

Causes and Consequences of Urban-associated Song Variation: A Study of Vocal
Behavior in the Northern Cardinal (*Cardinalis cardinalis*)

THESIS

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ABSTRACT

Animal communication systems, which rely upon complex cognitive behavior, specific social contexts, and environments that permit effective transmission, are vulnerable to disruption by anthropogenic disturbance. Forests in urban landscapes are known to differ from rural forests in terms of invasive exotic shrubs, avian communities, and anthropogenic noise. Although these urban-associated differences can elicit demographic consequences, little is known about the sub-lethal behavioral effects. Recent studies have implicated anthropogenic noise as a cause of changing bird song in urban areas; however, few have considered alternative explanations, nor the evolutionary and ecological consequences of altered songs. I investigated song variation in an urban landscape by asking the following questions: 1) How do the structural and behavioral components of bird song change across a rural-urban landscape gradient? 2) Which aspects of urbanization (e.g., noise pollution, invasive plants, avian community and morphology) best predict changes in song properties? and 3) Does urbanization alter relationships among song, indicators of fitness (e.g., reproductive output), and male quality (e.g., morphology, parental care and territory quality)? I investigated these questions by recording vocal behavior and monitoring the breeding activity of 54 individually-marked male Northern Cardinals (*Cardinalis cardinalis*) at nine sites distributed across riparian forests within a rural to urban landscape gradient in central Ohio in 2011.

Forests within urban versus rural landscapes differed ecologically so that urban forests had greater densities of conspecifics, denser understory vegetation with greater numbers of large trees, louder ambient noise (primarily from traffic), and smaller birds than more rural forests. As expected, cardinal song also changed with urbanization, with songs becoming longer, faster and with higher minimum, maximum and peak frequencies (Hz) as urbanization increased. Ambient noise at the territory level explained shifts in minimum frequency, whereas changes in conspecific densities best explained temporal variation in song structure (e.g., song length and syllable rate). Peak and maximum frequencies were not well explained by habitat or morphological models and instead may be driven by factors not considered in this study, such as cultural dialects.

Relationships between song and indicators of fitness and quality were not consistent across landscapes for some, but not all, song characteristics. In rural landscapes, the largest birds sang songs that were short and slow; however, song of urban males was not associated with body size. The lack of an association between song and body size in urban birds may be due to increased interspecific aggression from the aggregation of high numbers of territorial males. Thus urbanization may weaken the usefulness of temporal aspects of song as a reliable indicator of size. Relationships between song and parental care were consistent across landscapes, where birds that sang short, slow songs provisioned less and had nestlings in poorer condition. Males that used higher minimum frequencies also had nestlings in poor condition, a possible effect of habitat quality in noisy territories. Male song was not related to reproductive output or territory quality in either landscape.

To my knowledge, this is the first study to simultaneously evaluate the evidence for multiple potential mechanisms of urban-associated changes in song, as well as investigate consequences for signal reliability and fitness. These results suggest that a variety of factors, not anthropogenic noise alone, influence song in urban birds and these changes can affect signal reliability in novel environments.

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CHAPTER 1

SONG BEHAVIOR AND URBANIZATION: A LITERATURE REVIEW

INTRODUCTION

In recent years, biologists have recognized the enormous impact of urban development to ecosystems, which has stimulated a wide variety of research in urban ecology. Urbanization profoundly changes the landscape through increasing habitat fragmentation and spatial heterogeneity (Irwin and Bockstael 2007) and widespread homogenization of local biota (McKinney 2006). The amount of urbanization surrounding a forest can elicit a number of changes within interior habitat as well. Urban forests generally have altered vegetation (Porter et al. 2001, Borgmann and Rodewald 2005) and predator communities (Rodewald and Kearns 2011), as well as increases in artificial light (Longcore and Rich 2004), accelerated phenology (Neil and Wu 2006), environmental contaminants (Pouyat and McDonnell 1991), and noise pollution (Slabbekoorn and Peet 2003). These abiotic and biotic changes can have cascading effects on wildlife populations and behavioral interactions as well as impose novel selection parameters on the species that are able to persist in these areas.

Our understanding of the ecological impacts of urban development on birds has increased significantly in part because of their ease of study and persistence in urbanized areas. The direct and indirect effects of urbanization on birds can occur across multiple scales and have significant ecological impacts (Blair 1996). Generally, urban bird communities have lower species richness and density of sensitive species but higher

abundance of generalist, opportunistic species (Rottenborn 1999, Marzluff et al. 2001, Shochat et al. 2006). Urbanization can also affect reproduction by prompting earlier lay dates, smaller clutch sizes, lower nestling weights and lower productivity (Chamberlain et al. 2009; but see Leston and Rodewald 2006, Rodewald and Shustack 2008a). Urban areas can have abundant exotic vegetation (Borgmann and Rodewald 2005), supplemental resource subsidies (Atchison and Rodewald 2006, Robb et al. 2008), altered predation communities and pressure (Jokimäki and Huhta 2000, Ryder et al. 2010, Rodewald and Kearns 2011) and increases in environmental noise (Slabbekoorn and Peet 2003, Katti and Warren 2004, Patricelli and Blickley 2006, Slabbekoorn et al. 2007). However, to date our understanding of the ways that urban-associated changes in the environment, communities, and resources can affect birds at individual and population levels remains incomplete. While certain ecological changes may promote population persistence for some synanthropic species, there may be sub-lethal impacts on individuals and populations.

Unlike direct ecological impacts like predation or resource availability, ambient noise has the potential to indirectly affect wildlife communities. Noise is of high importance to birds because of their reliance on vocal communication for species and individual recognition, mate attraction and territorial defense (Bradbury and Vehrencamp 1998). A wide range of human activities including traffic, airplanes, and industry, produce low-frequency background noise in urban environments (Berglund 1996). Indeed, urban forests have higher noise than forests near rural areas (Slabbekoorn and Peet 2003, Seger et al. 2010) and noise can permeate large distances into adjacent woodlands from sources (Reijnen et al. 1995). Urban noise can radically alter acoustic

environments in ways that affect wildlife behavior and demographics (Katti and Warren 2004, Patricelli and Blickley 2006), and as such has been cited as the driver of changes in avian community structure (Francis et al. 2009), population densities (Reijnen et al. 1995, Bayne et al. 2008), vocal communication (Patricelli and Blickley 2006, Slabbekoorn and den Boer-Visser 2006) as well as reproductive success (Habib et al. 2007) and community interactions (Francis et al. 2009, Barber et al. 2010).

Currently, we have a poor understanding of the ways environmental change can influence behavior, especially for those traits used in communication and sexual selection. Studies in urban areas provide a unique opportunity to evaluate the impacts that novel environmental conditions have on song variation and reliability of the information contained in acoustic signals. Communication signals have important functions in conspecific attraction (Betts et al. 2008), territory acquisition & breeding success (Catchpole 1987) and sexual selection (Searcy and Andersson 1986, Catchpole 1987, Ballentine et al. 2004), and hence understanding the maintenance of mating signals is important for effective management within and between sensitive populations. Bird song can also be highly influenced by variation in the physical environment (Bradbury and Vehrencamp 1998, Slabbekoorn and Smith 2002), social interactions with other individuals (Ritchison 1988) and individual performance limits (Podos 1997, Podos et al. 2001). The conspicuous use and sensitivity to environmental conditions make song an ideal cue to investigate the influence of urbanization on sexual traits and mating patterns.

LITERATURE REVIEW

Song Ecology

In passerines, song is a conspicuous acoustic signal with primary functions in both mate acquisition and territory defense (Kroodsma and Miller 1996). One definition of ‘song’ is vocalizations that are made in a “sustained, quasi-rhythmic performance” (Smith 1996). Song is constrained by the ability of the individual to perform near its energetic, morphological or physiological limit as well as within contextual and environmental limitations (reviewed in Gil and Gahr 2002). Some song characteristics increase the difficulty of vocal performance (Podos 1997) or are limited by morphology (Ryan and Brenowitz 1985, Derryberry 2009) indicating that males should only perform songs that maximize transmission efficiency to the receiver while not exceeding performance ability (Lambrechts 1996).

Information about individual identity, motivation and quality may be expressed in the content of song through variation in song attributes (Becker 1982). For example, individual white-crowned sparrows (*Zonotrichia leucophrys*) from distinct populations can be identified by unique song elements (Nelson and Poesel 2007). Song may also represent carry-over effects from the non-breeding season, and produce a signal of dominance status (Otter et al. 1997, Christie et al. 2004). Generally, high among-individual variation in song characteristics and high variation in songs used in the presence of conspecifics suggests that song structural characteristics may be limited by individual abilities (Ritchison 1988).

Song is costly to develop and display (Nowicki et al. 2002, Gil and Gahr 2002) and vocalizations often act as reliable indicators of male quality (Searcy and Andersson 1986, Catchpole 1987, Andersson and Iwasa 1996). Mating signals and female response evolve together through intersexual selection so that females may prefer some elaborate attributes of song over others because of direct (i.e., territory quality) or indirect (i.e., genetic) benefits (Catchpole 1987). A synthesis of research to date suggests a general pattern of female preference for more complex song with higher vocalization rates over less variable song at low rates (Searcy and Yasukawa 1996) but this pattern may not always be the rule (Conner et al. 1986, Shutler and Weatherhead 1990). Song can also provide information to neighboring males and new recruits regarding the condition and status of the territorial male (Peake et al. 2001, Searcy and Beecher 2009), age/size (Ballentine 2009) and parental ability (Buchanan and Catchpole 2000). In addition, females display more often to songs that are challenging or of higher performance (Ballentine et al. 2004) thereby actively use song information to evaluate mates.

Song characteristics can also vary as they relate to fitness components. Song amplitude and complexity is related to reproductive success (Catchpole 1987), male longevity and extra pair paternity (Forstmeier et al. 2002). Song rates can be associated with early territory settlement and nesting success (Hoi-Leitner et al. 1995) as well as nest maintenance and defense (Greig-Smith 1982, Welling et al. 1997). Quality may also be indicated by the species' ability to perform certain songs along a continuous range and make plastic adjustments when necessary (Christie et al. 2004).

Environmental Constraints on Song

Sexual traits are developed not only by genes and female preference but also the social and environmental context (Badyaev and Qvarnström 2002) and this holds especially true for acoustic signals. Bird song is a highly variable behavior that is strongly influenced by the surrounding habitat to facilitate efficient transmission of the signal to the receiver (Wiley et al. 1991, Bradbury and Vehrencamp 1998, Lohr et al. 2003). The acoustic adaptation hypothesis supposes strong selection for vocalization traits that transmit most efficiently given a particular habitat type (Morton 1975). A plethora of physical and social environment attributes contribute to natural selection on bird song characteristics including wind, water currents, insects, vegetation, conspecifics and heterospecifics (Bradbury and Vehrencamp 1998, Brumm and Naguib 2009, Kirschel et al. 2009). In addition, urbanization drastically alters the physical environment that birds inhabit yet communication still occurs between individuals.

Noise

There is strong evidence of selection for vocalization structure in the presence of environmental noise (Ryan and Brenowitz 1985, Brumm and Slabbekoorn 2005) because environmental noise can mask sounds occurring in the same acoustic space. The song of tropical birds vary over different habitats due to the presence of different insect communities selecting against song that occurred in the same frequency (Slabbekoorn and Smith 2002, Kirschel et al. 2009). In more natural areas, birds compete with abiotic

background noise as well, in the form of wind, surf or torrent water, and favor high-pitched frequencies (Brumm and Slabbekoorn 2005). Within an avian community, a species' song tends to occupy an acoustic space that avoids overlap with other species with similar vocalizations (Nelson and Marler 1990). Shifting frequencies higher or lower to avoid masking can successfully improve transmission of signals, as long as the change can still be understood by the receiver.

Urban environmental noise is produced predominantly from surrounding anthropogenic sources and occurs in high amplitudes, with sound energy primarily in the lowest frequencies (<2 kHz) (Slabbekoorn and Peet 2003). Noise can occur in both predictable homogenous (i.e., chronic noise from traffic) and infrequent heterogeneous forms (e.g., fly-over planes, temporary constructions) (Katti and Warren 2004). Peak noise from rush-hour traffic also occurs in the morning during the highest bird activity (Warren et al. 2006) and traffic forms a noise gradient from major roads (Diaz et al. 2011). Presumably, anthropogenic noise has the potential to impact singing behavior and song structural characteristics by masking vocalizations that occur in the same frequency or overpowering vocalizations with higher amplitudes selecting for shifts to higher frequencies (Brumm and Slabbekoorn 2005).

Other Constraints on Song

Several studies have cited anthropogenic noise as the likely source of changes in urban vocal behavior (Slabbekoorn and Peet 2003, Brumm 2004, Slabbekoorn and den Boer-Visser 2006) although there may be other mechanisms in action. Aside from noise

pollution, urbanization can elicit dramatic changes in vegetation, wildlife densities and resource availability, which in turn can affect development and maintenance of acoustic signals.

Vegetation

Habitat composition and structure can impact the development and maintenance of acoustic signals because attenuation of sound depends on the sizes and numbers of objects that interfere with the acoustic wavelength (Bradbury and Vehrencamp 1998). For example, song frequencies in birds are dependent on how differences in habitat structure and openness influence transmission properties (Morton 1975, Wiley 1991, Kirschel et al. 2009). Indeed, birds that vocalize in open, low, or small-stem density habitats tend to utilize songs that are fast, have high frequencies and many modulations (Wiley et al. 1991, Bradbury and Vehrencamp 1998). Even within one coarse habitat type, song attributes can vary with vegetation structure, by way of tree densities (Anderson and Conner 1985). Birds in adjacent habitats where vegetation is structurally different can have concordant song divergence (Patten et al. 2004) which may eventually lead to species isolation through communication disconnection across large or fragmented spatial scales (Slabbekoorn and Smith 2002).

Urbanization often promotes changes in vegetative structure which could potentially influence bird song characteristics. For example, invasion of urban habitats by Amur honeysuckle (Borgmann and Rodewald 2005) creates a dense sub-canopy of vegetation that may impede vertical and understory song transmission. Dense woody

stems in young forests should select for song characteristics that are low pitched and at faster rates (Tobias et al. 2010). Urban forests can also have less overall trees but more large trees creating a patchy fragmented canopy with open understory (Porter et al. 2001). Alternatively, large trees can increase scattering effects, and birds should use vocalizations that have higher frequencies and slower rates (Wiley 1991, Bradbury and Vehrencamp 1998, Tobias et al. 2010). Urban forests are also characterized by advanced leaf phenology (Shustack et al. 2009), resulting in an early spring green-up that increase reverberations of song earlier in the season when territory acquisition and pair bonding is occurring.

Densities

Conspecific densities can also influence vocal behavior by affecting social opportunities and antagonistic motivational states. High densities promote competition for space and resources and territorial interactions between males. Males sing at faster rates (Ritchison 1988, Penteriani 2003) and higher frequencies (Shackleton and Ratcliffe 1994) when male-male competition is high or during aggressive contexts. Aggression can increase frequencies by tightening vocal organs (Bradbury and Vehrencamp 1998) or be an artifact of singing louder (Brumm 2004, Brumm and Slabbekoorn 2005, Nemeth and Brumm 2010). Birds can also use particular song types in antagonistic encounters to match the song of their neighbor, or signal aggressive intent (Vehrencamp 2001, Christie et al. 2004, Searcy and Beecher 2009). High densities may also strengthen sexual selection for ornamental traits by increasing competitive and mating opportunities

(Penteriani 2003, Ryder et al. 2012) and serving as a proxy for resource availability (Rodewald and Shustack 2008a).

Urban areas can prompt changes in the community structure of birds and population densities. Generally, urban areas support higher densities of resident, and short-distance migrant generalists and lower densities of long distance, neotropical migrant specialists (Shochat 2004, Rodewald and Bakermans 2006). Urban habitats are known to have more food and nesting cues that cardinals use to select breeding habitats and support up to five times higher densities than rural forests (Leston and Rodewald 2006). Given that noise alters soundscapes, urbanization can negatively impact densities as well. Areas near traffic noise support high-frequency vocalizing species and limit low-frequency species despite vegetative similarities (Hu and Cardoso 2010, Goodwin and Shriver 2011). Densities are also lower in areas that are noisy or near roads (Reijnen et al. 1995, Habib et al. 2007, Bayne et al. 2008, Francis et al. 2009, Slabbekoorn and Halfwerk 2009). If bird density is correlated with vegetative cues or physical inhibitors like noise, this may lead to spurious relationships with song variation.

Individual Performance

In addition to the social environment, the production of song can be constrained by morphology or physiology. Song can indicate a male's body size because larger birds tend to sing songs of lower frequencies (Wiley 1991, Ryan and Brenowitz 1985, Handford and Loughheed 1991, Gil and Gahr 2002, Ballentine 2009). Likewise, bill morphology can limit the ability of a singer to produce frequency or temporal

modulations (Podos 1997). Consequently, contemporary adaptations in bill shape and structure can drive subsequent variation in song (Podos et al. 2001, Ballentine 2006).

Urban-associated song changes may derive from morphological differences between urban and non-urban individuals. Slabbekoorn et al. (2007) hypothesized that smaller individuals with poorer song performance settle urban habitats. Indeed, in some species, smaller birds in poorer condition settle in urban or lower-quality areas (house sparrows, *Passer domesticus*: Liker et al. 2008, Acadian flycatcher, *Empidonax virescens*: Rodewald and Shustack 2008b), although, this may not always be the case for urban-adapting species (Black-Capped chickadees, *Poecile atricapillus*: Van Oort et al. 2006, Northern cardinals, *Cardinalis cardinalis*, Rodewald and Shustack 2008a). Changes in food availability, particularly a switch from an insectivorous diet to granivorous supplements, may drive bill changes that also promote song divergence between urban and rural birds (Badyaev et al. 2008, Derryberry 2009).

Physiologically, song modulations may incur a cost to the condition of the sender (Bradbury and Vehrencamp 1998), however, these costs may be minimal (Ward et al. 2003). Nevertheless, song production can negatively impact condition over time, when time spent singing means less time spent on somatic activities like foraging or vigilance. Birds that are released from food limitation perform higher difficulty songs such as increasing song rates or type switches (Strain and Mumme 1988) and those in poor habitat reduce song output especially in high-quality individuals (van Oort et al. 2007). Even natal nutritional stress can influence later vocal and cognitive performances of adult birds (Nowicki et al. 2002, Buchanan et al. 2003).

Urban areas may contribute differently to the food sources available for birds. Urban areas are characterized by surrounding anthropogenic food supplements (i.e., bird feeders, Atchison and Rodewald 2006) which may contribute to a weaker relationship between a condition-dependent signal and body condition (Jones et al 2010). Increases of invasive vegetation in urban areas (Borgmann and Rodewald 2005) can also facilitate decreases in prey quality and quantity (Magura et al. 2006, Isaksson and Andersson 2007).

Urban Song Variation.

Song variation between urban and rural populations may reflect long-term selective environments for effective communication (Tobias et al. 2010, Luther and Derryberry, 2009) or short-term behavioral plasticity in the production of bird song (Gross et al. 2010, Bermúdez-Cuamatzin et al. 2011). If noise is the driver of acoustic variation, birds can improve signal transmission by singing higher, louder and faster. Indeed, many studies have found consistent patterns of increases in song frequency across species (Great tit, *Parus major*: Slabbekoorn and den Boer Visser 2006, Mockford and Marshall 2009; European Blackbird, *Turdus merula*: Nemeth and Brumm 2009, Reed buntings, *Emberiza schoeniclus*, Gross et al. 2010; Northern Cardinal, *Cardinalis cardinalis*: Seger et al. 2010, Dowling et al. 2012; Song Sparrow, *Melospiza melodia*, Wood and Yezerinac 2006; Grey Flycatcher *Empidonax wrightii* & Ash-throated Flycatcher, *Myiarchus cinerascens*: Francis et al. 2011). Birds also sing shorter songs and at faster rates (i.e., shorter inter-song intervals) (Brumm & Slabbekoorn 2005; Slabbekoorn & den Boer-Visser 2006, Nemeth and Brumm 2009). Additional studies

have also illustrated a higher frequency shift in certain song syllables (Wood et al. 2006), lower energy in low frequency notes (Wood and Yezerinac 2006) as well as an increase in overall song amplitude (Brumm 2004) in the presence of acoustic disturbance. Some song characteristics are able to be immediately manipulated when in the presence of temporary noise such as song frequency (Wood et al. 2006, Gross et al. 2010, Bermúdez-Cuamatzin et al. 2011), amplitude (the Lombard effect: Brumm and Slabbekoorn 2005) or song type (Halfwerk and Slabbekoorn 2009).

Although structural changes are most often documented, birds can change other components of their singing behavior such as temporal or spatial characteristics. Behaviorally plastic aspects of song, such as bout duration or perch height can be manipulated according to contextual needs (Riebel and Slater 2000, Møller 2011). Birds can increase production of song during times of low noise, such as nocturnally (Fuller et al. 2007), during the weekends (Gross et al. 2010, Díaz et al. 2011) or times when traffic volumes are low (Katti and Warren 2004). Birds that sing at high frequencies are not masked by low frequency noise but can lengthen singing bouts in noisy areas to maximize likelihood of being heard (Díaz et al. 2011). Singing from a higher perch will also increase the broadcast area of sound (Møller 2011).

Noise may alter reproductive success of birds if it disrupts communication. Noise was attributed to the low pairing success in ovenbirds (*Seiurus aurocapillus*) (Habib et al. 2007) and reed buntings (*Emberiza schoeniclus*) (Gross et al. 2010). Their territories may be less attractive to females because they are noisy, or noise may be related to areas of poor habitat quality. However, areas near loud roads can be dominated by young males

who produce fewer young than pairs farther from the road despite similar vegetation (Foppen and Reijnen 1994). On the other hand, noise may contribute to higher reproductive success if chronic noise avoidance changes predator-prey dynamics (Francis et al. 2009) because of the sensitivity of non-flexible species that use low frequencies (Rheindt 2003).

Functional Consequences of Urban Song Variation

If songs in urban environments are different, the question remains, what implications do these changes have for the information contained in the signal? To date, our understanding of the functional consequences of changes in song is limited, though emerging evidence suggests the response of receivers varies between urban and non-urban systems. Both males and females inhabiting quieter territories responded more quickly and strongly to song recorded from a quiet territory than from a noisy territory and vice versa for birds in noisy areas (Mockford and Marshall 2009, Luther and Derryberry 2012, Halfwerk et al. 2011). Different responses may be indicative of a tradeoff between urban song variation and efficacy or an artifact of song familiarity between populations, however, a possible disconnection between song and signal information should be further explored. Even though habitats may impose different selective pressures on signals (Higginson and Reader 2009, Cornwallis and Uller 2010), few studies have investigated whether relationships between mating signals and fitness parameters hold across populations in different habitats. This may be because the current trend in behavioral research is to focus exclusively on a single population (Cornwallis

and Uller 2010). Despite this limitation, there is new recognition that functions of ornamental traits can differ between two isolated populations (Yeh 2004, Mitchell et al. 2007, Vortman et al. 2011) which may be due to changes in habitat and resource availability. Signals that do not change can also become unreliable if males that use high-quality signals prefer habitat attributes that are deleterious for fitness (Rodewald et al. 2011, Schlaepfer et al. 2002, Battin 2004). For example, cardinals that nest in *Lonicera spp.* early achieve lower annual reproductive output due to higher vulnerability to predation (Rodewald et. al., 2010) and territories dominated by *Lonicera* are preferred by males with bright plumage.

Signal divergence may also be the result of relaxed selection for ornamental traits. In less than 30 years, an urban population of dark-eyed juncos (*Junco hyemalis*), lost portions of white tail plumage, a sexually selected trait in this species (Yeh 2004). Relaxed selection for tail plumage may reflect reduced competition for mates, an interaction where this trait would have traditionally held social importance (Yeh and Price 2004). Alternatively, when competition should be higher, as in habitats with poor resources, males also reduced their sexual advertisement (Van Oort et al. 2006). Instead, birds in poor habitats, such as those assumed to be in urban areas, may preferentially select for parental care and competitor advantages for food rather than indirect socially-selected signals (Shochat et. al., 2004). Rapid changes in selection, signal output, and mate preference in urban habitat patches could eventually lead to population divergence and contemporary evolution (Reugg et al. 2006, Warren et. al, 2006, Cornwallis and Uller, 2009).

Study Species

This study used the Northern cardinal (*Cardinalis cardinalis*, here after ‘cardinal’) as a focal species because it is a synanthropic, resident generalist that breeds in both urban and rural forests and exhibits high site fidelity in my system (Narango, personal observation). Cardinals are socially monogamous, with low levels of extra pair paternity and high amounts of mate guarding (Ritchison et al. 1994). Nests are maintained by biparental care, but males consistently feed more than females and parental care varies between individuals (Filliater and Breitwisch 1997). Nest defense is shared equally between males and females and is not related to ornamental signals (Nealen and Breitwisch 1997).

Earlier studies have demonstrated flexibility of vocal performance for this species. Cardinals have a complex song repertoire with many different song and note types. Individuals possess 8 to 11 song types and 9 to 13 syllable types but a typical song contains only 1 to 2 syllables (Lemon 1965). Songs among male cardinals within a locality are similar but songs vary geographically over large scales (Lemon 1966). Cardinals sing with eventual variation meaning that one song type is repeated many times before switching to a new song type although function of song types and type switching is unknown in this species (Lemon 1965, Ritchison 1988). Unlike most passerines, female cardinals also sing occasionally, possibly to facilitate mate communication (Ritchison 1986).

