selection (P -values > 0.05). Predictor variables tested were beak size PC1, body size PC1, and body shape PC2.

The best model assessing male song parameters as predictors of nesting success ($n = 97$ nests, $n = 55$ males) included song phrase rate and an interaction between song

maximum frequency and habitat type (urban, suburban, or rural). The number of nestlings significantly increased as maximum frequency increased at urban sites ($Z = 3.506$, $\beta = 0.721 \pm 0.205$, $P < 0.001$). Although included in the model, phrase rate was not significantly correlated with number of nestlings, and there were no significant differences among habitat types - any combination of urban, suburban, or rural sites (P -values > 0.05). However, the interaction between habitat type and maximum frequency was significant such that at suburban and rural sites as maximum frequency decreased, number of nestlings increased, and this slope was significantly different from the correlation found at urban sites in which nesting success significantly increased as maximum frequency increased (Table 8, Figure 6). All final models remained statistically significant using a standard Bonferroni correction of $\alpha = 0.05/3 \text{ tests} = 0.0167$.

Table 8. Generalized linear mixed model (GLMM) and generalized linear model (GLM) results for number of nestlings. Impervious surface and canopy cover are for a 100m buffer around each nest's location. Significance indicated in bold, $\alpha = 0.017$ following Bonferroni correction.

Variable	N	Estimate ($\beta \pm \text{SE}$)	Z	P
I. Number of nestlings over an urban gradient				
	178			
Intercept		0.464 ± 0.076	6.142	<0.001
Impervious surface		0.251 ± 0.086	2.927	0.003
Noise		-0.215 ± 0.083	-2.577	0.010
Random effects		Variance	SD	
Male ID	122	0.087	0.295	
II. Number of nestlings male morphometrics				
	145	No sig. model		
III. Number of nestlings and male song features				
	97			
Intercept		0.365 ± 0.185	1.974	0.05
Phrase rate		-0.066 ± 0.096	-0.684	0.494
Max freq at urban sites		0.721 ± 0.205	3.506	<0.001
Habitat_suburban vs urban		0.298 ± 0.241	1.233	0.218
Habitat_rural vs urban		-0.154 ± 0.233	0.660	0.509
Max freq * Habitat_suburban vs urban		-0.857 ± 0.273	-3.141	0.002
Max freq:Habitat_rural vs urban		-1.014 ± 0.235	-4.308	<0.001

