

ABSTRACT

NOLKER, ALLISON JEANNE. Changes in Northern Mockingbird *Mimus polyglottos* Vocalizations in Central North Carolina Between 1981 and 2013. (Under the direction of Dr. Theodore R. Simons).

Increased urbanization and anthropogenic disturbance present new challenges to which some species cannot adapt. Others adapt to urban environments in a way which allows them to persist in acoustically variable environments. Adjustment of song frequency is one adaptation that enables some songbird species to prosper despite increased noise. Northern Mockingbirds (*Mimus polyglottos*) have the capacity for behavioral plasticity that allows them to navigate variable urban soundscapes. Using historical urban song recordings from 1981 and 1982 and contemporary recordings from urban and rural sites in 2013, we show that mockingbirds have modulated their song frequencies to higher pitches in response to low-frequency noise in urban habitats over time. Contrary to similar studies of other songbird species, we did not detect site-level frequency differences among contemporary rural and urban mockingbirds. This lack of site-dependent difference could be due to the synurbic nature of mockingbirds. Our data suggest a slight adjustment in the seasonal timing of singing between contemporary populations. In order to fully understand the underlying mechanisms which allow mockingbirds to flourish in variable acoustic environments, additional analyses with captive breeding, reciprocal transplants and genetic components must be conducted.

Changes in Northern Mockingbird *Mimus polyglottos* Vocalizations in Central North
Carolina Between 1981 and 2013

by
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DEDICATION

To Daniel, my Davy.

BIOGRAPHY

I grew up in Rockingham County, North Carolina on a piece of property that was my Giving Tree. My family's small farm played so many roles: laboratory, refuge, challenge, anchor, and teacher. I learned about nature, life, humility, and myself on our farm. No matter how well I did in school, there was always the back pasture's broken fence and the hungry livestock to keep me grounded. My passion for the outdoors was forged amongst the smell of pine trees next to my constant companion and best friend, my older brother, Daniel. Nothing was impossible if Daniel said it could be done. I was blessed to be raised in the most loving home by parents who valued both books and hard work. They supported my every pursuit and when I won a Park Scholarship to NC State, they were beyond proud. The Park allowed me to further stretch my academic wings and engage in experiences I would have otherwise not been able to.

I wanted to be the female Marty Stouffer since I can remember. I wanted to share my love of wildlife and wild places. During my undergraduate career, that vague dream developed into a particular passion for human-animal interactions and bioacoustics. I participated in the brand-new Accelerated Bachelor's/Master's program for the Zoology and Biology departments, which culminated in this thesis. I have now begun a new adventure with the North Carolina Wildlife Resources Commission as a wildlife biologist studying captive cervids. I look forward to the challenges and brilliant people I will meet in this new position. I have the opportunity to affect change in wildlife management. I will become Martina Stouffer yet.

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CHAPTER 1

Project Background and Literature Review

OBJECTIVES AND HYPOTHESES

We compared historical and contemporary recordings of urban Northern Mockingbirds and contemporary recordings of urban and rural Northern Mockingbirds to examine how the bird's vocalizations may have been shaped by their acoustic environment. To inform this, we measured spectral characteristics that captured the entire frequency range of mockingbird song and compared these characteristics across space and time using generalized linear mixed models. Furthermore, we collected ambient sound data to create a realistic view of the acoustic environments experienced by the three mockingbird populations and how they may or may not be different. The objectives of this study were to: 1) compare the spectral characteristics of the songs of the historical and contemporary urban populations; and 2) compare the spectral characteristics of the songs of the contemporary urban and rural populations.

Objective 1: Historical-contemporary urban analysis

The goal of this objective was to examine the differences, if any, in the spectral characteristics of historical and contemporary mockingbird song. The urbanization of Greensboro, North Carolina is well-documented and provided an appropriate model of increased anthropogenic disturbance. The historical and contemporary urban data provide a unique snapshot view of two mockingbird populations. Because the historical data was well

maintained, we conducted a repeated measures analysis on data collected 30 years apart. We predicted that the contemporary urban mockingbirds would sing at higher pitches than their historical counterparts.

Objective 2: Contemporary urban-rural analysis

The goal of this objective was to examine the differences in the spectral characteristics between contemporary urban and rural Northern Mockingbird song. We analyzed the same contemporary recordings used in the historical-contemporary urban study as well as recordings made in two rural sites. These data provide an interesting study on the implications of the perceived level of human development and land use and the adaptation of synurbic species. We hypothesized that there would be higher levels of ambient noise in urban areas. If there were higher ambient noise levels, we hypothesized that mockingbird song characters would change in response to the higher level of ambient noise akin to other studies of this kind. If no differences in background noise level were experienced, we did not expect a difference between urban and rural spectral characteristics.

BACKGROUND

A number of key studies over the past decade have illustrated how the characteristics of bird song are shaped by their acoustic environment. Anthropogenic disturbance is any form of disturbance caused by human activity (Bisson et al. 2009). A cursory internet search using the keywords “anthropogenic disturbance” yield hits that deal with the large-scale effects of

loss of canopy algae on rocky shores (*i.e.* Benedetti-Cecchi et al. 2001), the terrestrial water cycle (*i.e.* Vorosmarty et al. 2000), and the responses of bees to anthropogenic disturbance (*i.e.* Winfree et al. 2009). Those are just three of the 190,000 results given by Google Scholar. Researchers are clearly interested in what impacts humans are having on the ecosystems of the world.

A branch of this research focuses on the effects of acoustic disturbance on animal communication and its influences on mating strategies, sexual selection, behavior, and morphology (Derryberry 2009). Analysis has not been restricted to one or two taxa; cetaceans, anurans, primates, and sciurid rodents have all been extensively studied (Warren et al. 2006; Bee and Swanson 2007; Nowacek et al. 2007). *Aves* is one of the most well-represented taxa in the study of anthropogenic noise as acoustic disturbance because the primary form of communication in many species is vocalization. Birds serve as excellent models for studying effects of anthropogenic noise because of their diverse behaviors and because many species are readily found in rural, suburban, and urban habitats.

Birds have a suite of characteristics useful for informing questions about the effect of anthropogenic disturbance and urbanization. Chace and Walsh (2006) cite four patterns typical of urban bird communities: (1) species richness declines; (2) the density of successful urban species increases; (3) overall avian biomass increases; and (4) the abundance of introduced species increases.

In addition to population level changes, birds often exhibit individual behavioral changes associated with urban disturbance. For example, urban magpies (*Pica pica*) build their nests higher relative to their rural counterparts, presumably to avoid human interference

(Wang et al. 2008). Birds also have been found to change their song characteristics and timing to avoid masking by low-frequency anthropogenic noise (Slabbekoorn and Peet 2003).

