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Determining the impacts of urbanization on song structure and its function in territorial defense
for gray catbirds (*Dumetella carolinensis*)

Morgan L. Rhodes

A thesis submitted to the Graduate Faculty of

JAMES MADISON UNIVERSITY

In

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Dedication Page

I would like to dedicate this thesis to my friends and family, who helped me throughout this entire process.

Acknowledgements

I would like to acknowledge all of the people who put in time and effort to the gray catbird project – I would not be where I am without the work and support of the Moseley Lab team and my advisor, Dr. Dana Moseley. I would also like to thank both Jacob Peters and Julia Portmann for their edits and suggestions to this document and the input of my committee members, Dr. Heather Griscom, Dr. Rocky Parker, and Dr. Brandt Ryder.

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Chapter 1: Determining the effects of urbanization on song spectral parameters of a vocal mimic, the gray catbird (*Dumetella carolinensis*)

Abstract

In urbanized habitats, animals are faced with novel selection pressures such as differences in community structure and increased urban noise. Urban noise pollution can negatively impact songbirds as low-frequency noise often masks portions of birds' mating signal and reduces signal transmission. Previous research has demonstrated that songs of birds in more urban habitats have structural differences that enhance signal transmission when noise is present. These studies have focused on species that deliver short, stereotyped songs with limited repertoires. Gray catbirds (*Dumetella carolinensis*, family: Mimidae) sing long bouts containing imitated, improvised, and invented song elements, and therefore may have an increased ability to vary songs in response to noise. I hypothesize that urbanization impacts catbirds' song structural parameters, such as entropy, duration, and frequency. I recorded male catbird songs at sites along an urban gradient in Virginia and the Washington, D.C. metro region and quantified the degree of urbanization at each site. Song features such as minimum, maximum, and peak frequency increased significantly as noise levels increased, demonstrating that catbirds in more urban areas sing higher frequency songs likely in response to anthropogenic noise. These structural differences limit the negative effects of noise masking for catbirds, even for their long song bouts, and suggest that vocal mimics are responding to anthropogenic noise. Future studies should investigate repertoire size and composition along an urban gradient and if these features correspond with community composition.

Introduction

In an increasingly urbanized world, animals are faced with novel selection pressures such as anthropogenic light and noise, increased predation pressure, altered community structures, and highly modified habitats (reviewed by Slabbekoorn and Ripmeester, 2008; Swaddle et al., 2015). Specifically, urban noise pollution is an obstacle for animals that communicate acoustically, as it is high amplitude and can overlap with the frequencies at which they signal (reviewed by Barber et al., 2010). For example, reduced signal transmission affects organisms' ability to attract mates and defend territories: two crucial functions in animal communication. Many previous studies have investigated how anthropogenic noise affects communication in various vertebrate groups (e.g., Grenat et al., 2019, amphibians; Buckstaff, 2004, Melcón et al., 2012, Blair et al., 2016, cetaceans; Halfwerk and Slabbekoorn, 2009; Nemeth and Brumm, 2009, birds). A study by Buckstaff (2004) showed Bottlenose dolphins (*Tursiops truncatus*) increase whistle production as sea vessels approach, which potentially increases the number of signals and thus would improve signal transmission. Additionally, blue whales (*Balaenoptera musculus*) have been shown to decrease calling rates in the presence of mid-frequency active sonar and increase calling in relation to ship noise (Melcón et al., 2012). However, anthropogenic noise is not limited to aquatic systems. When exposed to traffic noise, the American ground frog (*Odontophrynus americanus*) increases the dominant frequency of its calls (Grenat et al., 2019). Similarly, the Asian particolored bat (*Vespertilio sinensis*) significantly decreases call complexity and increases call amplitude in response to simulated traffic noise, increasing signal transmission (Jiang et al., 2019). Additionally, anthropogenic noise is associated with altered song characteristics of multiple bird species (e.g., Nemeth and Brumm, 2009).

Birdsong as a Signal

Acoustic communication is essential for the vast majority of bird species. Birdsong is a sexually selected mode of communication used for mate attraction and territory defense that is learned either in early development or acquired throughout an individual's lifetime for oscine songbirds (Catchpole, 1980; Marler, 2004). Some receiver behaviors modified by a vocal signal include aggressive response to a rival male song, the attraction of a potential mate to a territory, or flock mates becoming alerted to a potential predator (reviewed by Catchpole and Slater, 2008). Masking by low-frequency noise interferes with the transmission of these signals and has been demonstrated to hinder avian alarm responses (Antze and Koper, 2018).

In general, vocalizations are constrained by any background noise, which limits the ability of signals to be received (Wiley, 1991). Background noise may consist of natural sources, like wind and streams, or anthropogenic sounds, like traffic and construction. Maximizing the signal-to-noise ratio (SNR) results in a detectable signal, meaning that the ratio of the vocalization to the background noise must allow the receiver to hear it (Wiley, 1991). There is evidence that species have evolved signals to optimize habitat-specific SNR, as different habitats possess different acoustic qualities (reviewed by Brumm and Slabbekoorn, 2005; Patricelli and Blickley, 2006). This adaptability allows organisms to communicate effectively in their respective surroundings.

Behavioral Adaptations to Anthropogenic Noise Masking

Features of urban environments such as impervious surfaces and anthropogenic noise specifically mask avian vocal signals and limit signal transmission. One way in which impervious surfaces alter signals is through reverberation, changing song features. Loud, low frequency anthropogenic noise masks the lower frequencies of birdsong and generally lowers the

SNR. In the last two decades, numerous studies have found a variety of differences in the way birds sing in noisy habitats compared to quieter habitats. Strategies that have been investigated include raising of minimum song frequency, singing with increased amplitude, and singing with more energy concentrated in a narrower bandwidth – all of which increase signal detectability. A study conducted by Slabbekoorn and Peet (2003) investigated how urban birds behave differently than their rural counterparts and first found evidence of differences in bird song with increased anthropogenic noise in birds. They found a correlation between noise level and birds singing with higher minimum frequencies in great tits. Raising minimum song frequency avoids low frequency noise, resulting in a more effective signal. A subsequent study conducted by Nemeth and Brumm (2009) further expanded the study of this phenomenon, investigating additional bird species and potential behavioral mechanisms resulting in song modification. Nemeth and Brumm (2009) found that blackbirds (*Turdus merula*) in cities sing with higher minimum frequencies and with shorter intervals between bouts than forest blackbirds. They proposed that these song differences may be an adaptation to urban noise, or alternatively, that this song divergence may be a side-effect of physiological adaptation to urban habitats (Nemeth and Brumm, 2009). Other previous studies have found that when broadcasting increased noise that overlaps the frequency of song, birds increase the amplitude (loudness) of their song which increases signal detection (e.g. Cynx et al., 1998; Brumm and Todt, 2002). Nightingales, however, do not maximize song amplitude but regulate vocal intensity depending on the level of masking noise (Brumm and Todt, 2002). To avoid noise masking, some species narrow the frequency bandwidth of their song, which further increases signal transmission by concentrating energy in a narrower frequency (Gentry et al., 2017). These vocal responses increase the detectability of a signal in noisy environments, allowing birds to communicate effectively.

Various mechanisms may be responsible for differences in song structure among populations such as genetic evolution, cultural evolution (Moseley et al., 2018; Moseley et al., 2019), or immediate flexibility whereby an individual can immediately alter its song in the presence of noise (e.g., Gentry et al., 2017). This behavioral plasticity is an important factor influencing which species persist in urban environments (e.g. ability to alter singing) (Slabbekoorn, 2013). Some species, such as house finches (*Haemorrhous mexicanus*), exhibit immediate signaling flexibility by immediately raising their minimum song frequency in response to noise playback (Bermúdez-Cuamatzin et al., 2011). Immediate shifting of minimum frequency reduces noise masking and promotes effective signal transmission in urban areas. Halfwerk and Slabbekoorn (2009) performed a playback experiment with great tits (*Parus major*) which resulted in birds switching to higher frequency song types when subjected to low-frequency noise. This is evidence of a short-term behavioral mechanism that may explain noise-dependent frequency use in birdsong (Halfwerk and Slabbekoorn, 2009). Additionally, white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) decrease frequency bandwidth when exposed to added noise, but shift regardless of the frequency of the experimental noise broadcast (low, high, and white) – a narrower frequency bandwidth which improves signal transmission (Gentry et al., 2017). Juvenile white-crowned sparrows that were reared with tutor songs masked by noise also selectively learn higher frequency song types more often than lower frequency song types (Moseley et al., 2018), providing evidence for an ontogenetic mechanism separate from immediate flexibility.

Minimum frequency shifting is not limited to passerines; some non-songbirds (suboscines) also raise the minimum frequency of their vocalizations and similarly avoid masking effects of low frequency noise (Hu and Cardoso, 2010). However, some species of

oscines and suboscines cannot shift song frequency immediately in response to noise (Hu and Cardoso, 2010). Such bird species unable to modify their song to avoid the masking effects of anthropogenic noise will not be able to effectively transmit information in an urban environment. An inability to transmit signals impacts how effectively individuals can attract mates and defend territories (Francis and Barber, 2013).

Alternatively, if masking effects are too great, birds may avoid an area (McClure et al., 2013; Ware et al., 2015). An experiment testing the effect of noise masking on bird presence played 2–10 kilohertz (kHz) pink noise, and this resulted in reduced bird presence, likely because it masked the entire bandwidth of their song (Swaddle et al., 2016). Species that do not exhibit behavioral plasticity may struggle to effectively communicate if unable to adapt. As a result, urbanization shapes the distribution of different species based on their ability to persist in human-dominated areas, creating a trait-based filter (Hagen et al. 2017). Species that can adapt or possess behavioral plasticity can persist in urban environments (Blair, 1996), but some still face increased mortality and stress (McClure et al., 2013). In addition, some species have higher population densities and success in urban areas than others due to their ability or inability to adapt (Blair, 1996).

Current Study

While the impact of urban noise is well documented for bird species with limited repertoire sizes, there is an incomplete understanding of how anthropogenic activities affect the repertoire and song features of more complex song, like that of vocal mimics. Here, I study the gray catbird (*Dumetella carolinensis*), as this species is found along rural-to-urban gradients and produces complex, mimicked song. They are common summer residents of areas in the urban/suburban-matrix, although suburban habitat suitability is highly variable (Balogh et al.,

2011) and, daily nest survival tends to increase with increasing prevalence of impervious surface (Ryder et al., 2010). However, catbird populations are declining, and the species is listed in the state of VA as a Tier IV Species of Greatest Conservation Need (VDGIF, 2020). Through studying how urbanization affects multiple aspects of gray catbird ecology and behavior, we may apply our findings to other related species and understand how a vocal mimic is impacted by urbanization and persists in multiple different habitat types and future conservation efforts.

A previous study by Dowling et al. (2011) found that gray catbird song bandwidth and maximum frequency decreased with increased urbanization, and minimum frequency increased with higher noise levels. This decrease in maximum frequency could be a response to the urban structural environment, making the song more tonal and better able to transmit without reverberation, while the increase in minimum frequency may avoid low-frequency masking noise (Dowling et al., 2011). However, this study analyzed few song structural features and had a sample size of eight individual catbirds, as it focused more on trends seen in several bird species. Lowering maximum frequency and the narrowing frequency bandwidth may increase signal transmission but may trade-off with attracting mates if singing broad frequency bandwidths is preferred by females (e.g., Halfwerk et al., 2011).

I hypothesized that catbird song features are impacted by varying degrees of urbanization. Specifically, I predict that song characteristics such as minimum frequency, maximum frequency, duration, and frequency bandwidth will differ between urban and rural males. While Dowling et al. (2011) showed that a limited number of song features differ between more urban and more rural habitats in gray catbirds, I aim to expand upon their findings through analyzing more song features, using an expanded urban-to-rural gradient, and sampling a larger number of individuals' song. I analyzed song features using both categorical site classifications

(urban, suburban, and rural) and continuous site classifications using geographical and noise data. There may also be within-population individual variation that differs from population-level trends in song frequency. Finally, determining how increased urbanization affects avian communication, especially mating signals, is essential to understand how to conserve vulnerable songbird species that persist in urban habitats.

Methods

Sites

From early May to early August, two field teams sampled at sites in the Shenandoah River Valley (2018-2019) and in Washington D.C. (2017-2019). I chose sites along an urban gradient, ranging from highly urban to highly rural. Sites in the Shenandoah River Valley region included the James Madison University Arboretum (38.428997, -78.862944), Westover Park (38.449385, -78.882563), Slate Lick Branch (38.6051173, -78.9539786), and a privately owned farm, Crusher Run (38.337585, -78.8298893). Field sites in Washington D.C. included the Smithsonian National Zoo (38.929569, -77.049807), along the National Mall at the Smithsonian Castle Haupt Gardens and National Museum of Natural History (38.889879, -77.022859), Dumbarton Oaks Park (38.913225, -77.060658), Opal Daniels Park (38.981641, -77.004761), and Brookside Gardens at Wheaton Regional Park (39.059710, -77.039204). See table 1 for corresponding site codes.