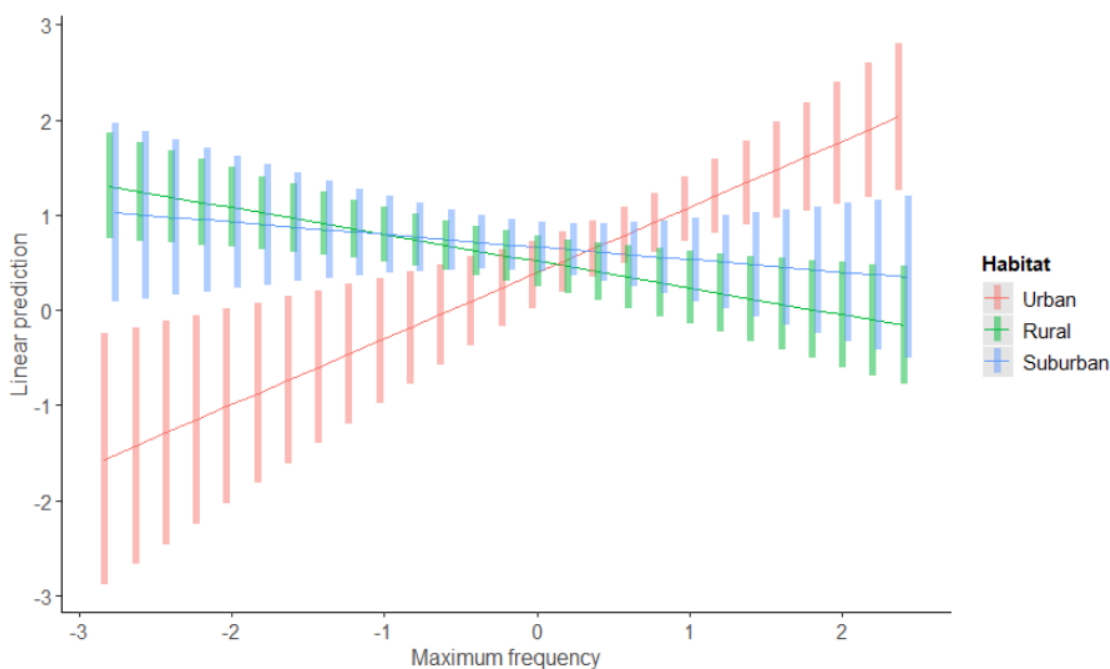


Figure 6. The interaction between maximum frequency and habitat for the final model predicting number of nestlings. The number of nestlings significantly increased as maximum frequency increased at urban (red) sites. At suburban (blue) and rural (green) sites, as maximum frequency increased nesting success decreased, and this slope was significantly different from the correlation found at urban sites (Table 8).

Discussion

While there is strong evidence of how birdsong is influenced by urban habitats and anthropogenic noise, still little is known about how differences in song may be affecting sexual selection and reproductive success. My research investigated the connection between birdsong and male fitness across the rural to urban gradient, which has implications for how urbanization may drive evolutionary change in a migratory songbird. Generally, I found further support that song features change across the urban gradient in line with previous literature – minimum peak frequencies increase with increased anthropogenic noise while maximum frequencies and bandwidth increase with

increasing percentages of impervious surface. Additionally, while dynamics of urban habitats affect song, general rules of body and beak size still drive song features, such as larger birds singing lower minimum frequencies and larger beaked birds singing lower peak and maximum frequencies, suggesting these song features may reveal physical traits that are subject to sexual selection pressure. Finally, I investigated the connection between song features, morphometrics, and nesting success across the urban gradient. While body and beak size showed no correlations with nesting success, certain song features, such as phrase rate, minimum frequency, and maximum frequency, predicted either success of fledging or the number of nestlings. Importantly, the direction of these correlated traits of song features on nesting success differed in direction across the urban gradient. These results indicate urbanization not only influences song features but also the nesting success of gray catbirds, with certain song features being more or less advantageous in different environments; thus, a potential shift in selection occurs in urban environments. Below, I discuss the relationships found between aspects of urban environments, birdsong, and nesting success and their implications.

First, my results align with past research showing correlations between song frequency and body or beak size (Ballentine, 2009; J. Podos, 2001). Due to the physics of sound, larger bodies and beaks produce notes at lower frequencies, and larger body sizes are often advantageous in both natural and sexual selection contexts. Consistent with my hypothesis and other studies, male catbirds with larger body sizes sang significantly lower minimum frequencies. Additionally, beak size was included in best-fit models of song characteristics showing larger beak sizes were associated with significantly lower maximum frequencies, qualitatively smaller bandwidths (non-significant), and

qualitatively lower peak frequencies (nonsignificant). These results corroborate those reported in previous studies, some looking at correlations across related species within a family, such as in tanagers, antbirds, woodcreepers, and finches (Demery et al., 2021; Derryberry et al., 2012; J. Podos, 2001) and others looking at correlations within a species (Giraudeau et al., 2014; Huber & Podos, 2006).

Second, I found impacts of anthropogenic noise and urban habitats on song characteristics which further confirm previous literature in other species but are novel for a species with a long song and large repertoire. Anthropogenic noise was a significant, single predictor of multiple song features from simple linear regression analysis (Appendix, Table S4), but I assessed all three predictors of level of urbanization along with both beak and body size predictor variables using model selection. Anthropogenic noise was included in best-fit models for both peak frequency (significant) and minimum frequency (non-significant). Both minimum and peak frequency were positively correlated with noise (i.e., higher in louder habitats). These results are consistent with a growing library of literature, which posits bird species sing at higher frequencies to avoid masking from low-frequency anthropogenic noise (Dowling et al., 2012; Luther et al., 2016; Roca et al., 2016; Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006).

Anthropogenic noise and percent impervious surface, two metrics that increase with degree of urbanization, were correlated ($r = 0.63$) but not considered colinear. The percent impervious surface of habitats was also included in best-fit models of other song features and significantly predicted maximum frequency and frequency bandwidth. The amount of impervious surface at a site was significantly and positively correlated with male maximum frequency: this indicates catbirds in urban environments are able to