Song performance plays an important role in the acquisition of mates and territory in cardinals. The majority of male singing occurs during the pre-nesting and nest building periods of each breeding attempt (Ritchison 1988). Males used songs with the highest number of different notes during interactions between females and conspecifics (Ritchison 1988). Cardinals share songs extensively within a neighborhood but high variation existed in song use between males for several temporal and structural features (Ritchison 1988), which suggests song characteristics may indicate condition or status. In a natural forest edge, cardinals with lower complexity and shorter song lengths had better territories and higher nesting success than males with more longer, variable songs (Conner et al. 1986). This contradicts prior assumptions that complex song signals high quality (Catchpole 1987) and a need to elucidate the variation of this signal between populations in different environmental and social contexts.

Implications

Communication is a vital component to the maintenance of avian populations, and as such, is important to further study. Urban habitats present novel selective pressures on birds, which may alter not just sexually selected traits (Cornwallis and Uller 2009, Badyaev and Qvarnstrom 2002), but also decouple once-reliable morphological and behavioral signals from fitness consequences. Cues, whether environmental or individual, that become unreliable can result in detrimental decisions that reduce survival and reproduction (Schlaepfer et al. 2002). Anthropogenic noise is assumed to be the primary driver in urban song variation and these changes could potentially have negative fitness

consequences due to changes in functionality of song. My study is one of the first to simultaneously test multiple urban-associated explanations for song variation as well as provide initial evidence of any consequences of urban song.

Changes in behavioral and social interactions can isolate fragmented populations and limit dispersal which affects maintenance of genetic diversity and persistence of populations. One of the most important anthropogenic factors to facilitate contemporary evolution is habitat fragmentation and degradation (Stockwell et. al. 2003), and we are beginning to recognize that some, but not all, species are able to persist despite our impacts to the environment. As metropolitan areas become increasingly more urbanized, effective conservation of remaining forest fragments will be crucial. Understanding the sub-lethal influence urbanization has on behavior and mating systems will be important for conserving remaining wildlife habitat in the shadow of a rapidly developing world.

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CHAPTER 2

URBAN-ASSOCIATED DRIVERS OF SONG VARIATION ALONG A RURAL-URBAN GRADIENT

Abstract

Most studies demonstrating associations between avian song and urbanization presume that noise is the driver, but alternative causes remain largely unexplored. In particular, urban-associated changes in vegetation, density of conspecifics, and morphology might contribute strongly to altered song. In this study I (1) identified relationships between urbanization and song characteristics and (2) evaluated the extent to which altered song was explained by variation in noise level, vegetation, social context, and morphology of individual birds. From March – August 2010 – 2011, I monitored the territories and recorded song of 54 color-banded northern cardinals (*Cardinalis cardinalis*) at 9 riparian forest fragments in central Ohio. As landscapes of surrounding forests urbanized, songs were longer, sung at faster rates and comprised of higher frequency notes. Noise best predicted minimum song frequency, with individuals singing at higher frequencies in louder environments. However, temporal attributes of song (e.g., syllable rate, length) were best explained by conspecific densities. These findings show that although anthropogenic noise may shape urban-associated changes in

song, other features of the urban environment may be more important contributors to patterns in song variation.

Introduction

Bird song is a conspicuous acoustic signal in passerines with primary functions in both mate acquisition and territory defense (Kroodsma and Miller, 1996). Song divergence has been explored in many different species and habitats both because of its sensitivity to environmental context (Morton 1975, Slabbekoorn and Smith 2002, Hansen et al. 2005, Kirschel et al. 2009) and fitness implications (Catchpole 1987, Buchanan and Catchpole 1997, Gil and Gahr 2002). Vocalizations are also highly variable among populations and individuals (Catchpole and Slater 2003, Nelson and Poesel 2007). Because certain habitat properties can impede or attenuate sound (Bradbury and Vehrencamp 1998), species are thought to optimize transmission by using vocalizations that propagate efficiently in a given habitat. Morton (1975) first proposed that habitats could shape songs via strong selective pressures of different acoustic environments (i.e., the acoustic adaptation hypothesis). Indeed, bird song is known to be affected by a wide variety of factors including wind (Bradbury and Vehrencamp 1998), conspecifics (Nelson and Marler 1994), heterospecifics (Nelson and Marler 1990), insects (Slabbekoorn and Smith 2002a), and vegetation (Morton 1975, Anderson and Conner 1985, Badyaev and Leaf 1997, Bradbury and Vehrencamp 1998).

Urbanization has been associated with shifts in structural attributes of avian song, with the most commonly cited pattern being a rise in minimum frequency in urban areas (Slabbekoorn and den Boer-Visser 2006, Mockford and Marshall 2009, Dowling et al. 2012). Urban birds also sing at faster rates than those in rural areas (Slabbekoorn and den Boer-Visser 2006), contrary to predictions that slower songs should transmit better in the presence of urban noise (Slabbekoorn et al. 2007). Song changes in cities may reflect adaptations to the introduction of noise (Luther and Derryberry 2012) or real-time structural and temporal adjustments through the use of behaviorally plastic vocal performance (Bermúdez-Cuamatzin et al. 2011).

Although urban-associated changes in song frequency may be driven by a variety of factors, the urban acoustic environment is the most frequently invoked explanation, in part because there is well-established link between environmental noise and song frequency (Ryan and Brenowitz 1985, Brumm and Slabbekoorn 2005). Whether the source of noise is abiotic or biotic, overlap with competing sounds can thwart effective communication (Bradbury and Vehrencamp 1998). Even under natural conditions, individual bird species compete for acoustic space, and song structures have evolved in order to maximize transmission by avoiding overlap with songs of other species (Nelson and Marler 1990). High frequency sounds from tropical insects are another example of ambient noise that can promote shifts in dominant frequencies in sympatric and locally co-occurring bird species (Slabbekoorn and Smith 2002, Kirschel et al. 2009). Animals associated with habitats with high amplitude abiotic sounds from wind, surf or torrent water favor higher pitched sounds (Brumm and Slabbekoorn 2005). Likewise,

environmental noise in urban habitats is composed primarily of sound energy in the lowest frequencies (<2 kHz) typical of traffic, construction and other anthropogenic sources (Slabbekoorn and Peet 2003). Presumably, urban environments select for higher frequencies to avoid masking of song by anthropogenic noise.

Irrespective of ambient noise, urban development can alter the acoustic environment via changes in vegetation. Because the size and number of objects affects propagation by attenuating sounds, birds vocalizing in structurally open habitats tend to use long vocalizations with high frequencies (Morton 1975, Bradbury and Vehrencamp 1998). Variation in vegetation can also favor efficient transmission of different vocalizations in forest stands (Anderson and Conner 1985) or strata (Nemeth et al. 2001) within a single habitat type. In urban landscapes, forests may be composed of younger stands with smaller trees than older, non-disturbed areas, which would relax degradation of high frequencies. In addition, urban landscapes can be characterized by increased densities of exotic vegetation (Borgmann and Rodewald 2005) that may select for faster, lower-pitch vocalizations.

As song occurs within particular social contexts, changes in avian densities in cities (Bakermans et al. 2006, Shochat et al. 2006, Rodewald and Shustack 2008a) represent an alternative hypothesis to noise as a driver of song variation. High densities promote increased competition for resources and territorial interactions between neighbors and floater males. Aggressive encounters can increase tension on the syrinx (Bradbury and Vehrencamp 1998) or louder amplitudes (Brumm 2004), both of which

result in vocalizations with higher frequencies. In addition, testosterone can also play a role in mediating song performance and structure (Ketterson et al. 1992, Ritschard et al. 2011). In high densities, birds sing at higher rates and vocalizations and are a more reliable signal of reproductive fitness, possibly resulting from increases in male-male competition (Ritchison 1988, Penteriani 2003).

Another possibility is that urban-associated song changes derive from morphological differences between rural and urban individuals. For example, Slabbekoorn et al. (2007) hypothesized that smaller individuals with poorer song performance settle urban habitats. Indeed studies have demonstrated that song is an indicator of interspecific male body size (Ryan and Brenowitz 1985, Gil and Gahr 2002), as larger birds tend to sing songs of lower frequencies (Handford and Loughheed 1991). In some species, smaller birds or those in poorer condition settle in urban territories (house sparrows (*Passer domesticus*): Liker et al. 2008, size only: Acadian flycatcher (*Empidonax vireescens*): Rodewald and Shustack 2008a), however, this may not be the case for urban-adapted species (Black-Capped chickadees (*Poecile atricapillus*): van Oort et al. 2007, Northern cardinals (*Cardinalis cardinalis*): Rodewald and Shustack 2008b). Differences in food sources in urban areas can also influence the development of bill morphology in ways that impact individual vocal performance (Badyaev et al. 2008).

Our understanding of the processes that result in altered song structure in urban habitats remains incomplete and largely focused on the effects of masking noise. This study evaluated the evidence for four non-mutually exclusive hypotheses explaining

urban-associated song variation. Specifically, I proposed that song could vary in response to increased urbanization because: 1) Loud anthropogenic noise will elicit upward shifts in frequencies and longer songs because urban ambient noise masks sound in the lowest frequencies and redundancy increases the likelihood of being heard, 2) Higher densities of conspecifics will promote faster and longer songs due to changes in motivational states, and higher frequencies because of increased aggressive encounters, 3) Higher densities of small plant stems will favor songs that are lower frequencies and at faster syllable repetition because these sounds suffer reduced degradation from scattering effects, and 4) Smaller body sizes will be related to increases in frequency and faster rates because of morphological limitations in song production and modulation and/or individual quality in song performance.

Methods

Study area. This study was conducted between March and August in 2010 and 2011 in 9 mature riparian forest fragments along three rivers (Olentangy, Darby and Alum Creek) in and around Columbus, Ohio (Figure 1). Digital orthophotos were used to quantify landscape composition (buildings, impermeable surface, agriculture, forest, shubland, wetland and open water) within a 1 km radius from the site, and these metrics were used in a principal components analysis to create an index of urbanization for each site (see Rodewald and Shustack 2008a for more details). Sites were separated by at least 2 km and were composed of contiguous linear riparian habitat with similar forest widths

and sizes (~4-6 Ha). Dominant tree species included maple (*Acer* spp.), sycamore (*Plantanus occidentalis*), elm (*Ulmus* spp.) and cottonwood (*Populus deltoids*). Dominant understory shrubs were Amur honeysuckle (*Lonicera* spp.), multiflora rose (*Rosa multiflora*), Ohio buckeye (*Aesculus glabra*), and box elder (*Acer negundo*).

Morphology and vegetation. Cardinals were captured at each site using mist-nets and fitted with a steel USGS band and a unique combination of 3 color bands. Upon capture, tarsus and wing were measured to quantify body size. Bill measurements were collected because bill size has been shown to influence trill rates (Derryberry 2009). Males that were unable to be captured were included in analyses if they were paired with a banded female (n=5) or exhibited reliable territory boundaries and song perches (n=4). Males were followed over the breeding season (March–August) to determine reproductive success. Two nesting attempts of each focal male were sampled for vegetation characteristics (one early and one late) in order to capture within-season variation. Trees and large woody shrubs were identified and classified using 4 size classes (3-8 dbh, 8-26 dbh, 26-38 dbh, and 38+ dbh) within a 11.3m radius sampling circle centered on the nest (Martin and Conway 1994). Percent shrub cover of the most abundant three shrubs (including exotic *Lonicera* spp.) was estimated for each quadrant of the circle. An additional vegetation plot was measured at a random bearing 25m from the first nest sampled. All vegetation measurements were averaged for each territory.

Conspecific Density. Sites were visited weekly ($n = 10$ visits) to spot-map densities of breeding birds (Bibby et al. 1998). Observers systematically walked a 2-ha

gridded area for 1 hour and noted observations of singing, calling and parental behavior of birds. At the end of the season, territories were delineated for each species to determine number of breeding territories for each site using 3 observations as a minimum for territory inclusion (Bibby et al. 1998). In addition, territorial mapping and nesting attempts for northern cardinals were used to accurately assign number of territories within a 2ha gridded plot.

Song recording. Recordings were completed between 15 minutes after sunrise and 5 hours after sunrise on weekdays between March and June of the breeding season. A focal watch was conducted for 30 min on each territory where at least one adult was banded in order to observe and record song behavior. Vocalizations were digitally recorded when a male was observed singing using a Marantz PMD 670 digital recorder and a Sennheiser directional microphone. Songs were sampled at 44.1 kHz with a bit rate of 32 kbps, and saved as mono .wav files. The male's identity was confirmed by visual identification of color bands and/or associations with known females or nesting attempts during the recording, or immediately thereafter. Noise decibel (dB) levels were measured following each recording using a sound pressure level meter (American Recorder Technologies, 0.1dB resolution) on A weighting calibrated to 94 dB using IEC651 Type II standards. The A weighting was chosen because it best measures the frequency bandwidth of sound that comprises the range of cardinal song (700 Hz -8000 Hz: Halkin and Linville 1999). At each song perch, a noise measurement was taken in each of the cardinal directions every 15 seconds and averaged for the location.

Song analysis. Songs from 2010 were recorded using a file type (.mp3) that compressed maximum and peak frequency measurements and thus could not be used for a multivariate analysis. In order to remain consistent with my measurements, I chose to only analyze songs from 2011 because they were recorded with the .wav file type. Digital spectrograms were created using Raven 1.4 Pro (Cornell lab of Ornithology). Songs were measured using Hann sampling (Time: 256 samples, 3dB filter bandwidth 248 Hz, overlap 50%, hop size 128 samples, dft size: 256 samples, grid spacing 172 Hz, Frequency: 1024 samples, 3dB filter bandwidth 61.9 Hz, overlap 50%, hop size 512 samples, dft size: 1024, grid spacing 43.1 Hz). Cardinals sing with eventual variation meaning individuals sing one type repeatedly before switching to a new song type. Because there is more difference between song types than within one song type, each song type was measured once per observation period to capture individual variation over all song types. Song types were defined according to Lemon (1965) such that a type was specified as a unique “utterance” of 1 or more syllable types where the time between syllables (<1 sec) was less than the time between songs (>1 sec). For example, a combination of syllable types ‘A’ and ‘B’ was called unique song type ‘AB’.

Songs were included in subsequent analyses only if they were (1) composed of 3 or more syllables, (2) clean recordings with minimal reverberations (3) free of overlap with other biological or ambient sounds, (4) able to be assigned to a territory based on color band combinations or associations with color-banded females. My intent was to capture song variation within males, and song types are inherently similar and non-independent, therefore the highest quality recording of each song type during the

sampling period was chosen for digital analysis. To account for individual repertoires in which some song types were used more often than others, identical song types sung on subsequent observation periods were considered a unique measurement. For each song sample I measured minimum frequency, maximum frequency, frequency range, peak frequency, song length, number of syllables, power, syllable types and syllable rate (definitions: Appendix C). All variables were measured using the manual cursor and by the same observer (DLN). Mean measures of individual characteristics per male are used in the following analyses.

Statistical Analysis.

I used a series of linked approaches to determine which of my alternative hypotheses best predicted urban song variation. First, I tested for variable redundancy using a Pearson's correlation matrix. Secondly, I conducted principal components analyses on both song and vegetation variables separately to extract components that best explained variation. Next, to examine changes in song characteristics as surrounding landscapes became more urban, I used the principal components of song in a linear regression with the urban index values. Then, I used a Pearson's correlation matrix to examine how my alternative hypotheses (noise, vegetation, density and morphology) were related with increasing urbanization. Finally, I used Akaike's Information Criteria (AIC) corrected for small sample sizes to test multiple nested predictive models of song variation.

Variables were tested for equal variance (Levene's test for homogeneity of variance) and normality (normal quantile plot, Shapiro-Wilks Test) and transformed if necessary. I used a Pearson's correlation to examine multicollinearity among variables. Variables that were highly correlated ($r > 0.7$) were assessed and one of the correlated variables was excluded from analysis to avoid redundancy. A correlation matrix revealed that average high frequency and average frequency bandwidth were highly correlated ($r = 0.99$, Table 2.1) as well as song length and number of syllables ($r = 0.80$, Table 2.1). I chose to remove frequency bandwidth as a redundant variable because maximum frequency was largely driving this relationship. I also chose to retain number of syllables and remove song length. I did not include power measurements because this variable was highly influenced by the position of the microphone relative to the bird.

A similar approach was used to reduce vegetation variables that were redundant. A correlation matrix (Table 4) revealed that total number of small stems (3-8 cm dbh) were highly correlated with number of 3-8cm dbh honeysuckle stems ($r = 0.99$, Table 2.3), given that the latter variable was included in the former. Likewise, total percent shrub density was correlated with percent honeysuckle shrubs (<3dbh) ($r=0.96$, Table 2.3), which reflected the fact that most shrubs were honeysuckle. Therefore I chose to drop individual honeysuckle measurements in order to capture structural densities within different strata.

To examine relationships between song and surrounding landscapes, I performed a linear regression between the song components and landscape index to determine if song attributes change as surrounding land becomes more urbanized.

Because each site had a unique urban index, site was not included as a separate variable in the models.

Model selection of environmental factors.

To examine the association between song variation and habitat factors associated with urbanization, I used an information theoretic approach for multiple models using Akaike's Information Criteria (AIC) corrected for small sample sizes (Burnham and Anderson 1998). I chose 4 unique *a priori* variables that represented alternative hypotheses to explain song variation: urban landscape (index), noise levels (noise), vegetation composition (understory density, large trees and small trees PCs), and body size. The model with the lowest $\Delta AICc$ value indicated the model with the best fit while minimizing the number of parameters. All models were generalized linear models using song characteristic as the dependent variable and each environmental hypothesis as an independent variable using Gaussian distribution and identity function (Zurr et al. 2009). Missing data points were included in the models by filling in mean values for the variable. All statistics were performed using program R 2.14 for Windows (R Development Core Team 2008).

Results

Recorded Males. In 2010 I recorded 32 males (14 from rural and 18 from urban landscapes) and in 2011 I recorded 66 males (26 from rural and 38 from urban

landscapes). Using my criteria for song inclusion and excluding 2010 recordings and males not recorded in the focal area, I measured 610 songs with 8.28 ± 4.55 song types from each male ($n=54$). Average cardinal frequency ranged between 1047.87 and 8694.15 Hz which overlaps with the bandwidth of typical low frequency ambient noise (<2 Hz, Slabbekoorn and Peet 2003).

Principal components analysis. I used a principal components analysis (PCA) to reduce the number of variables associated with song and vegetation characteristics. Using the song averages for each male, I reduced the variables, number of syllables, minimum frequency, maximum frequency, peak frequency and song rate, into three latent variables (eigenvalues >1) using a principal components analysis that explained 80.8% of the variance (Zurr et al. 2007). The first principal component (PC1) had factors that loaded heavily toward decreases in temporal aspects of song (number of syllables and rate) (Table 2.2, Figure 2.1). The component of temporal attributes (PC1), ranged from -3.18 to 2.60 which represented a difference of 18.22 to 6.17 average syllables and 5.67 to 2.41 average syllables per second. The second principal component (PC2) increased with peak frequency and high frequency, reflecting a range of average peak frequency from 2045.65 to 3560.13 Hz and average high frequency Hz from 3549.41 to 8131.40. The third principal component (PC3) was negatively related to minimum frequency such that increases in PC3 described decreases in minimum frequency (Table 2.2), and it represented a difference between 1047.87 and 1749.68 in average minimum frequency Hz. Hereafter I call these variables temporal components (PC1), peak/high frequency (PC2) and minimum frequency (PC3).

A principal components analysis of the variables, trees in 4 size classes (3-8, 8-23, 23-38 and 38+ dbh), and percent shrub cover, showed that three components explained 73.5% of the variance (Table 2.4). The first principal component (PC1) had factors that loaded positively toward high shrub densities and saplings (Table 2.4, Figure 2.2). The second principal component (PC2) had factors that loaded positively toward small and medium trees (Table 2.3, Figure 2.2). The third principal component (PC3) had factors that loaded negatively toward only large trees, therefore higher values contained low numbers of larger trees (Table 2.4). I described the latent variables as understory density (PC1), small trees (PC2) and large trees (PC3).

Urban-associated changes in song. Temporal components of song were negatively associated with urbanization (β : -0.31 ± 0.16 , $F_{1, 52}=3.45$, $p=0.07$; Figure 2.3) meaning urban songs were longer and faster. The component that represented minimum frequencies also decreased over the gradient (β : -0.28 ± 0.12 , $F_{1, 52} = 5.10$, $p = 0.03$) such that minimum frequencies rose as sites became more urban (figure 2.4). Peak and high frequency song components increased over the rural-urban gradient (β : 0.30 ± 0.14 , $F_{1, 52}=4.95$, $p=0.03$; Figure 2.5) so that urban songs had higher peak and high frequencies.

Evidence for alternative mechanisms. As expected, as landscapes surrounding forests urbanized, the environment changed in ways that could conceivably affect bird song. As urbanization increased, noise ($r = 0.81$), conspecific densities ($r = 0.89$), large trees ($r = -0.92$) and shrub densities ($r = 0.94$) (influenced by presence of the exotic

Lonicera maackii) increased, whereas body sizes decreased ($r = -0.79$) (Table 2.5).

Numbers of small trees had no relationship with urbanization ($r = -0.28$).

Model selection for song variation. When considering alternative mechanisms to explain urban-associated changes in temporal song characteristics (temporal PC1), the top model was number of conspecific territories at the site level (Table 2.6; $w = 0.93$). Song attributes became longer and faster as sites increased in conspecific densities ($\beta = -0.22 \pm 0.06$, 95% CI: -0.35, -0.10, $F=12.53$, $p<0.001$; Figure 2.6). Increases in minimum frequency was best explained by and negatively related to noise levels at the territory site (Table 2.8, Figure 2.7; $w = 0.90$); $\beta = -0.13 \pm 0.02$, 95% CI: -0.18, -0.09, $F=29.92$, $p<0.001$). Peak/high frequency (frequency PC2) of song was not well explained by any single model. Rather, six ecological models (body size, shrubs/saplings, noise, density, large trees and small trees) and the null model had a $\Delta AIC_C < 2$ (Table 2.7).

Discussion

Although loud acoustic environments are usually invoked to explain altered bird song in cities (Patricelli and Blickley 2006, Wood and Yezerinac 2006, Slabbekoorn and den Boer-Visser 2006, Mockford and Marshall 2009), my findings show that modifications in song may be the consequence of other ecological changes associated with urbanization. Whereas minimum song frequency was best explained by the acoustic environment within territories, temporal changes in song structure (e.g., syllable

rate) was a product of high densities within urban habitats. Peak/high frequencies were not explained by any of my ecological models.

Changes in temporal characteristics are reported less often in studies of urban song (but see: (Slabbekoorn and den Boer-Visser 2006, Nemeth and Brumm 2009, Hamao et al. 2011, Potvin et al. 2011). Here, temporal characteristics increased with urbanization as a result of increases in conspecific densities. Resident generalists tend to increase as landscapes become more developed, a characteristic of urban ‘adapter’ species. Cardinals can be found at up to 4x higher densities at urban sites, and cardinal prevalence is best predicted by understory and exotic stem densities (Leston and Rodewald 2006). Indeed, sites where honeysuckle had been experimentally removed had lower densities of cardinals (Rodewald, unpublished). A meta-analysis of acoustic adaptation studies found weak support for strong acoustic adaptation in vocalizations (Boncoraglio and Saino 2007), and contextual variation via population density may be an important factor that contributes to song changes in different habitats.

Accordingly, males from sites with the highest densities sang songs that were longer and faster. This difference supports that temporal attributes are driven by increases in conspecific densities within a site. These song changes could be a behavioral consequence of increased territorial interactions between neighbors (Searcy and Beecher 2009). In cardinals specifically, males use higher syllable rates and increased syllable types in songs used for interactions with conspecifics (Ritchison 1988). Cardinals settling in habitats with dense urban populations are likely subject to increased aggression

between individuals, which manifests in subtle behavioral change at the individual level. Although familiarity with neighbors may decrease aggression (e.g., dear enemy effect), birds often increase or change vocal behavior when confronted with an unfamiliar floater male attempting to settle territories. Anecdotally, rogue banded and unbanded males were more often observed mid-season attempting to usurp territories in urban sites than in rural sites (Narango, personal observation). Increases in aggression may be a behavioral compensation to avoid sites becoming over-saturated with cardinal territories.

On the other hand, temporal differences in song may be indicative of the quality of individuals settling in these habitats. For example, plumage brightness, another indicator of quality in cardinals, declined with surrounding urbanization (Jones et al. 2010). Song is also indicative of male quality in northern cardinals such that shorter, slower songs indicated higher territory quality and reproductive success in birds in a non-developed landscape (Conner et al. 1986). Urban birds may be experiencing early developmental stress that reduces production of high quality song (Buchanan et al. 2003). We did not, however, find support that lower quality individuals (e.g., smaller body size) best predicted changes in temporal characteristics, although size was negatively associated with urbanization.

Temporal increases such as song length and rate may also result from abundant food sources in areas with high densities. Song can be energetically expensive to develop and produce (Nowicki et al. 1998, Gil and Gahr 2002) and birds in lower quality habitat have reduced song output (Van Oort et al. 2006). Likewise, birds with access to

supplementary food sources exhibited sustained song production (Strain and Mumme 1988). In urban areas, generalist species have access to energetically-rich foods year round (e.g., bird seed). Although urban cardinals occur in higher densities, they appear to be resource-matching (Rodewald and Shustack 2008b) and adjusting song may be an indicator of relaxed response on the limits to song performance.

To my knowledge, this study is one of the first to simultaneously test multiple competing models of urban-associated habitat changes that may explain song variation (but see: Hamao et al. 2011). Because we explicitly tested several potential mechanisms, my study provides strong and compelling support that noise is, indeed, driving changes in frequency but changes in density contribute to shifts in temporal attributes of song. The insights made possible from this study are further strengthened by the fact that (1) the influence of habitat size and population dialects on behavior was minimized by utilizing similar sized forest fragments in close proximity that differed primarily in landscape context and (2) territory-level features were considered in addition to landscape-scale phenomena. The latter is especially important given that nearby objects such as buildings or impermeable surfaces are associated with frequency shifts (Warren et al. 2006, Dowling et al. 2012). My lack of evidence for noise as the driver of peak/high variation suggests that there were potentially behavioral mechanisms that were not accounted for in my study. These frequency changes may result from cultural or geographical drift of urban song dialects over time (Luther and Baptista 2009, Luther and Derryberry, 2012) or use of different song types (Slabbekoorn and den Boer-Visser 2006, Halfwerk and Slabbekoorn 2009).