Table 1. Study site state, code, and brief site description.

Site	State	Code	Description
JMU Arboretum	VA	JMUARB	James Madison University Arboretum
Westover Park	VA	WESTOV	Small suburban park
Hogpen Road	VA	HOGPEN	National forest campground
Crusher Run Farm	DC	CRUSHR	Privately-owned farmland
Opal Daniels Park	DC	OPALD	Small suburban park
Dumbarton Oaks Park	DC	DUMBO	Larger suburban park
Smithsonian Castle	DC	SMITHCAT	National mall and Haupt gardens
Smithsonian National Zoo	DC	SIZOO	National zoo in D.C.
Wheaton Regional Park	DC	WHEAT	Large, more heavily forested park

Quantification of Urban and Rural Sites

I obtained land cover raster data (30 m resolution), including percent developed imperviousness, percent tree canopy, and categorical land cover from the Multi-Resolution Land Characteristics Consortium (Homer et al., 2020). To ensure that proportional land cover metrics were comparable across sites that may contain open water, we used the categorical land cover layer to set the values of open water pixels to NA. For each site, we determined the site centroid as the median location of all catbird nesting location records. We then calculated the proportion of impervious surface and canopy cover (30 m resolution, Homer et al., 2020) within buffer distances of 100, 500, 1000, and 2000 m of the site centroids. These buffer distances are expected to represent biologically relevant scales for gray catbirds, as previous research has shown that they are predictive of catbird abundance (100 m, Evans et al., 2018), adult survival (500 m, Evans et al., 2015), nest success (1000 m, Ryder et al., 2010), and broad regional variation (2000 m).

In order to quantify the level of urbanization, I used these parameters, percent impervious surface, and percent canopy cover at the four distances, as well as noise level. I then ran two principal component analyses either including or not including noise level, and generated output loadings of PC1 for each site from VA to DC. I did not include noise level in one PCA to determine just how physical features of the sites categorized them along an urban gradient. Using the PC1 loadings, I scored sites along a rural-to-urban gradient to determine degree and category (urban, suburban, or rural) of urbanization. Previous studies have quantified urbanization using just impervious surface measurements (e.g., Evans et al., 2015; Evans et al., 2018), but I chose to incorporate additional parameters to determine how multiple environmental variables would describe a range of urbanization. Based on these PC scores, Smithsonian Castle and NMNH, Smithsonian Zoo, and Westover Park VA were ranked as urban; Opal Daniels Park MD, Dumbarton Oaks Park DC, and JMU Arboretum were ranked as suburban; while Wheaton Regional Park MD, Crusher Run Farm VA, and Hogpen Road VA in the National Forest were ranked as rural (Figure 1).

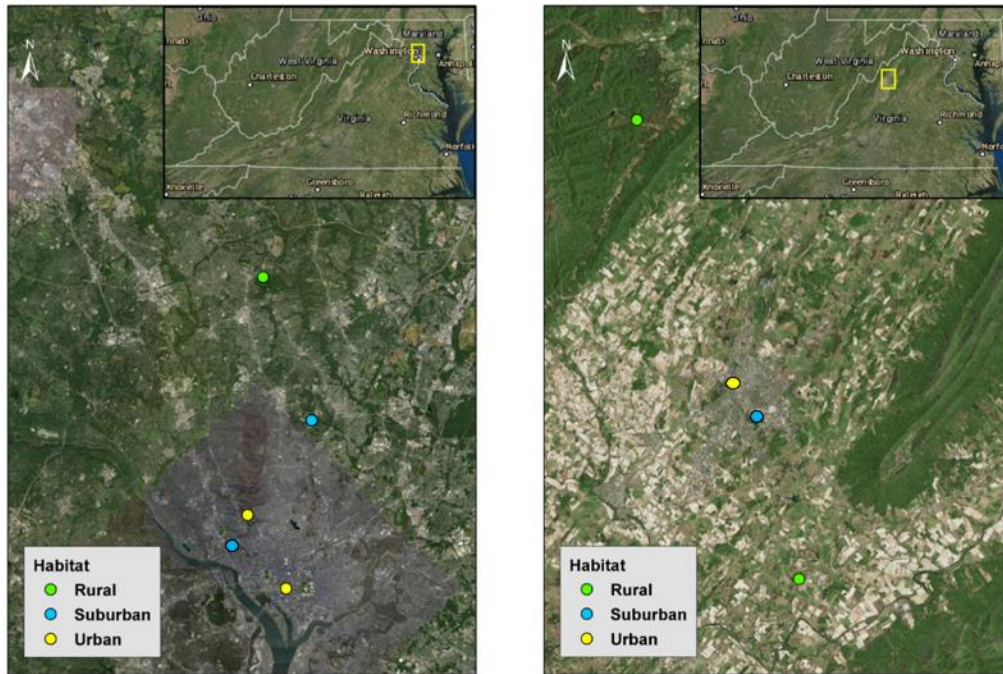


Figure 1. Site maps of Washington D.C. field sites (left) and Virginia field sites (right). Sites are marked by colored circles designating habitat type (green = rural, blue = suburban, and yellow = urban).

Banding

I captured catbirds using active and passive mist-netting and then banded birds with a unique color combination and a USGS band in order to allow for later identification. For adults I measured tarsus, wing, tail, and beak lengths (mm) in addition to body mass (g), but for nestlings I only measured mass. After measurements were taken, I then released the birds. Two observers took all measurements in VA (DLM and MLR), and four observers took measurements in DC (DLM, TBR, GD, DA). Two observers, DLM and TBR, compared measurements with field trainees to minimize variation and error. The same methods were used across all sampling years. To date, 352 birds have been banded across DC and VA sites in 2018 and 2019. The IACUC of James Madison University and IACUC at NZP approved all procedures involving the use of live vertebrates.

Song Collection

I visited each of the field sites in the Shenandoah Valley area 1-3 times per week and used both targeted recordings of focal males and ambient sampling to record catbird song. I used microphones (Sennheiser ME 66) and digital recorders (Marantz Professional PMD561 handheld solid-state recorder) for targeted sampling and song meters (Wildlife Acoustics SM4 song meter) for ambient sampling. I identified males by color band if possible; otherwise, unbanded territory-holding males were given a name based on site name (e.g. J1). In addition, I used a sound pressure level meter (SPLM) to take accurate noise measurements in each of our sites (Galaxy Audio CM-170 IEC 61672-1 Type II SPL). The D.C. field team used the same equipment models in Washington, D.C.

Song Processing

I measured multiple song parameters using sound analysis software (Raven v1.5, The Cornell Lab of Ornithology) including minimum and maximum frequency (Hz), average entropy (bits), bandwidth 90% (Hz), and duration 90% (s) (Table 2). View axes were configured to have a time scale of approximately 22 seconds and a frequency scale of 15600 Hz. Bouts were selected in each song file, and individual elements of song in 3 – 5 clear bouts were also selected per individual file (Figure 2). For a subset of males for which I had blood samples, nest data, and song recordings, I selected all elements in all recordings. I defined an element as a distinct song unit that could be separated from others temporally, while bouts were defined by 1-2 second pauses between utterances and a minimum of three elements.

Table 2. Measurements taken in Raven sound analysis software with definitions. Definitions taken from Raven Pro Manual.

Sound Parameter	Definition	Unit
Minimum Frequency	The lowest frequency of sound being measured.	Hz
Maximum Frequency	The highest frequency of sound being measured.	Hz
Average Entropy	The amount of disorder for a typical spectrum within the selection.	Bits
Bandwidth 90%	The difference between the 5% and 95% frequencies.	Hz
Duration 90%	The difference between the 5% and 95% times.	S

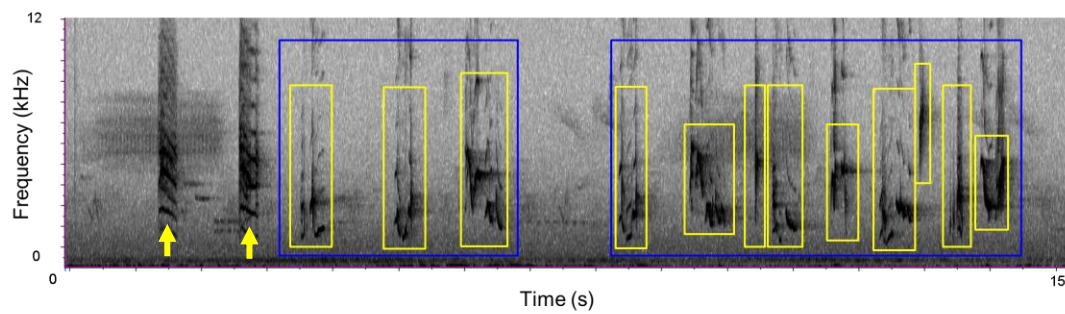


Figure 2. Example spectrogram of male gray catbird song with boxes drawn around bouts (blue) and elements (yellow). The catbird song is preceded by two meow calls (arrows) which are unique to the species.

Table 3. Sample sizes of male catbirds by site, two habitats (rural and urban), and three habitats (rural, suburban, and urban), as well as the total number of files, bouts, and elements processed.

Site	n(males)	habitat2	n(males)	habitat3	n(males)	n Files	Bouts	Elements
JMU Arboretum	8	urban	25	urban	12	106	859	16145
Westover Park	3	rural	17	suburban	16			
Hogpen Road	5			rural	14			
Crusher Run Farm	4							
Opal Daniels Park	3							
Dumbarton Oaks Park	5							
Smithsonian Castle	6							
Smithsonian Zoo	3							
Wheaton Park	5							
Total	42							

Study Design

I used recorded songs from Washington, D.C., and VA sites to quantify differences using sound analysis software. Through selection of catbird song in Raven sound analysis software I calculated peak frequency contour (PFC) minimum frequency of rural and urban song (Cornell Lab of Ornithology), which then measures the lowest frequency sound with a certain power. Interference from low-frequency noise rendered these measurements for bouts unreliable, so I used the peak frequency (Hz) of the five lowest frequency elements per bout of song in addition to using the PFC minimum frequency for elements. I averaged the selected elements per male and per site to obtain accurate minimum song frequency measurements.

Statistical Analysis

I used R v1.2 to run statistical analysis on collected data, including the song variables mentioned previously. I averaged each song feature by individual male and then analyzed by habitat type: either urban and rural (habitat 2) or urban, suburban, and rural (habitat 3). I used a t-test to test for differences between rural and urban song because minimum frequency was

normally distributed, and an ANOVA was used when analyzing across the three habitat types. Using outputs from the site urbanization PCA, regression was run to test for trends in degree of urbanization and song features. In addition to frequency measurements, I analyzed entropy, bandwidth, and duration of songs.

Results

Site Classification

Sites were classified based on percent impervious surface, canopy cover, and ambient noise level using principal component analysis (PCA). Several combinations of both the geographic raster data (impervious surface and canopy cover buffers) and ambient noise level (maximum, median, and average) were added to determine the best predictor of site urbanization level (Table 4; Table 5).

I found that urban sites have high impervious surface, low canopy cover, and high anthropogenic noise levels, while rural sites have the opposite: low impervious surface, high canopy cover, and low anthropogenic noise levels. Based upon these variables, there are unique groupings of sites along an urban gradient. While some sites (such as Dumbarton Oaks) would switch ranks with another site based on the geographic raster data and noise variables used in PCA the most urban and most rural sites stayed uniform. In all combinations the National Mall was the most urban site followed by Westover Park, due to high noise levels and lack of canopy cover. The only exception to this order is when just noise level was considered, which then placed Westover Park as less urban. The most rural site was consistently Slate Lick Branch in Virginia, a national forest site (Table 6, Figure 3). Ambient noise readings taken in multiple locations at each site were an accurate predictor of the degree of urbanization of a site (Figure 3).

Through examining the output principal component one (PC1 values) for the geographic raster data and noise measurements, sites were categorized as rural, suburban, and urban. Rural sites had PC1 geographic raster data values that ranged from -4.805 to -0.971, suburban sites ranged from -0.504 to 0.563, and urban sites ranged from 1.114 to 3.831 (Table 7). Sites were categorized based on natural breaks in PC1 values.