Human activities create relatively loud, low-frequency noise. Urban areas are permeated with noise from cars, airplanes, industrial machinery, construction, air compressors, and the like (Francis et al. 2009). The background noise in cities is considerably louder than most natural environments, especially in the lower registers (Ripmeester 2009). This low-frequency noise partially overlaps the song ranges of many species. Noisy conditions invariably alter what the birds are hearing, what they are responding to, and ultimately how they communicate (Patricelli and Blickley 2006). Sound plays an integral role in mate acquisition and recognition, territory defense, and predator avoidance (Wilkins et al. 2013). Species that are especially vocal rely heavily on clear and unobstructed signal transmission. Some species have developed ways to reduce the effect masking has on the efficacy of their vocalizations. As an analog compare this to how you would change your vocal output when trying to get a friend's attention at a noisy concert. You would likely increase the amplitude of your vocalizations by shouting. Birds in noisy

environments may increase the signal-to-noise ratio (SNR) by increasing the amplitude, or loudness, of their songs. This behavior is commonly termed the “Lombard effect” and is a widespread phenomenon throughout many species of birds and mammals (Brenowitz and Beecher 2005; Patricelli and Blickley 2006). Maximum possible amplitude is constrained by body size, so birds must often find other strategies to overcome anthropogenic noise (Ryan and Brenowitz 1985). Recall the example of the noisy concert. If shouting loudly did not work to gain your friend’s attention, you would perhaps change the type of vocalization from a shout to a whistle or continue shouting, but at a higher pitch. We instinctually utilize higher pitches over short distances to make ourselves heard, especially in loud surroundings. Songbirds, which have similar, though superior, hearing ranges to humans, show similar adaptations (Marler and Slabbekoorn 2004).

Birds make predictable behavioral adjustments to offset the effects of persistent low-frequency anthropogenic noise. These adjustments fall largely into two general categories: spectral adjustment and temporal adjustment. Spectral adjustment is the change in frequency characteristics of the songs themselves. Great tits (*Parus major*), song sparrows (*Melospiza melodia*), and plumbeous and grey vireos (*Vireo plumbeus*, *Vireo vicinior*) have all been shown to increase the pitch of some aspects of their songs to combat low-frequency interference (cf. Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Francis et al. 2009). In one study of urban habitats in The Netherlands, male Great Tits sang with fewer low-pitched notes that would have otherwise been masked. The result was a song with higher minimum frequency (Slabbekoorn and den Boer-Visser 2006). Song sparrows at the

noisier locations in a study conducted by Wood and Yezerinac (2006) had higher-frequency low notes and were quieter in the low-frequency ranges of their songs although lower-frequency song components remained fairly unchanged. In addition to changing the pitch structure of their songs birds can also alter their songs' repertoire components. Mimetic birds, like Northern Mockingbirds, tend to copy their neighbors songs when they can hear them clearly (Slabbekoorn and den Boer-Visser 2006). In this context, the term "copy" refers to either the songs of both conspecifics or heterospecifics. Songs that do not elicit a response may also be dropped from a bird's repertoire. Regardless of the specific mechanism, selective attrition of songs in noisy environments is thought to be based on the amount of spectral overlap between the song and the environment. Selective attrition is a consequence of the overproduction of song types and the subsequent paring down of the gross repertoire to include only those song types that prove the most beneficial in the immediate environment (Nelson and Marler 1994). This operative suite of phrases can change over time based on female response to mating signals, predator abundance and activity, and aggressive male response to territorial displays (Patricelli and Blickley 2006; Luther and Baptista 2010). Selective attrition may also be a key mechanism underlying a mockingbirds' ability to choose novel and environmentally suitable mimics. Nelson et al. (1995) found that migratory white-crowned sparrows (*Zonotrichia leucophrys oriantha*) use selective attrition after establishing their territories to develop song types that closely match their neighbors.

Temporal adjustment is the change in the timing of songs rather than a change in the song itself. *Timing* can be anything from a shift in the season during which birds are most active,

to changes in the temporal pattern of diurnal singing, to minute variations in silent periods between song phrases (Patricelli and Blickley 2006; Warren et al. 2006; Derryberry 2007). Shifts in the seasonality of singing could occur, for example, if urban-adapted species nest at higher densities in urban areas compared to rural environments. Male mockingbirds sing more readily when their neighbors are singing, (Derrickson 1987) so higher densities generally promote higher singing rates, especially early in the breeding season. Similarly, greater food abundance, or higher competition for mates or might cause urban males to pair earlier than rural birds (C. Botero, pers. comm.) Oscine singing activity typically peaks during the dawn chorus. Patricelli and Blickley (2006) proposed that timing of the dawn chorus could be altered in urban environments by traffic noise associated with rush hour, which changes throughout the year with day length and the implementation of Daylight Savings Time, or higher light levels in cities, which might act as a confusing analog for the natural sunrise to birds. We did not record during the dawn chorus in this study because it is difficult to isolate mockingbird song from the myriad other simultaneous bird song. Mockingbirds sing throughout the day, so recording during the dawn chorus was not necessary. Finally, birds, including mockingbirds, may change or extend the inter-phrase silent periods within their song (Derrickson 1988; Derryberry 2009). Rather than expend energy singing during times of heightened anthropogenic noise when the likelihood of being heard is very low, some birds may very temporarily cease singing altogether until the disturbance is over (Gross et al. 2010). We observed urban mockingbirds that stopped singing when extremely loud (over 80 dB) street cleaning equipment was in use nearby. The

birds resumed singing as soon as the equipment moved away from their territories. Although interesting, we did not analyze the intra-phrase silent periods in this study. Rather, we focused on coarse seasonal timing of songs between urban and rural sites.

STUDY SITES

Urbanization causes a shift in species composition. Although low levels of urbanization have been linked to an increase in bird community composition, higher levels of urbanization serve only to yield avian communities dominated by a few species (Chace and Walsh 2006; Gross et al. 2010). Contemporary rural species composition remains less changed, although urban exploiters are typically absent and urban adapters are found less abundantly (Blair 1996).

Rural habitats

The term “rural” encompasses a wide array of environments and an objective, scientific definition of “rural” is not readily found. Definitions based on cultural perceptions of the rural-urban gradient dominate both the sociological and ecological literature (Dewey 2014). This is a fluid gradient and as such the term “rural” embraces a more robust suite of habitats than it did in previous decades (Dewey 2014). Typically, rural habitats are primarily agrarian with minimal human development. Structures do not dominate the landscape. The ground is generally vegetated but distinct from natural forests and paved surfaces are uncommon (Ripmeester et al. 2010). Roadways tend to be smaller and more dispersed compared to urban

areas. For the purposes of this study, “rural” sites were farmland and the surrounding edge forest plots, as well as the adjacent roads.

Urban habitats

Urban habitats provide excellent opportunities to study how populations diverge in novel ecosystems compared to in their original system (Ripmeester 2009; Stracey 2010). Although the value of natural habitats will generally exceed that of urban habitats for conserving biodiversity, urbanized sites provide unique opportunities for innovative conservation efforts (Miller and Hobbs 2002). Like “rural”, the term “urban” encompasses a range of habitats, all experiencing human disturbance to some consequential degree. Typically, urban habitats are characterized by large, closely-spaced buildings, ground covered primarily by asphalt and concrete rather than undergrowth, and constant human presence (Sih et al. 2011; Francis and Chadwick 2012). Urbanization has major effects on flora and fauna including increased competition from introduced non-native species (Smith and Bernatchez 2008); habitat loss and fragmentation, (Sol et al. 2013), and air, light, and noise pollution (Mockford and Marshall 2009). From an evolutionary perspective, urbanization is often a rapid process that requires species to adapt quickly in order to survive. Species that are unable to cope with human disturbance, termed ‘urban avoiders’, do not have traits shaped by past selection that allow them to be successful around humans or human modified environments (Blair 1996;

Sih et al. 2011). Thriving species, ‘urban adaptable’ and ‘urban exploiters’, are highly tolerant of these new environments and they often have the capacity to quickly learn and integrate novel behaviors (Dowling et al. 2011; Sol et al. 2013). Urban adaptable species tend to reside in both their natural habitats as well as in urban areas. These species may undergo trait divergence as a result of conflicting selective pressures, and thus provide useful models of intraspecific population differentiation (Ripmeester 2009).