mostly maintain their bandwidth even when minimum frequencies are increased. Other studies have reported a decrease in bandwidth due to increasing minimum frequencies in areas of high anthropogenic noise (Luther et al., 2016; Patricelli & Blickley, 2006). In a study on six urban species including catbirds ($n = 8$), Dowling and colleagues (2012) reported no correlation between impervious surface and maximum frequencies in gray catbirds when analyzed on its own. However, they did find an interaction between impervious surface and noise: there was a significant correlation with increasing impervious surfaces and increasing maximum frequencies at sites with low noise levels but no correlation at higher noise levels. I did not test for an interaction between noise and impervious surface, but it should be considered in future studies in order to parse out which aspects of urbanization are influencing observed changes in urban populations. Taken together, these song parameters, which have been shown to be evaluated in female mate choice in other songbirds, all vary predictably across the urban gradient. Because male birdsong plays an important role in territory defense and mate attraction (Catchpole & Slater, 1995) both signal transmission and signal quality are paramount for reproductive success in this taxon.

From these sets of results (lower frequencies for larger birds, higher frequencies in more urban environments), a conflict arises between female mate attraction and signal transmission. Studies on several species of birds have shown females have a preference for males that sing at lower frequencies and wider frequency bandwidths (Ballentine et al., 2004; Halfwerk et al., 2011; Pasteau et al., 2007). However, in two studies using birds known to prefer low-frequency song, females displayed a significantly reduced response to low-frequency songs when exposed to noise (Halfwerk, Bot, et al., 2011; Huet des

Aunay et al., 2014). These studies indicate noise pollution is influencing communication. What is not known is how this affects reproductive success and thus potentially drives evolution in an urban landscape (reviewed in Cronin et al., 2022).

Although studies have shown that females change their preference for song frequencies when exposed to noise (Halfwerk et al., 2011; Huet des Aunay et al., 2014), it has not been investigated whether this correlates with changes in male reproductive success in environments with higher ambient noise. Here, my research addressed how urbanization impacts male birdsong and how song traits are linked to nesting success across the gradient. I found both nesting success and number of nestlings showed interactions between level of urbanization and frequency measures of male song. Habitat classifications represent levels of urbanization, and noise loaded positively on the PCA used to determine sites as rural, suburban, or urban (Table 2). Male catbirds nesting in urban environments that sang at higher minimum frequencies had greater probability of successfully fledging their nests whereas males in suburban and rural habitats were more likely to have nesting success if they sang at lower minimum frequencies (Figure 5). Therefore, suburban and rural catbirds appear to follow the trends seen in many other bird species insofar as females can select males based on this song feature in less noisy habitats. Similarly, catbirds that sang at higher maximum frequencies in urban environments were correlated with a higher number of nestlings; conversely, their suburban and rural counterparts had more nestlings when their maximum frequencies were lower (Figure 6).

Another song feature that could be linked to nesting success and characteristics of urbanization is phrase rate. Male phrase rate significantly increased with an increase in

canopy cover. This result may be explained by investigating the relationships I found between nesting success and canopy cover and nesting success and male phrase rate. Nests with greater canopy cover were significantly more likely to fail, and male catbirds that sang at lower phrase rates were significantly more likely to fledge their nest. At first glance, the inverse relationship between phrase rate and reproductive success could be interpreted as contradicting the results of other studies such as one that showed female zebra finches (*Taeniopygia guttata*) prefer males with a higher song rate; another reported that male willow warblers (*Phylloscopus trochilus*) with higher song rates had earlier dates of mate pairing (Collins et al., 1994; Radesäter et al., 1987). It takes more energy for a male to sing at a higher song rate or phrase rate. Song rate was correlated with male body condition in willow warblers and thus may be an honest signal (Nystrom, 1997). Therefore, it is plausible for males to increase song rate at relevant times, such as during the breeding season or when guarding a mate that is laying eggs. Catbirds are known to participate in extra-pair copulations (Ryder et al., 2012), meaning females will breed with males other than their social mate, thus increasing a males motivation to mate guard. A study on rufous bush chats (*Cercotrichas galactotes*) found males sang at highest rates early in the breeding season during mate formation and territory acquisition (Alvarez, 1996). Males that have fewer nest failures are likely to spend less time and energy on mate guarding, whereas a pair of catbirds with nest failures will have more renesting attempts in a season which correlates with more egg laying and more time that the male would be motivated to expend energy increasing phrase rate for mate guarding purposes.