Song Structural Features

A total of 69 banded males were recorded across 2017-2019, as well as several unbanded males. I used 42 males, both banded and unbanded, with several quality recordings for analysis (Table 3). Recordings were ranked based on background noise, amount of song, and quality of song. Upon analyzing mean minimum frequency across three habitat types (urban, suburban, and rural), mean urban minimum frequency was 2660.91 +/- 209.53 Hz (n = 12), while mean rural minimum frequency was 2476.93 +/- 266.08 Hz (n = 14). Suburban minimum frequency was the lowest, at 2432.288 +/- 222.10 Hz (n = 16). Minimum song frequency did not significantly differ between rural and urban habitat types, but suburban sites had a significantly lower song frequency than urban sites ($F = 3.503$, $p = 0.0399$, pairwise suburban-rural = 0.8619, urban-rural = 0.1269, urban-suburban = 0.0382, $df = 2$). Neither PFC maximum frequency nor peak frequency differed between the three habitat types ($p > 0.05$)

I found that both minimum and maximum song frequency increased with increasing noise levels. Using the principal component one (PC1) values for both site geographical raster data and noise measurements, minimum song frequency did not vary significantly ($p > 0.05$, Table 8). Using PC1 values for just noise levels, including maximum, median, and average noise in a linear regression, I found minimum song frequency did vary significantly, with positive values representing noisier sites ($p = 0.016$, Table 8). Maximum frequency showed a similar trend, with

a non-significant relationship with geographical raster data and noise, and a significant relationship with noise levels based on a linear regression ($p = 0.0108$, Table 8).

Like minimum and maximum, peak frequency did not show a significant relationship with both geographical raster data and noise but did with noise level alone as a predictor ($p = 0.0471$, Figure 4). However, frequency bandwidth did not differ based on noise levels or geographical raster data and noise (Table 7). Additionally, song duration did not differ across the urban gradient ($p > 0.05$, Figure 5). Average and aggregate entropy did not differ significantly based on PC1 values of geodata and noise or with PC1 noise values ($p > 0.05$, Table 8).

Finally, I calculated phrase rate using the number of individual song elements per bout duration 90% (phrase rate 90) and per delta time (phrase rate). Neither phrase rate nor phrase rate 90 correlated with noise levels or combined geodata and noise PC1 values ($p > 0.05$, Figure 6).

Table 4. Variables and PC1 loadings used in noise PCA with Eigen Value and variance explained.

Variable Name	Loading
Average Noise	0.5807
Maximum Noise	0.5733
Median Noise	0.578
Eigen Value	2.9467
Variance Explained	98.22%

Table 5. Variables and PC1 loadings used in geographic raster data PCA with Eigen Value and variance explained.

Variable Name	PC1
Impervious surface 100 m	-0.3373
Impervious surface 500 m	-0.3594
Impervious surface 1000 m	-0.3628
Impervious surface 2000 m	-0.3425
Canopy cover 100 m	0.3662
Canopy cover 500 m	0.344
Canopy cover 1000 m	0.3594
Canopy cover 2000 m	0.3556
Eigen Value	6.1612
Percent Variance	77.01%

Table 6. Average, maximum, and median noise levels (dB) at each site.

site	siteID	Average Noise	Maximum Noise	Median Noise
Crusher Run Farm	CRUSHRUVA1	48.74	53.20	49.95
Dumbarton Oaks Park	DUMBOPKDC1	50.38	54.40	51.20
Hogpen Road	HOGPENRVA1	43.35	46.40	44.15
JMU Arboretum	JMUARBOVA1	58.74	66.75	57.70
Opal Daniels Park	OPALDPKMD1	49.73	50.55	49.73
Smithsonian Zoo	SIZOOPKDC1	56.93	66.40	56.55
Smithsonian Castle	SMITHCADC1	59.00	69.50	57.70
Westover Park	WESTOPKVA1	55.78	60.35	56.25
Wheaton Park	WHEATPKMD1	52.54	57.00	53.03

Table 7. PC1 values for geographic raster data (PC1Geo), noise measurements (PC1Noise) and geographic raster data and noise measurements (PC1GeoNoise) across sites. Sites were categorized as either urban or rural (habitat2) and either urban, suburban, or rural (habitat3).

Site	habitat2	habitat3	PC1Noise	PC1GeoNoise	PC1Geo
Smithsonian Castle	urban	urban	2.091551	-4.35385	3.831229
Westover Park	urban	urban	0.897206	-2.43041	2.315517
Smithsonian Zoo	urban	urban	1.495629	-1.75978	1.114381
JMU Arboretum	urban	suburban	1.865696	-1.4902	0.563192
Dumbarton Oaks Park	urban	suburban	-0.76148	0.177074	0.279824
Opal Daniels Park	rural	suburban	-1.29595	1.134721	-0.50392
Crusher Run Farm	rural	rural	-1.18611	1.493265	-0.97113
Wheaton Park	rural	rural	-0.1068	1.573664	-1.82412
Hogpen Road	rural	rural	-2.99975	5.655507	-4.80498

Table 8. Statistical values for regression analysis of all variables. Significance is denoted with an asterisk (n = 42).

Independent	Dependent	Adjusted R ²	F-value	p-value
PC1 Noise	Peak Frequency (Hz)	0.0723	4.195	0.0471*
PC1 Geo Noise	Peak Frequency (Hz)	0.03283	2.222	0.145
PC1 Noise	PFC Minimum Frequency (Hz)	0.1151	6.332	0.016*
PC1 Geo Noise	PFC Minimum Frequency (Hz)	0.0657	3.883	0.0557
PC1 Noise	PFC Maximum Frequency (Hz)	0.1305	7.155	0.0108*
PC1 Geo Noise	PFC Maximum Frequency (Hz)	0.02517	1.93	0.1736
PC1 Noise	Duration 90% (s)	-0.00322	0.8684	0.357
PC1 Geo Noise	Duration 90% (s)	-0.0188	0.2436	0.6243
PC1 Noise	Average Entropy (Bits)	-0.0127	0.5469	0.465
PC1 Geo Noise	Average Entropy (Bits)	0.02703	2	0.166
PC1 Noise	Phrase Rate	0.01544	1.643	0.2073
PC1 Geo Noise	Phrase Rate	0.01104	1.458	0.2344
PC1 Noise	Phrase Rate 90	0.06902	4.04	0.05122
PC1 Geo Noise	Phrase Rate 90	0.05107	3.207	0.05107

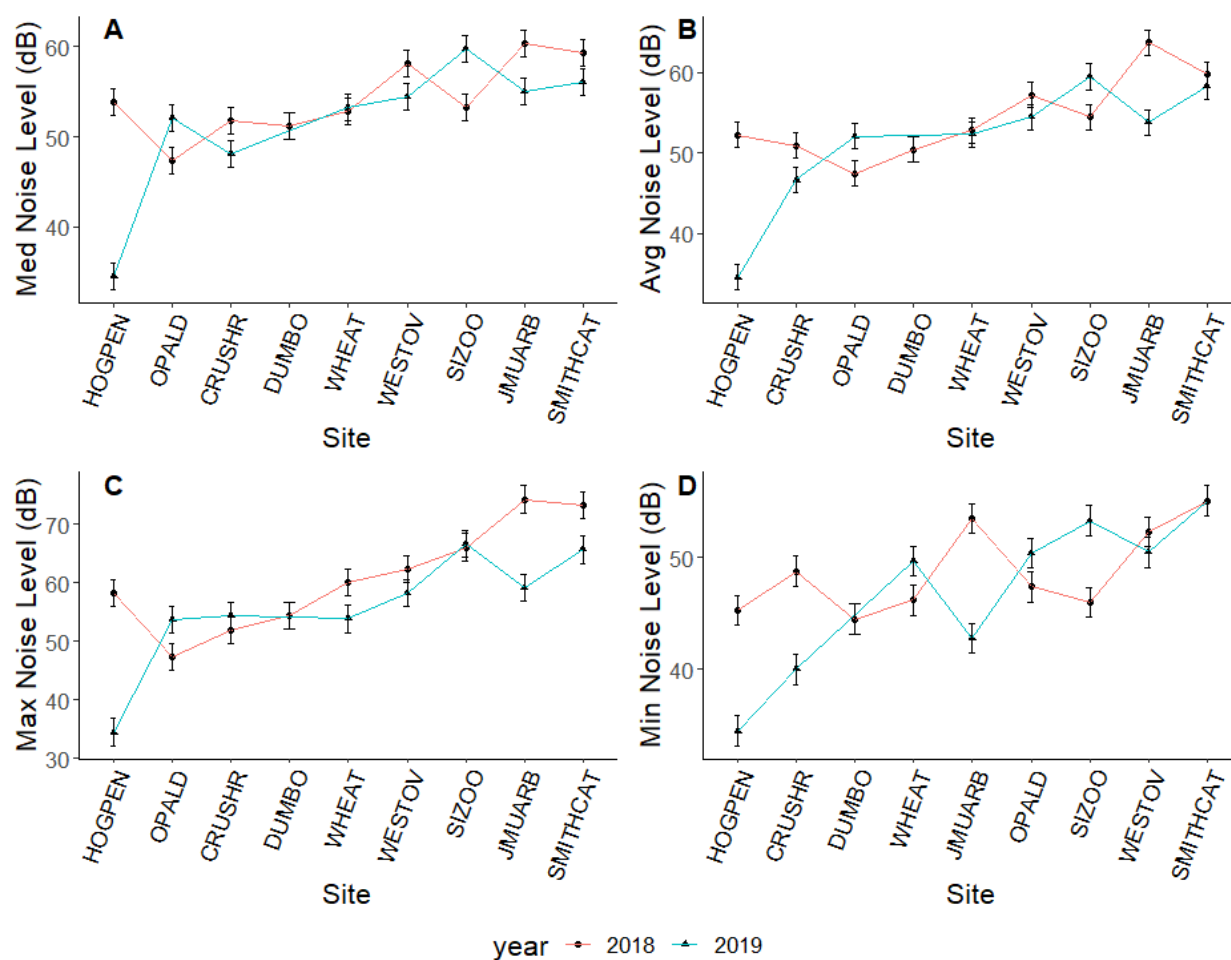


Figure 3. Median (A), Average (B), Maximum (C), and Minimum (D) averaged ambient noise level readings taken at each site across 2018 and 2019. Sites are arranged by average noise level.

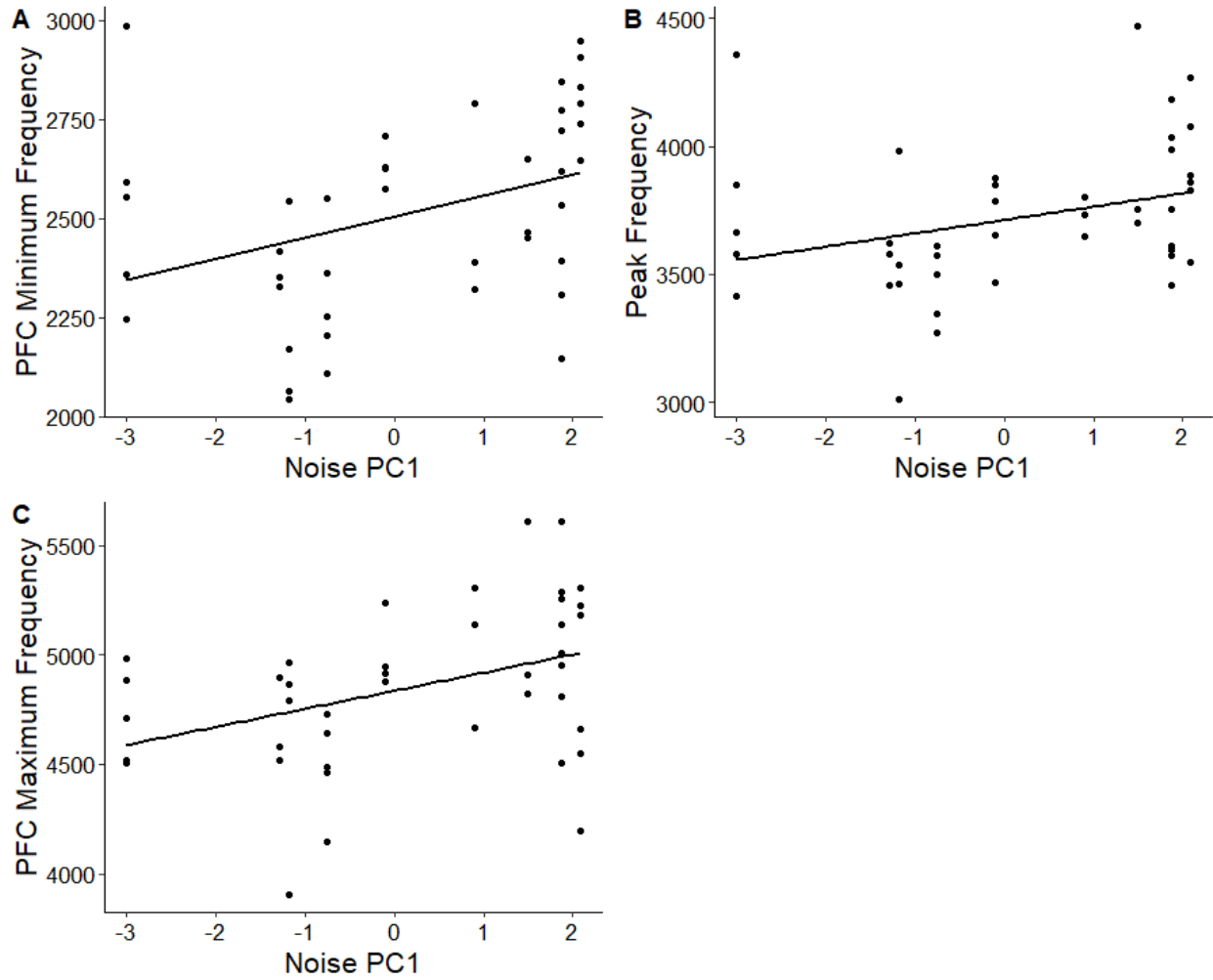


Figure 4. PFC minimum frequency (A, $p = 0.016$), peak frequency (B, $p = 0.0471$), and PFC maximum frequency (C, $p = 0.0108$) with noise PC1 values (maximum, median, and average noise levels). Positive noise PC1 values represent noisier sites. All three measures of song frequency significantly correlated with noise PC1 values, increasing with increasing noise levels.