Urban study sites

Historical recordings of mockingbird vocalizations were made between February and June of 1981 and 1982 by Logan and Fulk (1984) as part of a larger study conducted from 1979-1987. The recordings were originally collected using a focal animal study examining reproductively dependent song cyclicality (Logan 1983), the characteristics of spring and fall song (Logan and Fulk 1984), and territorial aggression in mockingbirds (Logan and Wingfield 1990). The recordings were made along a 487-meter route on College Avenue at The University of North Carolina at Greensboro (UNCG). The study area consisted of nine discrete plots delineated by individual birds’ territories. These territories were approximated using nest location and abundance, along with meticulous behavioral observations (Logan 1983, Logan pers. comm. 2011). My contemporary study sites were established in the same manner and territory boundaries were similar to those mapped by Logan, although two historic territories were not available due to campus construction activities. UNCG is a public university in Greensboro, Guilford County, North Carolina that currently has over 17,000 enrolled students. At the time of the original recordings, there were only 10,201

students (IRE, 2014). UNCG is located near the center of Greensboro, an area that has experienced marked and rapid population growth and urban sprawl in the past two decades. The population of the city of Greensboro has grown by almost 80% since 1980 (155,642 in 1980 to 279,639 in 2013; 2013 U.S. Census data). College Avenue is bordered by large academic buildings including the main campus library. The buildings are landscaped such that each is closely surrounded by low, ornamental shrubs and other non-native plants. There are small trees every five to seven feet down the entire median of the street. There are also large trees on the lawns of many of the academic buildings. Most of these trees and shrubs are utilized as nesting sites by the resident mockingbirds while the lawns are prime foraging sites shared by multiple territorial individuals. When the historical recordings were taken, cars were able to drive unrestrictedly on College Avenue. Vehicles other than University Maintenance vehicles are now prohibited from driving on College Avenue. Although this difference suggests that campus is now quieter than in the past, the surrounding areas of Greensboro have grown so much that ambient noise levels have likely increased substantially as well.

Rural study sites

I originally planned to locate my rural study sites on the R. Wayne Bailey-Caswell Game Lands outside of Yanceyville, Caswell County, North Carolina. Sites were surveyed from September-November 2012, but unfortunately, mockingbirds were found not in sufficient abundance. Mockingbirds were observed on telephone lines and the front lawns of farm houses adjacent to the Game Lands, but not on the Game Lands themselves. Therefore rural

study sites were selected near the Upper Piedmont Research Station (UPRS) between Reidsville and Wentworth, Rockingham County, North Carolina. The UPRS is a 835-acre working cattle and tobacco farm owned by North Carolina State University for the purpose of agricultural research. The UPRS is dedicated to feed studies on the resident Black Angus herds and research on burley and flue-cured tobacco, wine grapes, herbs, and Paulownia trees. The Station is located on the historic Chinqua-Penn plantation. The habitat is characterized by small trees abutting agricultural fields and the plantation is divided by a moderately busy roadway. Most of the anthropogenic noise is caused by light vehicle traffic and the farm equipment such as tractors and all-terrain vehicles (ATVs) that use this road. Mockingbirds were common on the UPRS, although territories were much more dispersed than those at UNCG. In addition to the UPRS territories, we sampled mockingbird vocalizations on a small farm at the eastern edge of Rockingham County between Reidsville and Yanceyville, North Carolina. The Grooms Road site had habitat characteristics similar to those at the UPRS: low shrubs bordering agricultural fields with moderately busy roadways.

STUDY SPECIES: *Northern Mockingbird*

The Northern Mockingbird (*Mimus polyglottos*) is a medium-sized member of the family Mimidae this monomorphic species has predominately gray plumage, pale breasts, dark eyelines, and white wingbars that become large white patches during flight. Mockingbirds have long legs and short, broad wings which make them appear to have quite long tails. North American *Mimidae* consists of mockingbirds, including the Tropical Mockingbird (*Mimus gilvus*) and the Blue Mockingbird (*Melatonis caerulescens*), and thrashers, including

the Brown Thrasher (*Toxostoma rufum*) and the Sage Thrasher (*Oreoscoptes montanus*). Other closely related species are Starlings (family *Sturnidae*) (Sibley et al. 1984).

Northern Mockingbird males and females both sing, but females sing only during the fall and winter and not nearly as often as the males. Males have distinct spring and autumn songs. Males will sing up to 24 hours per day during the breeding season. Paired males are comparatively silent during the early nestling phase of each clutch (Logan 1983; Logan and Hyatt 1991).

Mockingbirds have a widespread distribution throughout the continental United States and into Canada and Mexico. Although some of the northernmost residents may migrate south for the winter, populations are predominately non-migratory. Historically, mockingbirds could be found along forest edges in the southeastern coast of the United States, feeding on insects and fruits. During the nineteenth century, a staggering number were captured as pets and sold around the country (Kaufman 1996). This drastically increased their range. They adapted to cities well and now mockingbirds are much more common in suburban landscapes than forests (Stracey 2010).

Research indicates that mockingbirds have adapted their ecology and behavior to urban environments. Levey et al. (2009) found that mockingbirds are capable of recognizing individual human intruders to their territories. Stracey (2010) concluded that urban nest predation is lower than non-urban nest predation, although avian predators are more abundant in cities. Typically, there are more mockingbirds per unit area in urban sites and

productivity of urban pairs exceeds rural pairs (Stracey 2010). As yet, there have been no published comparisons between urban and rural mockingbirds to determine whether genetic divergence of urban and rural populations exists as suggested by morphological differences.

Song has important sexual signaling functions associated with mate acquisition and territorial defense. Male mockingbirds sing from high perches within their territories. Songs show individual variation but general song types are often shared by regional populations (Laskey 1944). Mockingbirds mimic the songs of other species in their communities, as well as other biotic and abiotic sounds including squirrels, tree frogs, horns, sirens, and even crosswalk signals. A mockingbird's repertoire consists of a combination of these mimics and their unique individual. Birds in the same population do not share all of their repertoire elements (Laskey 1944), and repertoires can consist of hundreds of songs (Michener and Michener 1935). Males constantly add mimics to their repertoire to maximize novelty and peak female interest, but they will also drop songs that are not effective in attracting mates (Laskey 1944). There is not a stereotypical structure to their song; rather males sing an almost constant and seemingly random string of song snippets. Mockingbird song has historically been broken down into discrete structural units defined by Wildenthal (1965). The most basic element of mockingbird song is a *syllable*, which is the group of sounds, possibly of varying pitches, that occur singly or together (*syllable-clusters*) to form the mimicked motif. Similar *syllables* or *syllable-clusters* are grouped into *syllable-patterns*. Performances of the same *syllable-patterns* are further grouped into *phrases*, which are the most generally useful descriptive unit of mockingbird song.