My work shows that changes associated with urbanization, such as ambient noise and population densities, can influence subtle communication behavior by affecting motivational states of singers, food resources or relaxing energetic constraints on song performance. Future studies should consider how noise and densities may be contributing to other behavioral variation in urban birds, either by affecting motivational states of singers or food resources. Researchers should investigate whether urban-associated changes might also impact communication in species that do not exhibit behavioral plasticity in vocal performance, as with non- or sub-oscines. In addition, because environmental and social heterogeneity may also influence signal reliability (Penteriani 2003, Cornwallis and Uller 2010), additional studies should consider whether there are fitness-related consequences to song variation for urban birds, or if the informational content of song may be changing urban systems.

Table 2.1. Correlation Matrix (Pearson's correlation) for variables measured on male Northern Cardinal song in central Ohio, 2011 (n=54). *P*-values are in italics.

Table 2.1

| | Song length | Minimum frequency | Maximum frequency | Frequency bandwidth | Power | Peak frequency | Syllables | Syllable type | Syllable rate |
|---------------------|--------------------------------|----------------------|--------------------------------|--------------------------------|----------------------|---------------------|----------------------------|---------------------|----------------------|
| Song length | 1.00 | -0.23 <i>0.11</i> | 0.08 <i>0.54</i> | 0.11 <i>0.68</i> | 0.27 <i>0.33</i> | 0.18 <i>0.94</i> | 0.80 0.01 | 0.07 <i>0.49</i> | 0.11 <i>0.71</i> |
| Minimum Frequency | -0.23 <i>0.11</i> | 1.00 | 0.01 <i>0.60</i> | -0.13 <i>0.41</i> | -0.36 <i>0.03</i> | 0.00 <i>0.59</i> | 0.03 <i>0.66</i> | 0.15 <i>0.85</i> | 0.23 <i>0.40</i> |
| Maximum Frequency | 0.08 <i>0.54</i> | 0.01 <i>0.60</i> | 1.00 | 0.99 <i><0.01</i> | -0.09 <i>0.44</i> | 0.17 <i>0.84</i> | -0.06 <i>0.11</i> | 0.13 <i>0.81</i> | -0.18 <i>0.05</i> |
| Frequency Bandwidth | 0.11 <i>0.68</i> | -0.13 <i>0.41</i> | 0.99 <0.01 | 1.00 | -0.04 <i>0.60</i> | 0.17 <i>0.79</i> | -0.07 <i>0.14</i> | 0.11 <i>0.80</i> | -0.21 <i>0.04</i> |
| Power | 0.27 <i>0.33</i> | -0.36 <i>0.03</i> | -0.09 <i>0.44</i> | -0.04 <i>0.60</i> | 1.00 | 0.05 <i>0.88</i> | 0.11 <i>0.82</i> | 0.20 <i>0.72</i> | -0.07 <i>0.56</i> |
| Peak Frequency | 0.18 <i>0.94</i> | 0.00 <i>0.59</i> | 0.17 <i>0.84</i> | 0.17 <i>0.79</i> | 0.05 <i>0.88</i> | 1.00 | 0.15 <i>0.80</i> | 0.16 <i>0.91</i> | 0.04 <i>0.56</i> |
| Syllables | 0.80 <0.01 | 0.03 <i>0.66</i> | -0.06 <i>0.11</i> | -0.07 <i>0.14</i> | 0.11 <i>0.82</i> | 0.15 <i>0.80</i> | 1.00 | 0.10 <i>0.49</i> | 0.61 <i>0.04</i> |
| Syllable Type | 0.07 <i>0.49</i> | 0.15 <i>0.85</i> | 0.13 <i>0.81</i> | 0.11 <i>0.80</i> | 0.20 <i>0.72</i> | 0.16 <i>0.91</i> | 0.10 <i>0.49</i> | 1.00 | 0.12 <i>0.79</i> |
| Syllable Rate | 0.11 <i>0.71</i> | 0.23 <i>0.40</i> | -0.18 <i>0.05</i> | -0.21 <i>0.04</i> | -0.07 <i>0.56</i> | 0.04 <i>0.56</i> | 0.61 <i>0.04</i> | 0.12 <i>0.79</i> | 1.00 |

| Variable | PC1 | PC2 | PC3 | PC4 | PC5 |
|--------------------------|-------------------------------------|--------------------------------|--------------------------|-------------|-------------|
| <i>eigenvalues</i> | <i>1.31</i> | <i>1.09</i> | <i>1.00</i> | <i>0.87</i> | <i>0.58</i> |
| minimum frequency | -0.32 | -0.04 | -0.92 | -0.17 | 0.13 |
| maximum frequency | 0.26 | 0.73 | -0.25 | 0.58 | -0.07 |
| peak frequency | -0.16 | 0.79 | 0.12 | -0.58 | -0.05 |
| number of syllables | -0.84 | 0.17 | 0.27 | 0.23 | 0.38 |
| syllable rate | -0.90 | -0.07 | -0.02 | 0.13 | -0.41 |
| Component Interpretation | Decreasing Temporal Characteristics | Increasing Peak/High Frequency | Decreasing Low Frequency | - | - |

Table 2.2. Factor loadings and eigenvalues for the principal components analysis of song variables measured of male Northern Cardinals in central Ohio, 2011.

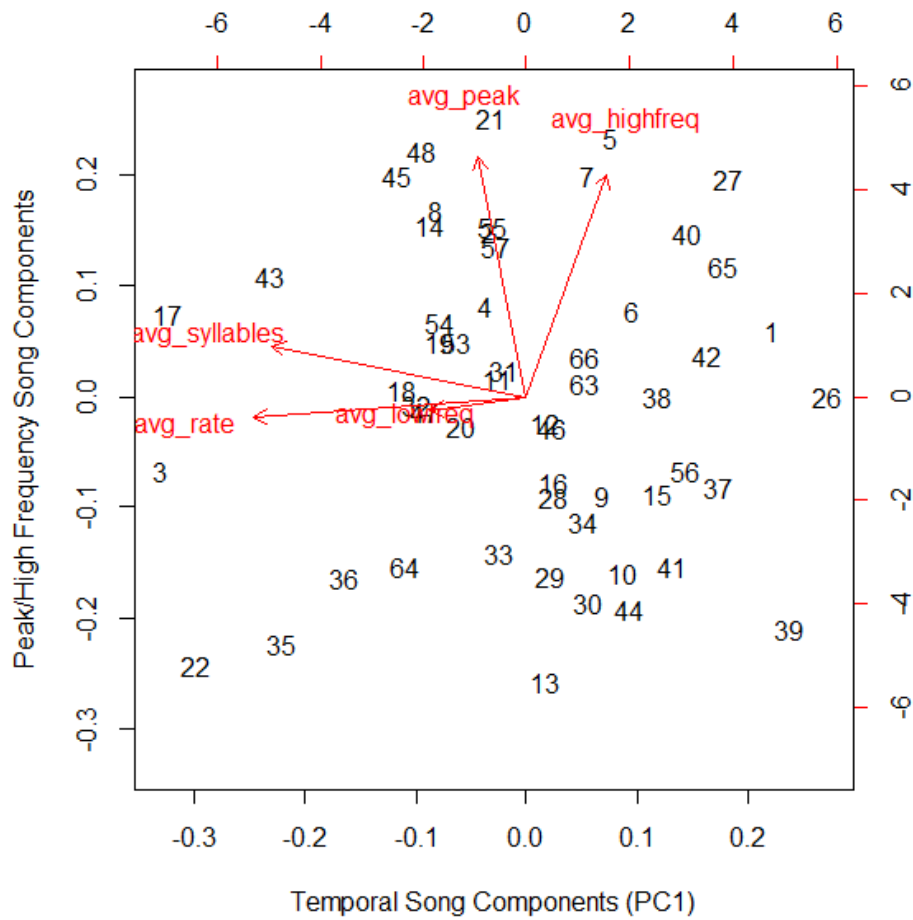


Figure 2.1. A biplot of the factor loadings from PC1 and PC2 of the principal components analysis on song variables of male Northern Cardinals in central Ohio, 2011. For PC1, songs become shorter and slower as the component increases. For PC2, songs increase in both peak and high frequency measurements as the component increases.

| | Saplings (3-8 dbh) | Small trees (8-23 dbh) | Medium trees (23-38 dbh) | Large Trees (38+ dbh) | Large honeysuckle shrubs (3-8 dbh) | % shrub cover (all species) | % shrub cover (honeysuckle) |
|--|--------------------------------|---------------------------|-----------------------------|--------------------------|---------------------------------------|--------------------------------|--------------------------------|
| Saplings (3-8 dbh) | 1.00 | -0.64 0.12 | -0.33 0.47 | -0.36 0.43 | 0.99 <0.01 | 0.40 0.38 | 0.57 0.19 |
| Small trees (8-23 dbh) | -0.64 0.12 | 1.00 | 0.23 0.62 | -0.25 0.59 | -0.69 0.09 | -0.40 0.37 | -0.51 0.25 |
| Medium trees (23-38 dbh) | -0.33 0.47 | 0.23 0.62 | 1.00 | -0.15 0.75 | -0.30 0.51 | -0.80 0.03 | -0.80 0.03 |
| Large Trees (38+ dbh) | -0.36 0.43 | -0.25 0.59 | -0.15 0.75 | 1.00 | -0.32 0.49 | -0.17 0.72 | -0.15 0.75 |
| Large honeysuckle shrubs (3-8 dbh) | 0.99 <0.01 | -0.69 0.09 | -0.30 0.51 | -0.32 0.49 | 1.00 | 0.38 0.40 | 0.56 0.19 |
| % shrub cover (all species) | 0.40 0.38 | -0.40 0.38 | -0.80 0.03 | -0.17 0.72 | 0.38 0.40 | 1.00 | 0.96 <0.01 |
| % shrub cover (honeysuckle) | 0.57 0.19 | -0.51 0.25 | -0.80 0.03 | -0.15 0.74 | 0.56 0.19 | 0.96 <0.01 | 1.00 |

Table 2.3 Correlation matrix (Pearson's correlation) for vegetation variables measures at male Northern Cardinal territories in Central Ohio, 2011 (n=54). *P*-values are in italics.

| Variable | PC1 | PC2 | PC3 | PC4 | PC5 |
|--------------------------|--------------------------|-------------|------------------------|------------|------------|
| <i>eigenvalues</i> | 1.18 | 1.13 | 0.98 | 0.94 | 0.7 |
| Saplings | 0.77 | 0.15 | 0.24 | 0.43 | 0.38 |
| Small trees | -0.05 | 0.69 | 0.32 | -0.62 | 0.21 |
| Medium trees | -0.13 | 0.81 | 0.07 | 0.46 | -0.33 |
| Large trees | 0.28 | 0.34 | -0.88 | -0.11 | 0.1 |
| % Shrub cover | 0.84 | -0.08 | 0.11 | -0.32 | -0.42 |
| Component Interpretation | Increasing Shrub Density | Small Trees | Decreasing Large Trees | - | - |

Table 2.4. Factor loadings and eigenvalues for the principal components analysis of vegetation variables of male Northern Cardinal territories in central Ohio, 2011.

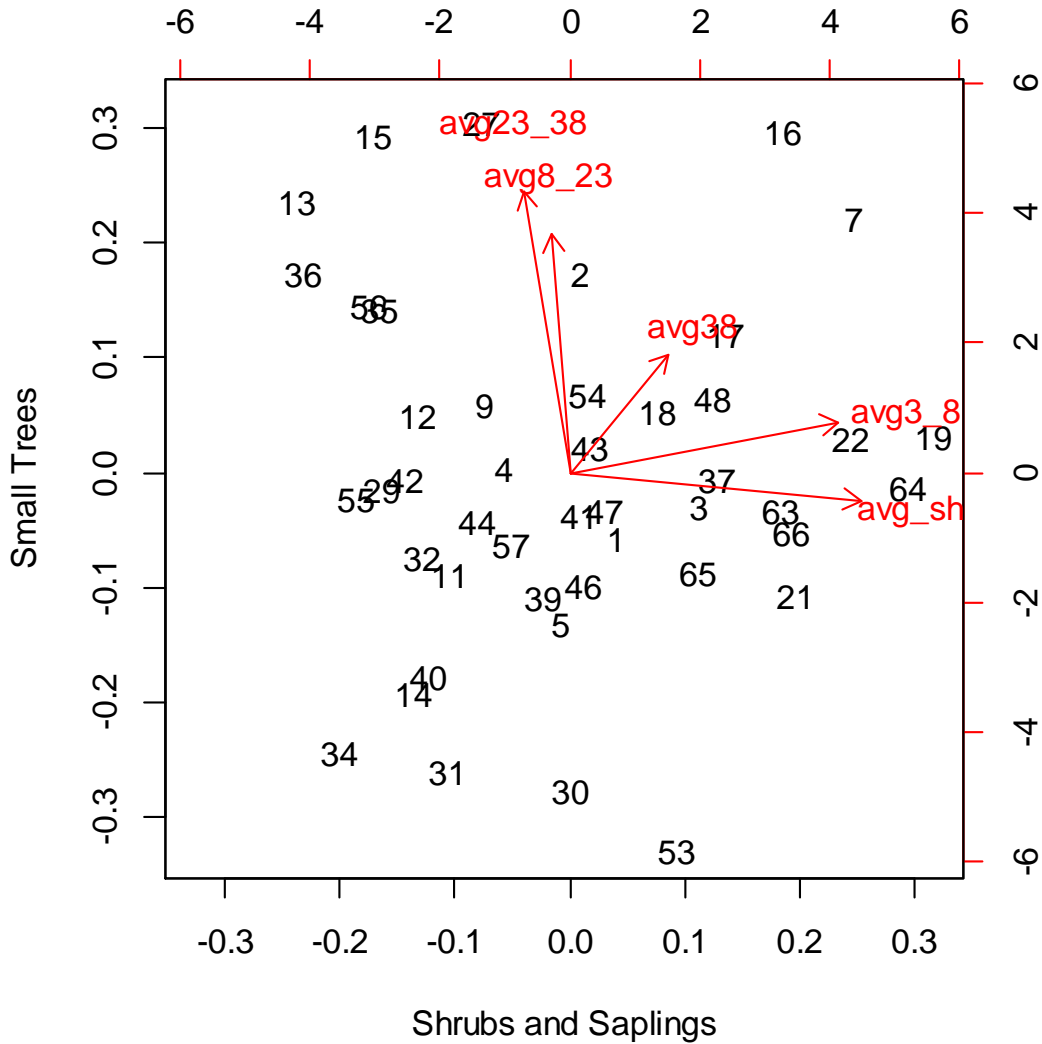


Figure 2.2. A biplot of the factor loadings from PC1 and PC2 of the principal components analysis on vegetation variables from male Northern Cardinal territories in central Ohio, 2011. For PC1, shrubs and saplings increase as the component increases. For PC2, small trees (8-23 and 23-38) increase as the component increases.

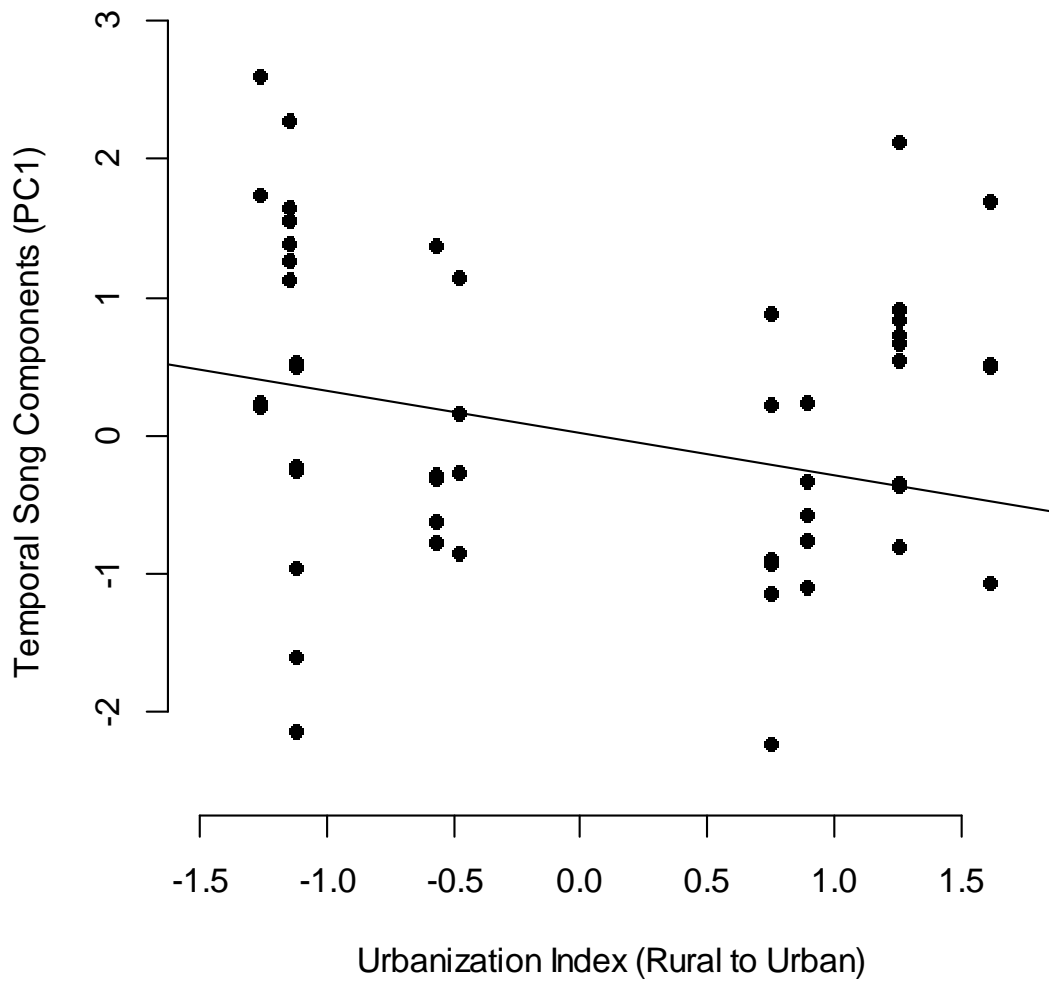


Figure 2.3. Temporal song components (PC1) as surrounding landscape changes. As urbanization increased, males sang songs that were longer and faster (decreases in PC1) (β : -0.31 ± 0.16 , $F_{1, 52}=3.45$, $p=0.07$).

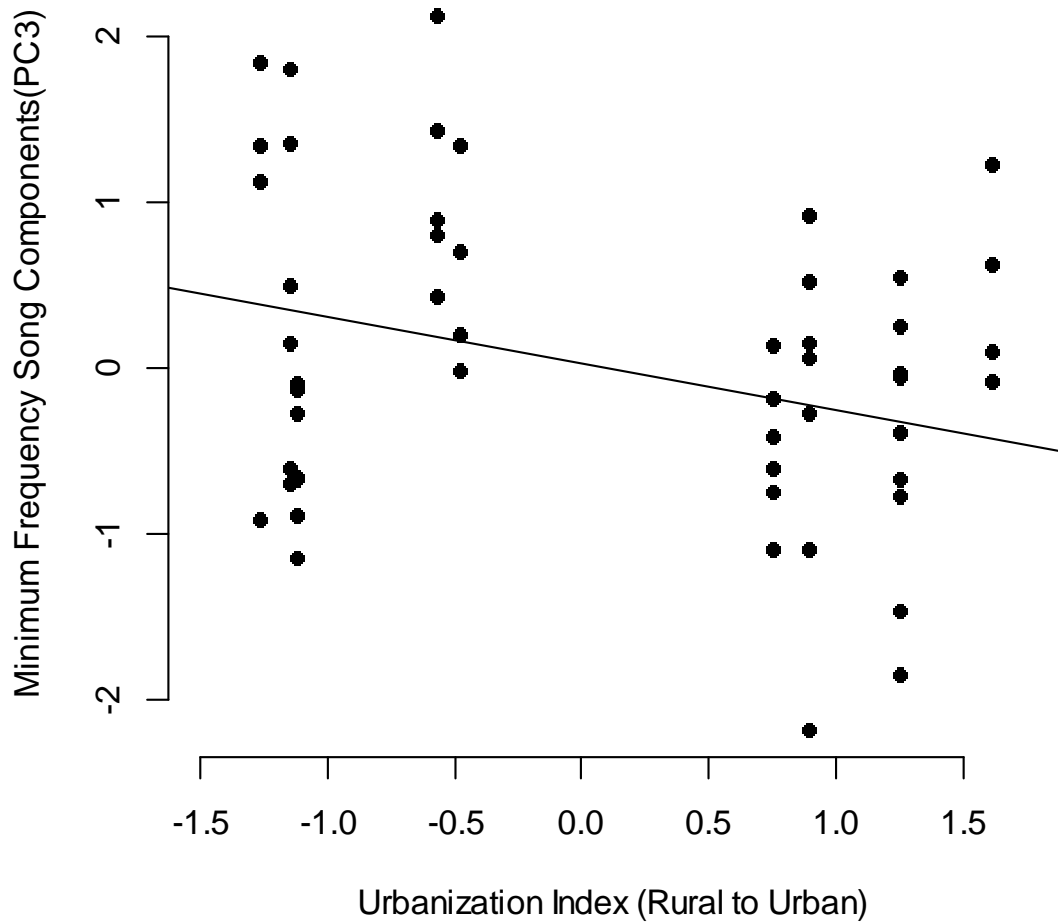


Figure 2.4. Low frequency song component (PC3) as surrounding landscape changes. As urbanization increased, males sang songs with higher minimum frequencies (decreases in PC3) (β : -0.28 ± 0.12 , $F_{1, 52} = 5.10$, $p=0.03$).

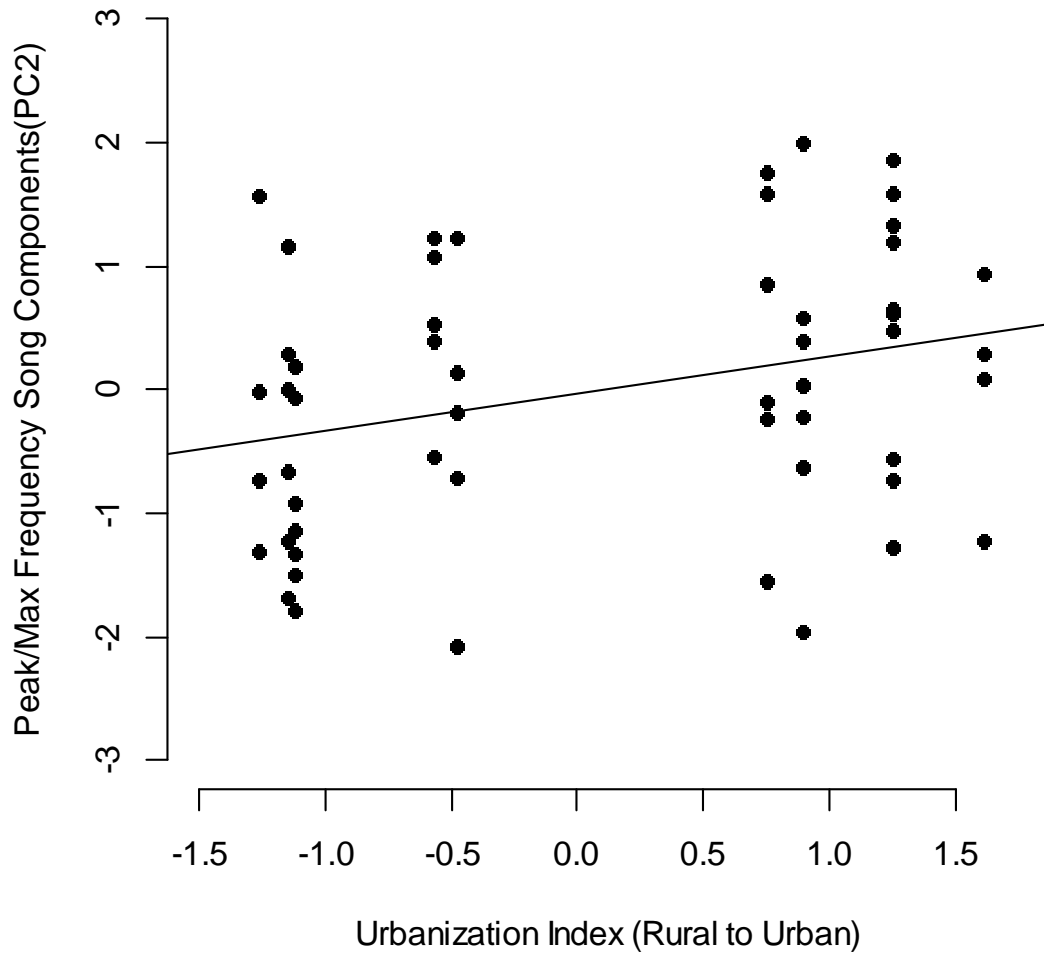


Figure 2.5. Peak and high frequency song components (PC2) as surrounding landscape changes.