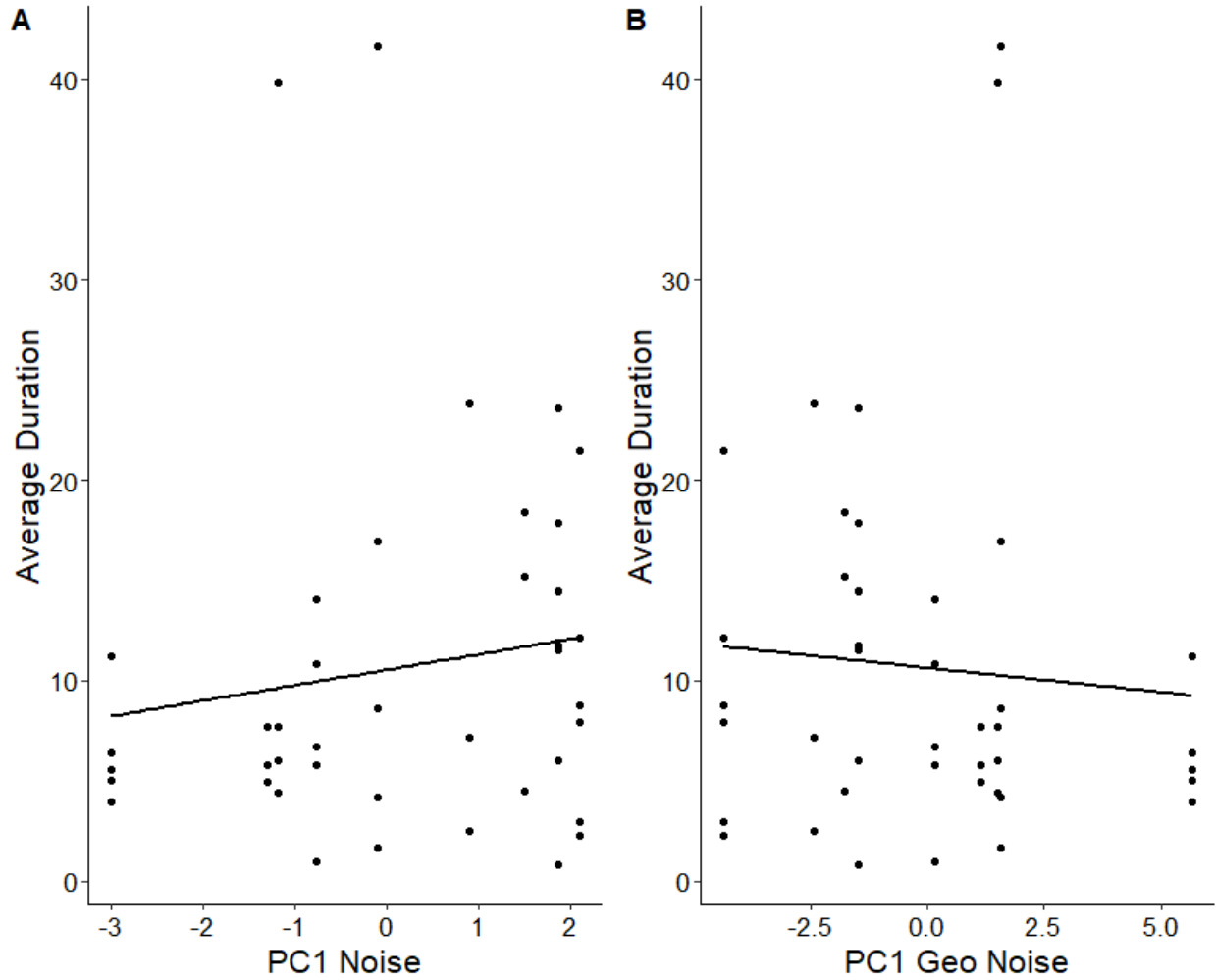


Figure 5. Average bout duration (s) correlated with PC1 noise ($p = 0.357$) and PC1 geographic raster data and noise values ($p = 0.6243$). Positive noise PC1 values represent noisier sites, and negative geographic raster data and noise values represent more urban sites. There was no correlation between either PC1 measurement and average bout duration.

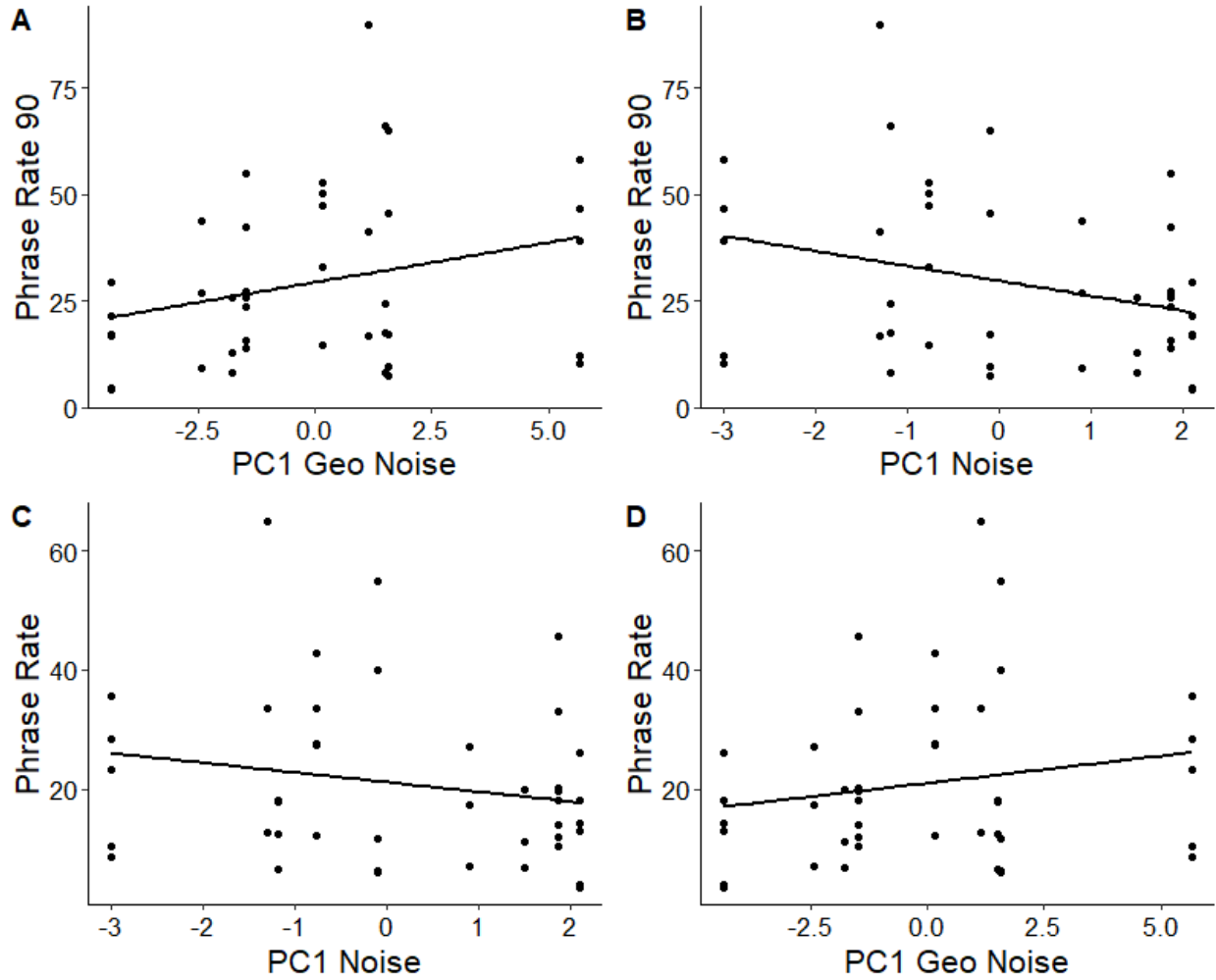


Figure 6. Phrase rate 90 (A and B) and phrase rate (C and D) correlated with both PC1 noise ($p > 0.05$) and PC1 geographic raster data and noise ($p > 0.05$). Positive noise PC1 values represent noisier sites, and negative geographic raster data and noise values represent more urban sites. There was no significant relationship between either PC1 measurement and phase rate measures.

Discussion

Song Structural Features

In line with a multitude of previous studies, I found that urban male catbirds sing at higher minimum frequencies than their rural counterparts (e.g., Dowling et al., 2011; Hu and Cardoso, 2010; Halfwerk and Slabbekoorn, 2009; Nemeth and Brumm, 2009). I hypothesized that urban and rural catbird song would differ structurally and predicted that urban males would have higher minimum song frequencies, lower maximum frequencies, and smaller frequency bandwidths. Compared to the majority of previous studies, I studied a species with a very different singing style that also imitates the sounds of other species. Previously, the question of whether similar structural differences associated with noisy habitats would be found in a bird species that does not deliver short, stereotyped songs was largely unanswered.

These song structural differences are in line with the masking avoiding hypothesis, as they increase signal transmission in the presence of low-frequency anthropogenic noise. Avoidance of low-frequency noise by shifting song minimum frequency may help to limit signal masking and enhance signal transmission (Dowling et al., 2011; Hu and Cardoso, 2010; Bemudez-Cuamatzin et al., 2010; Nemeth and Brumm, 2009). However, it is unclear if urban birds have adapted across generations to possess a higher minimum frequency, or if catbirds are generally able to immediately shift their song frequency in response to low-frequency noise. Moseley et al. (2018) found that nestling white-crowned sparrows tutored with noise learned less-masked songs significantly more often, suggesting that cultural evolution may be a potential mechanism for acoustic adaptation. The possibility of cultural selection may also be the case for gray catbirds, but a similar experiment would have to be conducted.

Additionally, the effect of modified signaling in urban catbirds on their reproductive success is unknown. While shifting song minimum frequency may assist in signal transmission, certain aspects that make song attractive to females may be negatively impacted. For example, lower frequency vocalizations are correlated with larger body size, which may mean that urban males are perceived as smaller and less threatening by rural males and may be less appealing to females. A study conducted by Francis et al. (2011) suggested that masking of lower-frequency signals, which are associated with higher quality males, may result in maladaptive mating decisions made by females.

I found opposite trends in maximum frequency than previous studies, such as Phillips et al. (2020). Phillips et al. found that urban birds sang with lower maximum frequencies and narrower bandwidths than rural birds. These findings support the acoustic adaptation hypothesis (AAH), as songs with narrower bandwidths may transmit better in urban areas. The AAH states that signals are endowed with optimal characteristics for transmission to overcome environmental constraints (Morton, 1975). Dowling et al. (2011) found similar trends in gray catbirds, as urban birds had increased minimum song frequencies, decreased maximum frequencies, and narrower bandwidths. However, only eight males were sampled which may not have been sufficient to fully observe song trends along an urban gradient. With an expanded sample size, I found that gray catbirds in urban environments sang with a higher maximum frequency than rural birds, and that bandwidth between habitats did not differ. Even though urban catbirds have higher minimum song frequencies, it appears that there is compensation through higher maximum frequencies as well, resulting in a similar bandwidth. This compensation may be a result of sexual selection as urban males, with their increased minimum frequency, may be less appealing to females. Through increasing maximum frequency, urban

males are able to maintain a similar bandwidth, which has been shown to be attractive to females in other bird species (e.g., Ballentine et al., 2004).

Urbanization and Conservation

Examining the impacts of urbanization on birds is vital from a conservation perspective, as populations have decreased by 29% since 1970, resulting in a net loss of approximately 3 billion individuals (Rosenberg et al., 2019). Urbanization and its consequences, such as increased traffic noise and large-scale artificial surfaces, influence the vocalizations and behavior of multiple bird species (e.g., Halfwerk and Slabbekoorn, 2009; Nemeth and Brumm, 2009; Bermudez-Cuamatzin et al., 2010; Hu and Cardoso, 2010; Dowling et al., 2012). Determining how increased urbanization affects avian communication, reproductive success, and behavior is essential to future conservation efforts of vulnerable songbird species as well as understanding how humans influence the natural world.