The Northern Mockingbird is a challenging model species for investigations on the effects of increased anthropogenic noise on avian song. Although large song samples are easily collected due to mockingbirds' loud, conspicuous, and nearly continuous song, the complexity of their song and their innate song learning capabilities make them less inclined to respond strongly and directly to anthropogenic disturbance. Mockingbirds are commensal with humans (Stracey 2010), which means that even in rural areas they are found near human settlement. A stronger response is likely to be seen in a species that has a smaller natural song repertoire and lives in more contrasting habitats, such as the Carolina Chickadee (*Poecile carolinensis*) or the Tufted Titmouse (*Baeolophus bicolor*). However, the mimetic nature of mockingbird song allows for the eventual discussion of the importance of the conspecific community composition (*i.e.* what is *available* to serve as a mimic model) versus individual- or population-level behavioral plasticity (*i.e.* what is *selected* as a mimic model by mockingbirds) on song spectral characteristics. Regardless of the challenges associated with studying mockingbirds, it seems likely from anecdotal evidence that mockingbirds have modified their singing behavior and/or song characteristics as they have become increasingly synurbic.

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CHAPTER 2

INTRODUCTION

The modern acoustical environment of much of the world has been drastically altered in recent years. The effects of anthropogenic noise created by industry and infrastructure on signal transmission is well documented for many taxa, particularly birds (Patricelli and Blickley 2006; Nowacek et al. 2007). Some species combat this acoustic disturbance by altering their communication strategies (Slabbekoorn and Peet 2003).

Sound plays an integral role in mate acquisition and recognition, territory defense, and predator avoidance in birds (Wilkins et al. 2013). Species that are especially vocal rely heavily on clear and unobstructed signal transmission. Some species of songbirds, like Great Tits (*Parus major*), Plumbeous and Grey Vireos (*Vireo plumbeus*, *Vireo vicinior*), and Song Sparrows (*Melospiza melodia*) have changed the spectral characteristics of their song to avoid low-frequency interference caused by traffic and other industrial noise (*cf.* Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Francis et al. 2009). Other songbirds, such as European Blackbirds (*Turdus melura*), have changed the temporal characteristics of their songs in response to similar forms of interference (Ripmeester et al. 2010).

Urbanization effects on the biomass and richness of avian populations (Chace and Walsh 2006). Although low levels of urbanization have been linked to an increase in bird community diversity, higher levels of urbanization often yield avian communities dominated by a few species that are well-adapted to urban environments (Gross et al. 2010). The

Northern Mockingbird (*Mimus polyglottos*) is one such species. Mockingbirds are a bold and prolific synurbic species (Shochat et al. 2006; Francis and Chadwick 2012) that dominates anthropogenically disturbed environments. The Northern Mockingbird is a permanent resident across most of North and Central America, and a widely recognized member of the *Mimidae* family. Classified by Blair (1996) as “suburban adaptable”, mockingbirds are more likely to be found in a recreational park or lawn than in more natural or wooded areas.

Many songbirds have more than one song type; most have between 5 and 10, although it is not unusual for repertoires of some species to stretch to 20-40 (Macdougall-Shackleton 1997). Mockingbirds, as mimics of their conspecific community members, have staggering repertoires that consist of 200 or more songs (Michener and Michener 1935; Kroodsma and Verner 1978). Mockingbird song functions in mate acquisition, individual recognition, and territory maintenance. Paired males are comparatively silent during the early nestling phase of each clutch (Logan 1983; Logan and Hyatt 1991). The timing of this quiet period can be used as an analog for the timing of mate acquisition, breeding season, and nesting cycle (Logan et al. 1983; Derrickson 1987). Unpaired males will sing longer into the season in an attempt to attract mates (Derrickson 1987).

We used historical data from The University of North Carolina at Greensboro (UNCG) and contemporary data from sites in a nearby rural community to assess the response of mockingbirds to anthropogenic noise by measuring eight metrics of energy distribution. The population of Greensboro, North Carolina has grown by almost 80% since 1980 (155,642 in 1980 to 279,639 in 2013; 2013 U.S. Census data). This population increase has brought with it drastic infrastructural expansion and increased traffic, both of which

create persistent, low-frequency noise. In order for mockingbirds to not only survive but also thrive in this acoustic turbulence, they must be able to rapidly adapt, most likely through phenotypic plasticity (Wood and Yezerinac 2006; Gross et al. 2010).

We predicted that mockingbird song would reflect the pattern seen in other species which modulate their song frequencies to higher pitches in response to low-frequency noise. We also predicted that there would be differences in song spectral characteristics between contemporary urban and rural populations associated with differences in the ambient noise of urban and rural sites.

STUDY AREAS AND METHODS

We compared digitized historic song recordings of Northern Mockingbird with contemporary digital song recordings, and ambient noise levels at urban and rural nesting sites, to assess changes in song energy distribution over space and time. Historic recordings were digitized in Audacity (Audacity Team, version 1.3.9, <http://audacity.sourceforge.net>). We analyzed frequencies between 1200 and 12000 Hz and used batch band filtering (Charif 2010) to exclude frequencies below 1200 Hz in order to negate low-frequency interference. We found no evidence of mockingbird vocalizations above 12000 Hz. We compared vocalizations from one urban site in the middle of Greensboro, North Carolina to a pair of rural sites in an agricultural part of eastern Rockingham County, North Carolina.

Urban Study Area and Recordings

Historical recordings were collected between February and June of 1981 and 1982 by Logan

and Fulk (1984) using a focal animal sampling protocol. Researchers made recordings of territorial Mockingbirds along a 487-meter route on the campus of The University of North Carolina at Greensboro (UNCG). UNCG is a residential campus located in north-central North Carolina that has grown from a student population of 10,201 students in 1981 to a current population of 17,707 students (IRE 2014). Habitat in 1981 was characterized by academic buildings bordered by low, dense, non-native ornamental vegetation (Logan and Fulk 1984). The densely planted trees and shrubs provided abundant nest and foraging sites for mockingbirds. Logan and Fulk (1984) observed and recorded focal mockingbirds in nine territories using an Uher 4000-Report IC portable analog tape recorder and a Dan Gibson microphone with a 47.6-cm parabola. Each territory housed a nesting pair of mockingbirds and occasional single males (~11 individuals total; Logan and Fulk 1984; Logan, pers. comm.).

We collected contemporary recordings between 0600 and 1030 on days with little to no rainfall and low wind between February and June 2013 following the historical route at the same locations used by Logan and Fulk (1984). Despite some landscaping changes over the intervening years, the habitat of dense ornamental trees and low shrubs was little changed, and we found territorial mockingbirds in many of the same locations observed in 1981 (Fig. 1). Although mockingbirds aggressively defend their nesting territories, we noted multiple birds utilizing the same small areas, especially for foraging. Altogether, we recorded 7 territorial pairs and up to 5 lone birds (11 individuals total; Table 1). None of the birds in the study were individually marked, but we mapped existing territories (Bibby et al. 2000) and assumed that singing birds in discrete territories were unique individuals. Songs

were recorded using a Sennheiser K6/ME62 shotgun microphone (Sennheiser Electronic Corporation, Fort Lyne, Connecticut, USA) and a Zoom H2 Handy Recorder (Zoom Corporation, Tokyo, Japan).