It should be noted that Dolby et al. (2005) reported male catbirds with higher phrase rates gave significantly more parental care to nestlings. Although a higher nestling feeding rate by males may correlate with nesting success, those authors did not report on number of nestlings or whether nests successfully fledged. Perhaps the most pertinent difference in the Dolby et al. study is that they collected all song recordings before mated pairs had formed; the song recordings I used, however, were collected throughout the breeding season. In my study, it is possible catbird recordings were made once males were already mated, and thus phrase rates were slower as the motivation to attract a mate had passed. Robbins et al. (2009) reported unmated male cerulean warblers (*Dendroica cerulea*) had twice the average song rate compared to mated conspecifics. For these reasons, caution should be taken when comparing my results with the findings of Dolby and colleagues. Future studies should include Julian date and/or a variable that represents pairing status and breeding stage as a potential confounding variables for song phrase rate.

An understanding of how aspects of urbanization affect reproductive success in a migratory songbird is critical as human populations and cities continue to grow. My prediction that nesting success will increase with increasing amounts of impervious surfaces and reduced amounts of canopy cover was supported: the probability of a nest successfully fledging significantly increased with increases in impervious surface and significantly decreased with increases in percent canopy cover. One possible explanation could be due to changes in predator pressures. Gering and Blair (1999) tested predation on artificial bird nests and found that predation rates decreased with increasing intensities of urbanization metrics. Similarly, my findings corroborate those found by Ryder and

colleagues (2010) who assessed nesting survival of catbirds and impervious surfaces and canopy cover and found that the greatest predictor of nest fate was canopy cover and that nest survival decreased with increasing amounts of canopy cover. A future study should take measures of more types of landcover such as shrubland and agricultural land classifications to better determine which habitat factors most influence nesting success.

Our knowledge of the connections between noise pollution and nesting success in birds is significantly lacking. My results show nesting success and number of nestlings were both significantly and negatively correlated with ambient noise. These results are especially notable because it is inverse to the relationship between impervious surface and measures of reproductive success, although impervious surface and ambient noise measures used for these analyses were positively correlated ($r = 0.63$). Similar results of decreased nesting success in areas with higher noise levels have been reported for two cavity nesters, great tits and eastern bluebirds (*Sialia sialia*) (Halfwerk et al., 2011; Kight et al., 2012). However, these studies did not parse out the effects of other environmental factors that could be influencing reproductive success. Bernaith-Plaisted and Koper (2016) assessed nesting of grassland birds near active and inactive oil and gas wells and reported the presence of physical structures, rather than noise or human activity, was negatively correlated with nesting success. In contrast, a similar study that used gas wells to isolate noise as the predictor variable (whether compressors were on or off) reported nests were more likely to fledge in noisy habitats which they attributed to a decrease in the presence of a major nest predator, the western scrub-jay (*Aphelocoma californica*) (Francis et al., 2009). Perhaps an explanation for my results could be driven in part by one site, Wheaton Regional Park, which had the largest sample size ($n = 49$ of 193), low

impervious surface cover (19.1% at 1000m buffer), high noise level ($LA_{90} = 47.5$ dB), and the lowest rate of nesting success (38.8%) across the nine sites (Appendix, Table S1). It is clear that more research is still needed to understand the relationships between noise, urban development, predator-prey dynamics, and nesting success.

Since my study does not assess post fledging success, the results should be interpreted only through the nesting stage for urban planners and conservationists as they may not reflect total reproductive success. For example, a study on catbird reproductive success in suburban areas deemed two of three sites as ecological traps which they attributed mainly to low fledgling survival, 47% of which was attributed to predation by domestic cats (Balogh et al., 2011). Additionally, a study conducted at a park reserve in Oregon found that spotted towhees preferred nesting nearer residential edges. While distance to edge did not have an effect on whether the nest fledged or failed, nests closer to residential edges had significantly lower rates of fledgling survival than those nesting farther away (Shipley et al., 2013). Furthermore, although this study does convey more of the story than just a species presence or nesting density survey, a full understanding of how varying levels of development are affecting species reproductive success is critical for sound land use planning. Future research should use camera trap arrays and conduct aerial predator surveys at study sites to determine differences in predator pressures that may be affecting fitness across the urban gradient.

In summary, my study contributes more evidence that male birds sing higher frequency song in urban environments likely to avoid signal masking, suggesting that singing higher is adaptive. Specifically, male catbirds sing significantly higher peak frequency in louder areas and significantly higher maximum frequencies in areas with

higher impervious surface, both of which may aid in signal transmission. In addition, I found that males in urban areas that sing higher minimum and maximum frequencies have more reproductive success, but suburban and rural males that sing lower have more reproductive success. Growing empirical evidence suggests noise pollution as the main driver for such changes. I also found nests were significantly more likely to fail in areas of higher noise which was inverse to the relationship found for another urbanization metric, impervious surface. Future studies should focus specifically on the effects of noise pollution on reproductive success in songbirds perhaps by selecting study sites with similar impervious surface and canopy cover measures, but differing noise levels. My research suggests urbanization may lead to evolutionary changes in different populations of gray catbirds and adds to the growing testimony that anthropogenic noise impacts wildlife.