As urbanization increased, males sang songs with higher peak and maximum frequencies

(increases in PC2) (β : 0.30 ± 0.14 , $F_{1, 52} = 4.95$, $p=0.03$).

| | Urban | Conspecific densities | Noise levels | Body size | Shrub/sapling density | Small trees | Large trees |
|-----------------------|----------------|-----------------------|---------------|---------------|-----------------------|---------------|----------------|
| Urban | 1.00 | 0.89 <0.01 | 0.81 0.02 | -0.79 0.02 | 0.94 <0.01 | -0.28 0.50 | -0.92 <0.01 |
| Conspecific densities | 0.89 <0.01 | 1.00 | 0.96 <0.01 | -0.47 0.24 | 0.96 <0.01 | -0.21 0.62 | -0.64 0.08 |
| Noise levels | 0.81 0.02 | 0.96 <0.01 | 1.00 | -0.31 0.45 | 0.90 <0.01 | -0.33 0.42 | -0.54 0.17 |
| Body size | -0.79 0.02 | -0.47 0.24 | -0.31 0.45 | 1.00 | -0.58 0.13 | 0.23 0.59 | 0.96 <0.01 |
| Shrub/sapling density | 0.94 <0.01 | 0.96 <0.01 | 0.90 <0.01 | -0.58 0.13 | 1.00 | -0.32 0.44 | -0.74 0.04 |
| Small trees | -0.28 0.50 | -0.21 0.62 | -0.33 0.42 | 0.23 0.59 | -0.32 0.44 | 1.00 | 0.26 0.54 |
| Large trees | -0.92 <0.01 | -0.64 0.08 | -0.54 0.17 | 0.96 <0.01 | -0.74 0.04 | 0.26 0.54 | 1.00 |

Table 2.5. Correlation matrix (Pearson's correlation) between urbanization index, and average conspecific densities, body size, noise levels, shrub & sapling densities, small trees and large trees at the site (n=9).

| <i>Model</i> | <i>k</i> | <i>AIC</i> | <i>AIC_C</i> | ΔAIC_C | <i>AIC_C</i> <i>Weight</i> | <i>evid.rat</i> |
|-------------------|----------|------------|------------------------|----------------|---|-----------------|
| Density | 2 | 175.67 | 175.92 | 0 | 0.93 | 1 |
| Noise | 2 | 182.22 | 182.47 | 6.55 | 0.04 | 26.43 |
| Null | 1 | 185.33 | 185.41 | 9.49 | 0.01 | 114.82 |
| Shrubs & saplings | 2 | 185.32 | 185.58 | 9.65 | 0.01 | 124.82 |
| Body Size | 2 | 185.91 | 186.17 | 10.24 | 0.01 | 167.75 |
| Global | 8 | 183.79 | 187.31 | 11.38 | 0 | 296.26 |
| Small Trees | 2 | 187.11 | 187.37 | 11.45 | 0 | 305.7 |
| Large Trees | 2 | 187.32 | 187.58 | 11.65 | 0 | 339.11 |
| All Trees | 3 | 189.11 | 189.63 | 13.71 | 0 | 946.46 |
| All Veg | 4 | 189.09 | 189.98 | 14.06 | 0 | 1129.69 |

Table 2.6. Northern Cardinal ($n = 54$) temporal song models using Akaike's Information Criterion corrected for small sample sizes (AIC_C). Models include variables that represent alternative hypotheses for song variation: density of conspecifics at the site level, noise levels (dbA) at the territory level, body size of the vocalizing male, vegetation at the territory level (tree classes and shrub densities) as well as a global and null model.

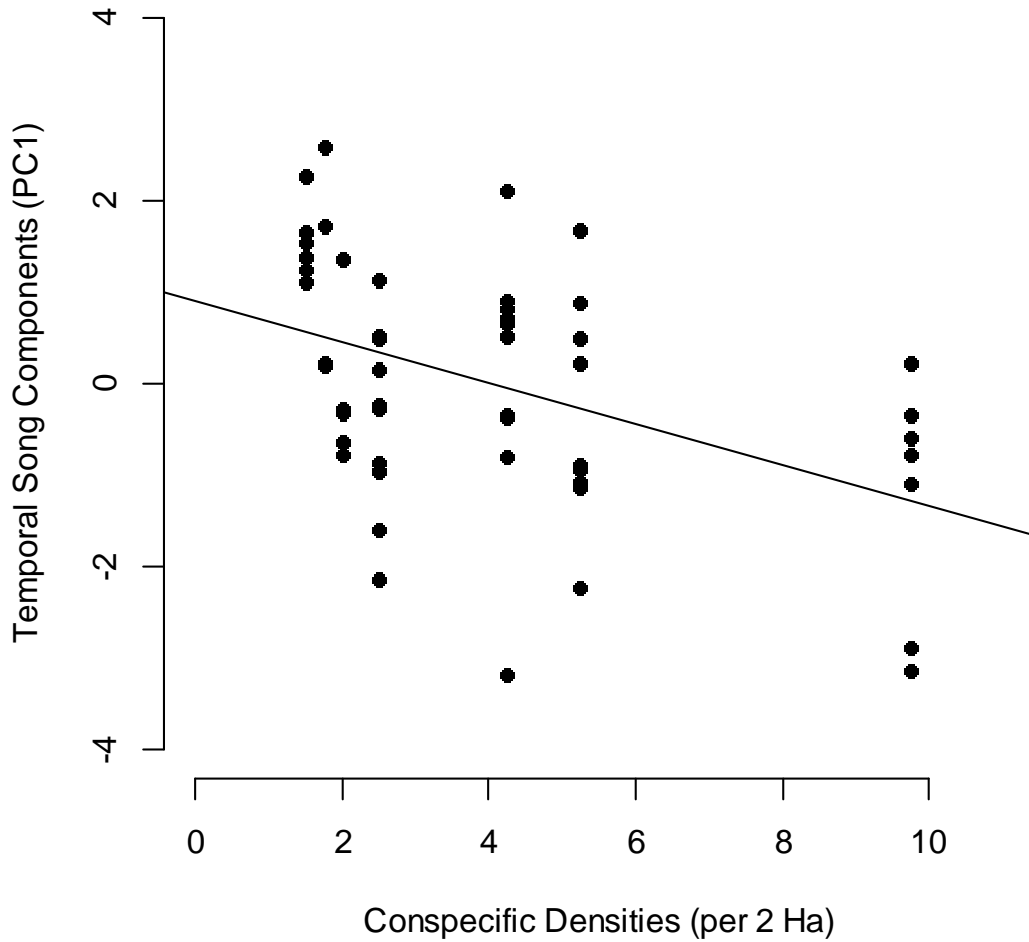


Figure 2.6. The relationship between temporal song characteristics and conspecific densities.

Males sing songs that are longer and faster (decreases in PC1) as sites have more cardinal territories ($\beta = -0.22 \pm 0.06$, 95% CI: -0.35, -0.10, $F=12.53$, $p<0.001$).

| <i>Model</i> | <i>k</i> | <i>AIC</i> | <i>AIC_C</i> | ΔAIC_C | <i>AIC_C</i> <i>Weight</i> | <i>evid.rat</i> |
|---------------------|----------|------------|------------------------|----------------|---|-----------------|
| Null | 1 | 165.48 | 165.56 | 0 | 0.19 | 1 |
| Body size | 2 | 165.5 | 165.75 | 0.19 | 0.18 | 1.1 |
| Shrubs and saplings | 2 | 165.55 | 165.81 | 0.25 | 0.17 | 1.13 |
| Noise | 2 | 166.21 | 166.46 | 0.9 | 0.12 | 1.57 |
| Density | 2 | 166.6 | 166.86 | 1.3 | 0.1 | 1.91 |
| Large Trees | 2 | 166.78 | 167.04 | 1.47 | 0.09 | 2.09 |
| Small Trees | 2 | 167.2 | 167.45 | 1.89 | 0.08 | 2.57 |
| All Trees | 3 | 168.49 | 169.02 | 3.46 | 0.03 | 5.63 |
| All Veg | 4 | 168.53 | 169.42 | 3.86 | 0.03 | 6.9 |
| Global | 8 | 172.44 | 175.96 | 10.4 | 0 | 180.96 |

Table 2.7. Northern Cardinal ($n = 54$) peak/high frequency song models using Akaike's Information Criterion corrected for small sample sizes (AIC_C). Models include variables that represent alternative hypotheses for song variation: density of conspecifics at the site level, noise levels (dbA) at the territory level, body size of the vocalizing male, vegetation at the territory level (tree classes and shrub densities) as well as a global and null model.

| <i>Model</i> | <i>k</i> | <i>AIC</i> | <i>AIC_C</i> | ΔAIC_C | <i>AIC_C</i> <i>Weight</i> | <i>evid.rat</i> |
|-------------------|----------|------------|------------------------|----------------|---|-----------------|
| Noise | 2 | 133.66 | 133.91 | 0 | 0.9 | 1 |
| Global | 8 | 134.88 | 138.39 | 4.48 | 0.1 | 9.37 |
| Density | 2 | 154.16 | 154.41 | 20.5 | 0 | 28275.1 |
| Small Trees | 2 | 155.95 | 156.2 | 22.29 | 0 | 69255.8 |
| Null | 1 | 156.2 | 156.28 | 22.37 | 0 | 71993.4 |
| All Trees | 3 | 156.24 | 156.76 | 22.85 | 0 | 91454.9 |
| Large Trees | 2 | 156.56 | 156.81 | 22.9 | 0 | 93949.8 |
| Shrubs & saplings | 2 | 158.08 | 158.33 | 24.42 | 0 | 200964 |
| Body Size | 2 | 158.17 | 158.43 | 24.52 | 0 | 210700 |
| All Veg | 4 | 158.11 | 159 | 25.09 | 0 | 280170 |

Table 2.8. Northern Cardinal (n=54) minimum frequency song models using Akaike’s Information Criterion corrected for small sample sizes (AIC_C). Models include variables that represent alternative hypotheses for song variation: density of conspecifics at the site level, noise levels (dbA) at the territory level, the percent urbanization in the surrounding landscape (index), body size of the vocalizing male, vegetation at the territory level (tree classes and shrub densities) as well as a global and null model.

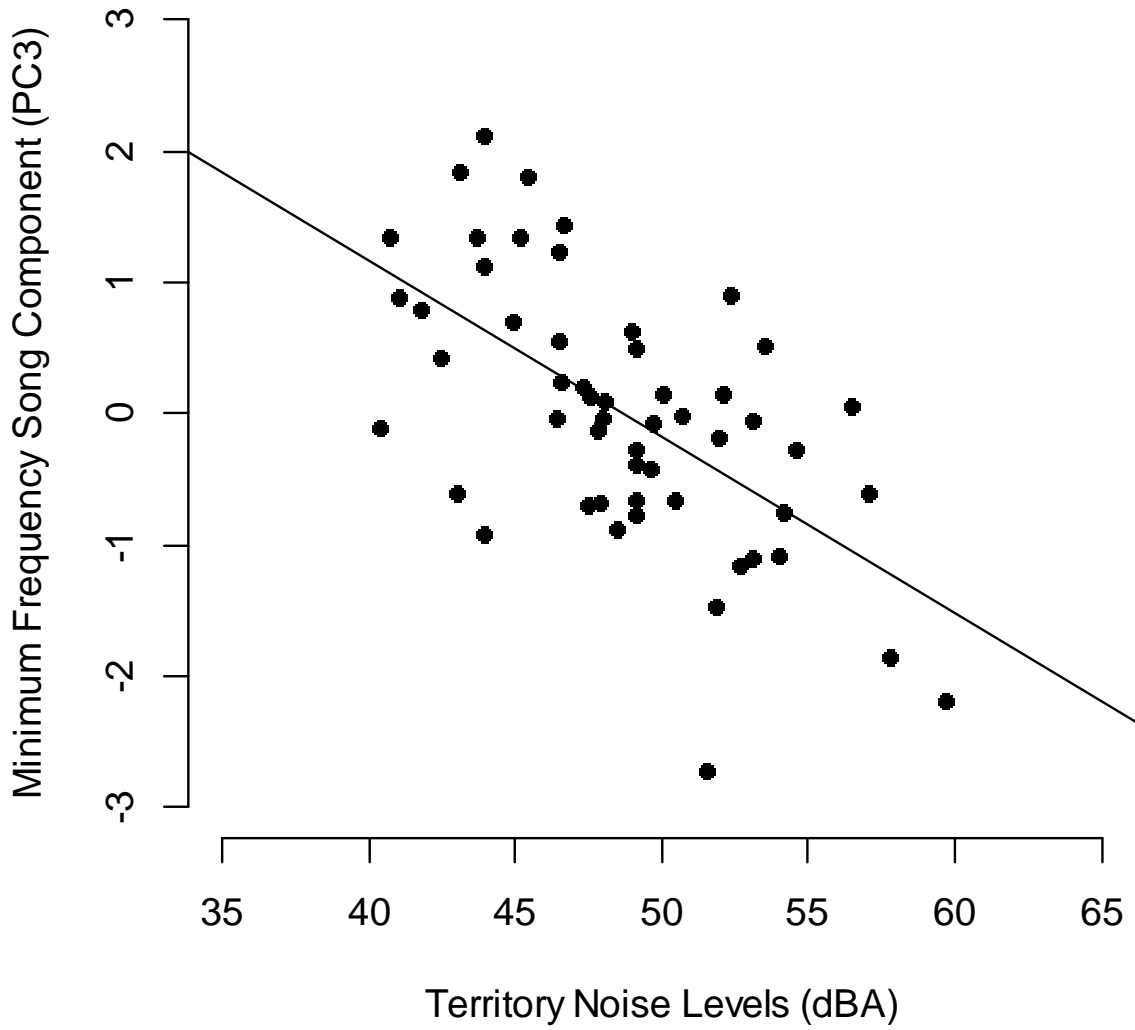


Figure 2.7. The relationship between minimum frequency and environmental noise. Males sing songs with higher minimum frequencies (decreases in PC3) as territories become louder ($\beta = -0.13 \pm 0.02$, 95% CI: -0.18, -0.09, $F=29.92$, $p<0.001$).

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CHAPTER 3

SIGNAL RELIABILITY OF BIRD SONG IN HUMAN-DOMINATED LANDSCAPES

Abstract

Communication systems, which rely upon specific social contexts and environments that permit effective transmission, are particularly vulnerable to disruption by anthropogenic disturbance. Indeed, recent studies have implicated anthropogenic noise as a cause of changing bird song in urban areas. Urban-associated variation in the transmission or reception of song can profoundly influence conspecific interactions in ways that ultimately affect fitness; however, the evolutionary and ecological consequences of altered songs remain poorly understood. I hypothesized that the relationship between song attributes and fitness metrics would be landscape-dependent, differing between urban and rural habitats. I investigated this hypothesis by measuring vocal and breeding behavior of 54 individually-marked male Northern Cardinals (*Cardinalis cardinalis*) at nine sites distributed across a rural to urban landscape gradient in Columbus, Ohio in 2010—2011. I quantified male fitness and quality by determining seasonal reproductive output, body size, nest provisioning, and territory attributes. I found that relationships between quality and song attributes varied across landscapes for some, but not all, song characteristics. Relationships between body size and temporal features were landscape-dependent, such that in rural landscapes alone, larger males sang

shorter, slower songs. There was no relationship between song and body size in urban landscapes. Relationships between parental care and song attributes were consistent across landscapes, and males that sang short, slower songs provisioned nests less often and had nestlings in poorer condition. Interestingly, males that sang higher minimum frequencies had nestlings in poorer condition. Song attributes were not significantly associated with reproductive output or territory quality. My results indicate that, in addition to favoring modifications that promote effective transmission in cities, urban landscapes may also change the reliability of song as a signal of quality. To my knowledge, this is the first study to investigate signal reliability and potential fitness of song variation in urban systems, thereby providing insight into micro-evolutionary processes operating within novel environments.

Introduction

The degree to which sexually-selected traits serve as reliable signals of quality can vary spatially with environmental and social context (Dunn et al. 2008, Higginson and Reader 2009, Cornwallis and Uller 2010, Rodewald et al. 2011). Heterogeneity in signal reliability should be most pronounced for traits that vary widely in the effectiveness of signal transmission among environments. Avian song is an excellent example of a trait for which (1) the effectiveness of signal transmission is strongly mediated by social and environmental context (Ryan and Brenowitz 1985, Bradbury and Vehrencamp 1998, Slabbekoorn and Smith 2002, Slabbekoorn et al. 2007) and (2) the fitness consequences, as related to territory and/or mate quality, can be substantial (Catchpole 1987, Andersson 1994, Mennill et al. 2006). In a time of rapid land transformation, understanding how selective environments for song are shaped by anthropogenic disturbance is necessary to anticipate the ecological and evolutionary responses of native species.

Urban development imposes rapid and dramatic change on the acoustic environment of birds, and thus, offers a unique opportunity to study variable selective pressures on sexual traits. For example, urban forests are characterized by abundant invasive vegetation (Borgmann and Rodewald 2005), high densities of generalist species (Shochat et al. 2006, Bakermans et al. 2006), high activity patterns of predators (Rodewald et al. 2011a), and loud sources of anthropogenic noise (Slabbekoorn and Peet 2003). Consequently, urban pressures have the potential to alter the expression of

ornamental traits as well (Yeh 2004, Slabbekoorn and den Boer-Visser 2006, Isaksson and Andersson 2007, Badyaev et al. 2008c, Evans et al. 2010, Jones et al. 2010). Indeed, a growing number of studies have described a pattern of urban-associated song alterations (Wood and Yezerinac 2006, Slabbekoorn and den Boer-Visser 2006, Mockford and Marshall 2009, Dowling et al. 2012). Yet even within cities, sufficient variation in song traits among individuals remains for sexual selection to operate; in other words, the cities do not “fix” the traits. Thus, if sexual traits are changing within urban environments, they may no longer act as reliable sources of information. Evolutionary traps can develop in contexts where conspecifics prefer traits that have recently become associated with unreliable information such as poor territories (Rodewald et al. 2011b) or mates of lower quality (Schlaepfer et al. 2002).

Song performance can signal age (Ballentine 2009), size (Ballentine 2009), condition (Rehsteiner et al. 1998), dominance rank (Otter et al. 1997b, Rehsteiner et al. 1998), reproductive success (Conner et al. 1986, Mennill et al. 2006), territory quality (Conner et al. 1986, Van Oort et al. 2006) and parental investment (Buchanan and Catchpole 2000). However, the extent to which urbanization influences the function of song as an informative signal remains poorly understood. In natural or non-noisy areas, high frequency songs tend to elicit lower territorial responses from conspecifics (Mockford and Marshall 2009, Ripmeester et al. 2010, Luther and Derryberry 2012) and females (Halfwerk et al. 2011a), yet high frequencies are prevalent in cities. Higher minimum frequencies also can give erroneous information about a singer’s status, such as pairing success, which could result in more unpaired males in urban areas (Gross et al.

2010). Extra-pair paternity may be correlated with song output, but become decoupled in noisy areas (Wisner 2011).

To better understand the consequences of urban-associated acoustic changes, I investigated the reliability of song as an informative signal across a rural-urban landscape gradient. Using the cosmopolitan Northern Cardinal (*Cardinalis cardinalis*) as a model species, I examined relationships between song traits and fitness parameters (i.e., reproductive output) as well as indicators of male quality (morphology, provisioning rates and territory vegetation). I hypothesized that relationships among song traits, fitness and quality parameters would change with urbanization, such that song characteristics indicating high fitness and quality in rural landscapes would be different than those in urban landscapes. Specifically, I predicted that males that use song characteristics that transmit most efficiently in urban environments (e.g., increases in frequencies and longer, faster songs) would have higher fitness and associated quality traits.

Methods

Study Area. This study was conducted between March-September, 2010-2011 in nine mature riparian forests ($\geq 250\text{m}$ long and $\geq 100\text{m}$ wide) along three rivers (Olentangy, Darby and Alum Creek) in and around Columbus, Ohio. Digital orthophotos were used to quantify landscape composition within a 1km radius from the site, and these metrics were used in a principal components analysis to create an index of urbanization for each site (see Rodewald and Shustack 2008 for more details). Index values were

correlated with surrounding composition such that values loaded positively with number of buildings, and percent cover by roads, pavement and lawn and negatively with percent cover by agriculture. Hereafter, positive values are considered sites within an ‘urban’ landscape and negative values are embedded within a ‘rural’ landscape although analysis is conducted on a continuous scale. Sites were separated by at least 2 km and were similar in size and shape and differed primarily in respect to surrounding landscape matrix.

Study species. I used Northern cardinals as a model synanthropic species to investigate consequences of song variation. Individual males were captured using mist-nets and fitted with a unique color band combination for individual identification. Few individuals were not captured, but could be followed because of reliable song perches and/or were mated with banded females. Upon capture, tarsus and wing were measured and subsequently used in a principal components analysis to construct a body size index (Zurr et al. 2007) which explained 57% of the variation in measurements and loaded positively with increases in wing ($r=0.75$) and tarsus size ($r=0.75$). Body condition was acquired by obtaining the residuals of a regression of mass with body size (Jakob et al. 1996). As size and condition were highly correlated ($r=0.96$), I focused only on body size because size is an indicator of male quality (Kodric-Brown and Brown 1984) and may be related to song characteristics (Ryan and Brenowitz 1985, Gil and Gahr 2002).

Song Recording and Analysis. Songs were recorded for 5 hours following sunrise on weekdays between March and June when peak cardinal singing occurs. Territories

were monitored for 30 minutes, during which I attempted to record all song bouts. The order of visits to territories alternated so that time of day of the recording observation was arbitrary. Identity of singing individuals was confirmed by color bands or associations with paired color-banded females. All recordings were made with a Marantz PMD 670 digital recorder and a Sennheiser directional microphone. Songs were sampled at 44.1 kHz with a bit rate of 32 kbps, and saved as mono .wav files.

Songs from 2010 were recorded using a file type (.mp3) that compressed maximum and peak frequency measurements and thus could not be used for a multivariate analysis. In order to remain consistent with my measurements, I chose to only analyze songs from 2011 because they were recorded with the .wav file type. Digital spectrograms were created using Raven 1.4 Pro (Cornell lab of Ornithology). Songs were measured using Hann sampling (Time: 256 samples, 3dB filter bandwidth 248 Hz, overlap 50%, hop size 128 samples, dft size: 256 samples, grid spacing 172 Hz, Frequency: 1024 samples, 3dB filter bandwidth 61.9 Hz, overlap 50%, hop size 512 samples, dft size: 1024, grid spacing 43.1 Hz). Cardinals sing with eventual variety meaning individuals sing one type repeatedly before switching to a new song type. As there is more difference between song types than within, song types were measured as unique samples to capture individual variation. Song types were defined according to Lemon (1965) such that a type was specified as a unique “utterance” of 1 or more syllable types where the time between syllables (<1sec) was less than the time between songs (>1 sec). For example, a combination of syllable type ‘A’ and ‘B’ was called unique song type ‘AB’. Sample size was limited by the number and quality of the

recordings taken, thus some males were dropped because of insufficient recording samples (<3 song types). These males were mostly from urban landscapes due to accidental recordings of males adjacent to focal territories, or overall poor recording quality from unusually high ambient noise (>70 dBA, 1 male). Because I was predominantly limited by rural rather than urban males in my sampling, these deletions likely do not bias my results.

Songs were visually inspected to measure the best recording of each song type during the observation period. Songs were included for spectrogram analysis if they: 1) were clean recordings with minimal reverberations 2) were not overlapped by any other biological or ambient sounds 3) could be assigned to a territory. My goal was to capture the variation across song types; hence to account for song types that were used more often, I measured the best recording of each song type per day. Songs of the same type that were recorded on different days were considered unique samples. Each song type was measured for minimum and maximum frequency (Hz), frequency bandwidth (range), frequency at the highest amplitude ('peak frequency'), song length, and number of syllables, syllable rate (syllables/sec), and number of syllable types. All variables were measured using the manual cursor and by the same observer (DLN). Mean measures of individual characteristics per male are used in analyses here.

Reproductive Success. From mid-March to September, males were followed for extensive territory monitoring to determine reproductive success. Territories were monitored every 2-3 days to locate and monitor nests. Nesting attempts were considered

successful if young were visually observed and counted following day of fledging. Fledges from multiple nesting attempts were summed for each male for seasonal reproductive success. The number of young fledged over the course of a season was considered a reasonable estimate of paternity because cardinals exhibit low extra-pair fertilizations and high levels of mate-guarding (Ritchison et al. 1994).

Territory Quality. Territory quality was quantified by measuring vegetative attributes known to be strongly selected by cardinals, particularly high understory shrub density and exotic shrubs (Conner et al. 1986, Leston and Rodewald 2006). We quantified territory vegetation composition and structure by selecting one early-season and one later season nest along with one random point within the territory for sampling (25m in a random direction from the early nest). Vegetation was measured in an 11.3m radius circle centered on the nest or random point. Trees and large woody shrubs were identified and classified in 4 size classes (3-8 dbh, 8-26 dbh, 26-38 dbh, and 38+ dbh). A large proportion of vegetation in the 3-8 dbh size class was comprised by native tree saplings and Amur honeysuckle (*Lonicera maackii*) > 3m high. Shrubs < 3m were quantified by percent cover within the circle.

Parental Care. Male parental care was estimated by quantifying provisioning visits during the nestling stage. A one hour observation was conducted between days 5-7 to control for variation at different nestling ages. Age was obtained from known hatch date or estimated by nestling development (at next visit following hatch). During an observation, the observer was positioned in a concealed location >10m from the nest.

Observations were completed in the afternoon, during times of clear weather, and only when adults were not disturbed by the observer's presence. The observer counted number of feeding visits by each adult as well as behaviors around the nest area. Number of nestlings was visually confirmed following each observation and adult visits were divided by nest size to obtain feeding visits per nestling.

For nests within reach (<4m high), nestlings were weighed to the nearest 0.01g and tarsi measured to the nearest 0.1mm. Tarsus length was highly correlated with nestling age ($r > 0.7$) so tarsus was only included as a measure of size. The model with the best fit (lowest AIC) included both tarsus and weight time as main effects, therefore condition was obtained by regressing mass by tarsus and time (Jakob et al. 1996). Because the interaction between tarsus and time was not significant ($p > 0.1$), only main effects were used in the model (Bradbury et al. 2003). Since nestlings from the same brood cannot be considered independent, mean nestling condition was calculated for each nest.