Unlike previous studies on gray catbirds, I also measured song duration and entropy across an urban-to-rural gradient. However, I did not find any significant trends in either variable. A previous study by Slabbekoorn et al. (2007) showed a non-significant trend in song duration, with birds in urban environments more commonly singing for a shorter duration. Impervious surfaces present in urban areas lead to echoes that potentially degrade acoustic signals, which would more severely impact lower frequency songs that are longer in duration (Slabbekoorn et al., 2007). Therefore, urban birds should sing songs shorter in duration to avoid further signal degradation. I found the opposite trend, with song duration increasing slightly in noisier sites. Urban catbirds may be singing for a longer duration so that their signal is more likely to be detected over noise instead of limiting duration to avoid echoes. Although song entropy did not differ along an urban gradient, it should be further investigated. There may be

more fine-scale differences in entropy that I did not detect, or perhaps both urban and rural catbirds just sing with similar levels of entropy.

Further study of gray catbird song and what factors may be impacting structural song differences is warranted. Being vocal mimics, gray catbirds are unique in their ability to copy the sounds of other species, and the interplay of mimicry and urbanization is relatively understudied. Through understanding how urbanization is impacting vocal mimics, particularly migratory ones, may better inform conservation efforts and future city planning. Future directions should include correlating minimum frequency with body size and investigating how this influences male mating success. It is well-established that many bird species in urban environments sing with a higher minimum frequency than rural birds, but the impact on mating success and female choice is less known.

In summary, I found that song structural features do not differ when catbirds are grouped by two (rural and urban) or three (rural, suburban, urban) habitats, but when site urbanization is characterized by geographical data such as impervious surface and canopy cover or by noise levels, song frequency features differ significantly. Noise as a predictor variable seemed to highlight these differences the most, suggesting that variables such as impervious surface and canopy cover may have less of an impact on gray catbird song than background noise.

Chapter 2: Urban and rural gray catbird (*Dumetella carolinensis*) songs elicit different territorial responses

Abstract

The acoustic signals of animals can be partially masked by low-frequency urban noise and subsequently limited in the effectiveness of their transmission and signal function. Birdsong is a sexually selected mode of communication used for mate attraction and territory defense. Previous studies demonstrated that the structure of birdsong in urban and rural habitats differs, for example many species sing higher minimum frequencies in noisy environments which avoids masking by urban noise. However, few studies have tested the territorial response of birds to song from different habitats along an urban gradient, and no study tests impacts of urbanization on the behavior of vocal mimics. I hypothesized that male gray catbirds (*Dumetella carolinensis*), which imitate vocalizations of other species, would respond differentially to song from more urban versus more rural habitats. Specifically, I predicted that males would respond more aggressively to songs from similar habitat types, as they may be more familiar in their structure and composition. Across an urban gradient from western Virginia to Washington D.C., I measured aggressive behavioral responses of 32 males to paired trials of more urban versus more rural song stimuli. Individual male response varied significantly between urban and rural song treatments based on the habitat of the subject males, such that suburban males responded more strongly to more urban stimuli as compared to rural males who tended to respond more strongly to more rural stimuli. Structural differences between urban and rural catbird song exist, and the results of this experiment suggest these differences may affect the degree of aggressive response. These findings provide evidence that songs across an urban gradient may be diverging, as individuals can distinguish between urban and rural song and modify their aggressive responses accordingly to songs that are more familiar in structure or composition.

Introduction

Since 1950, the world has undergone rapid urbanization, and these trends are expected to continue (United Nations, 2018), with wide-reaching implications for wildlife. Increased urbanization results in light and noise pollution, the latter impacting all organisms that communicate acoustically. Low-frequency anthropogenic noise such as traffic and construction often overlap with the frequencies at which various species vocalize (reviewed by Barber et al., 2010), limiting signal transmission. The impact of anthropogenic noise on various vertebrate groups has been widely documented, ranging from cetaceans (e.g., Melcón et al., 2012) to amphibians (e.g., Grenat et al., 2019). Birds, a taxon for which acoustic communication is a key part of their natural history, also experience such signal masking in urban environments.

For some species, the masking effects of anthropogenic noise are associated with song structural differences which allow better signal transmission, thus leading to differences between song among bird populations along an urban-to-rural gradient. Several previous studies have found quantifiable structural differences between urban and rural birdsong (e.g. Slabbekoorn and Peet, 2003; Nemeth and Brumm, 2009; Bermúdez-Cuamatzin, 2011). Moseley et al. (2019) found that over almost 50 years, urban white-crowned sparrows had increased vocal performance, while rural birds did not. These results may be attributed to increased sexual selection pressure, which is driving cultural evolution of song. One study found males in noisier habitats were slower to respond to simulated territorial intrusion by song playback than males in quieter habitats, suggesting that anthropogenic noise may interfere with territorial defense in response to vocal signals (Lenis & Guillermo-Ferreira, 2020).

Not only does urbanization impact vocal signals, but it also changes how organisms behave. Previous studies show that individuals in urban habitats display increased aggression

(e.g., Foltz et al., 2015; Phillips and Derryberry, 2018). Foltz et al. (2015) investigated the relationship between population density, availability of nesting vegetation, and aggression in song sparrows (*Melospiza melodia*). They found no correlation between these variables and territorial aggression, but did find a significant relationship between aggression and food availability through food supplementation experiments. These results suggest that food availability is the main factor influencing aggression levels in urban and rural song sparrows (Foltz et al., 2015). Additionally, a playback experiment conducted by Phillips and Derryberry (2018) on white-crowned sparrows showed that males on noisier territories approached the speaker more closely than males in quieter territories regardless of stimulus type. Approach distance is commonly used to quantify aggression in playback experiments, with closer approaches signifying a higher likelihood of attack (Phillips and Derryberry, 2018; Searcy et al., 2006).

Previous playback experiments have also investigated how male birds respond to conspecific song from different geographic locations. The scale of these experiments ranges from within the same site to completely different geographic areas. For example, Mackin (2005) found that male Audubon's shearwater (*Puffinus l. lherminieri*) responded with calls longer in duration to playbacks of stranger males than those of neighboring males, signifying higher levels of aggression. This response is in line with the "dear enemy" effect, proposed by Fisher (1954) suggesting that territorial songbirds are less aggressive with neighboring males than strange males because they already have established territories and relationships. Over a larger geographic range, Searcy et al. (1997) tested if male and female song sparrows (*Melospiza melodia*) could discriminate between local (Pennsylvania) and foreign (New York) songs. They found that both males and females responded more strongly to local song than foreign song

(Searcy et al., 1997). These results suggest that there are acoustic differences in song between the two populations that enables birds to distinguish between them.

While multiple playback experiments have addressed differences in response to ecologically diverged songs, fewer studies have determined if males in urban or rural environments react differently to urban or rural conspecific song. (e.g., Brambilla et al., 2008; Patten et al., 2004; Ripmeester et al., 2010). Ripmeester et al. (2010) played songs with high and low frequency motifs to urban and forest male European blackbirds (*Turdus merula*) to determine if habitat-related song divergence impacts male response. They used number of strangled songs and number of flights to quantify aggression to the different song stimuli. Urban birds reacted more aggressively to song with high frequency motifs while rural birds were more aggressive towards song with low frequency motifs (Ripmeester et al., 2010). They also found that songs played from the same population as the focal male elicited a more aggressive response than songs recorded at a different site. Differential aggressive reactions to song stimuli characteristic of different populations and habitat types may indicate habitat-related song divergence.

A second study by Phillips and Derryberry (2018) conducted a playback experiment comparing song attributes associated with rural birds (wide frequency bandwidths) to those associated with urban birds (narrow frequency bandwidths) in white-crowned sparrows as many species in urban habitats have higher minimum frequencies and lower maximum frequencies, limiting bandwidth. They found urban birds responded more aggressively to wide-bandwidth songs. Mockford and Marshall (2009) report that great tits (*Parus major*) were faster to sing over playback song, approached the speaker more closely, and spent more time interacting with the playback song if it was from their own habitat type (urban versus rural), suggesting males react

more aggressively to homotypic songs. Results from these three studies warrant further investigation into the question of whether divergence in urban and rural songs impact how song functions in territorial defense and competition, especially for a species that does not sing short stereotyped songs.

To address the question of the effects of urbanization on song function and territoriality for a species with a large and mimicked repertoire, I chose to study gray catbirds (*Dumetella carolinensis*) as they are present along a rural-to-urban gradient and their songs differ with noise level (Dowling et al., 2011; Rhodes unpublished data). Given these structural differences, I designed an experiment to test if urban and rural songs differ in effectiveness in territorial defense across an urban gradient. I quantified aggression using several behaviors previously demonstrated to accurately represent male aggression towards playback (e.g., number of flights, closest approach, and number of songs). I hypothesized that urban, suburban, and rural males would react differently to song stimuli from more urban as compared to more rural environments. I had four main predictions to potentially explain differences in aggressive reaction: (1) Familiarity hypothesis: song stimuli from similar habitat types would elicit more aggressive reactions than stimuli recorded in different habitat types, (2) Novelty hypothesis: song stimuli from dissimilar habitat types would elicit more aggressive reactions, as a more strange male would be considered a higher threat than a familiar male, with which the focal male has an established relationship with (Fisher, 1954), (3) Rural song as higher quality hypothesis: catbird song recorded in more rural habitats would elicit more aggressive reactions from birds in all different habitat types, and (4) Urban aggression hypothesis: males in more urban habitats would generally be more aggressive as a result of increased competition for resources (e.g., Philips and Derryberry, 2018).

Methods

Experimental Protocol

Using the same study sites as my observational study (Chapter 1), I conducted a playback experiment testing the effectiveness of urban and rural catbird song in functions of territoriality through playback of urban and rural catbird song. Song playback is an experimental technique in which natural or synthetic signals are broadcast in the field and the responses of animals are recorded (McGregor, 2000). Each male received a unique pairing of one urban and one rural song stimulus (Figure 7). I followed traditional playback protocol (See Pegan et al., 2015), which involved placing a speaker just within a male's territory and measuring behavioral responses of territorial male gray catbirds to a simulated conspecific intruder's song played from the speaker.

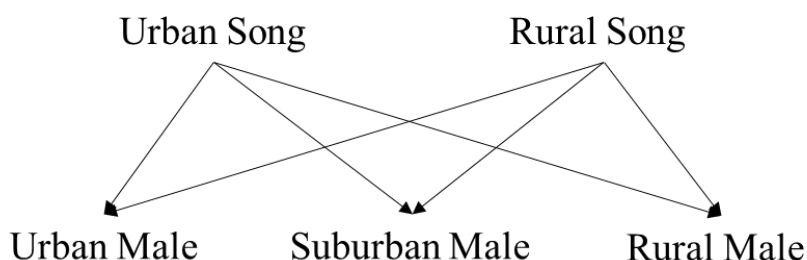


Figure 7. Paired design of urban and rural song playbacks. Urban, suburban, and rural males received a unique combination of one rural and one urban playback in a balanced design.

Creation of Playback Stimuli

I used urban and rural catbird songs recorded from previous years (2017-2019) in Virginia and Washington, D.C. to create playback stimuli for the urban versus rural experiment. I selected stimuli based on results from the observational study. Specifically, I chose representative songs from each habitat type that were within one standard deviation of the mean for a particular song parameter such as duration.

I selected playback bouts using Raven sound analysis software, and then I used SIGNAL 5 software to create playback stimuli. Each rural or urban playback consisted of three different bouts from one male, which were randomly repeated until the desired duration of two minutes was reached. I filtered each bout from 0 to 1900 Hz to remove low frequency background noise and used a low pass filter for filtering frequencies above 8000 Hz to remove any high-frequency noise. I also normalized the amplitude of each bout to control for differences across recordings and saved these as uncompressed WAV files.

Playback of Rural and Urban Song

Experiments were carried out from May 2019 - July 2019 at both D.C. and VA sites (see Chapter 1) during the gray catbird breeding season and conducted in the morning (between 5:30am and 11:00am). A total of 34 males across D.C. and VA sites received successful pairings of rural and urban playbacks (see Table 8), however the dictation files were unclear for two males resulting in a sample size of 64 playback trials to 32 males. Both banded and unbanded males were used for the experiment, but unbanded males were only used if they were singing, which signified potential territoriality. Banded males that were not actively singing were still used because they were deemed territorial from consistent observation. Once I gave a playback to an unbanded male in a certain area, I avoided unbanded males in adjoining territories to prevent resampling. I conducted playback during times in which male catbirds were territorial, either during the period of mate attraction or mate and territory defense from other males and during these phases in between successive clutches of nestlings. I avoided conducting playbacks while males were feeding nestlings and young fledglings and avoided the mid-to-late stages of incubation when males would be less likely to react to a simulated intruder. As demonstrated by Wingfield et al. (1987), male testosterone levels are highest when territories are first being

established and while females are sexually receptive, yielding more aggressive behavior. Timing my playbacks with certain temporal behavioral patterns ensured that males predictably reacted to the song of a simulated intruder. I also avoided playing songs to the neighbors of focal males on the same day, as their motivational state may have been altered by earlier playbacks.