Appendix

Table S1. Summary of site urbanization metrics and nesting success. Nesting success is the number of nests that successfully fledged divided by total number of nests at a given site.

site	Impervious surface (%)		Canopy cover (%)		Noise (dB)		Nesting success	Urbanization PC1	Habitat
	500m buffer	1000m buffer	500m buffer	1000m buffer	avg LAeq	avg LA90			
CRU	2.12	5.55	21.67	17.70	42.28	33.44	0.72	-2.892	Rural
BEL	2.26	3.38	13.84	13.00	44.12	36.58	0.57	-2.548	Rural
WHE	8.69	19.07	84.94	73.36	50.63	47.46	0.39	-0.339	Rural
OPA	36.95	30.95	66.92	71.56	46.70	43.18	0.44	-0.313	Suburb
WES	46.64	49.97	17.63	17.70	47.84	42.04	0.77	0.032	Suburb
JMU	34.85	49.07	35.14	21.58	51.65	45.12	0.57	0.442	Suburb
DUM	39.64	53.97	57.64	41.88	50.05	45.62	0.40	0.624	Urban
SIZ	44.14	59.16	59.97	42.99	57.47	51.78	0.52	1.999	Urban
SMI	75.15	79.54	14.50	10.72	57.76	53.76	0.67	2.995	Urban

Table S2. Sample sizes per site for all banded males used to create summary statistics, determine outliers, and replace missing data (n = 304).

Plot	n
1 BELLSLNVA1	20
2 CRUSHRUVA1	41
3 DUMBOPKDC1	18
4 HOGPENRVA1	7
5 HQUARRYVA1	8
6 JMUARBOVA1	40
7 OPALDPKMD1	27
8 SIZOOPKDC1	37
9 SMITHCATDC1	31
10 WESTOPKVA1	10
11 WHEATPKMD1	65

Table S3. Summary statistics of male morphometrics from all banded males (n = 304).

Mass	Wing	Tail
Min. : 30.50	Min. : 82.00	Min. : 81.00
1st Qu.: 34.00	1st Qu.: 88.00	1st Qu.: 91.00
Median : 35.15	Median : 89.33	Median : 94.00
Mean : 35.31	Mean : 89.42	Mean : 93.65
3rd Qu.: 36.50	3rd Qu.: 91.00	3rd Qu.: 96.00
Max. : 42.30	Max. : 95.00	Max. : 103.00
NA's : 11	NA's : 3	NA's : 6
Bill Depth	Bill Width	Bill Length: culmen
Min. : 4.190	Min. : 3.730	Min. : 15.1
1st Qu.: 5.010	1st Qu.: 4.430	1st Qu.: 17.0
Median : 5.170	Median : 5.125	Median : 17.5
Mean : 5.182	Mean : 5.017	Mean : 17.5
3rd Qu.: 5.340	3rd Qu.: 5.555	3rd Qu.: 18.1
Max. : 6.040	Max. : 6.460	Max. : 19.7
NA's : 17	NA's : 17	NA's : 20
Bill Length: nares	Tarsus	
Min. : 10.02	Min. : 19.52	
1st Qu.: 11.44	1st Qu.: 27.11	
Median : 11.78	Median : 27.67	
Mean : 11.78	Mean : 27.66	
3rd Qu.: 12.10	3rd Qu.: 28.25	
Max. : 13.40	Max. : 30.14	
NA's : 17	NA's : 17	

Table S4. Simple linear regression results with noise (LA90) as the predictor variable and the indicated song feature as the response variable (n = 73 males). Significant p values indicated in bold.

Variable	F	R ²	Estimate ($\beta \pm \text{SE}$)	P value
Min freq	4.535	0.0600	3.175 \pm 1.491	0.037
Peak freq	12.25	0.1471	15.28 \pm 4.367	< 0.001
Max freq	7.864	0.0997	23.25 \pm 8.290	0.006
Bandwidth	5.824	0.0758	20.07 \pm 8.318	0.018
Phrase rate	4.662	0.0616	0.002 \pm 0.001	0.034

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