Statistical Analysis. I first assessed multicollinearity among variables using a correlation matrix. When variables were highly correlated ($r > 0.70$) only one of the two variables were used based on which was most biologically relevant for my study. All variables were assessed for normality using histograms, normal quantile plots and a Shapiro-Wilk test. All variables satisfied assumptions of normality, except provisioning rates, which I log-transformed.

Next, I used a principal components analysis to reduce the number of variables associated with song and vegetation characteristics (see chapter 2 for more details). Principal component 1 (PC1) had factors that reflected decreases in temporal features of song (number of syllables and rate), whereas PC2 indicated increases in peak frequency and maximum frequency. PC3 was negatively related to minimum frequency such that increases in PC3 described decreases in minimum frequencies. Hereafter I call these variables temporal components (PC1), peak/high frequency (PC2) and minimum frequency (PC3).

Finally, I used linear (LMM) and generalized linear mixed-effect models (GLMM) to test for the relationships between fitness parameters and song parameters and urbanization. Changes in the relationship between urban and rural landscapes were tested using the interaction between song and a continuous index of urbanization. Therefore all full models included one of the song scores as a fixed factor (temporal, peak/high frequency and minimum frequency), urbanization and the interaction between song and urbanization. Since multiple males were recorded at each site, and I was interested in the effect of surrounding urbanization, site was used as a random effect in the model. Separate models were run for each indicator of fitness. Sample sizes vary for each model, because I was unable to collect every fitness parameter for each male. If the interaction term was non-significant ($p > 0.1$) this term was deleted and re-run with the subsequent simpler model (Zuur et al. 2009). I validated model fit assumptions by plotting and visually inspecting residuals against fitted values and a normal quantile plot of residuals (Zuur et al. 2007). The fledgling count model was run with a poisson distribution with a log

link (Zuur et al. 2009, O'Hara and Kotze 2010) using the `glmmML` function in R (package MASS, version 7.3-16). All other models were run with a Gaussian distribution using the `lme` function in R (package nlme, version 3.1-102).

Results

Summary of means. In 2010 I recorded 32 males (14 from rural and 18 from urban landscapes) and in 2011 I recorded 66 males (26 from rural and 36 from urban landscapes). Using my criteria for song inclusion and excluding 2010 recordings and males not recorded in the focal area, I measured 610 songs with 8.28 ± 4.55 song types from each male ($n=54$).

Relationships between quality attributes and song. Interestingly, the relationship between temporal song traits (PC1) and body size was dependent on the surrounding landscape ($\beta=0.28 \pm 0.11$ SE, $F=7.12$, $p=0.01$; Table 3.1). Males with the shortest and slowest songs had the largest body size in rural landscapes, but this pattern was absent in urban landscapes (Figure 3.1). No relationship existed between body size and peak frequency (Figure 3.2) and low frequency song traits (Figure 3.3). There was no significant interaction between any song traits and urbanization (Table 3.1).

Increases in song length and rate were negatively related to male feeding rates and nestling condition such that males singing short, slow songs made fewer feeding visits per nestling ($\beta=-0.09 \pm 0.05$, $F=3.57$, $p=0.07$; Table 3.2; Figure 3.4) and had nestlings in

poorer condition ($\beta=-0.40 \pm 0.21$, $F=3.57$, $p=0.08$; Table 3.2; Figure 3.5). This relationship persisted across the landscape as indicated by the non-significant interaction between temporal song components and urbanization (Table 3.2). There was no relationship between feeding rates and either frequency component, nor the interaction between frequency traits and urbanization (Table 3.2). Minimum frequencies of song were positively related to nestling condition ($\beta=0.65 \pm 0.25$, $F=6.61$, $p=0.02$; Table 3.2), a relationship that persisted in either landscape. Here, males that sang higher minimum frequencies (a PC3 with low values) had nestlings in poorer condition between days 5-7 (Figure 3.5). The relationship between the peak/high frequency component was landscape dependent ($\beta=0.45 \pm 0.24$, $F=3.64$, $p=0.07$; Table 3.2) but relationships appeared weak for both landscapes (Figure 3.5).

Density of shrubs and saplings was positively related to urbanization but unrelated to any song components (Table 3.3). There was no significant effect of an interaction between song features and urbanization or between landscapes for vegetation features.

Relationships between reproductive fitness and song. Contrary to my predictions, seasonal fledgling success was unrelated to any song component or the effect of urbanization. In addition, there was no significant interaction between song features and urbanization between landscapes for reproductive output (Table 3.4).

Discussion

My study provides evidence that urban environments can alter the reliability of song as a signal of male quality for some, but not all, fitness attributes. The relationship between body size and song characteristics was landscape dependent such that males with the shortest and slowest songs were larger, but only in rural forests. Other relationships were consistent across landscapes, including the pattern that males singing short, slow songs provided less parental care and males singing short, slow, high frequency song had nestlings in poorer condition. That said, I found no evidence of strong relationships between song attributes and reproductive success or territory attributes.

Despite a plethora of studies documenting that songs of urban birds differ from their non-urban counterparts (Chapter 1, Wood and Yezerinac 2006, Slabbekoorn and den Boer-Visser 2006, Mockford and Marshall 2009), few have evaluated the functional consequences of urban-associated changes in song. To my knowledge, my study is the first to show that relationships between song and quality traits may differ in rural and urban landscapes. Specifically I found that anthropogenic disturbance not only shapes acoustic temporal attributes, but also the relationship between song and body size. Males that were larger sang songs that were shorter and slower in rural landscapes. This is consistent with Conner et al. (1986), who demonstrated that males in a non-developed landscape that sang short songs of low complexity secured better territories and fledged more young. Many studies have shown that large body size provides fitness advantages in interspecific competition, survival and reproduction (Kodric-Brown and Brown 1984,

Jennions et al. 2001). Thus, temporal features of song may have evolved relationships with body morphology in cardinals.

I found that the relationship between song and morphology was landscape-dependent, such that song failed to signal information about body size in urban landscapes. In addition to background levels of spatial heterogeneity in selection (Cornwallis and Uller 2010), environments may decouple relationships between sexual traits and the information they once signaled (Higginson and Reader 2009). Indeed, the degree to which sexual traits indicate morphology or reproductive output varies widely across geographic ranges and landscapes (Yeh 2004, Badyaev et al. 2008, Jones et al. 2010, Vortman et al. 2011). One explanation for reduced reliability of sexual traits is that males in poor habitat reduce advertisement when resources are low (Van Oort et al. 2006). Alternatively, the selective environment for ornamental traits may be modified by anthropogenic resource subsidies or evolutionary traps (Rodewald et al. 2011). Song that provides unreliable information about a signaler's condition or intent may increase time spent defending the territory against intruders (Conner et al. 1986) or reduce mating opportunities with prospective females (Catchpole 1987, Swaddle and Page 2007, Halfwerk et al. 2011). Smaller males that are able to secure better territories may eventually result in higher fitness and decouple the relationships between quality and song.

Irrespective of landscape context, temporal features of song were associated with male feeding rates and nestling condition, but not to reproductive output. In multi-modal

signaling systems, song may be a more honest indicator of parental care than other ornamental traits such as plumage (Linville et al. 1998), as in the case of some species (Greig-Smith 1982, Buchanan and Catchpole 2000). Male quality is often negatively related to resources provided to nestlings, and this differential allocation may reflect strategies of lower quality males to improve reproductive success by increasing parental care (Burley 1988, Sheldon 2000). Males of higher quality may spend more time in territory defense or sexual advertisement. The lack of a difference across landscapes suggests that males may adjust parental care depending on their own attractiveness (Burley 1988, Smith 1995). I found no evidence that females were increasing their provisioning rates to compensate for low male investment (Pearson's correlation, male and female feeding visits; $r = 0.15$, $p = 0.41$) (Burley 1988) which could result in lower nestling condition. Although differential allocation has been well studied in some species, investigating this strategy in dynamic systems where ornamental traits have become unreliable may reveal the adaptability of this mechanism.

Despite consistent patterns that minimum song frequencies increase in loud urban environments (Wood and Yezerinac 2006, Slabbekoorn and den Boer-Visser 2006, Mockford and Marshall 2009, Bermúdez-Cuamatzin et al. 2011; Chapter 1), few studies have explicitly tested for relationships between urban-associated frequency variation and other aspects of quality. Contrary to my predictions, I did not find support that increases in either peak/high frequency or minimum frequency provides reproductive benefits (or handicaps) in urban systems. The sole pattern observed between minimum frequency and breeding status was that nestling condition was negatively related to minimum

frequencies of song. This relationship was not explained by feeding rates, which were unrelated to frequency (Pearson's correlation, $r = 0.17$, $p = 0.41$). The relationship between peak/high frequency and nestling condition also changed across landscapes, but as the behavioral mechanism behind this variation is unknown and may be due to cultural drift, this interaction may result from differences in song types associated with other song attributes, and the limitations of sample size.

I propose two explanations for the relationship between minimum frequency and nestling condition. First, minimum frequencies may indicate a male's ability to deliver large food items because frequency is constrained by body size (Ryan and Brenowitz 1985, Podos 2001). However, because I failed to find a relationship between song frequency and body size, this explanation is unlikely. An alternative explanation is that males that sing high minimum frequencies have secured territories in habitat that is poor for nestling birds. Because birds increase frequencies in response to noise (Gross et al. 2010, Bermúdez-Cuamatzin et al. 2011), song may be a proxy for noisy areas that contribute to lower condition of young. Noisy territories are located close to high anthropogenic activity (e.g., roads) regardless of landscape type. Noise can reduce the ability of adults to communicate or hear nestlings begging (Warren et al. 2006). Roads and developed edges are also dominated by invasive vegetation (Borgmann and Rodewald 2005) which support fewer and lower quality prey items (Magura et al. 2006, Isaksson and Andersson 2007). Further investigation of the interplay between noise, vegetation and other forms of avian behavior is needed to elucidate these patterns.

One important limitation to my study is that, I used an observational approach to investigate natural song behavior in urban birds. Birds may respond to changes in environmental noise in real-time by adjusting song structure (Hu and Cardoso 2009, Gross et al. 2010, Bermúdez-Cuamatzin et al. 2011), types (Halfwerk and Slabbekoorn 2009), amplitude (Brumm and Slabbekoorn 2005) or activity (Díaz et al. 2011) to increase transmission efficiency (Slabbekoorn et al. 2007, Mockford et al. 2011), and birds that prosper in urban areas may be more behaviorally plastic. In many species, females evaluate mates by complex changes in vocalizations because this potentially indicates an individual's cognitive ability (Boogert et al. 2008). If structural components of song do not translate into direct fitness benefits, behavioral syndromes correlated with song plasticity could be a more reliable signal. Future studies should utilize an experimental approach to test whether an individual's ability to respond to changes the acoustic environment provides reproductive benefits. Another important caveat to my findings is that frequency may not be an important signal of quality for cardinals, unlike other species (Gil and Gahr 2002, Christie et al. 2004). Indeed, I did not find a relationship between body size and song frequency, although large size may constrain the ability to produce low frequency vocalizations (Ryan and Brenowitz 1985). Moreover, I found no evidence of a fitness advantage to singing higher frequencies in urban environments. Similarly, Conner et al. (1986) found no positive correlations between frequency attributes and territory quality or reproduction. In cardinals, individual fitness may be highly driven by other ornamental cues, such as plumage (Wolfenbarger 1999), or territory vegetation and predation pressure, which was outside the scope of this study.

In addition, reproductive output may not be different in territories that are inherently noisy (Barron et al. 2012, but see: Francis et al. 2009, Halfwerk et al. 2011).

In this study, changes in frequency and temporal characteristics of song may be due to immediate responses to changes in environmental and motivational states. The most parsimonious predictive model for temporal song traits was number of conspecific territories and noise for minimum frequencies (chapter 1). Higher competition in urban areas increases the necessity for even large males to defend territories and to change lengths and rates of songs during responses to territorial intrusions (Ritchison 1988). Indeed, number of vocalizing individuals (Spearman's Correlation, $r = 0.82$, $p = <0.01$) and observed recordings directed at conspecifics (Spearman's Correlation, $r = 0.69$, $p = 0.04$) were positively related to amount of urbanization, suggesting increased antagonistic competition in urban birds. Increases in minimum frequency may also be a response to noise levels at the time of recording to maintain transmission efficiency. The lack of any relationship between frequency and reproductive output may be the result of males compensating their song output in order to reduce the fitness costs of not being heard. Anecdotally, males in noisy territories tended to sing more (Narango, personal observation), another mechanism that may offset the chances of not being heard.

A growing paradigm in behavioral ecology is that relationships between sexually selected traits and fitness attributes are not static, but vary in a heterogeneous environment (Cornwallis and Uller 2010). Given the rapid expansion of urban areas, this raises the strong possibility that selective environments might quickly change in cities.

This study is one of the first to provide evidence that urban landscape changes may alter the usefulness of song as an indicator of quality. I found that urbanization decouples the relationship between song and morphology but relationships between song and parental care remain largely consistent across landscapes. In contrast, the complex social use of song, coupled with high behavioral plasticity, may make this behavior less susceptible to significant changes in fitness consequences. Future studies should combine experimental and observational based designs to further elucidate possible mechanisms behind dynamic sexual selection in human-dominated systems and the influence of urban-associated habitat changes on the development and maintenance avian behavior.

| Body Size | | | |
|-----------------------------|--------------|------------|-------------|
| <i>Factor</i> | β (SE) | $F_{7,32}$ | <i>P</i> |
| Temporal | -0.16 (0.12) | 2.05 | 0.16 |
| Urban | 0.18 (0.14) | 1.95 | 0.21 |
| Temporal x Urban | 0.28 (0.11) | 7.12 | 0.01 |
| Peak/High Frequency | 0.16 (0.15) | 1.31 | 0.3 |
| Urban | 0.21 (0.20) | 1.26 | 0.3 |
| Peak/High Frequency X Urban | -0.06 (0.15) | 0.21 | 0.65 |
| Minimum Frequency | -0.00 (0.17) | 0 | 0.98 |
| Urban | 0.30 (0.17) | 3.27 | 0.11 |
| Minimum Frequency X Urban | 0.22 (0.16) | 2.19 | 0.15 |

Table 3.1. Linear mixed model results between morphometrics and song parameters for male cardinals in central Ohio, 2011 ($n = 42$). Factors are principal components of song, urbanization and the interaction between song and urbanization. Urbanization is represented by the index of percent development around the site.

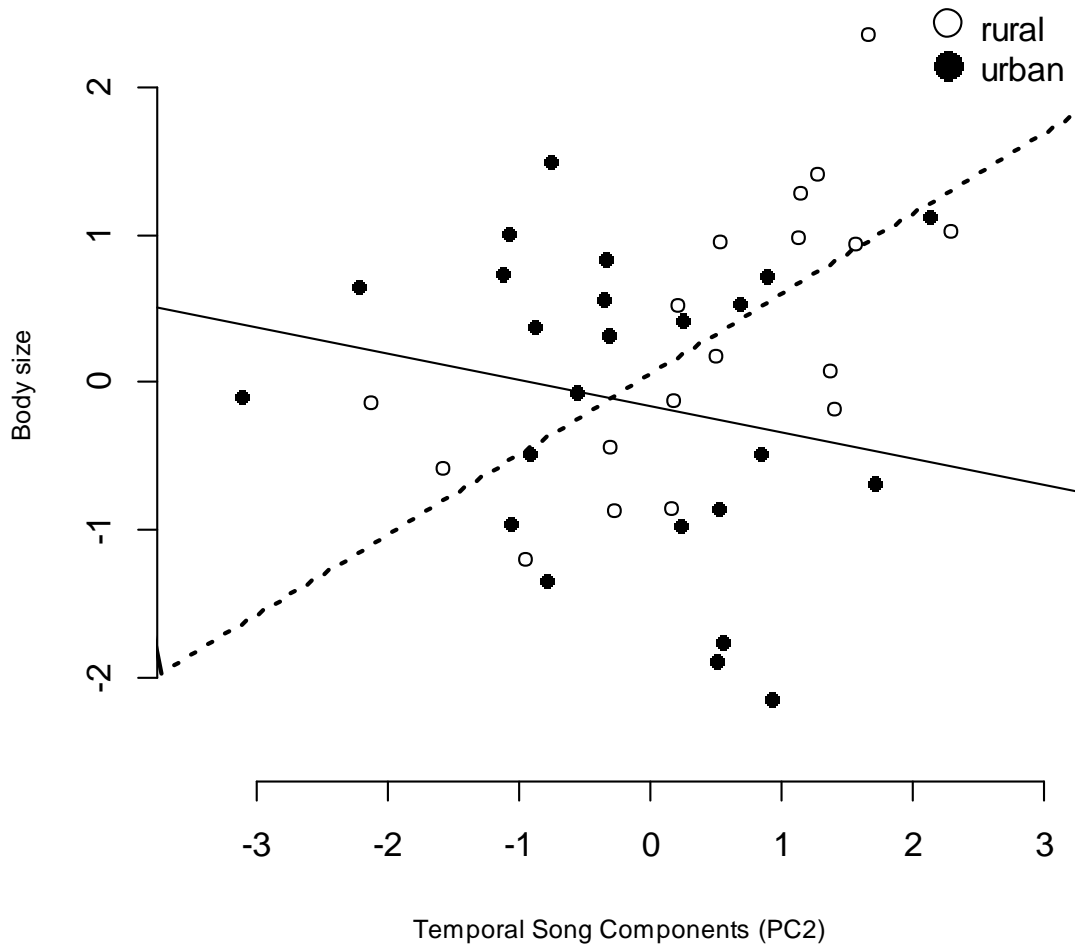


Figure 3.1 Relationship between body size and temporal song characteristics between urban (urban index >0, solid line) and rural (urban index <0, dashed line) landscapes for male cardinals in central Ohio, 2011 ($n = 42$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

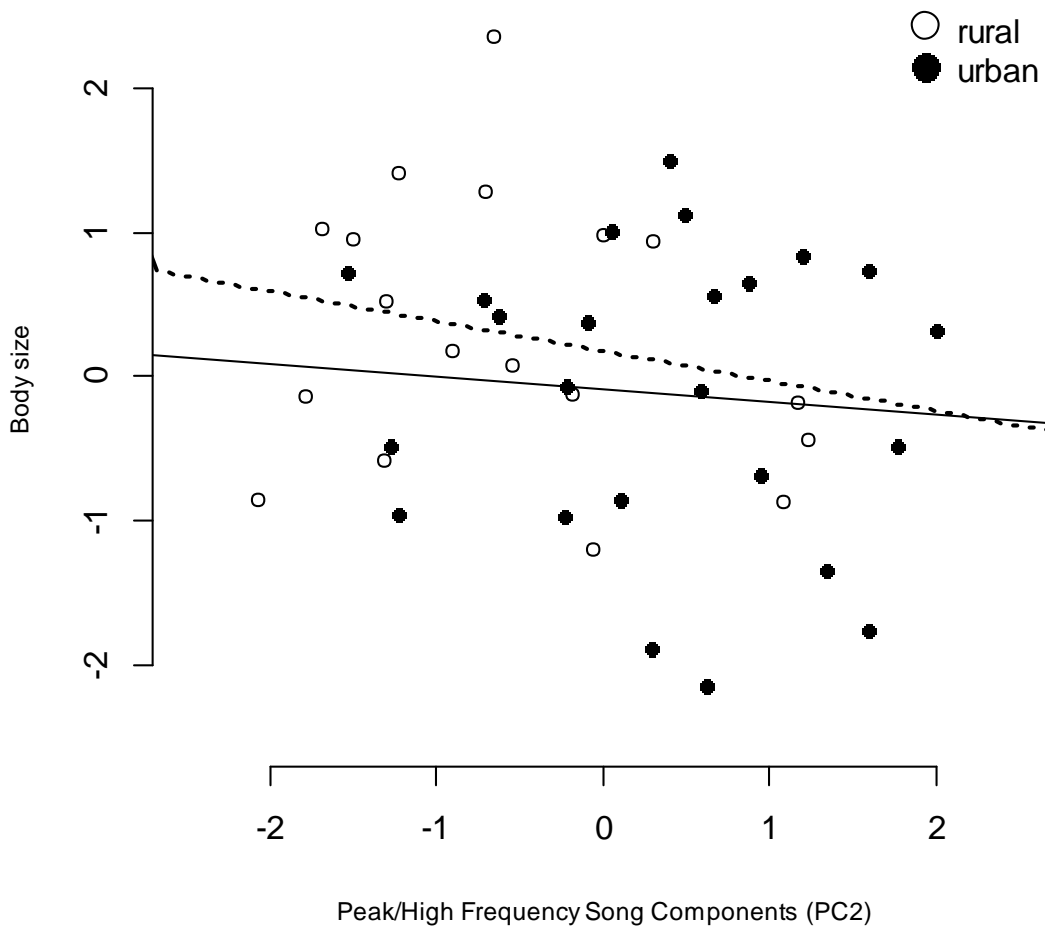


Figure 3.2. Relationship between body size and peak/high frequency (Hz) song characteristics between urban (urban index >0, solid line) and rural (urban index <0, dashed line) landscapes for male cardinals in central Ohio, 2011 ($n = 42$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

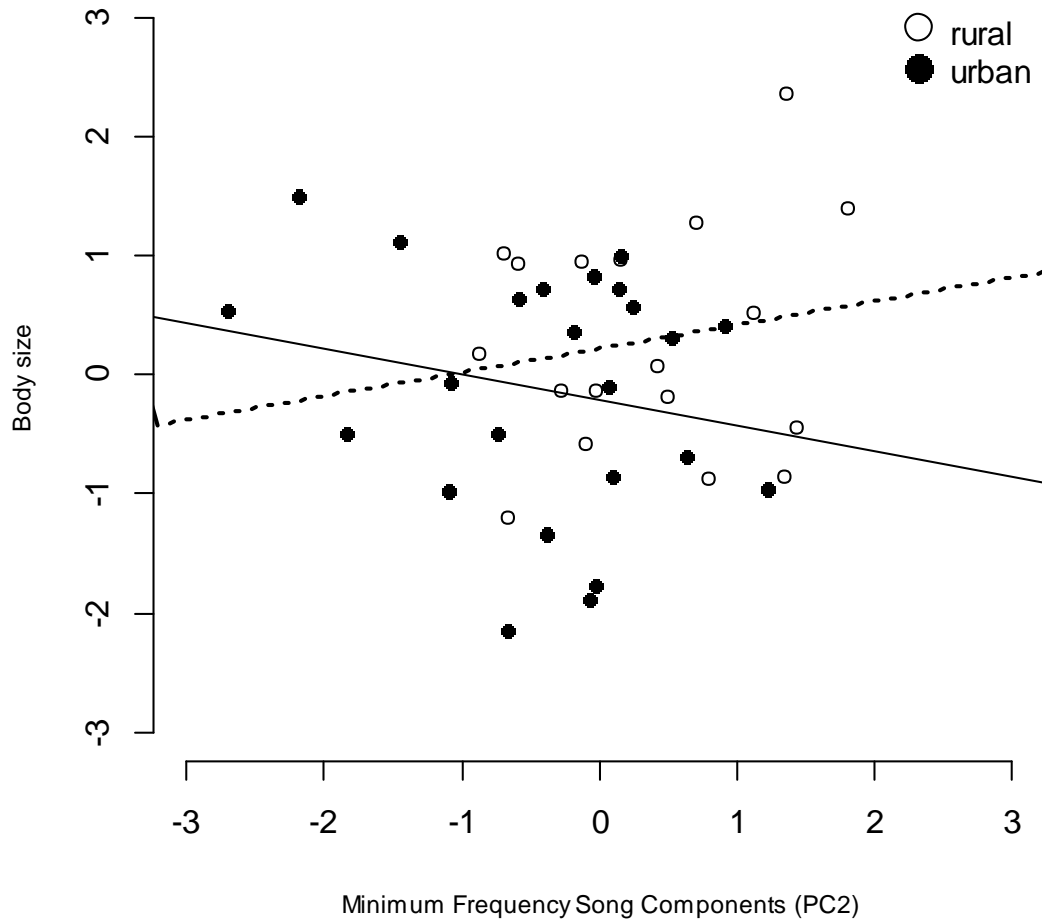


Figure 3.3. Relationship between body size and minimum frequency (Hz) song characteristics between urban (urban index >0, solid line) and rural (urban index <0, dashed line) landscapes for male cardinals in central Ohio, 2011 ($n = 42$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

| <i>Factor</i> | Nestling Condition | | | Provisioning Rates | | |
|-----------------------------|---------------------|-------------|-------------|---------------------|-------------|-------------|
| | β (SE) | $F_{6,16}$ | P | β (SE) | $F_{7,23}$ | P |
| Temporal | -0.40 (0.21) | 3.57 | 0.08 | -0.09 (0.05) | 3.57 | 0.07 |
| Urban | -0.02 (0.45) | 0.01 | 0.96 | -0.01 (0.07) | 0.00 | 0.96 |
| Temporal x Urban | 0.11 (0.18) | 0.36 | 0.56 | - | - | - |
| Peak/High Frequency | 0.17 (0.25) | 0.43 | 0.52 | -0.05 (0.07) | 0.50 | 0.49 |
| Urban | 0.03 (0.45) | 0.01 | 0.94 | 0.05 (0.07) | 0.51 | 0.50 |
| Peak/High Frequency X Urban | 0.45 (0.24) | 3.64 | 0.07 | 0.03 (0.07) | 0.15 | 0.70 |
| Minimum Frequency | 0.65 (0.25) | 6.61 | 0.02 | 0.02 (0.08) | 0.08 | 0.77 |
| Urban | 0.26 (0.43) | 0.36 | 0.57 | 0.04 (0.07) | 0.27 | 0.62 |
| Minimum Frequency X Urban | -0.22 (0.21) | 1.05 | 0.32 | 0.02 (0.07) | 0.05 | 0.83 |

Table 3.2. Linear mixed model results for nestling condition ($n = 26$) and provisioning rates ($n = 33$) for male cardinals in central Ohio, 2011.