Table 9. Summary table of playbacks performed by site, two habitats (rural or urban), and three habitats (rural, suburban, and urban).

Site	n	habitat2	n	habitat3	n
JMU Arboretum	5	urban	15	urban	14
Westover Park	1	rural	17	suburban	9
Hogpen Road	0			rural	9
Crusher Run Farm	4				
Opal Daniels Park	5				
Dumbarton Oaks Park	0				
Smithsonian Castle	3				
Smithsonian Zoo	6				
Wheaton Park	8				
Total	32				

I placed the speaker just within the boundary of a male's territory to simulate a realistic intrusion from another male. Playbacks included two minutes of pre-playback silence for recording/habituation, two minutes of playback, and three minutes of post-playback silence for observation, with observers positioned at least 10 m away from speaker to prevent interference. I presented both urban and rural stimuli on the same day to each focal male in a balanced experimental design. I used a cool-off period of a minimum of 30-minutes between playbacks to the same male. This inter-trial interval is within the range used by similar playback studies (e.g., 20 min, Mockford and Marshall, 2009; up to two hours, Luther et al., 2017).

Before playback began, a male had to be within 20 m of the speaker in his territory, and exact distance was noted. Playing a conspecific song from the focal male's habitat type (e.g. rural to rural or urban to urban) served as a baseline aggressive response for each individual, and I used a balanced design for the order of song presentation for each male. The selected playbacks were broadcast using a portable field speaker at an amplitude of 75 dB measured at 1 m, and I took ambient noise level measurements within 1 m of the speaker before a trial.

I quantified degree of aggression through recording the number of flights toward the speaker, distance of closest approach to the speaker, latency to approach, number of flights, number of passes by the speaker, body posture, number of songs, and number of soft songs. Fletcher and Smith (1978) used similar behavioral responses to score gray catbird reaction to playbacks of manipulated song. A previous study conducted by Searcy et al. (2006) showed that soft song is an indicator of impending attack in other species, so I also recorded soft songs. The observer dictated these behaviors in addition to distances such that I could later calculate duration spent within 1, 3, or 5 meters of the speaker.

I made song recordings using a parabola, microphones (Sennheiser ME 66) and digital recorders (Marantz Professional PMD561 handheld solid-state recorder). A simple lapel mic and smartphones were used to record additional dictation from observers. All collected song recordings were saved as uncompressed WAV files at a 44.1 kHz sampling rate.

Analysis

In Raven, I annotated the dictation files to quantify number of flights, songs, and passes, as well as the closest approach (m) and duration (s) within five meters of the speaker. These values were added to obtain a single number for each trial for comparison of aggression between males. All aggressive response variables were decomposed into one variable using principal

component analysis (PCA) in R statistical analysis software, to generate one variable describing aggressive response: PC1-Aggression (see Table 10). Principal component one (PC1-Aggression) values were plotted for rural and urban playbacks with male PC1-Aggression values grouped by the males' focal habitat type after running a generalized linear mixed model (GLMM). I also used two-way repeated measure ANOVAs to test for differences in individual variables, such as latency to approach the speaker. The factors used in ANOVA were stimulus habitat and focal male habitat.

Results

Playback Experiment

A total of 68 playback trials were successfully completed to 34 males, and 32 were included in analysis, as two males were dropped due to insufficient data and difficulty interpreting the dictation file (Table 9). Principal component analysis yielded positive loadings for closest approach and latency to approach, and negative loadings for the remaining variables (Table 10). Because responding more quickly in fewer seconds and approaching the speaker more closely (small distance) are more aggressive, a lower PC1-Aggression value signified a more aggressive response.

Results of the GLMM show males significantly varied as to which stimulus – the more urban or the more rural song – they responded to more aggressively (Table 11). Two factors explained this variation, as males in different habitat types (urban, suburban, or rural) reacted differently to urban versus rural stimuli (Figure 10). When conducting the GLMM, I used PC1 noise (see chapter 1) for the site at which a playback stimulus was recorded instead of a categorical classification of “rural” or “urban”. The GLMM interaction between stimulus PC1

noise (maximum, median, and average noise at each site) and subject males' habitat type was significant ($t = -2.068$, $p = 0.0442$, Table 11, Figure 10). Suburban males responded significantly more aggressively to stimuli recorded from noisier sites, while rural males tended to respond more aggressively to stimuli originally recorded from quieter sites. It is important to note that there was a high level of variability between males and within sites (Figure 11).

To further investigate how these responses differed, I also analyzed individual variables using a two-way repeated measures ANOVA, such as latency to approach, closest approach, and duration spent within 1, 3, and 5 m of the speaker. Rural, suburban, and urban males did not differ in their latency to approach the speaker ($F = 1.029$, $p > 0.05$, $df = 2$, Figure 12), their closest approach to the speaker ($p > 0.05$, Figure 14), or in the amount of time they spent near the speaker depending on the stimuli habitat ($p > 0.05$, Figure 13).

Table 10. List of variables that were included in principal component analysis and PC1 loadings. Both closest approach and latency to approach loaded positively, while all other variables loaded negatively.

Variable Name	PC1
number of flights in toward speaker	-0.331
number of flights away from speaker	-0.289
number of songs	-0.143
number of passes	-0.26
duration in 1m of speaker	-0.271
duration in 3m of speaker	-0.365
duration in 5m of speaker	-0.406
closest approach to speaker	0.418
latency approach to speaker	0.398
song duration	-0.114
Eigen Value	4.42
Variance Explained	44.20%

Table 11. GLMM output of PC1-Aggression and PC1-noise. There was a significant interaction between stimulus PC1-noise and PC1-Aggression.

	Estimate	Standard Error	t	p-value
PC1-Aggression and noise				
(Intercept)	0.381	0.4907	0.776	0.5005
Stimulus PC1-noise	0.3256	0.2009	1.621	0.1137
habitat suburban	-1.0113	1.0085	-1.003	0.3873
habitat urban	-0.5013	0.7783	-0.644	0.5595
Stimulus PC1-noise x habitat suburban	-1.2132	0.5867	-2.068	0.0442*
Stimulus PC1-noise x habitat urban	0.3873	0.4369	0.866	0.3809

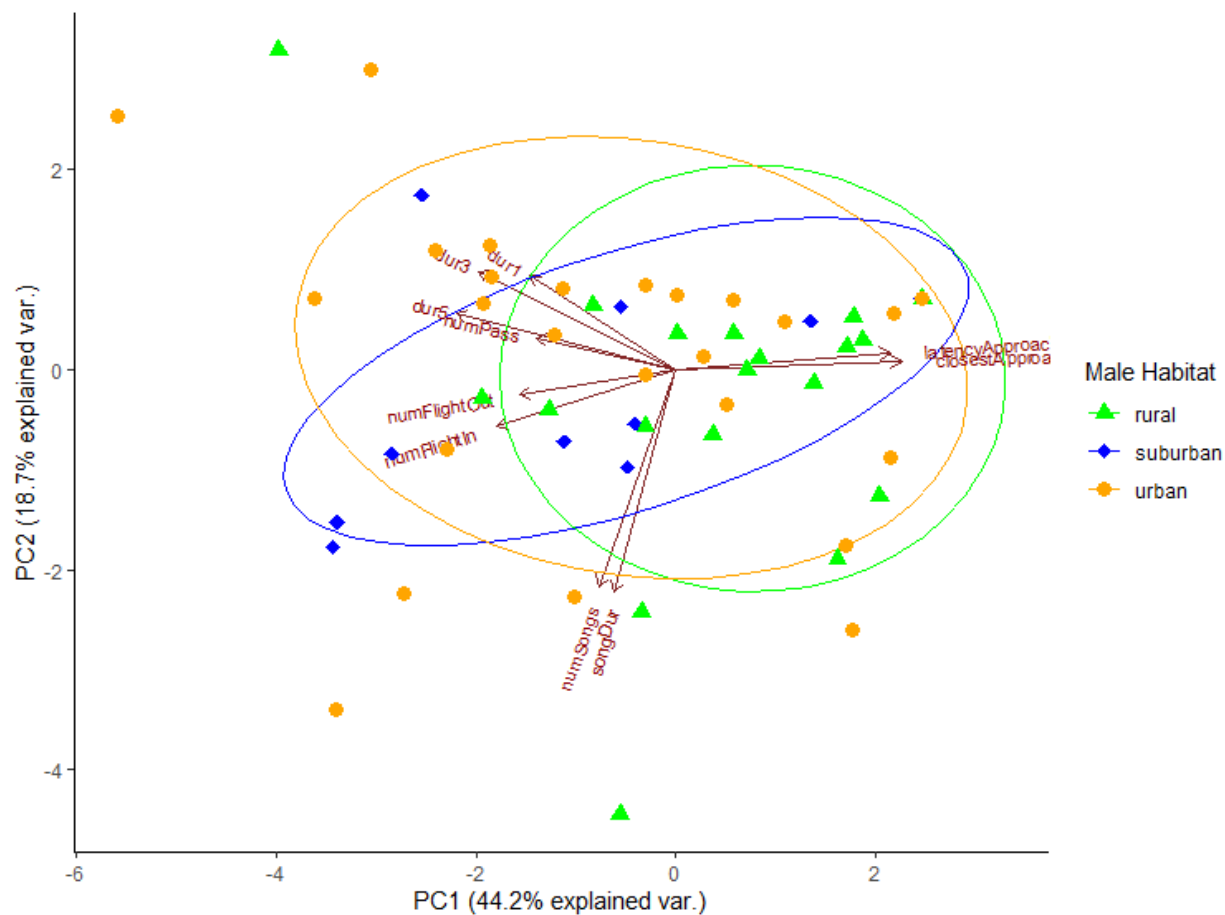


Figure 8. Principal component analysis visualized using 'ggbiplot', plotting principal component one aggression (PC1) and principal component two (PC2) values. Variable arrows represent direction of loading (positive or negative) and each point is a male sorted into rural, suburban, or urban sites.

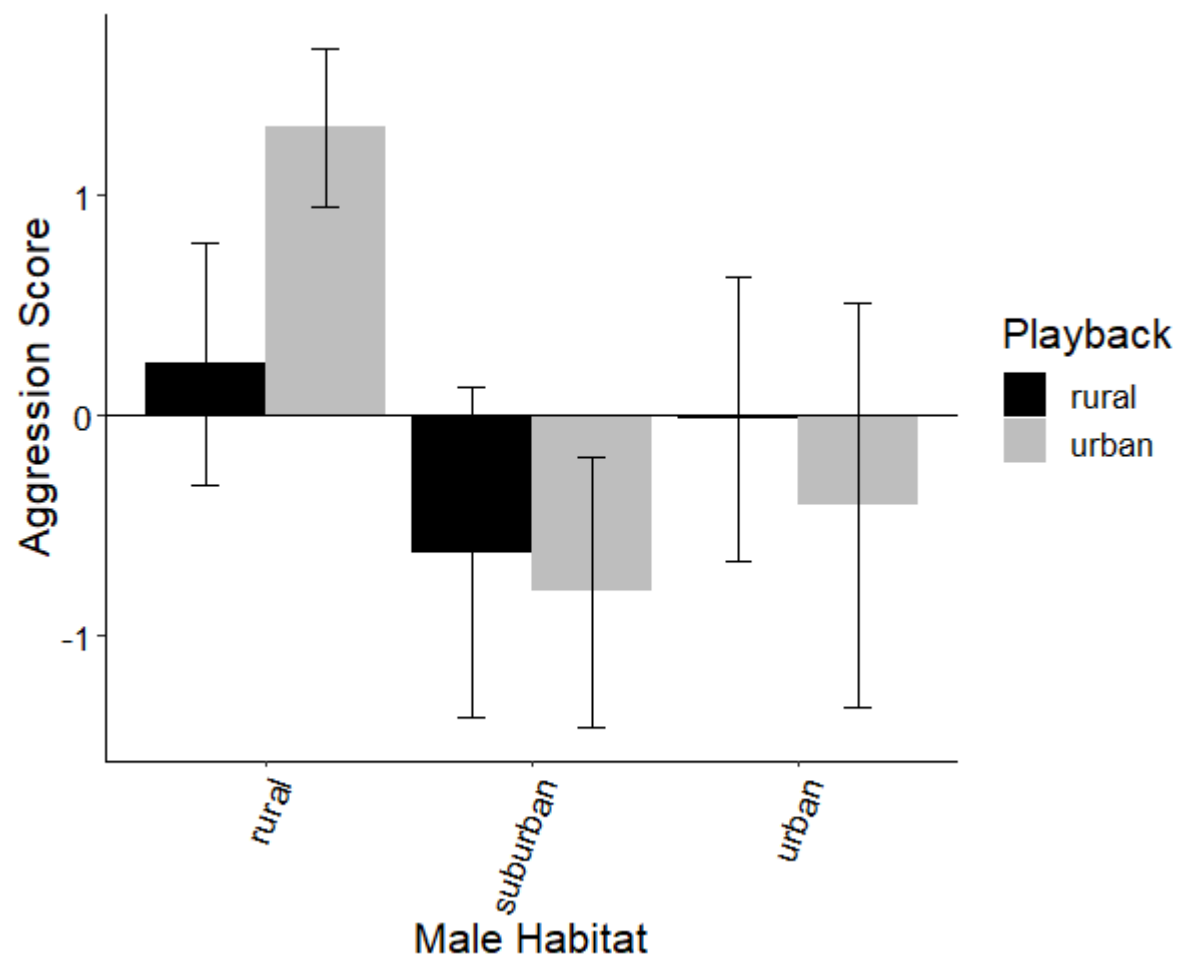


Figure 9. Mean aggression scores based on male habitat when presented with rural and urban playback stimuli. Higher levels of aggression are more negative and error bars represent standard error.