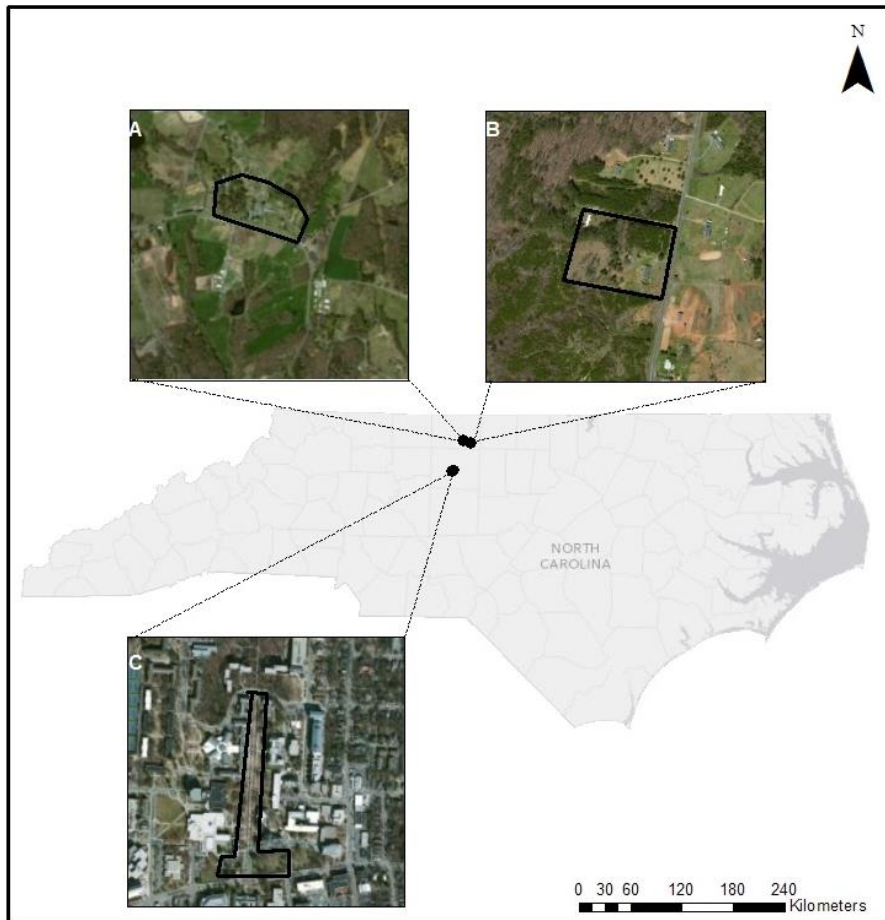


Figure 1. Map showing the 3 study locations in North Carolina, which consisted of 7 contemporary rural territories ((a) 4 at the Upper Piedmont Research Station and (b) 3 at the Grooms Rd site); (c) 9 historical urban territories; and (c) 7 contemporary urban territories. Both historical and contemporary urban sites are at UNCG in Greensboro, NC. Both rural sites are located in southeastern Rockingham County. UNCG and UPRS are 43.13 km apart; UNCG and GR are 48.44 km apart; UPRS and GR are 17.54 km apart. A, B, and C are all at the same scale. Note the difference in land development between A-B and C.

Rural Study Area and Recordings

We collected recordings at four territories from February through June of 2013 at the Upper Piedmont Research Station (UPRS) located in Wentworth, North Carolina. Each territory

consistently contained at least one nesting pair and sporadically contained up to 4 single birds. The UPRS is a working cattle and tobacco research farm characterized by a few large trees surrounded by low shrubs that bordered agricultural fields and adjacent roadways. Like UNCG, the UPRS is located within the Piedmont ecoregion of North Carolina. We also recorded at an additional rural site off of Grooms Road outside of Reidsville, NC. This location had 3 mockingbird territories, each with a single nesting pair. Altogether, there were 11 total rural individual males (Table 1). Habitat structure and composition was similar between both UPRS and Grooms Road. The main sources of noise on both sites were other birds and farm equipment (*e.g.* tractors, large trucks).

Table 1. Summary of data collected for historical and contemporary urban and contemporary rural sites. Recordings ranged from 5-50 minutes in length. Samples were each 30-seconds long.

Site Type	Individuals	Territories	Recordings	Selections
Urban _{Historical}	11	9	37	589
Urban _{Contemporary}	11	7	21	207
Rural _{Contemporary}	11	7	14	930

Equal sampling effort was exerted for both the contemporary urban and rural sites. Sampling began on February 8, 2013, although the first rural recording was not made until March 5, 2013. Each site was visited 7 – 10 times per month and each visit lasted approximately 2 hours.

Ambient Noise Recording

Sound pressure was measured 1.5 meters above the ground before, during, and after all recordings of mockingbird vocalizations at contemporary urban and rural sites using a

CheckMate CM-140 handheld sound pressure level meter (Galaxy Audio, Wichita, Kansas, USA). Ambient sound measurements were used to determine the difference, if any, between the background noise levels of the urban and rural sites. For our purposes, background noise is any noise not made by the bird itself, especially anthropogenic noise. Comparable measurements were not available for the historical recordings.

Recording Analysis

Spectral characteristics of historical and contemporary recordings were analyzed using RavenPro (version 1.5) sound analysis software (www.birds.cornell.edu/raven). Sound below 1200 Hz was primarily anthropogenic and contained no reliable mockingbird song. Frequencies below 1200 Hz were therefore removed from analysis. Sound spectrograms of each song were constructed using 16-bit resolution, 44100 Hz sampling rate, 90% overlap, 1025 FFT, and a Hamming window. We chose 30-second selections from the highest quality segments of the recordings for analysis. High-quality recordings were those with low background noise, minimal conspecific and other types of interference. We modified the approach of Francis et al. (2011) and Slabbekoorn (2003, 2006, 2013) who measured minimum, maximum, and peak frequencies (Hz) as evidence of frequency shifts in bird song by also including the: first and third quartile frequency (Hz), interquartile bandwidth (Hz), 5% and 95% frequency (Hz), peak frequency (Hz), and center frequency (Hz).

Statistical analysis

We compared historical and contemporary energy distribution metrics using a linear mixed effects model (LME) fitted by restricted maximum likelihood (REML) (Francis et al.

2011). This approach suited the unbalanced and observational nature of the study design and reinforced our inferences by including both fixed and random effects (Zurr et al. 2009). Recording location and historical status (contemporary or historical) were included as fixed effects within the model. Date and seasonality were included as random effects within the model. *Date* was the specific day-month-year while *seasonality* encapsulates larger units of time: *month* and *quarter*. *Quarter* broke the entire study duration into two intervals, February – March and April – June. We incorporated both these random factors: date and seasonality into the model to determine the effect of temporally-mediated song characteristics (Ripmeester et al. 2010). Model selection procedures based on second-order Akaike's Information Criterion (AICc) were used to identify the most parsimonious models with small sample sizes (Bolker et al. 2009). We fit models using package lme4 (Bates et al. 2014) in program R (R Development Core Team 2012).