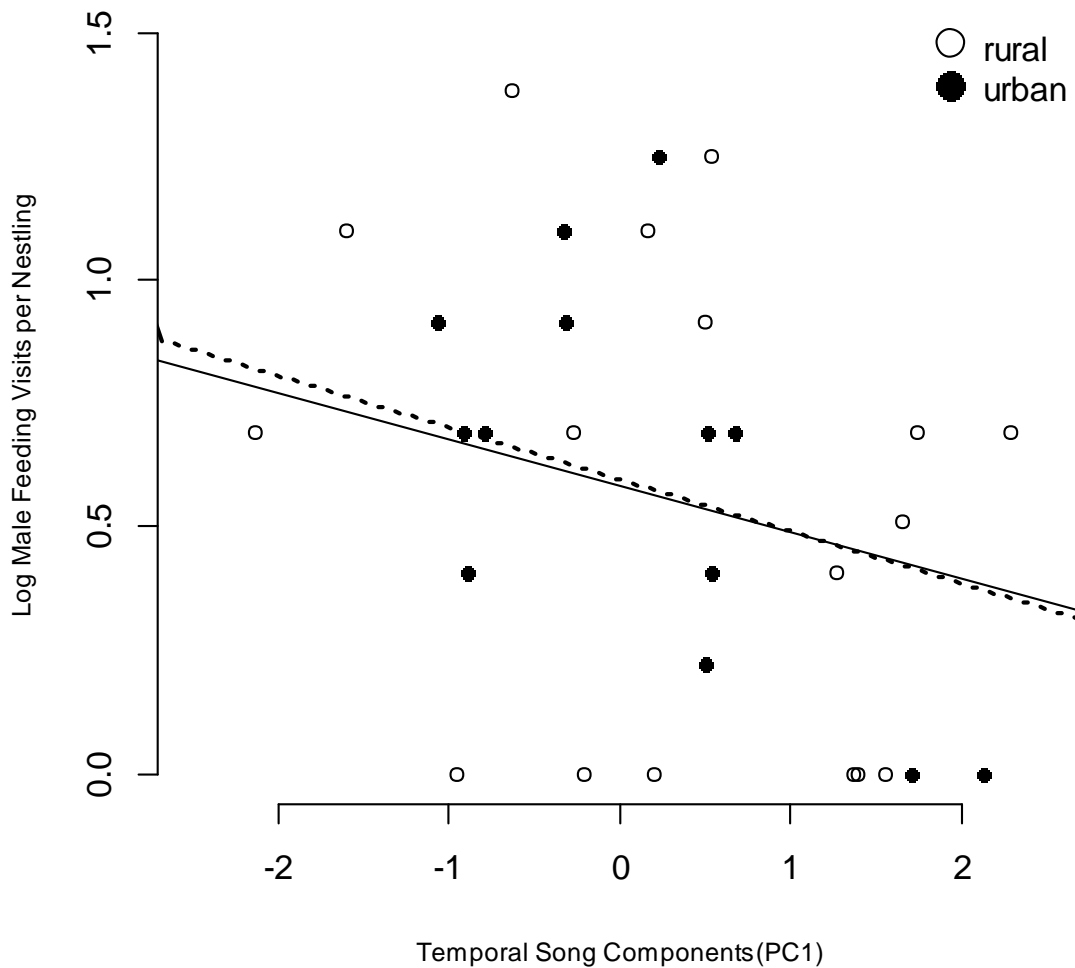


Table 3.4. Relationship between male feeding visits and temporal song characteristics between urban (urban index >0, solid line) and rural (urban index <0, dashed line) landscapes for male cardinals in central Ohio, 2011 ($n = 33$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

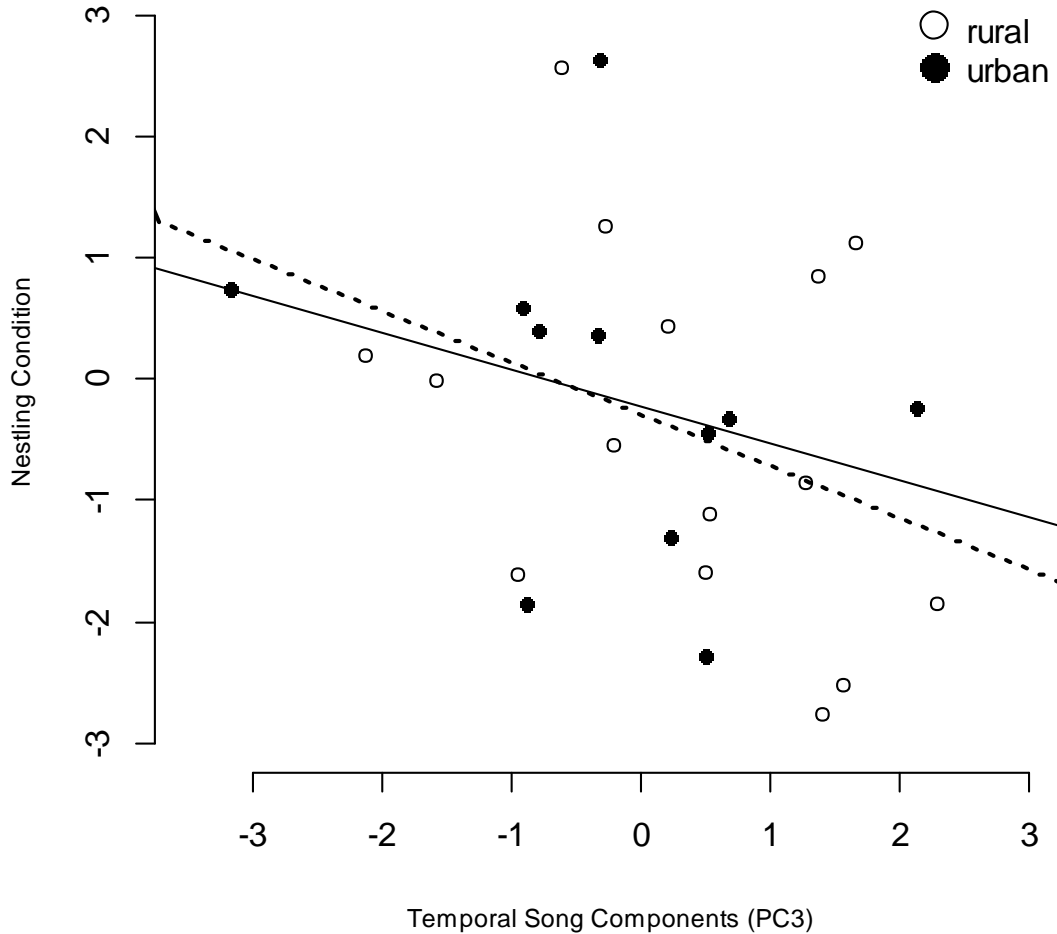


Table 3.4. Relationship between nestling condition and temporal song characteristics between urban (urban index >0, solid line) and rural (urban index <0, dashed line) landscapes for male cardinals in central Ohio, 2011 ($n = 26$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

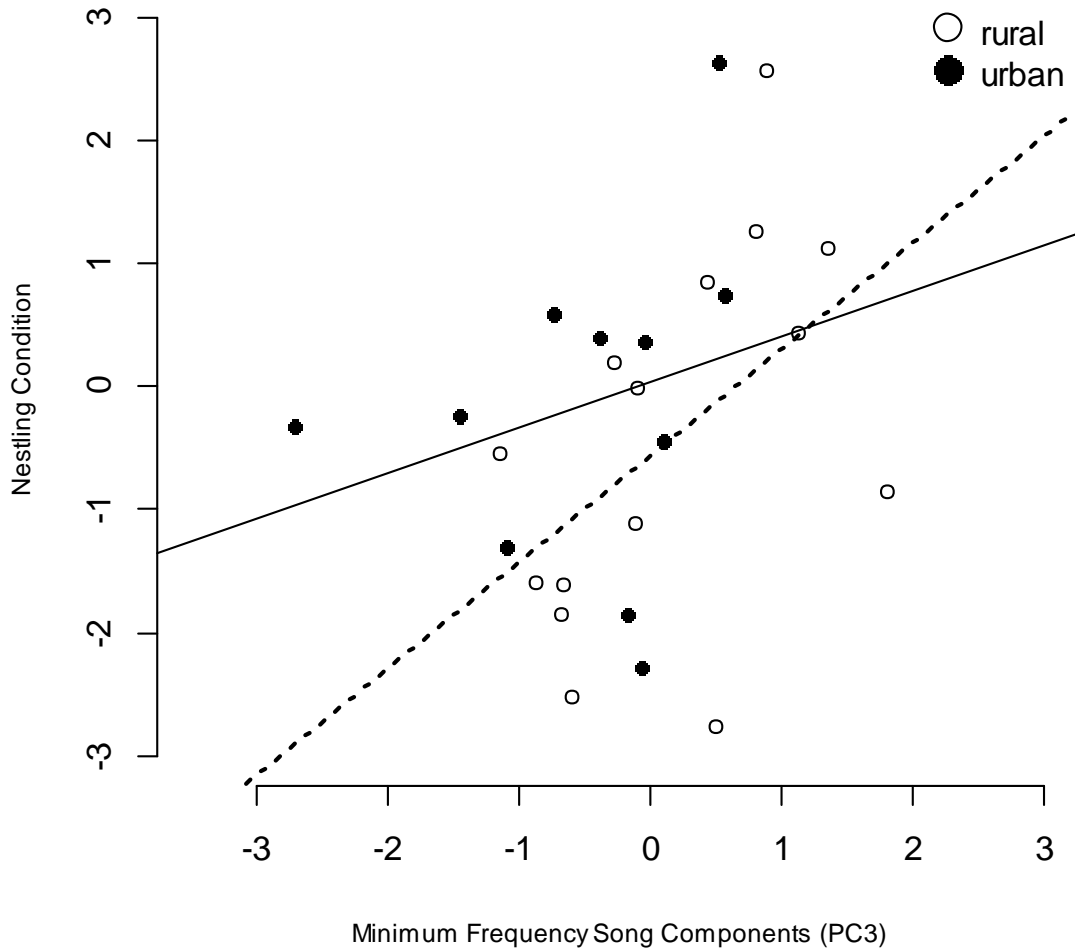


Table 3.5. Relationship between nestling condition and minimum frequency song characteristics between urban (urban index >0, solid line) and rural (urban index <0, dashed line) landscapes for male cardinals in central Ohio, 2011 ($n = 26$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

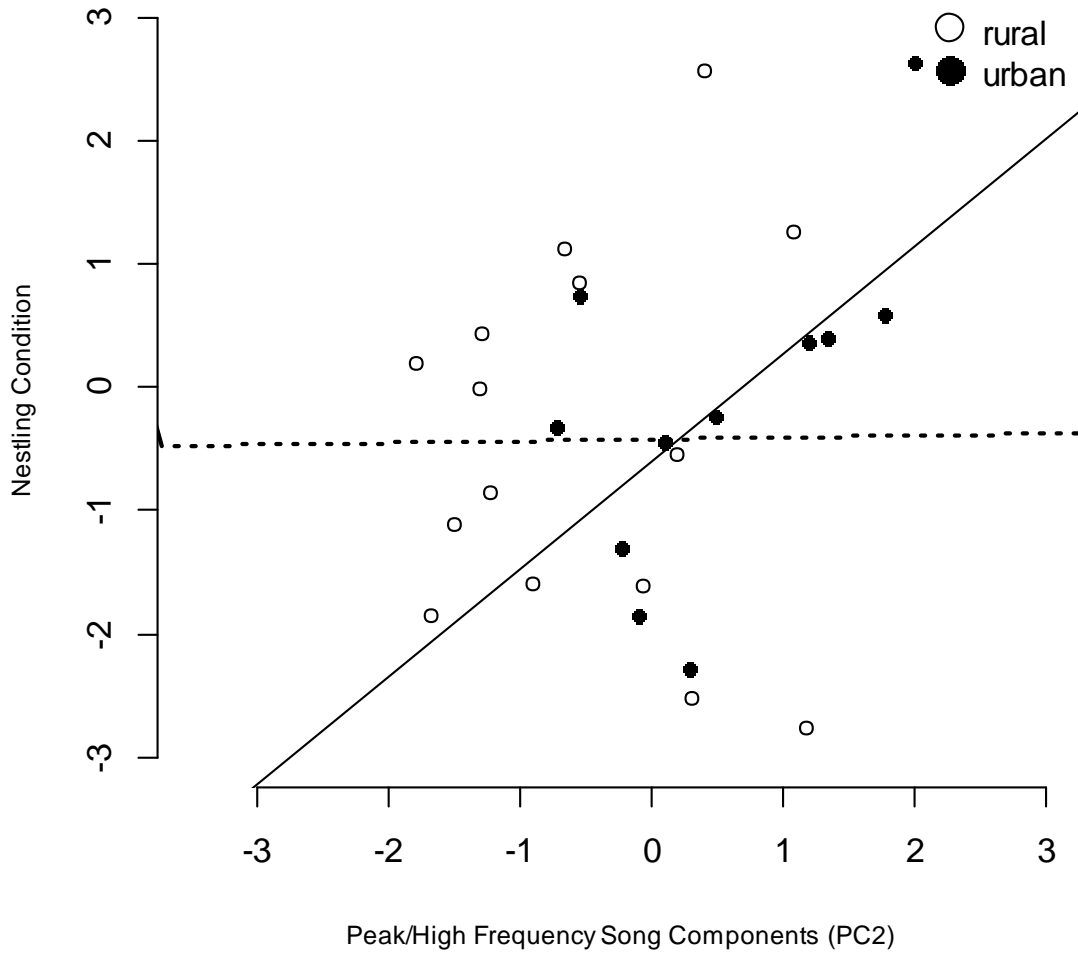


Table 3.5. Relationship between nestling condition and Peak/High frequency song characteristics between urban (urban index >0) and rural (urban index <0) landscapes for male cardinals in central Ohio, 2011 ($n = 26$). Landscapes are graphically displayed as categories here, but analyses were conducted on the continuous urban index.

| Shrubs and Saplings | | | |
|-----------------------------|--------------|------------|------|
| <i>Factor</i> | β (SE) | $F_{7,34}$ | P |
| Temporal | 0.00 (0.11) | 0.00 | 1.00 |
| Urban | 0.80 (0.19) | 17.87 | 0.01 |
| Temporal x Urban | -0.16 (0.10) | 2.77 | 0.11 |
| Peak/High Frequency | 0.05 (0.11) | 0.17 | 0.68 |
| Urban | 0.76 (0.21) | 13.61 | 0.01 |
| Peak/High Frequency X Urban | 0.01 (0.11) | 0.01 | 0.93 |
| Minimum Frequency | 0.14 (0.14) | 0.98 | 0.33 |
| Urban | 0.82 (0.21) | 15.35 | 0.01 |
| Minimum Frequency X Urban | -0.05 (0.13) | 0.17 | 0.68 |

Table 3.3. Linear mixed model results for vegetation and song for male cardinals in central Ohio, 2011 ($n = 45$).

| <i>Factor</i> | Reproductive Output | | |
|-----------------------------|---------------------|------------|------|
| | β (SE) | $F_{7,30}$ | P |
| Temporal | 0.13 (0.08) | 2.68 | 0.11 |
| Urban | -0.19 (0.11) | 3.65 | 0.10 |
| Temporal x Urban | -0.09 (0.08) | 1.69 | 0.20 |
| Peak/High Frequency | -0.07 (0.10) | 0.57 | 0.46 |
| Urban | -0.26 (0.12) | 3.38 | 0.11 |
| Peak/High Frequency X Urban | -0.06 (0.09) | 0.38 | 0.54 |
| Minimum Frequency | 0.02 (0.12) | 0.05 | 0.82 |
| Urban | -0.23 (0.11) | 4.57 | 0.07 |
| Minimum Frequency X Urban | 0.10 (0.11) | 0.99 | 0.33 |

Table 3.4. Generalized linear mixed model results for reproductive output and song for male cardinals in central Ohio, 2011 ($n = 41$).

LITERATURE CITED

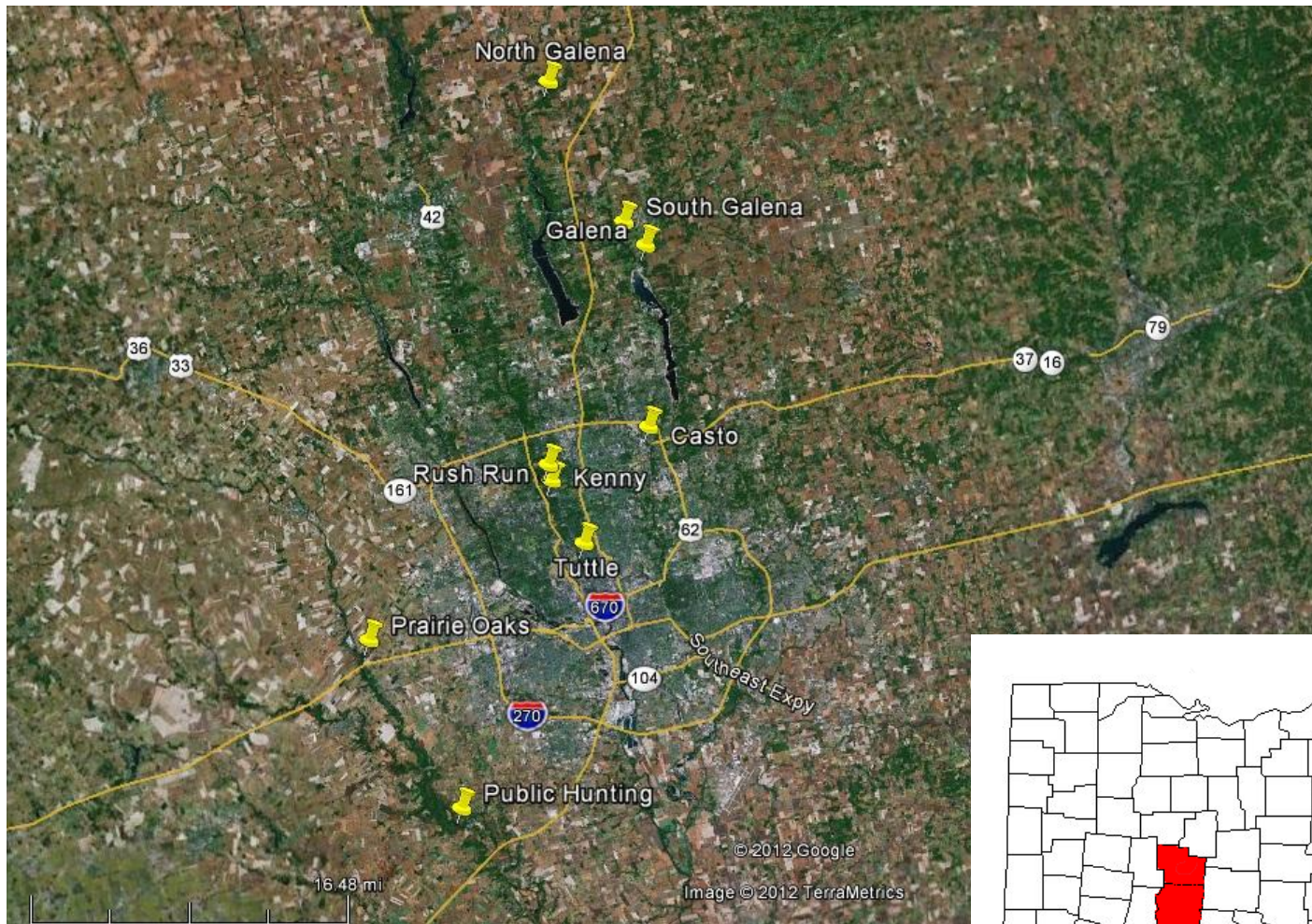
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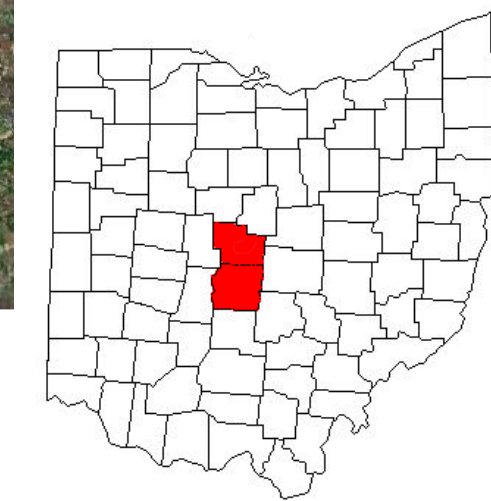
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Appendix A: Map of riparian forest study sites where males were recorded and territories monitored in Delaware and Franklin Counties, Ohio, 2011.



Appendix B: Surrounding landscape composition, site characteristics and coordinates for study sites central Ohio, 2011. Site descriptions include urbanization index (component of percent surrounding development), plot type, coordinates, and study site averages of habitat and morphology covariates used for alternative models of song variation.

UI=Urbanization index, D=Cardinal densities per 2 Ha, NL=Territory mean noise levels (SE), BS=Mean body size component, SS=Mean shrubs and saplings component, SE=Mean small trees principal component, LT=Mean large trees principle component.

Appendix B

| <i>Site</i> | <i>UI</i> | <i>Experimental Plot</i> | <i>Latitude</i> | <i>Longitude</i> | <i>D</i> | <i>NL</i> | <i>BS</i> | <i>SS</i> | <i>ST</i> | <i>LT</i> |
|---------------|-----------|--------------------------|-----------------|------------------|----------|--------------|-----------|-----------|-----------|-----------|
| Casto | 1.25 | no | 40.082777 | -82.92212 | 4.25 | 50.23 (3.57) | -0.26 | 0.30 | 0.28 | -0.71 |
| Galena | -0.48 | no | 40.21565 | -82.8789 | 2.5 | 46.89 (2.76) | 0.08 | -1.24 | 0.47 | -0.15 |
| Kenny North | 0.89 | control | 40.066 | -83.031 | 9.75 | 54.64 (2.66) | 0.45 | 1.53 | 0.55 | 0.44 |
| Kenny South | 0.89 | experimental | 40.066 | -83.031 | 4.25 | 58.02 (3.40) | - | - | - | - |
| North galena | -1.27 | no | 40.353074 | -82.926825 | 1.75 | 42.93 (1.51) | 0.17 | -0.95 | 1.11 | 0.47 |
| Prairie Oaks | -1.12 | no | 39.98628 | -83.24587 | 2.5 | 47.92 (3.69) | -0.10 | -1.10 | -0.66 | 0.17 |
| Pubhunt | -1.15 | no | 39.84723 | -83.2028 | 1.5 | 46.69 (2.65) | 1.09 | -0.24 | -0.49 | 0.60 |
| Rushrun North | 0.75 | control | 40.07663 | -83.03103 | 5.25 | 52.22 (3.36) | 0.17 | 0.16 | -0.12 | 0.02 |
| Rushrun South | 0.75 | experimental | 40.07663 | -83.03103 | 5.5 | 48.84 (3.48) | - | - | - | - |
| South Galena | -0.57 | no | 40.23683 | -82.89458 | 2 | 43.16 (2.23) | -0.22 | -0.48 | -0.29 | 0.42 |
| Tuttle North | 1.61 | experimental | 40.012 | -83.017 | 2.5 | 48.57 (2.20) | - | - | - | - |
| Tuttle South | 1.61 | control | 40.012 | -83.017 | 5.25 | 48.28 (1.41) | -1.10 | 1.55 | -0.33 | -1.01 |

| <i>Trait</i> | <i>Definition</i> |
|---------------------|---|
| Minimum frequency | Absolute lowest frequency of the song type (Hz) |
| Maximum frequency | Absolute highest frequency of song type (Hz) |
| Peak frequency | Frequency with the most energy throughout the song (Hz) |
| Frequency Bandwidth | Range of frequency for the song, Maximum minus minimum frequency (Hz) |
| Number of syllables | Number of temporally distinct (interval <1sec) elements in the song |
| Song length | Duration of the entire song (seconds) |
| Power | Highest amplitude of the song (dB) |
| Syllable Types | Number of visually unique syllable types within a song on the spectrogram |
| Syllable Rate | Number of syllables produced per second within the length of the song |

Appendix C: Song measurement definitions for measurements taken from spectrograms of Northern Cardinal song. All males were recorded in central Ohio, 2011.

Appendix D: Song variables of recorded male Northern Cardinals in central Ohio, 2011
expressed as territory mean. SL=Song length, MIN= Minimum frequency,
MAX=Maximum frequency, FB=Frequency bandwidth, POW=Power, PF=Peak
frequency, SYLL=Number of Syllables, ST=Number of syllable types, SR=Syllable rate
(syllables per second), NS=Number of songs recorded.