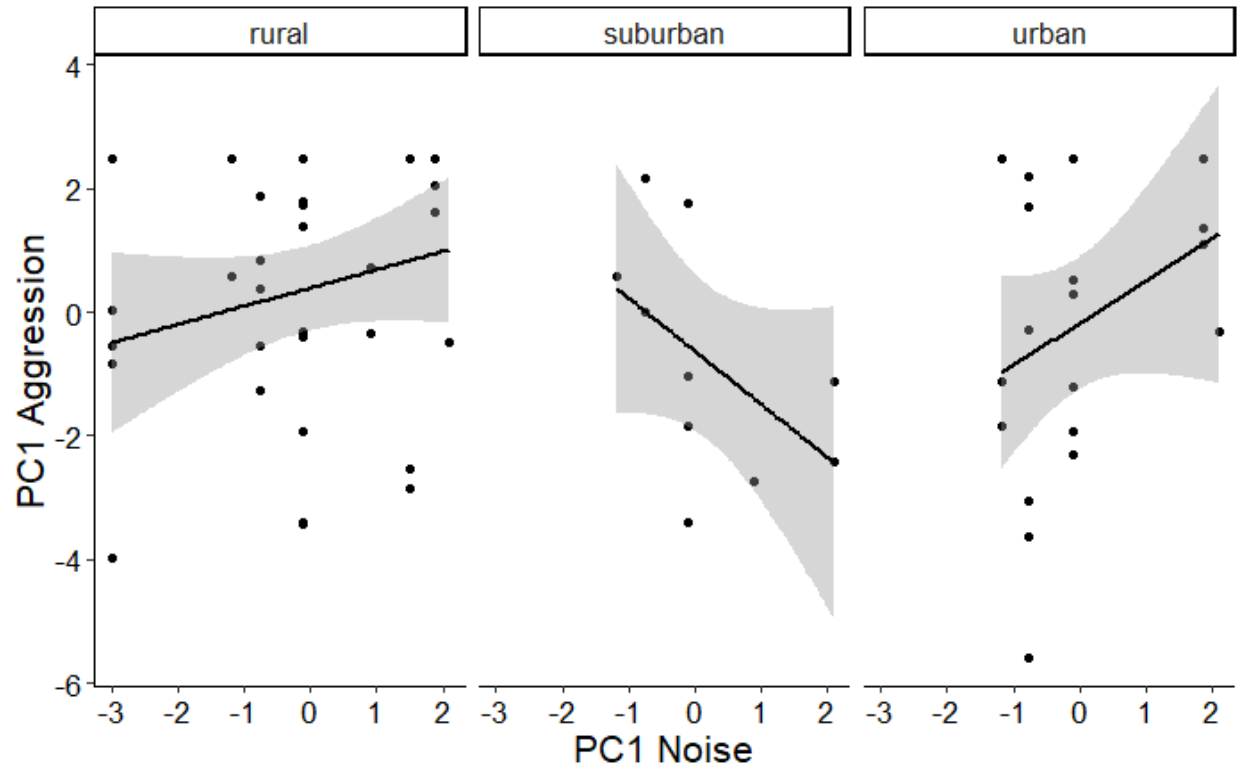


Figure 10. PC1 aggression based on PC1 noise levels for rural, suburban, and urban males. A more negative aggression score is a more aggressive response, and a more positive PC1 noise value is a noisier habitat in which the stimulus song was recorded for use in the playback experiments. Both rural and urban males responded more aggressively to songs that were recorded in quieter habitats. Suburban males responded significantly more aggressively to songs recorded in noisier habitats ($t = -2.068$, $p = 0.0442$).

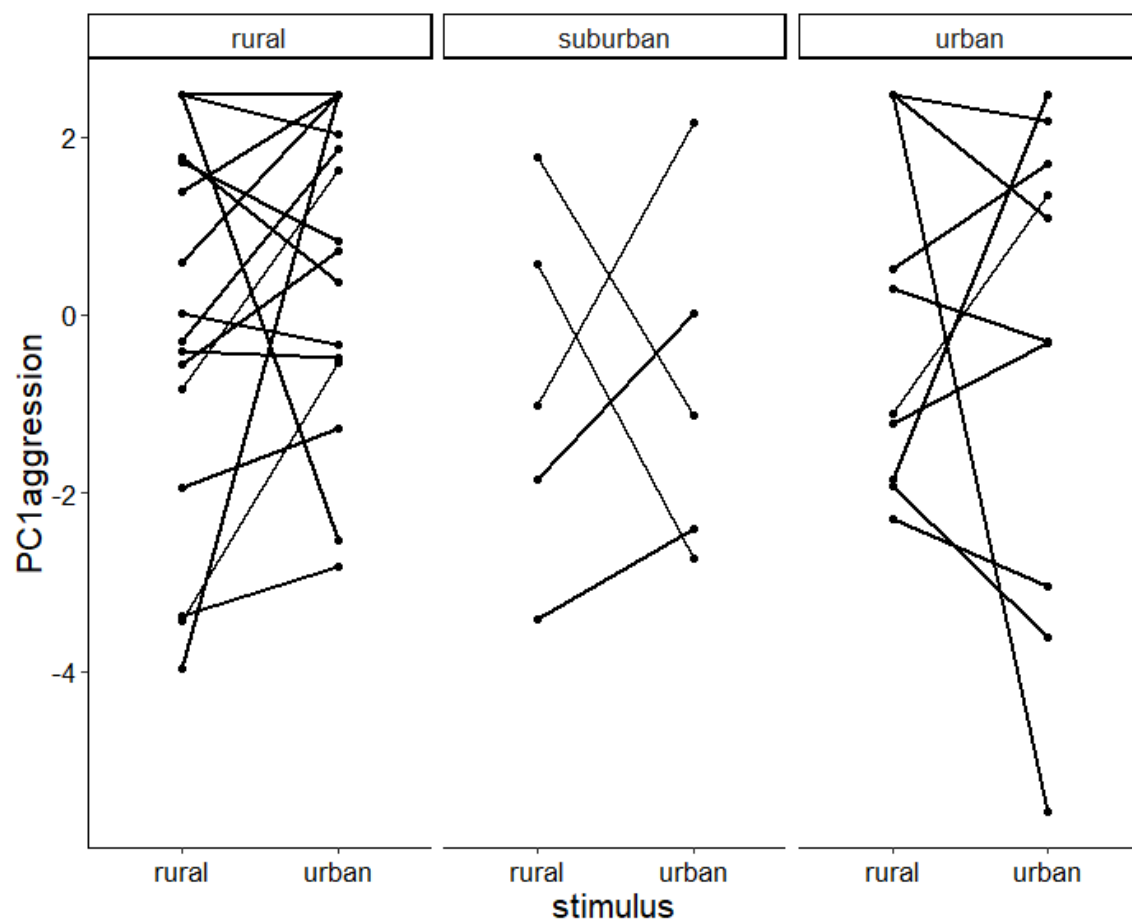


Figure 11. PC1 aggression values to urban and rural song stimuli grouped by focal male habitat. Connected points show playback reaction to both stimuli from the same male.

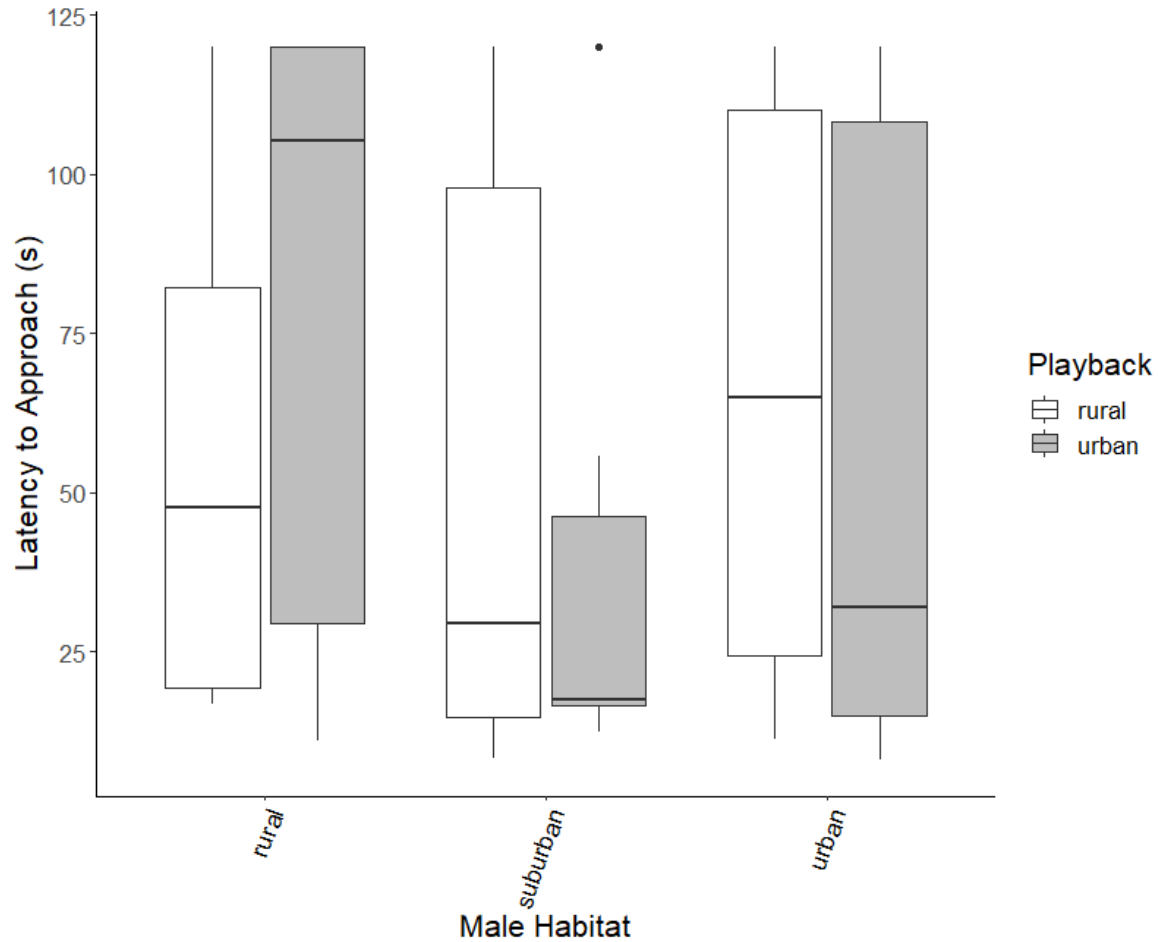


Figure 12. Boxplot showing latency to approach the speaker based on habitat type (rural, suburban, or urban). Bold horizontal lines signify the median latency to approach, the ends of each box show the 1st and 3rd quartiles, and the vertical lines show the minimum and maximum values excluding outliers. Greater latencies to approach signify less aggression, while more rapid approaches (fewer seconds to respond) are more aggressive. No differences were detected across groups or playback type.