We were unable to compare historical and contemporary ambient sound levels due to a lack of historical ambient sound level measurements. We conducted t-tests and F-tests (Markowski and Markowski 1990) to compare ambient sound levels for contemporary urban and rural sites.

RESULTS

In total, we analyzed 863 useable song-minutes from 33 individuals (11 U_H, 11 U_C, 11 R_C). The mean noise level was 49.367 dB in the rural site ($\min_{\text{avg}} = 40.017$ dB; $\max_{\text{avg}} = 57.382$ dB) and the mean noise level in the urban site was 60.862 dB ($\min_{\text{avg}} = 52.610$ dB; $\max_{\text{avg}} = 67.130$ dB); ($t_{1,90.118} = -5.7679$, $p < 0.001$).

Historical-Contemporary Urban comparison

Mockingbirds at the historical site had songs with lower high-frequency values but similar low-frequency values compared to contemporary urban mockingbirds (Fig. 2). We found significant differences between historical and contemporary sites for all of the metrics that described high-frequency bands of the spectrograms (i.e. 95% frequency (Hz), third quartile frequency (Hz), and peak frequency (Hz)). Center frequency (Hz), first quartile frequency (Hz), and 5% frequency (Hz) did not show significant differences. Range metrics (i.e. 90% bandwidth (Hz) and interquartile range bandwidth) were significant, confirming the presence of the high-frequency shifts within the urban mockingbird songs.

Historical mockingbird songs had lower peak frequencies (LME ANOVA χ^2 $p < 0.001$) and less energy in the higher bands of the spectrogram (95% frequency (Hz) χ^2 $p < 0.001$; third quartile frequency (Hz) χ^2 $p < 0.001$). Historical and contemporary songs had similar low-frequency band usage (5% frequency (Hz) χ^2 $p = 0.469$; first quartile frequency (Hz) χ^2 $p = 0.974$). Center frequency (Hz) did not differ significantly (χ^2 $p = 0.119$).

Two of the historic territories were unavailable for contemporary comparisons due to campus construction activities. Therefore, these two sites were excluded from the U_h-U_c comparisons.

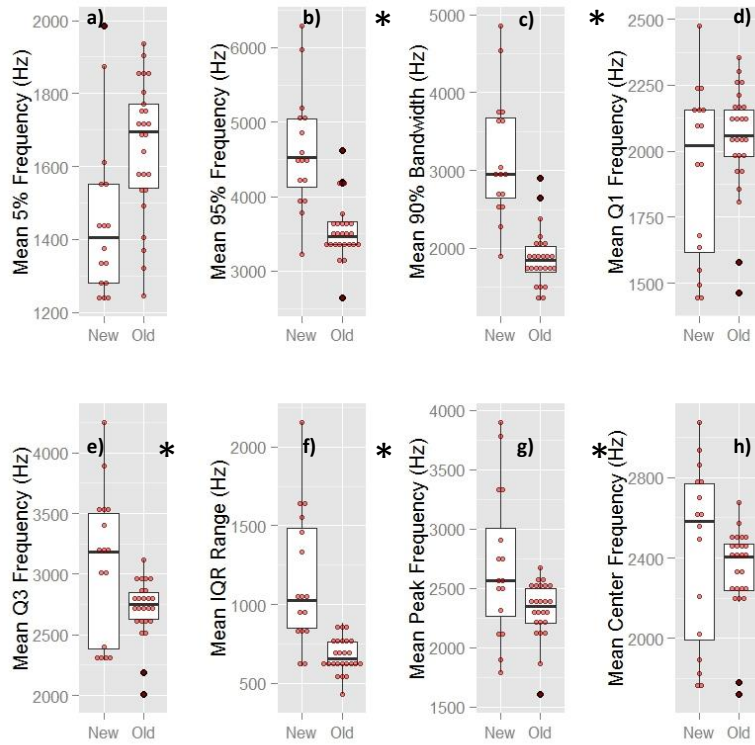


Figure 2. Overview of the spectral differences between historical urban males (n=11) and contemporary urban males (n=11). The boxplots show median (line), interquartile range (box), 95% range (whiskers), outliers (dark dots), and a horizontal dot plot for each group (light dots). Plots **b**, **c**, **e**, **f**, and **g** show significant differences. Each of these significant plots is marked with an asterisk (*). All of these are associated with either high-frequency bands (**b**, **e**, **g**) or range metrics (**c**, **f**). Plots **a**, **d**, and **h** do not show significant differences between historical and contemporary birds and are associated with low-frequency metrics.

Contemporary Urban-Rural comparison

Mockingbirds were actively singing at our urban site when we began sampling on February

8, 2013 but the first singing birds were not detected at our rural sites until March 11, 2013.

Mockingbirds were seen at the rural sites and at residences near the rural sites before they

began singing. We detected a lack of site level frequency differences between rural and urban

sites (5% frequency (Hz) χ^2 p= 0.542; 95% frequency (Hz) χ^2 p= 0.140; 90% bandwidth (Hz)

χ^2 p= 0.299; first quartile frequency (Hz) χ^2 p= 0.305; third quartile frequency (Hz) χ^2 p=

0.338; interquartile bandwidth (Hz) χ^2 p= 0.637; peak frequency (Hz) χ^2 p= 0.945; center frequency (Hz) χ^2 p= 0.406; Fig. 3), contrary to many recent studies of other passerines (*cf.* Slabbekoorn and Peet 2003; Brumm 2004; Francis et al. 2009; Francis et al. 2011; Slabbekoorn 2013). Contemporary urban and rural populations sang at the same higher frequency range compared to the historical urban song characteristics. We detected a territorial pair level difference among all metrics except for IQR bandwidth and peak frequency (Table 2). These differences indicate a general variation in frequency distribution change across the summer season.

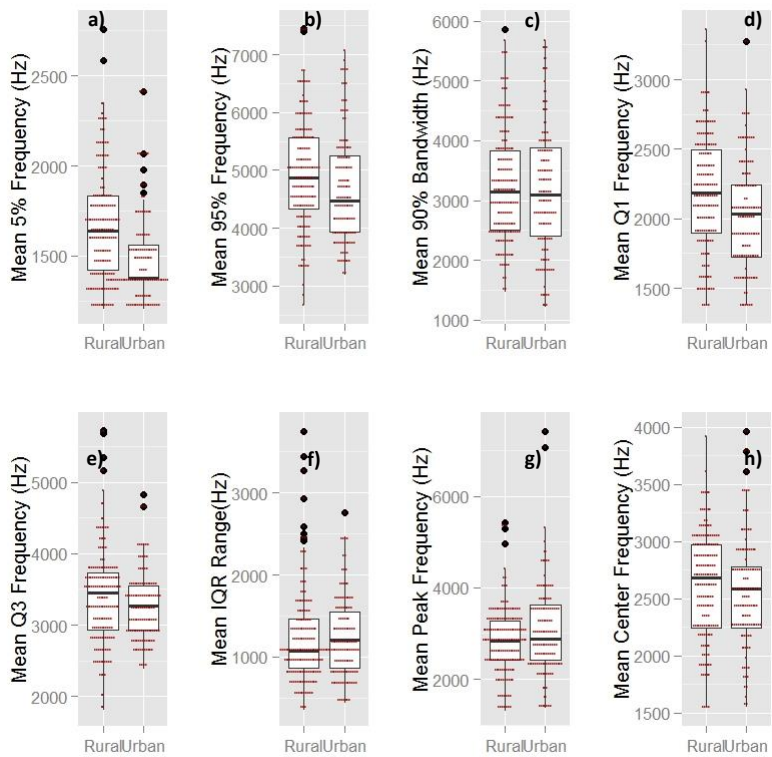


Figure 3. Overview of the spectral differences between contemporary urban (n=11) and rural (n=11) males at each of the 8 spectral characteristics. The boxplots show median (line), interquartile range (box), 95% range (whiskers), outliers (dark dots), and a horizontal dot plot for each group (light dots). No plots show significant differences at the site level.