Appendix D

| Site | Color Combo | SL | MIN | MAX | FB | POW | PF | SYL | ST | SR | NS |
|------------|-------------|------|---------|---------|---------|--------|---------|-------|------|------|----|
| casto | bgys | 2.18 | 1489.52 | 7219.62 | 5730.12 | 95.07 | 2806.48 | 6.17 | 1.67 | 2.89 | 6 |
| casto | gsyo | 4.24 | 1455.69 | 6008.27 | 4552.59 | 96.11 | 3275.91 | 12.87 | 1.53 | 3.18 | 15 |
| casto | pows | 3.39 | 1356.33 | 5238.43 | 3882.10 | 98.93 | 2828.03 | 13.33 | 2.33 | 5.67 | 6 |
| casto | sbgg | 3.93 | 1411.50 | 5717.58 | 4306.10 | 95.54 | 3118.00 | 13.00 | 1.80 | 3.24 | 5 |
| casto | unb+osgo | 2.58 | 1431.20 | 7740.45 | 6309.28 | 95.32 | 3201.25 | 9.00 | 1.83 | 3.48 | 6 |
| casto | wbps | 3.79 | 1402.15 | 8131.40 | 6729.30 | 96.35 | 2465.58 | 11.75 | 2.50 | 3.06 | 4 |
| casto | woos | 3.65 | 1373.04 | 7157.74 | 5784.67 | 102.43 | 3162.29 | 11.29 | 2.29 | 3.13 | 7 |
| casto | wspp | 3.79 | 1489.49 | 6634.53 | 5145.03 | 91.47 | 3168.44 | 13.57 | 1.86 | 3.51 | 7 |
| casto | yswp | 1.83 | 1710.10 | 6424.43 | 4714.33 | 90.57 | 2555.30 | 6.67 | 2.33 | 3.67 | 3 |
| casto | ywbs | 3.06 | 1664.60 | 5102.70 | 3438.13 | 98.68 | 2583.98 | 8.75 | 2.50 | 2.90 | 4 |
| galena | A0 | 3.14 | 1439.14 | 5019.11 | 3579.97 | 95.94 | 3167.53 | 10.57 | 1.52 | 3.53 | 21 |
| galena | gpys | 3.57 | 1390.94 | 6116.27 | 4725.36 | 99.90 | 2676.27 | 11.86 | 1.86 | 3.29 | 7 |
| galena | sggo | 2.96 | 1236.85 | 3549.41 | 2312.55 | 102.21 | 2605.53 | 10.25 | 2.00 | 3.48 | 8 |
| galena | unb+spbo | 3.63 | 1437.02 | 5625.63 | 4188.62 | 98.07 | 3416.60 | 12.83 | 2.17 | 3.54 | 6 |
| galena | wbws | 3.24 | 1272.90 | 5302.16 | 4029.27 | 99.56 | 2701.43 | 9.79 | 1.79 | 2.95 | 14 |
| kennynorth | obos | 3.96 | 1281.16 | 5291.10 | 4009.94 | 102.94 | 2683.04 | 12.30 | 1.90 | 3.15 | 10 |
| kennynorth | oosw | 4.01 | 1479.42 | 6430.51 | 4951.09 | 94.86 | 2823.26 | 18.22 | 2.11 | 4.55 | 9 |
| kennynorth | ppsp | 3.81 | 1452.09 | 5148.19 | 3696.09 | 101.90 | 3014.64 | 13.71 | 1.86 | 3.59 | 7 |
| kennynorth | sbbw | 3.01 | 1749.68 | 5929.65 | 4179.97 | 97.25 | 3064.33 | 10.85 | 2.00 | 3.64 | 13 |
| kennynorth | sgyo | 3.38 | 1597.99 | 5346.39 | 3748.40 | 101.13 | 2922.36 | 11.43 | 1.86 | 3.52 | 7 |
| kennynorth | wgos | 4.07 | 1353.63 | 6766.18 | 5412.58 | 101.43 | 3391.48 | 13.50 | 2.50 | 3.26 | 4 |
| kennynorth | wspo | 3.43 | 1573.15 | 3771.30 | 2198.14 | 98.98 | 2534.30 | 15.69 | 1.85 | 4.44 | 13 |

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Appendix D

| Site | Color Combo | SL | MIN | MAX | FB | POW | PF | SYL | ST | SR | NS |
|------------|-------------|------|---------|---------|---------|--------|---------|-------|------|------|----|
| kennysouth | boos | 3.32 | 1528.18 | 5093.58 | 3565.38 | 98.04 | 2815.88 | 10.08 | 2.08 | 3.08 | 13 |
| kennysouth | sbgy | 3.28 | 1628.91 | 5776.67 | 4147.75 | 95.00 | 2584.00 | 10.27 | 2.09 | 3.21 | 11 |
| kennysouth | wyso | 3.33 | 1655.01 | 4662.94 | 3007.96 | 93.50 | 2444.02 | 12.75 | 1.58 | 3.70 | 12 |
| ngalena | c0 | 2.60 | 1427.27 | 6669.60 | 5242.33 | 96.65 | 2706.02 | 6.67 | 1.83 | 2.41 | 6 |
| ngalena | e100 | 3.27 | 1047.87 | 7114.20 | 6066.37 | 100.13 | 3158.20 | 9.67 | 2.00 | 2.92 | 3 |
| ngalena | ne | 3.12 | 1219.42 | 4666.28 | 3446.86 | 99.87 | 2858.04 | 10.73 | 2.00 | 3.43 | 11 |
| ngalena | swob | 3.17 | 1134.20 | 6718.30 | 5584.10 | 101.95 | 2045.65 | 11.50 | 1.50 | 4.02 | 2 |
| prairie | gpos | 2.55 | 1389.79 | 4898.15 | 3508.36 | 96.94 | 2540.91 | 8.73 | 2.18 | 3.53 | 11 |
| prairie | parkinglot | 2.75 | 1537.08 | 6411.98 | 4874.89 | 98.85 | 2845.71 | 10.08 | 2.00 | 3.80 | 13 |
| prairie | pbbs | 3.40 | 1549.67 | 5385.12 | 3835.43 | 93.42 | 2950.03 | 12.50 | 1.83 | 3.67 | 6 |
| prairie | peninsula | 2.56 | 1500.83 | 4890.90 | 3390.07 | 99.53 | 2698.83 | 9.67 | 2.33 | 3.78 | 3 |
| prairie | spbo | 3.08 | 1531.70 | 5086.86 | 3555.16 | 95.71 | 2719.79 | 9.57 | 1.71 | 3.14 | 14 |
| prairie | sygy | 3.38 | 1512.74 | 4408.80 | 2896.06 | 95.72 | 2472.04 | 13.80 | 1.80 | 4.44 | 5 |
| prairie | ysgw | 3.81 | 1462.21 | 5408.19 | 3945.96 | 90.28 | 2337.32 | 15.09 | 1.55 | 3.97 | 11 |
| pubhunt | bsop | 3.23 | 1197.62 | 4483.76 | 3286.12 | 96.68 | 2955.93 | 8.64 | 1.64 | 2.65 | 11 |
| pubhunt | ppys | 2.54 | 1352.89 | 5301.31 | 3948.43 | 93.57 | 3074.94 | 8.00 | 1.50 | 3.12 | 10 |
| pubhunt | sbby | 2.46 | 1427.58 | 5139.49 | 3711.89 | 100.81 | 2416.50 | 6.44 | 1.33 | 2.58 | 9 |
| pubhunt | sygb | 2.97 | 1242.00 | 7217.27 | 5975.27 | 97.20 | 3000.30 | 9.33 | 2.00 | 3.09 | 3 |
| pubhunt | spyg | 2.91 | 1115.30 | 4457.20 | 3341.90 | 96.61 | 2719.33 | 9.00 | 2.00 | 3.10 | 7 |
| pubhunt | wsgp | 2.79 | 1404.27 | 6849.96 | 5445.69 | 97.10 | 2756.26 | 8.56 | 1.72 | 2.92 | 18 |

Appendix D

| Site | Color Combo | SL | MIN | MAX | FB | POW | PF | SYL | ST | SR | NS |
|--------------|-------------|------|---------|---------|---------|--------|---------|-------|------|------|----|
| rushrunnorth | bsww | 2.60 | 1516.44 | 5926.48 | 4410.00 | 93.22 | 3281.66 | 11.60 | 1.60 | 4.98 | 5 |
| rushrunnorth | osgb | 2.83 | 1400.20 | 4039.83 | 2639.64 | 95.73 | 2725.47 | 9.00 | 2.00 | 2.95 | 7 |
| rushrunnorth | posb | 3.51 | 1491.60 | 6698.26 | 5206.68 | 101.63 | 3283.81 | 13.25 | 2.13 | 3.84 | 8 |
| rushrunnorth | wsop | 2.41 | 1556.66 | 5291.59 | 3734.93 | 98.74 | 3002.33 | 8.57 | 2.00 | 3.50 | 7 |
| rushrunnorth | ybsy | 2.70 | 1461.54 | 5127.22 | 3665.67 | 96.25 | 3046.94 | 11.08 | 2.08 | 3.98 | 12 |
| rushrunnorth | ypps | 3.29 | 1535.93 | 6685.47 | 5149.53 | 101.10 | 3387.87 | 12.33 | 2.33 | 3.76 | 3 |
| rushrunsouth | bwos | 2.98 | 1640.18 | 6155.55 | 4515.35 | 88.18 | 2540.93 | 12.25 | 2.50 | 3.98 | 4 |
| rushrunsouth | gbbs | 2.92 | 1595.87 | 4107.47 | 2511.60 | 88.23 | 2024.13 | 10.00 | 1.33 | 3.36 | 3 |
| rushrunsouth | gsgg | 3.23 | 1351.27 | 7741.30 | 6390.03 | 94.03 | 2325.57 | 8.33 | 1.00 | 2.55 | 3 |
| rushrunsouth | obys | 2.69 | 1548.08 | 4678.20 | 3130.15 | 99.90 | 3326.85 | 9.00 | 2.25 | 3.29 | 4 |
| sgalena | ...S | 3.46 | 1294.87 | 5785.44 | 4490.56 | 98.04 | 2998.08 | 12.93 | 2.14 | 3.70 | 14 |
| sgalena | b50 | 3.22 | 1185.27 | 3998.93 | 2813.70 | 100.23 | 3560.13 | 12.00 | 2.00 | 3.70 | 3 |
| sgalena | ggsww | 3.93 | 1196.83 | 6384.37 | 5187.53 | 103.33 | 3172.53 | 13.00 | 2.00 | 3.59 | 3 |
| sgalena | psyp | 3.54 | 1304.45 | 5557.80 | 4253.36 | 97.82 | 2703.25 | 9.57 | 2.21 | 2.80 | 13 |
| sgalena | sywb | 3.53 | 1293.19 | 6239.51 | 4946.33 | 97.53 | 3177.67 | 12.33 | 1.87 | 3.55 | 15 |
| tuttlenorth | ppso | 3.13 | 1595.45 | 8694.15 | 7098.75 | 89.10 | 2928.50 | 8.00 | 1.50 | 2.52 | 2 |
| tuttlenorth | psoo | 2.95 | 1428.10 | 4012.96 | 2584.87 | 96.89 | 2553.23 | 9.14 | 2.00 | 3.00 | 7 |
| tuttlenorth | s/b | 2.12 | 1356.50 | 3669.13 | 2312.63 | 98.40 | 2627.03 | 6.67 | 1.67 | 3.47 | 3 |
| tuttlenorth | unb+spbg | 2.84 | 1671.75 | 4451.08 | 2779.35 | 99.85 | 2691.65 | 10.75 | 2.25 | 3.70 | 4 |
| tuttlenorth | ypys | 3.28 | 1295.51 | 4852.34 | 3556.83 | 97.04 | 3134.60 | 12.71 | 1.86 | 3.79 | 14 |
| tuttlesouth | gsyp | 3.24 | 1376.69 | 5768.05 | 4391.36 | 97.02 | 2926.36 | 10.45 | 2.05 | 3.19 | 20 |
| tuttlesouth | osoy | 3.85 | 1267.99 | 4818.34 | 3550.35 | 101.58 | 2536.61 | 14.10 | 1.60 | 3.85 | 10 |
| tuttlesouth | psgg | 3.20 | 1211.53 | 7282.20 | 6070.67 | 96.53 | 2871.07 | 9.33 | 1.67 | 2.93 | 3 |
| tuttlesouth | sbpw | 3.74 | 1361.03 | 7117.33 | 5756.30 | 98.46 | 2590.14 | 12.14 | 1.86 | 3.18 | 7 |

Appendix E: Morphology measurements of recorded male Northern Cardinals in central Ohio, 2011. Wing, tarsus and bill measurements were measured in millimeters. Mass was measured in grams and body measurements in millimeters.

Appendix E

| Site | Combo | Wing | Tarsus | Mass | Bill Length | Bill Depth | Bill Width | Body Size | Body Condition |
|------------|----------|-------|--------|-------|-------------|------------|------------|-----------|----------------|
| casto | bgys | 96.00 | 24.90 | 44.00 | . | . | . | 1.12 | 0.84 |
| casto | gsyo | 95.00 | 24.90 | 44.00 | 12.20 | 11.00 | 8.90 | 0.83 | 0.55 |
| casto | pows | . | . | . | . | . | . | . | . |
| casto | sbgg | 97.00 | 24.00 | 43.00 | . | . | . | 0.57 | 0.52 |
| casto | unb+osgo | . | . | . | . | . | . | . | . |
| casto | wbps | 91.50 | 22.80 | 38.03 | 12.25 | 12.20 | 8.60 | -2.14 | -1.01 |
| casto | woos | 87.00 | 24.60 | 40.91 | 13.25 | 12.30 | 9.50 | -1.76 | -1.31 |
| casto | wspp | 92.00 | 23.50 | 44.00 | . | . | . | -1.34 | -1.63 |
| casto | yswp | 93.00 | 25.20 | 43.36 | 12.60 | 11.80 | 8.60 | 0.53 | 0.40 |
| casto | ywbs | 94.00 | 23.80 | 43.35 | 13.10 | 12.00 | 9.00 | -0.48 | -0.61 |
| galena | A0 | . | . | . | . | . | . | . | . |
| galena | gpys | 92.00 | 24.80 | 46.39 | 12.60 | 11.90 | 9.30 | -0.13 | -0.98 |
| galena | sggo | 89.50 | 24.80 | 40.79 | 12.30 | 11.85 | 9.10 | -0.85 | -0.38 |
| galena | unb+spbo | . | . | . | . | . | . | . | . |
| galena | wbws | 93.00 | 26.00 | 45.47 | 13.00 | 12.00 | 8.70 | 1.28 | 0.64 |
| kennynorth | obos | 95.50 | 24.30 | 41.18 | 12.00 | 11.40 | 8.80 | 0.42 | 0.80 |
| kennynorth | oosp | 95.00 | 23.90 | 41.00 | 12.15 | 11.30 | 8.90 | -0.10 | 0.33 |
| kennynorth | ppsp | 99.50 | 23.70 | 44.00 | 12.70 | 10.15 | 8.10 | 1.01 | 0.73 |
| kennynorth | sbbw | 97.00 | 25.00 | 48.00 | . | . | . | 1.50 | 0.27 |
| kennynorth | sgyo | 94.00 | 24.25 | 42.60 | 13.25 | 12.70 | 9.00 | -0.06 | -0.02 |
| kennynorth | wgos | 95.50 | 24.20 | 45.21 | 13.20 | 11.70 | 9.10 | 0.32 | -0.25 |
| kennynorth | wspo | . | . | . | . | . | . | . | . |
| ngalena | c0 | . | . | . | . | . | . | . | . |
| ngalena | e100 | . | . | . | . | . | . | . | . |
| ngalena | ne | . | . | . | . | . | . | . | . |

Appendix E

| Site | Combo | Wing | Tarsus | Mass | Bill Length | Bill Depth | Bill Width | Body Size | Body Condition |
|--------------|------------|-------|--------|-------|-------------|------------|------------|-----------|----------------|
| ngalena | swob | 92.00 | 25.50 | 41.50 | . | . | . | 0.52 | 0.83 |
| prairie | gpos | 93.50 | 25.50 | 47.69 | 12.20 | 12.30 | 9.50 | 0.96 | -0.20 |
| prairie | parkinglot | . | . | . | . | . | . | . | . |
| prairie | pbbs | 92.50 | 23.50 | 39.91 | 13.50 | 12.10 | 9.10 | -1.20 | -0.51 |
| prairie | peninsula | . | . | . | . | . | . | . | . |
| prairie | spbo | 90.50 | 25.60 | 45.48 | 13.10 | 11.95 | 9.15 | 0.18 | -0.45 |
| prairie | sygy | 91.00 | 25.10 | 41.16 | 13.00 | 11.90 | 8.90 | -0.14 | 0.25 |
| prairie | ysgw | 93.00 | 24.00 | 42.97 | 11.65 | 11.70 | 8.70 | -0.59 | -0.63 |
| pubhunt | bsop | 99.00 | 25.30 | 47.00 | . | . | . | 2.36 | 1.36 |
| pubhunt | ppys | 95.50 | 24.90 | 37.51 | 12.50 | 11.70 | 9.10 | 0.98 | 2.23 |
| pubhunt | sbby | 95.00 | 25.10 | 44.29 | 12.85 | 12.00 | 9.10 | 1.02 | 0.66 |
| pubhunt | sgbo | 92.00 | 24.75 | 45.54 | 13.25 | 13.50 | 9.20 | -0.18 | -0.83 |
| pubhunt | spyg | 97.00 | 24.90 | 47.01 | 12.35 | 11.30 | 9.10 | 1.41 | 0.41 |
| pubhunt | wsgp | 96.00 | 24.70 | 42.11 | 13.80 | 12.60 | 9.70 | 0.93 | 1.10 |
| rushrunnorth | bsww | 95.00 | 24.70 | 41.62 | 12.50 | 12.00 | 9.10 | 0.64 | 0.92 |
| rushrunnorth | osgb | 94.00 | 25.10 | 43.60 | 12.70 | 11.80 | 9.00 | 0.73 | 0.54 |
| rushrunnorth | posb | 90.00 | 26.35 | 44.59 | 13.20 | 12.30 | 9.40 | 0.74 | 0.31 |
| rushrunnorth | wsop | 92.00 | 23.90 | 40.50 | 13.00 | 11.50 | 8.90 | -0.97 | -0.42 |
| rushrunnorth | ybsy | 96.00 | 24.10 | 42.00 | . | . | . | 0.37 | 0.56 |
| rushrunnorth | ypps | 94.00 | 23.80 | 42.98 | 12.65 | 11.95 | 9.20 | -0.48 | -0.53 |

Appendix E

| Site | Combo | Wing | Tarsus | Mass | Bill Length | Bill Depth | Bill Width | Body Size | Body Condition |
|-------------|-------|-------|--------|-------|-------------|------------|------------|-----------|----------------|
| sgalena | ...S | . | . | . | . | . | . | . | . |
| sgalena | b50 | . | . | . | . | . | . | . | . |
| sgalena | ggsw | 94.50 | 23.70 | 42.00 | . | . | . | -0.43 | -0.24 |
| sgalena | psyp | 94.00 | 24.40 | 44.50 | . | . | . | 0.08 | -0.33 |
| sgalena | sywb | 92.00 | 24.00 | 40.00 | . | . | . | -0.88 | -0.21 |
| tuttlesouth | gsyp | 94.00 | 23.40 | 38.95 | 12.90 | 11.50 | 9.20 | -0.86 | 0.06 |
| tuttlesouth | osoy | 93.00 | 23.60 | 41.58 | 12.70 | 11.60 | 9.40 | -0.96 | -0.67 |
| tuttlesouth | psgg | 92.00 | 24.20 | 40.29 | 12.00 | 11.40 | 9.30 | -0.69 | -0.09 |
| tuttlesouth | sbpw | 89.00 | 23.85 | 37.53 | 13.60 | 11.70 | 8.40 | -1.88 | -0.63 |

Appendix F: Reproductive output of recorded male Northern Cardinals in central Ohio, 2011. Territories were monitored every 2-3 days between March and August. Only territories with high confidence of fledge output are shown. Total fledges indicated number of cardinal fledges plus number of brown-headed cowbird (*Molothrus ater*) fledges (n=2 territories).

Appendix F

| Site | Combo | # of cardinal fledges | Total fledges | Nests | Fledges per nest |
|------------|----------|--------------------------|------------------|-------|------------------|
| casto | bgys | 1 | 1 | 4 | 0.25 |
| casto | gsyo | 2 | 2 | 2 | 1.00 |
| casto | pows | 0 | 0 | 4 | 0.00 |
| casto | sbgg | . | . | . | . |
| casto | unb+osgo | 1 | 1 | 5 | 0.20 |
| casto | wbps | . | . | . | . |
| casto | woos | 3 | 3 | 4 | 0.75 |
| casto | wsp | . | . | . | . |
| casto | yswp | 2 | 2 | 1 | 2.00 |
| casto | ywbs | . | . | . | . |
| galena | A0 | 1 | 1 | 4 | 0.25 |
| galena | gpys | 2 | 2 | 2 | 1.00 |
| galena | sggo | 0 | 0 | 4 | 0.00 |
| galena | unb+spbo | 4 | 5 | 2 | 2.50 |
| galena | wbws | 1 | 1 | 2 | 0.50 |
| kennynorth | obos | 2 | 2 | 4 | 0.50 |
| kennynorth | oosw | 2 | 2 | 5 | 0.40 |
| kennynorth | ppsp | 1 | 1 | 5 | 0.20 |
| kennynorth | sbbw | 0 | 0 | 7 | 0.00 |
| kennynorth | sgyo | 1 | 1 | 3 | 0.33 |
| kennynorth | wgos | 0 | 0 | 6 | 0.00 |
| kennynorth | wspo | 2 | 2 | 6 | 0.33 |
| kennysouth | boos | 5 | 5 | 5 | 1.00 |
| kennysouth | sbg | 1 | 1 | 5 | 0.20 |
| kennysouth | wyso | 4 | 4 | 7 | 0.43 |

Appendix F

| Site | Combo | # of Cardinal fledges | Total fledges | Nests | Fledges per nest |
|--------------|------------|--------------------------|------------------|-------|------------------|
| ngalena | c0 | . | . | . | . |
| ngalena | e100 | 2 | 2 | 4 | 0.50 |
| ngalena | ne | . | . | . | . |
| ngalena | swob | 1 | 1 | 4 | 0.25 |
| prairie | gpos | 5 | 5 | 2 | 2.50 |
| prairie | parkinglot | 2 | 2 | 4 | 0.50 |
| prairie | pbbs | 5 | 5 | 2 | 2.50 |
| prairie | peninsula | . | . | . | . |
| prairie | spbo | 3 | 3 | 2 | 1.50 |
| prairie | sygy | 2 | 2 | 2 | 1.00 |
| prairie | ysgw | 2 | 3 | 1 | 3.00 |
| pubhunt | bsop | 5 | 5 | 2 | 1.50 |
| pubhunt | ppys | . | . | . | . |
| pubhunt | sbby | 4 | 4 | 3 | 1.33 |
| pubhunt | sgbo | 3 | 3 | 3 | 1.00 |
| pubhunt | spyg | 4 | 4 | 3 | 1.33 |
| pubhunt | wsgp | 4 | 4 | 3 | 1.33 |
| rushrunnorth | bsww | 2 | 2 | 5 | 0.40 |
| rushrunnorth | osgb | 2 | 2 | 2 | 1.00 |
| rushrunnorth | posb | . | . | . | . |
| rushrunnorth | wsop | 0 | 0 | 5 | 0.00 |
| rushrunnorth | ybsy | 3 | 3 | 4 | 0.75 |
| rushrunnorth | ypps | 0 | 0 | 7 | 0.00 |

Appendix F

| Site | Combo | # of Cardinal fledges | Total fledges | Nests | Fledges per nest |
|--------------|----------|--------------------------|------------------|-------|------------------|
| rushrunsouth | bwos | 4 | 4 | 4 | 1.00 |
| rushrunsouth | gbbs | 5 | 5 | 5 | 1.00 |
| rushrunsouth | gsgg | 1 | 1 | 6 | 0.17 |
| rushrunsouth | obys | 6 | 7 | 3 | 1.67 |
| sgalena | ...S | 2 | 2 | 4 | 0.50 |
| sgalena | b50 | 2 | 2 | 2 | 1.00 |
| sgalena | ggsW | 0 | 0 | 1 | 0.00 |
| sgalena | psyp | 2 | 2 | 6 | 0.33 |
| sgalena | sywb | 2 | 4 | 5 | 0.20 |
| tuttlenorth | ppso | 1 | 2 | 3 | 0.67 |
| tuttlenorth | psoo | 3 | 3 | 6 | 0.50 |
| tuttlenorth | s/b | . | . | . | . |
| tuttlenorth | unb+spbg | 4 | 4 | 3 | 1.33 |
| tuttlenorth | ypys | 4 | 4 | 5 | 0.80 |
| tuttlesouth | gsyp | 2 | 2 | 7 | 0.29 |
| tuttlesouth | osoy | 3 | 3 | 3 | 1.00 |
| tuttlesouth | psgg | 1 | 1 | 2 | 0.50 |
| tuttlesouth | sbpw | 3 | 3 | 4 | 0.75 |

Appendix G: Territory vegetation of recorded male Northern Cardinals in central Ohio, 2011. Territory quality was quantified by measuring vegetation around two nests and one random point within the focal territory.