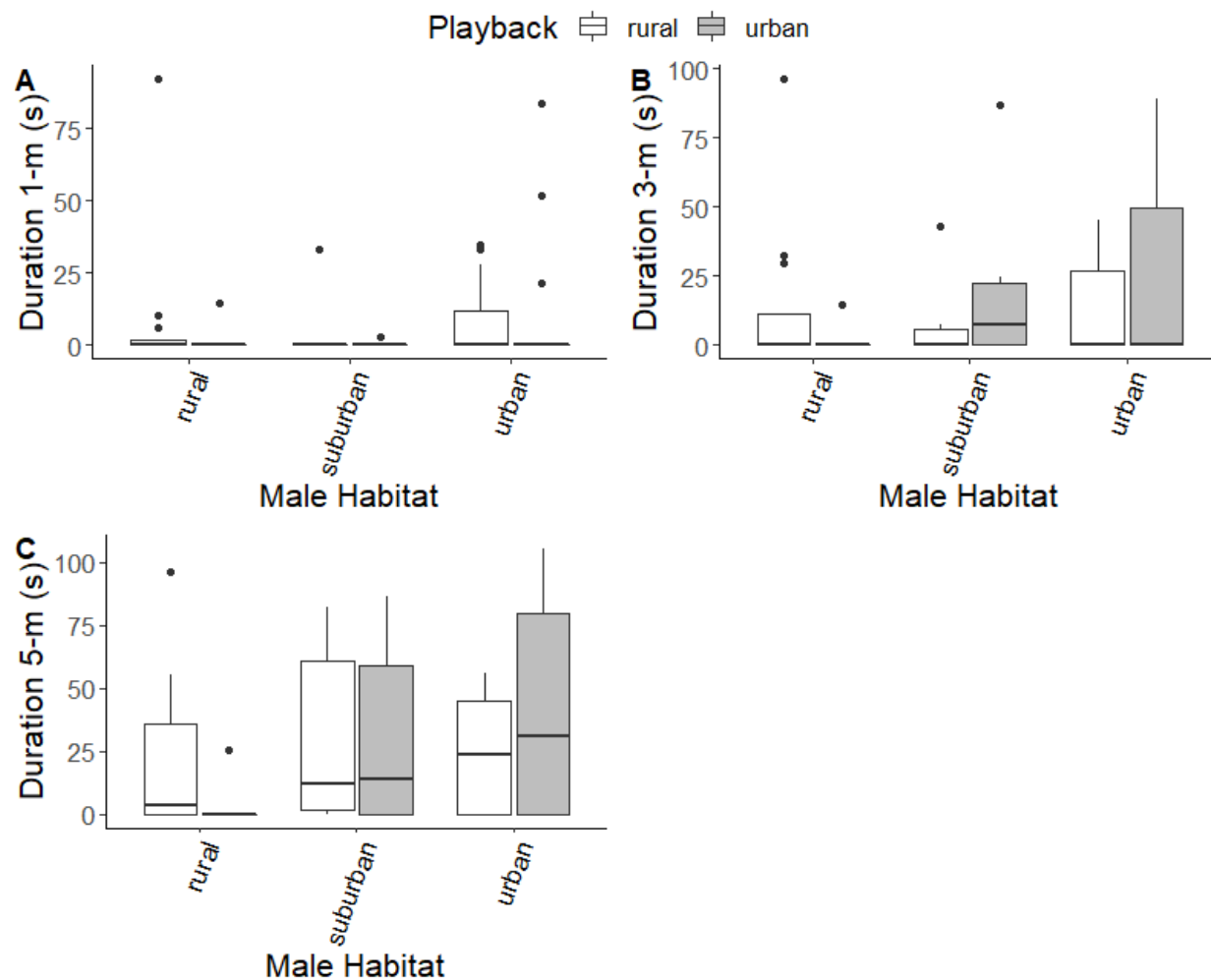


Figure 13. Duration spent within 1, 3, and 5 m of the speaker by habitat type. A greater duration of time spent close to the speaker signifies higher aggression. Bold horizontal lines signify the median duration, the ends of each box show the 1st and 3rd quartiles, and the vertical lines show the minimum and maximum values excluding outliers. Birds from all three habitat types spent a similar amount of time within 1, 3, and 5 m of the speaker for both stimuli.

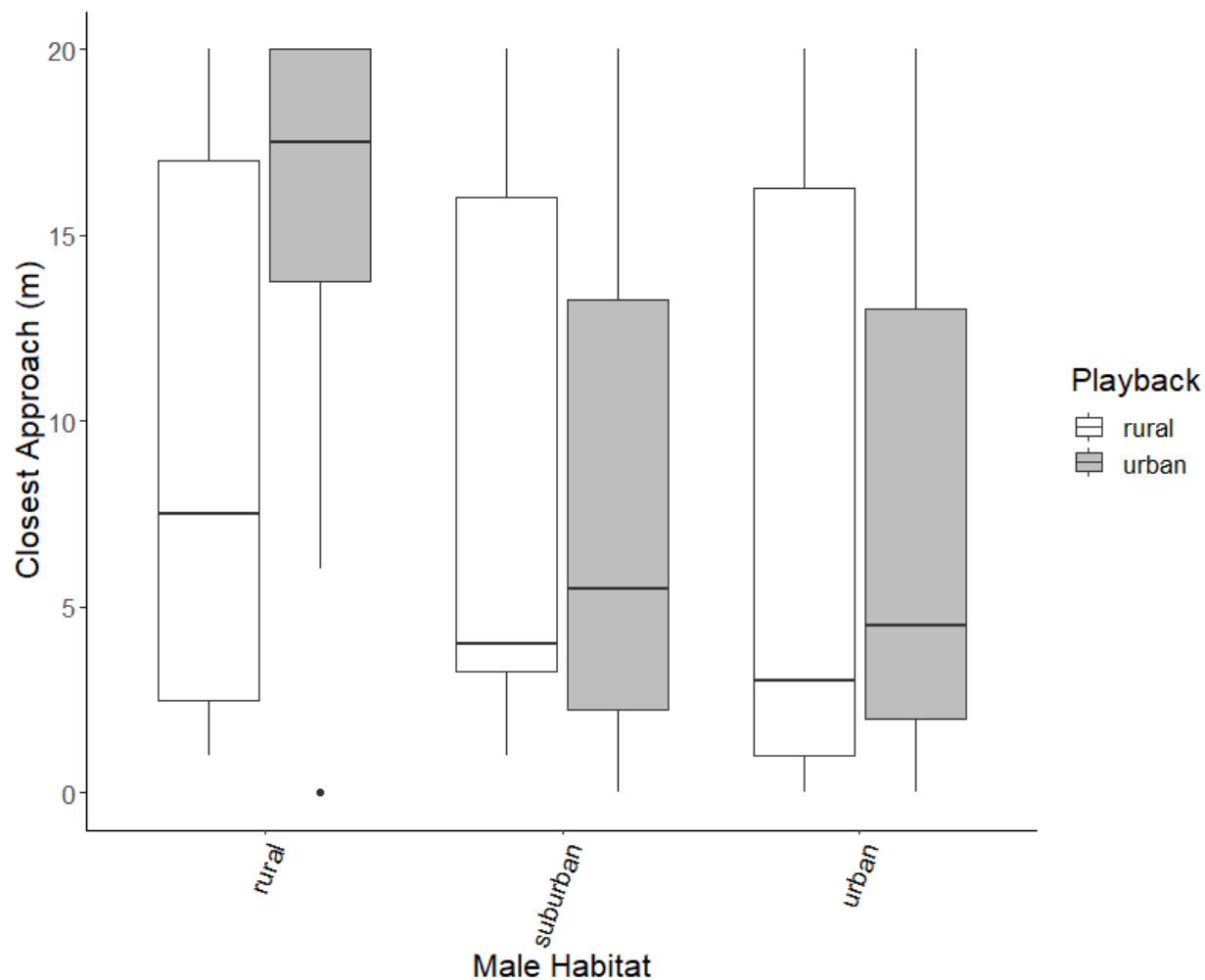


Figure 14. Closest approach to playback stimuli grouped by habitat type. Approaches with smaller values are more aggressive. Bold horizontal lines signify the median closest approach, the ends of each box show the 1st and 3rd quartiles, and the vertical lines show the 1st and 3rd quartiles, and the vertical lines show the minimum and maximum values excluding outliers.

Discussion

I investigated if both rural and urban catbird song function as effectively in territorial defense using a paired playback experiment. I set forth four main predictions drawing from the results of previous studies: (1) Song stimuli from similar habitat types would elicit more aggressive reactions than stimuli recorded in different habitat types, (2) Song stimuli from dissimilar habitat types would elicit more aggressive reactions, as they would be more novel, (3) Catbird song recorded in more rural habitats may be of higher quality and thus would elicit more aggressive reactions from birds in all different habitat types, and (4) Males in more urban habitats would generally be more aggressive as a result of increased competition for resources.

Addressing my first prediction, I did find evidence of males responding more aggressively to playback songs from similar habitat types. Rural males tended to respond more aggressively to song stimuli recorded in quieter sites and suburban males responded significantly more aggressively to stimuli recorded in noisier sites. Interestingly, urban males were more aggressive towards stimuli recorded in quieter sites. An experiment conducted by Mockford and Marshall (2009) found that birds approached the speaker more closely when a homotypic song was played, signifying higher aggression levels. The results of my playback experiment support these findings, other than urban males showing more aggression towards rural song stimuli. Urban males may have shown a different trend for several reasons; one of which may be that song stimuli recorded in quieter habitats was perceived as a higher threat. The lower minimum frequency of rural catbird song could indicate that the simulated intruder is a larger competitor, as lower frequency vocalizations are correlated with larger body size (e.g., Martin et al., 2011), and are also more attractive to females (e.g., Francis et al., 2011). Additionally, my quantification of structural differences between urban and rural catbird song did not consider all

possible variables, such as repertoire size, composition, or instances of mimicry, which could also account for any differences in aggression. Future study should investigate if urban and rural male catbirds show differences in both of these measures, and if this influences aggressive reaction.

My second prediction was that stimuli from dissimilar habitat types would elicit more aggressive reactions because of its novelty. I did not find support for this prediction, as rural birds reacted more aggressively to rural songs. However, as discussed above, urban males reacted nearly as aggressively for some response variables to rural song. Rural males may be mimicking different species than urban birds because their community structures differ. Thus, urban males may react more aggressively to rural song because it contains unique vocalizations from species not present in urban areas. Again, repertoire size, composition, and mimicry should be quantified to further investigate this question.

My third prediction was that rural song would generally elicit the most aggressive reactions from all habitat types. This prediction hinges on the assumption that rural male catbirds are indeed mimicking a wider range of species than their urban counterparts, and therefore have larger or more diverse repertoires. Several previous studies demonstrate that repertoire size is linked to both male quality and reproductive success (reviewed by Robinson and Creanza, 2019). If rural males have larger song repertoires they may be perceived as a higher threat and elicit more aggressive behavior. While both urban and rural males reacted most aggressively to rural songs, suburban males reacted most aggressively to urban songs. If rural song had universally elicited the most aggressive responses in all three habitat types, then there may be sufficient support for this prediction.

My final prediction was that regardless of stimulus type, urban birds would react more aggressively than rural and suburban birds. Previous studies have shown that birds in urban habitats tend to be more aggressive than birds in rural habitats (e.g., Foltz et al., 2015; Phillips and Derryberry, 2018), likely as a result of increased competition for limited food resources. Additionally, small urban and suburban parks may be limiting in resources and set up more intense competition among males in small but dense populations (Ryder et al., 2012). Suburban birds had the highest mean aggression scores, followed by urban birds, and then rural – specifically urban and suburban males tended to fly in more quickly, approach more closely, and spend longer closer to the speaker compared to rural males regardless of stimulus type. However, these trends did not achieve statistical significance, so solid conclusions cannot be made without further investigation.

For direct comparison to previous playback studies quantifying aggression, I also tested for differences in individual variables (e.g., latency to approach). I found no significant differences in closest approach, because of wide variation male approach within each habitat type. Additionally, I did not find any significant differences in amount of time spent close to the speaker based on the song being broadcast, with birds spending similar amounts of time within 1, 3, and 5 m of the speaker. There are non-significant trends, with rural birds spending more time within 3 and 5 m of the speaker when rural songs were played.

Finally, there was no difference in latency to response between urban and rural birds, unlike the experiment performed by Lenis and Guillermo-Ferreira (2020). Lenis and Guillermo-Ferreira found that response latency correlated positively with increased noise pollution, suggesting that urbanization negatively impacts signal transmission and the time it takes territory holders to detect and respond to simulated intruders. My findings suggest that gray catbird song

is still successfully transmitted in urban environments, as urban birds did not take longer to approach the speaker. Had urban birds had a greater latency to respond, then perhaps urban noise impedes signal transmission in catbirds. Playing back two stimuli that differed in the acoustic environment from which they were recorded to males in various habitats likely entails differences in how the soundscape and ecological community has shaped those stimuli and corresponding male reaction.

In addition to the song structural components that differ with background noise that I measured in chapter 1, the soundscape of how sound affects presence of other species in ecological communities should be considered. Previous studies have demonstrated that certain species will avoid noisy areas, especially those with lower frequency vocalizations, which are more heavily masked by anthropogenic noise (e.g., Goodwin and Shriver, 2011). Additionally, habitat modification through urbanization shapes species distribution and presence (e.g., Francis et al., 2009).

Features of different soundscapes likely shape catbird songs in ways I have not yet investigated, such as mimicked repertoire size and composition. Importantly, the three categories of habitats (rural, suburban, and urban) and the individual sites themselves differ in their quality, resources, and could vary in gray catbird population density (Ryder et al., 2012). The interplay between catbird site density and sexual selection pressures was investigated by Ryder et al. (2012) in suburban parks, showing that habitat modification changes fine-scale ecological conditions, which then drives breeding density and sexual selection. While this study focused primarily on breeding success and strategies, future studies could determine how these same site differences impact male aggression and territoriality. Site-level differences may explain the high level of variability in male aggressive reactions in my playback experiment and should be

considered in the future. These factors should be further investigated to determine the role that soundscape, among other individual site features, influence male catbird behavior.

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