Table 2. Summary ANOVA (Analysis of Variance and Deviance) results for changes in temporal characteristics (song timing throughout summer season) among urban and rural territories. We used a LME model with specific date and site type as random effects and the interaction of site type, specific territory, and month as fixed effects. *Month* encompasses April, May, and June of 2013.

Response	χ^2	df	F-value	χ^2 p-value
5% Freq (Hz)	24.0	8	3.73	<0.001
95% Freq (Hz)	30.0	8	5.12	0.03
90% Bandwidth (Hz)	22.8	8	5.80	<0.001
First Quartile Freq (Hz)	36.9	8	1.03	<0.001
Third Quartile Freq (Hz)	17.6	8	4.18	0.02
IQR Bandwidth (Hz)	8.0	8	3.58	0.43
Peak Freq (Hz)	13.2	8	1.48	0.10
Center Freq (Hz)	41.8	8	1.63	<0.001

Ambient sound

The minimum mean ambient noise levels and maximum ambient noise levels differed between urban and rural locations. Urban sites had consistently higher maximum noise levels (rural: 57.382 dB, urban: 67.130 dB; $t_{1,49} = -4.147$, p-value < 0.001) and rural sites had consistently lower minimum noise levels (rural: 40.017 dB, urban: 52.610 dB; $t_{1,49} = -8.568$, p-value < 0.001). Shapiro-Wilks tests were run to ensure the assumption of normality held (Urban_{max}: $W = 0.9624$, p-value = 0.148; Rural_{max}: $W = 0.945$; p-value = 0.356). The overall mean ambient noise levels differed as well (Rural_{mean} = 49.367; Urban_{mean} = 60.862; $t_{1,90} = -5.768$, p-value < 0.001).

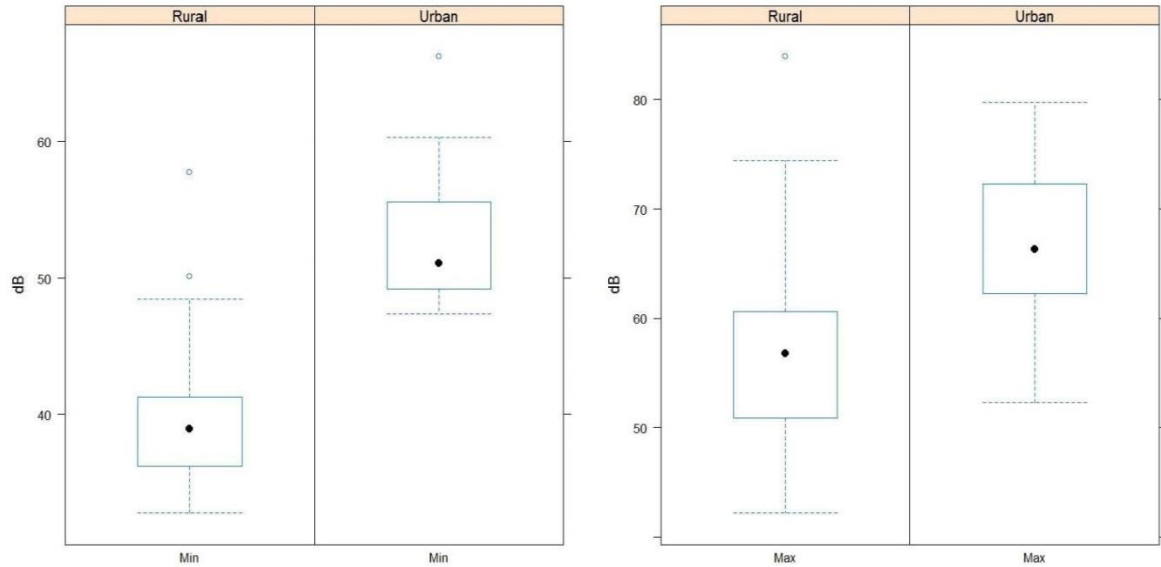


Figure 4. Plots of the average ambient sound data between the contemporary urban and rural sites. The rural sites had lower minimum and maximum average ambient noise. There was roughly 10 dB difference each between the minimum means, maximum means, and overall means of the rural and urban sites.

DISCUSSION

Our historical-contemporary comparison results were similar to those of other recent studies (*cf.* Wood and Yezerinac 2006; Francis et al. 2009; Gross et al. 2010; Ripmeester et al. 2010). Contemporary male mockingbirds increased the high-frequency components of their song while the low-frequency content remained unchanged compared to the mockingbird population occupying the same territories thirty years prior. These findings support Dowling et al. (2011)'s claim that minimum and maximum frequency modulation cannot happen simultaneously. We did not detect any site level frequency differences between contemporary urban and rural sites. The results of this study are contrary to findings for some comparisons of urban and rural bird populations (*cf.* Slabbekoorn and den Boer-

Visser 2006; Gross et al. 2010; Francis et al. 2011), but they are similar to results for forest and city dwelling European Blackbird populations; neither European Blackbird population showed differences between spectral characteristics and ambient noise (Ripmeester et al. 2010). Contemporary urban and rural mockingbird song differed in their frequency distributions among months. These differences may be associated with a novel adjustment to differing levels of anthropogenic disturbance or may simply be capturing natural temporal variability or individual variation among resident mockingbirds. More intensive studies focused on song timing and singing rates are necessary to tease out the mechanism responsible for the observed changes. However, differences in song timing but not spectral characteristics of the song suggest that both populations have similarly acoustically adjusted to the increasingly noisy environment while finding different mating and/or nesting strategies to maximize breeding and survival potential. Given the synurbic nature of mockingbirds, it is not surprising that differences in song frequency were not significant between rural and urban populations. Even in the rural habitats, mockingbirds are tied almost exclusively to people. They do not exhibit an extreme habitat contrast like other species that are more prevalent in acoustic disturbance studies.

Although the rural and urban individuals were experiencing different levels of acoustical disturbance, the birds appeared to have responded to changing sound environments over the past thirty years similarly. In our study, on average, rural areas tended to be quieter than urban areas. It should be noted that the decibel scale is log-based rather than linear. The average 10 decibel difference between the urban and rural sites are interpreted by the average human as a doubling of sound intensity (Sataloff and Sataloff 2006). The rural mockingbirds

were found close to roads and buildings where anthropogenic noise was concentrated. Mockingbirds, therefore, tend to experience more similar acoustic environments in urban- and rural-classified habitats than do classic “urban avoider” species. Mockingbirds, in both our urban and rural plots, chose nesting and foraging sites that included at least one high perch (e.g. a tall tree or utility pole) for singing, an area of low, dense cover (i.e. bushes or shrubs) for nesting, and an open, grassy area for foraging. The similarity of microhabitat selection by birds at both our rural and urban sites suggests that differences in habitat structure may not have a large influence on the characteristics of mockingbird song in our sites (Wilkins et al. 2013).