Appendix G

| Site | Combo | Saplings (3-8 dbh) | Small trees (8- 23 dbh) | Medium trees (23-38 dbh) | Large trees (38+) | Honeysuckle stems (3-8 dbh) | Native trees stems (3-8 dbh) | % Shrub cover | % Honeysuckle cover | % Native shrub cover |
|------------|----------|-----------------------|-------------------------------|--------------------------------|-------------------------|-----------------------------------|------------------------------------|------------------|------------------------|-------------------------|
| casto | bgys | 17.00 | 9.67 | 2.67 | 2.00 | 5.67 | 11.33 | 50.75 | 21.17 | 29.58 |
| casto | gsyo | 28.67 | 14.67 | 4.00 | 2.67 | 0.67 | 28.00 | 33.63 | 25.88 | 7.75 |
| casto | pows | 35.00 | 12.50 | 2.00 | 2.00 | 3.50 | 31.50 | 50.38 | 26.38 | 24.00 |
| casto | sbgg | 14.00 | 10.50 | 2.50 | 3.00 | 9.50 | 4.50 | 25.31 | 17.25 | 8.06 |
| casto | unb+osgo | 24.50 | 13.00 | 1.00 | 1.00 | 3.50 | 21.00 | 38.88 | 13.75 | 25.13 |
| casto | wbps | . | . | . | . | . | . | . | . | . |
| casto | woos | 33.50 | 19.00 | 3.50 | 3.00 | 7.50 | 26.00 | 78.38 | 71.88 | 6.50 |
| casto | yswp | 13.00 | 19.50 | 1.00 | 2.50 | 0.00 | 13.00 | 25.50 | 3.33 | 22.17 |
| casto | ywbs | . | . | . | . | . | . | . | . | . |
| galena | a0 | 16.00 | 7.33 | 2.67 | 2.00 | 0.33 | 15.67 | 20.33 | 1.50 | 18.83 |
| galena | gpys | 24.33 | 19.00 | 2.33 | 0.33 | 0.67 | 23.67 | 21.92 | 2.00 | 21.42 |
| galena | s bpy | 18.00 | 7.00 | 1.00 | 2.00 | 0.00 | 18.00 | 8.30 | 0.00 | 8.30 |
| galena | sggo | 17.00 | 15.00 | 6.00 | 1.00 | 0.00 | 17.00 | 7.13 | 0.00 | 7.13 |
| galena | unb+swby | 12.50 | 8.00 | 3.00 | 2.00 | 0.00 | 12.50 | 10.05 | 0.40 | 9.65 |
| galena | wbws | 24.33 | 14.33 | 6.33 | 2.00 | 0.00 | 24.33 | 8.25 | 0.17 | 8.08 |
| kennynorth | obos | 68.00 | 17.33 | 4.67 | 2.67 | 55.00 | 13.00 | 40.17 | 40.00 | 0.17 |
| kennynorth | oosw | 68.33 | 12.33 | 4.33 | 1.33 | 63.00 | 5.33 | 36.58 | 33.08 | 3.50 |
| kennynorth | ppsp | 59.33 | 9.67 | 4.67 | 0.67 | 50.00 | 9.33 | 36.13 | 36.00 | 0.13 |
| kennynorth | sbbw | 113.67 | 12.00 | 2.67 | 1.00 | 92.67 | 21.00 | 35.67 | 32.67 | 3.00 |
| kennynorth | sgyo | . | . | . | . | . | . | . | . | . |
| kennynorth | wgos | 33.50 | 13.50 | 1.00 | 1.50 | 19.00 | 14.50 | 71.50 | 68.38 | 3.13 |
| kennynorth | wspo | 60.67 | 14.00 | 1.67 | 2.67 | 50.33 | 10.33 | 52.00 | 45.25 | 6.75 |
| kennysouth | boos | 16.67 | 6.00 | 2.00 | 2.00 | 6.00 | 10.67 | 8.17 | 7.83 | 25.75 |
| kennysouth | sbgy | 46.00 | 4.33 | 4.33 | 4.00 | 43.00 | 3.00 | 12.13 | 43.25 | 46.63 |
| kennysouth | wyso | 8.00 | 6.33 | 1.00 | 1.67 | 0.00 | 8.00 | 3.29 | 2.33 | 5.29 |

Appendix G

| Site | Combo | Saplings (3-8 dbh) | Small trees (8- 23 dbh) | Medium trees (23-38 dbh) | Large trees (38+) | Honeysuckle stems (3-8 dbh) | Native trees stems (3-8 dbh) | % Shrub cover | % Honeysuckle cover | % Native shrub cover |
|--------------|------------|-----------------------|-------------------------------|--------------------------------|-------------------------|-----------------------------------|------------------------------------|------------------|------------------------|-------------------------|
| ngalena | c0 | . | . | . | . | . | . | . | . | . |
| ngalena | e100 | 33.00 | 20.00 | 5.00 | 1.67 | 0.00 | 33.00 | 22.33 | 0.42 | 21.92 |
| ngalena | ne | . | . | . | . | . | . | . | . | . |
| ngalena | swob | 23.00 | 15.00 | 2.00 | 1.00 | 0.00 | 23.00 | 9.75 | 0.63 | 9.13 |
| prairie | gpos | 43.33 | 5.67 | 1.33 | 0.00 | 0.33 | 43.00 | 30.67 | 9.13 | 24.58 |
| prairie | parkinglot | 23.67 | 7.67 | 0.67 | 0.67 | 0.33 | 23.33 | 18.92 | 2.75 | 16.17 |
| prairie | pbbs | 23.00 | 12.33 | 1.67 | 1.33 | 2.67 | 20.33 | 13.25 | 8.50 | 4.75 |
| prairie | peninsula | . | . | . | . | . | . | . | . | . |
| prairie | spbo | 10.33 | 7.00 | 1.00 | 1.00 | 0.33 | 10.00 | 8.25 | 2.33 | 5.92 |
| prairie | sygy | 17.00 | 21.00 | 2.00 | 2.00 | 0.00 | 17.00 | 9.00 | 0.50 | 8.50 |
| prairie | ysgw | 15.67 | 14.00 | 5.33 | 1.00 | 0.00 | 15.67 | 7.71 | 1.67 | 6.04 |
| pubhunt | bsop | 36.33 | 18.67 | 2.00 | 0.00 | 22.33 | 14.00 | 68.83 | 56.42 | 12.42 |
| pubhunt | ppys | . | . | . | . | . | . | . | . | . |
| pubhunt | sbby | 17.67 | 10.67 | 1.67 | 1.67 | 10.00 | 7.67 | 37.67 | 30.08 | 7.58 |
| pubhunt | spyg | 31.67 | 16.67 | 2.00 | 0.00 | 12.00 | 19.67 | 46.58 | 41.33 | 5.25 |
| pubhunt | sygb | 16.25 | 6.00 | 2.75 | 0.50 | 5.75 | 10.50 | 26.38 | 18.95 | 7.43 |
| pubhunt | wsgp | 15.33 | 10.33 | 3.00 | 2.00 | 1.67 | 13.67 | 14.17 | 8.92 | 5.25 |
| rushrunnorth | bsww | 41.33 | 17.33 | 2.33 | 0.33 | 14.33 | 27.00 | 38.67 | 27.83 | 10.83 |
| rushrunnorth | osgb | 35.00 | 14.00 | 1.00 | 2.00 | 0.00 | 35.00 | 7.75 | 5.75 | 2.00 |
| rushrunnorth | posb | . | . | . | . | . | . | . | . | . |
| rushrunnorth | wsop | 41.00 | 10.50 | 2.00 | 1.00 | 9.50 | 31.50 | 30.38 | 22.75 | 7.63 |
| rushrunnorth | ybsy | 34.67 | 11.00 | 2.00 | 2.33 | 16.00 | 18.67 | 30.58 | 26.83 | 3.75 |
| rushrunnorth | ygps | 37.50 | 14.50 | 3.25 | 0.50 | 21.75 | 15.75 | 48.28 | 42.15 | 5.25 |
| rushrunnorth | ypps | 41.67 | 14.00 | 2.67 | 2.33 | 18.00 | 23.67 | 47.00 | 40.92 | 6.08 |

Appendix G

| Site | Combo | Saplings (3-8 dbh) | Small trees (8-23 dbh) | Medium trees (23-38 dbh) | Large trees (38+) | Honeysuckle stems (3-8 dbh) | Native trees stems (3-8 dbh) | % Shrub cover | % Honeysuckle cover | % Native shrub cover |
|--------------|----------|-----------------------|---------------------------|-----------------------------|-------------------------|--------------------------------|------------------------------------|------------------|------------------------|-------------------------|
| rushrunsouth | bwos | 37.25 | 22.75 | 1.25 | 3.25 | 8.25 | 29.00 | 19.55 | 6.90 | 12.65 |
| rushrunsouth | gbbs | 16.75 | 12.50 | 3.25 | 1.25 | 0.00 | 16.75 | 20.35 | 5.18 | 15.18 |
| rushrunsouth | gsgg | 19.00 | 16.00 | 8.00 | 1.00 | 4.00 | 15.00 | 30.30 | 24.00 | 6.30 |
| rushrunsouth | obys | 19.00 | 10.85 | 3.15 | 2.00 | 7.50 | 11.50 | 14.48 | 1.95 | 12.53 |
| rushrunsouth | pwos | 20.50 | 24.50 | 5.00 | 1.00 | 0.00 | 20.50 | 16.50 | 6.53 | 9.98 |
| rushrunsouth | ppbs | 31.00 | 14.50 | 3.00 | 1.50 | 12.00 | 19.00 | 61.80 | 43.30 | 18.50 |
| rushrunsouth | ygps | 33.00 | 16.00 | 5.00 | 1.00 | 20.00 | 13.00 | 26.00 | 23.00 | 3.00 |
| sgalena | ...s | 25.00 | 8.00 | 0.30 | 0.00 | 2.70 | 22.30 | 64.50 | 24.80 | 39.70 |
| sgalena | b50 | 16.50 | 13.00 | 4.00 | 1.50 | 0.00 | 16.50 | 53.25 | 0.00 | 53.25 |
| sgalena | ggsw | 10.67 | 10.33 | 3.00 | 1.67 | 0.00 | 10.67 | 11.25 | 0.13 | 11.17 |
| sgalena | psyp | 14.67 | 17.00 | 4.33 | 0.67 | 3.33 | 11.33 | 21.93 | 13.96 | 7.97 |
| sgalena | sywb | 21.67 | 15.33 | 1.33 | 1.00 | 2.33 | 19.33 | 33.42 | 21.33 | 12.08 |
| sgalena | unb+bygs | 53.00 | 25.00 | 6.00 | 2.00 | 14.00 | 39.00 | 23.30 | 16.80 | 6.50 |
| tuttlenorth | ppso | 24.00 | 4.00 | 2.00 | 5.00 | 5.00 | 19.00 | 30.30 | 12.00 | 18.30 |
| tuttlenorth | psoo | 22.33 | 18.67 | 1.00 | 1.33 | 9.33 | 13.00 | 56.33 | 50.00 | 6.33 |
| tuttlenorth | s/b | . | . | . | . | . | . | . | . | . |
| tuttlenorth | unb+sbgp | 19.50 | 11.25 | 4.50 | 4.00 | 9.00 | 10.50 | 51.75 | 43.68 | 8.08 |
| tuttlenorth | ypys | 21.67 | 7.33 | 1.67 | 1.00 | 3.00 | 18.67 | 35.33 | 18.75 | 16.58 |
| tuttlesouth | gsyp | 45.67 | 7.33 | 2.67 | 3.00 | 21.00 | 24.67 | 49.42 | 41.67 | 7.75 |
| tuttlesouth | osoy | 80.67 | 6.00 | 3.67 | 2.00 | 70.67 | 10.00 | 52.00 | 47.00 | 5.00 |
| tuttlesouth | psgg | 49.00 | 13.50 | 0.50 | 2.00 | 35.50 | 13.50 | 35.75 | 33.75 | 2.00 |
| tuttlesouth | sbpw | 35.00 | 10.67 | 1.33 | 3.33 | 14.33 | 20.67 | 56.58 | 47.25 | 9.33 |
| tuttlesouth | wsgb | 34.00 | 3.00 | 3.00 | 4.00 | 20.00 | 14.00 | 36.80 | 35.80 | 1.00 |

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Appendix H: Parental care and mean nestling condition of recorded male Northern Cardinals in central Ohio, 2011. Nestling condition is the residuals of a model that includes both tarsus and weight time as covariates.

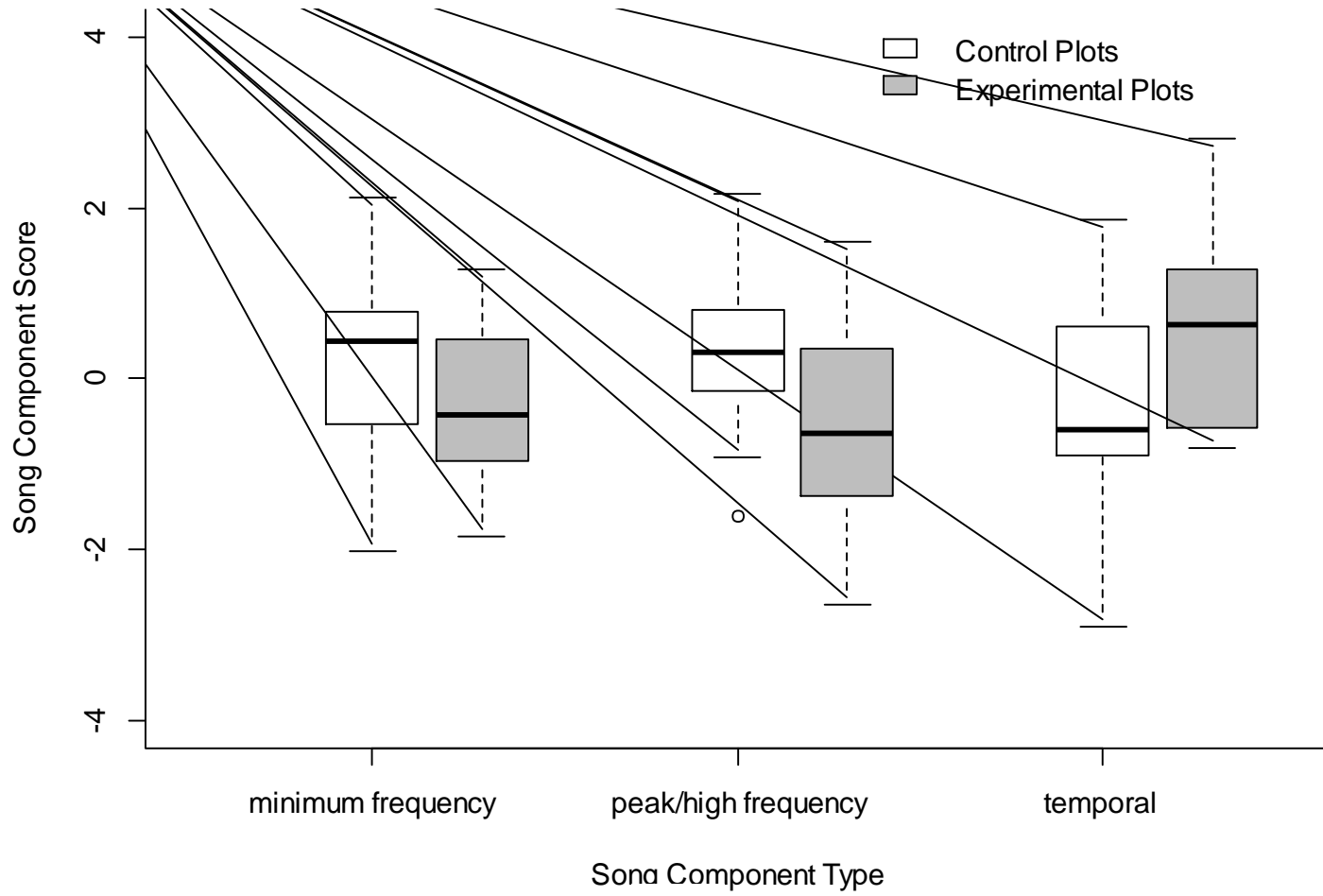
Appendix H

| Site | Combo | Male feeding visits | Male feeding visits per nestling | Female feeding visits | Female feeding visits per nestling | Nestling condition |
|------------|----------|---------------------|----------------------------------|-----------------------|------------------------------------|--------------------|
| casto | bgys | 0.00 | 0.00 | 4.00 | 4.00 | -0.24 |
| casto | gsyo | 2.00 | 2.00 | 1.00 | 1.00 | 0.36 |
| casto | pows | 3.00 | 1.50 | 3.00 | 1.50 | 0.75 |
| casto | sbgg | . | . | . | . | . |
| casto | unb+osgo | . | . | . | . | . |
| casto | wbps | . | . | . | . | . |
| casto | woos | 1.00 | 0.50 | 0.00 | 0.00 | . |
| casto | wspp | 1.00 | 1.00 | 5.00 | 5.00 | 0.41 |
| casto | yswp | 3.00 | 1.00 | 4.00 | 1.33 | -0.31 |
| casto | ywbs | . | . | . | . | . |
| galena | A0 | . | . | . | . | . |
| galena | gpys | 4.00 | 2.00 | 1.00 | 0.50 | . |
| galena | sggo | . | . | . | . | . |
| galena | unb+spbo | . | . | . | . | . |
| galena | wbws | . | . | . | . | . |
| kennynorth | obos | . | . | . | . | . |
| kennynorth | oosw | 2.00 | 1.00 | 2.00 | 1.00 | . |
| kennynorth | ppsp | . | . | . | . | . |
| kennynorth | sbbw | . | . | . | . | . |
| kennynorth | sgyo | . | . | . | . | . |
| kennynorth | wgos | 3.00 | 1.50 | 0.00 | 0.00 | 2.64 |
| kennynorth | wspo | 1.00 | 0.50 | 1.00 | 0.50 | . |
| kennysouth | boos | 2.00 | 2.00 | 2.00 | 2.00 | 1.21 |
| kennysouth | sbgy | 2.00 | 1.00 | 5.00 | 2.50 | -0.92 |
| kennysouth | wyso | 2.00 | 1.00 | 1.00 | 0.50 | . |
| ngalena | c0 | . | . | . | . | . |
| ngalena | e100 | 2.00 | 1.00 | 1.00 | 0.50 | . |
| ngalena | ne | . | . | . | . | . |
| ngalena | swob | 0.00 | 0.00 | 0.00 | 0.00 | 0.44 |

Appendix H

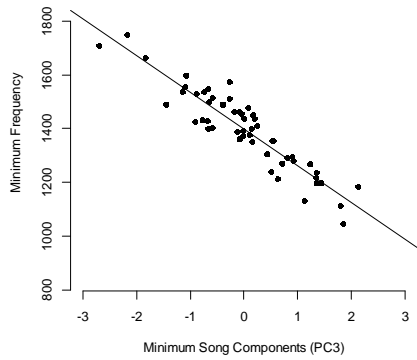
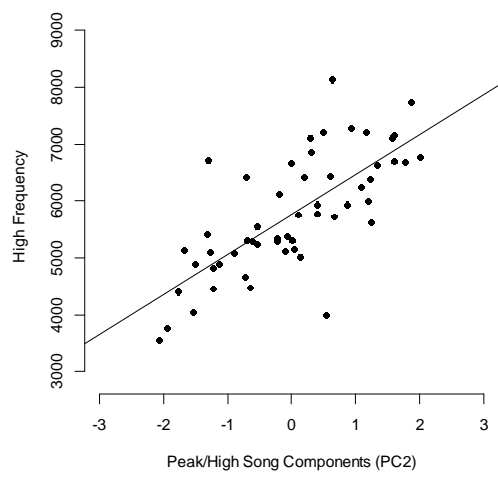
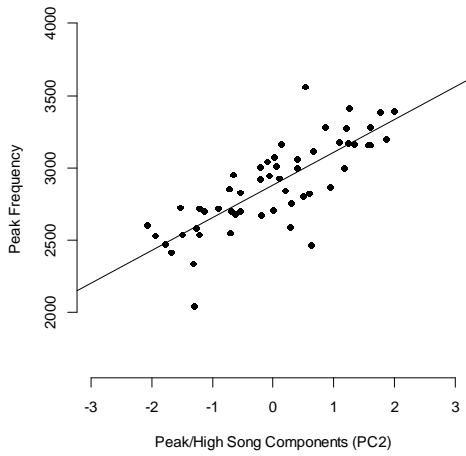
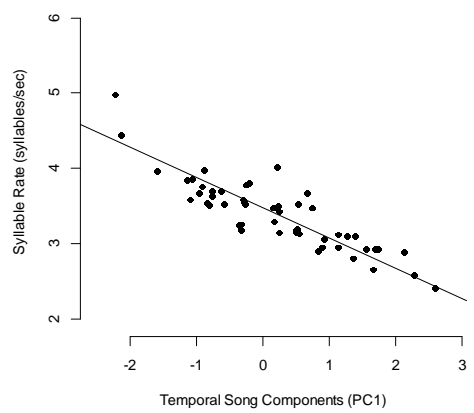
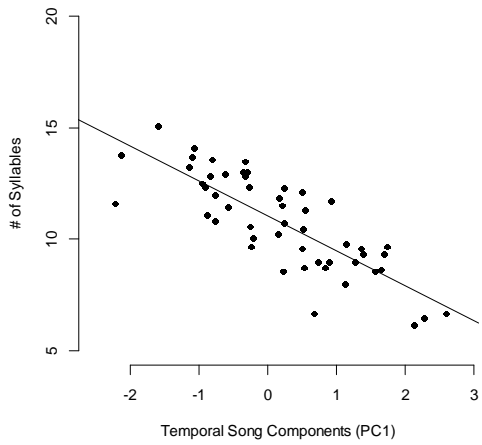
| Site | Combo | Male feeding visits | Male feeding visits per nestling | Female feeding visits | Female feeding visits per nestling | Nestling condition |
|--------------|------------|---------------------|----------------------------------|-----------------------|------------------------------------|--------------------|
| prairie | gpos | 5.00 | 2.50 | 4.00 | 2.00 | -1.11 |
| prairie | parkinglot | 0.00 | 0.00 | 2.00 | 2.00 | -0.55 |
| prairie | pbbs | 0.00 | 0.00 | 1.00 | 0.50 | -1.61 |
| prairie | peninsula | . | . | . | . | . |
| prairie | spbo | 3.00 | 1.50 | 1.00 | 0.50 | -1.59 |
| prairie | sygy | 2.00 | 1.00 | 2.00 | 1.00 | 0.19 |
| prairie | ysgw | 6.00 | 2.00 | 5.00 | 1.67 | -0.01 |
| pubhunt | bsop | 2.00 | 0.67 | 2.00 | 0.67 | 1.13 |
| pubhunt | ppys | . | . | . | . | . |
| pubhunt | sbby | 2.00 | 1.00 | 2.00 | 1.00 | -1.85 |
| pubhunt | sgbo | 1.00 | 0.00 | 0.00 | 3.00 | -2.76 |
| pubhunt | spyg | 1.00 | 0.50 | 0.00 | 0.00 | -0.85 |
| pubhunt | wsgp | 0.00 | 0.00 | 2.00 | 1.00 | -2.53 |
| rushrunnorth | bsww | . | . | . | . | . |
| rushrunnorth | osgb | . | . | . | . | . |
| rushrunnorth | posb | . | . | . | . | . |
| rushrunnorth | wsop | 5.00 | 2.50 | 2.00 | 1.00 | -1.30 |
| rushrunnorth | ybsy | 1.00 | 0.50 | 1.00 | 0.50 | -1.85 |
| rushrunnorth | ypps | 3.00 | 1.00 | 1.00 | 0.33 | 0.59 |
| rushrunsouth | bwos | . | . | . | . | . |
| rushrunsouth | gbbs | 1.00 | 0.50 | 2.00 | 1.00 | . |
| rushrunsouth | gsgg | . | . | . | . | . |
| rushrunsouth | obys | 3.00 | 1.50 | 1.00 | 0.50 | -0.99 |
| sgalena | ...S | 3.00 | 3.00 | 3.00 | 3.00 | 2.57 |
| sgalena | b50 | . | . | . | . | . |
| sgalena | ggsw | . | . | . | . | . |
| sgalena | psyp | 0.00 | 0.00 | 0.00 | 0.00 | 0.86 |
| sgalena | sywb | 3.00 | 1.00 | 3.00 | 1.00 | 1.27 |
| tuttlenorth | ppso | 3.00 | 1.50 | 2.00 | 1.00 | 1.86 |
| tuttlenorth | psoo | 1.00 | 0.50 | 1.00 | 0.50 | -2.38 |
| tuttlenorth | s/b | 0.00 | 0.00 | 6.00 | 3.00 | 0.24 |
| tuttlenorth | unb+spbg | . | . | . | . | . |
| tuttlenorth | ypys | 1.00 | 0.50 | 1.00 | 0.50 | 1.50 |
| tuttlesouth | gsyp | 2.00 | 1.00 | 1.00 | 0.50 | -0.45 |
| tuttlesouth | osoy | 3.00 | 1.50 | 4.00 | 2.00 | . |
| tuttlesouth | psgg | 0.00 | 0.00 | 1.00 | 1.00 | . |
| tuttlesouth | sbpw | 1.00 | 0.25 | 0.00 | 0.00 | -2.28 |

Appendix I: A description of a subset of Northern Cardinal males recorded on experimental honeysuckle removal plots in central Ohio in 2011 and a comparison of song components between control and experimental sites.



Appendix I. Prior to the initiation of this study, three urban sites (Kenny, Rush Run and Tuttle) were included in a complementary study of the impacts of Amur honeysuckle (*Lonicera maackii*) on avian communities and demographic parameters in Central Ohio. In 2007-08 one of two 2-ha grids was randomly selected for removal of honeysuckle and the other to act as a control. All removal was completed in the winter season when birds were not breeding. No vegetation manipulation took place on the control sites. Following experimental removal, these sites differed from adjacent control site by having lower densities of saplings and shrubs, primarily from the removal of Amur honeysuckle. In addition, experimental removal grids had lower densities of cardinals and higher ambient noise than controls (Rodewald, unpublished). The decrease in cardinal densities is likely due to the dramatic reduction of preferred understory vegetation. Increases in ambient noise likely reflect traffic noise permeating farther through the forest, as a result of the lack of vegetation at the strata where measurements took place (1.5m). In 2011, I recorded a small subset of birds located within these removal sites using the same methodology as presented in chapters 2 and 3. Mean song components of Northern Cardinal males between control (honeysuckle present) (n=17) and experimental (honeysuckle removed) sites (n=12) in are presented here. Males on control plots sang longer & faster songs (2 sample t-test, $t=-2.16$, $df=27$, $p = 0.04$), and higher peak/high frequencies (2 sample t-test, $t=2.51$, $df=27$, $p = 0.02$) than males on experimental plots.

Appendix J: Relationships between principal components of song and original song measurements for male Northern Cardinals in central Ohio, 2011 (n=54).



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