In this study, differences measured between rural and urban birdsong were seasonal rather than frequency-based. It should be noted that these data are not comprehensive and should be expanded upon in future studies. Our preliminary data suggest that rural mockingbirds at our sites sang later in the season than urban mockingbirds. Urban males begin singing earlier than rural males because there is likely greater competition for urban habitats (Ripmeester et al. 2010). Conversely, higher availability of habitat and less competition for mates in rural areas may result in relatively later mating displays. Urban mockingbird territories are smaller and more densely arranged than those of rural mockingbirds (Stracey 2010). Male mockingbirds cease singing after they find a mate and continue in relative silence until after the chicks have fledged (Michener and Michener 1935; Laskey 1944). Our data suggest that urban males begin their post-clutch song in earnest earlier than rural males, which suggests earlier pairing. Additionally, an increase in the number of neighbors is correlated with an increase in song output by territorial male

mockingbirds (Michener and Michener 1935; Derrickson 1987). The larger proportion of mockingbirds per unit area could naturally result in higher and earlier song output as well (Stracey 2010).

The mechanisms driving the observed frequency shifts and behavioral changes are not well-understood, but persuasive theories have been put forth by Gross et al. (2010) and Wood and Yezerinac (2006). Gross et al. (2010) found that Reed Buntings (*Emberiza schoeniclus*) rely on short-term vocal adjustments to adapt to increasingly noisy environments. These adjustments, manifest as song length, minimum frequency, and/or song rate modification, are evidence of plastic behaviors that serve to increase a male's chances of pairing success during the breeding season. Evidence from our study suggests that vocal adjustment may occur over longer time scales because the changes are seen between data taken thirty years apart.

Based on the available data, it is impossible to assert any genetic cause for the vocal adjustments seen in the urban populations except to note that adult male mockingbirds are typically faithful to their territories, especially if foraging and nest sites are abundant and despite the fact that there is strong competition for mates and habitats (Michener and Michener 1935; Logan and Fulk 1984). Regardless of the mechanism, it is clear that our rural and urban populations of mockingbirds show distinct song frequency distributions. Similar patterns observed in Song Sparrows (*Melospiza melodia*) have been discussed by Wood and Yezerinac (2006) who identify four possible pathways for frequency modification that are in birds relevant to this study: (1) *Mockingbirds change only the frequency (not the content) of their songs to negotiate around low-frequency anthropogenic noise and*

subsequent masking. This change is an immediate, extemporaneous, and reversible shift that may result from the mockingbird's inherent behavioral plasticity. Birds not exposed to this sort of variable noise do not exhibit the same degree of behaviors, although they possess the plastic capacity. (2) *Mockingbirds change the suite of songs that they choose to mimic so as to avoid low-frequency interference with anthropogenic noise*. This behavioral modification could be the result of plastic behaviors that, due to sexual selective pressure and male success, could result in microevolutionary change. Notably, there is currently no evidence of microevolution and subsequent genetic differentiation in the Great Tits whose genetics have been extensively studied (Slabbekoorn and Ripmeester 2008). There must be some element of choice, however conscious, in mockingbird song since new mimics are constantly added, some being only temporary acquisitions (Laskey 1944; Brenowitz and Beecher 2005). (3) *The actual community of conspecifics has changed in such a way that the songs available to comprise present-day mockingbird repertoires are markedly and measurably different than those available in the past*. The makeup of the avian community has been winnowed to mainly urban exploiters and urban adapters, so contemporary mockingbirds' repertoires are likely comprised of different songs than past repertoires. The mockingbirds have not modified their own behaviors, but are simply an observable symptom of long-term changes in the local community. (4) *Individuals have experienced an ontogenic change influenced by early song learning*. The result of this change would be songs that more accurately match the noisiness of the mockingbird's environment. This seems unlikely given the evolutionarily short time between our measurements of the historical and contemporary population and the fact that mockingbirds do not have a critical period of song learning followed by song

crystallization as other songbird species do (Derrickson 1988; Wood and Yezerinac 2006). However, this could induce a long-term adaptation if there is significant sexually selective pressure. Ontogenic explanations for frequency shifts are not as convincing as those of behavioral plasticity or community change because mockingbird songs do not include mimics until aged 4.5 months or so (Laskey 1944) although they start singing around one month after fledging (Michener and Michener 1935; Laskey 1944).

Evidence that the content of mockingbird songs is dependent on the makeup of the community in which they live (Michener and Michener 1935; Stracey 2010) suggests that community composition may be the main driver of the frequency shifts we observed, although alternative hypotheses, such as a combination of hypotheses two and three are certainly plausible. We might expect smaller differences in contemporary comparisons of urban and rural populations because mockingbirds are strong urban adapters. Therefore differences in the sound environment experienced by urban and rural birds may be less than it is for species more tied to undisturbed habitats. In contrast the differences in the sound environment experienced by our contemporary and historic urban mockingbirds may have been relatively larger. We predict different patterns in a comparison of urban avoider species such as a Red-eyed Vireo (*Vireo olivaceus*) at contemporary urban and rural sites. In such a case, results would be more likely to resemble those of Francis et al. (2011) which found changes in both timing and frequency distribution of Plumbeous and Gray Vireos due to increased anthropogenic noise. Species with songs comprised of lower mean frequencies might have been driven from the urban territories due to an inability to communicate in the

altered noise environment. If this is the case, urban mockingbirds would have been left with fewer low-frequency mimetic options, regardless of their actual ability to alter their song composition. This explanation could be tested by rigorous analyses of the song constituents of many individuals from both rural and urban habitats. Mockingbirds are also pre-adapted for vocal adjustment due to their mimetic capabilities. Irrespective of acoustic disturbance, mockingbirds naturally fit their songs to their environment by means of repertoire modification. For these reasons, a mockingbird's responses to urbanization might not be as distinct, both in vocalizations and ecology, as a songbird species with a simple song and extreme habitat contrasts such as the Carolina Chickadee (*Poecile carolinensis*) or the Tufted Titmouse (*Baeolophus bicolor*).

Understanding the mechanisms behind the differences in the distribution of sound energy and singing rates that we observed will require more intensive studies of banded individuals and detailed genetic data. Captive breeding and reciprocal transplant experiments could be employed to get at the underlying behavioral modifications that lead to frequency shifts. Although we used AICc values to select the most parsimonious models of our data, we recognize the limitations of our conclusions due to relatively small sample sizes to and possible confounding factors that were beyond the scope of this study. We further acknowledge that the diverse and unique song repertoires of mockingbirds may have resulted in conclusions that were less clear cut than they might have been in other Passerines with simpler songs. The Northern Mockingbird is a unique and challenging species in many aspects of its biology. Nevertheless, mockingbirds clearly alter both the spectral characteristics of their song in order to mitigate interference by anthropogenic noise.

Although more work is necessary to define the mechanisms by which these alterations occur, the results of this and similar studies have important implications for understanding and possibly mitigating the effects of anthropogenic noise on wildlife.

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