ABSTRACT

Signals that are efficiently transmitted and easily detected in their signaling environment are favored by natural selection. Anthropogenic disturbance can rapidly alter the signaling environment, and recent studies have shown that acoustic and visual signals change in response to these altered habitats. Although these studies provide important insight into the effects of urbanization on animal signals and have served as experiments testing the role of the environment in shaping signal design, several key aspects of how signal design can be influenced by environmental changes remain unclear.

Previous studies have focused on signals used between adults, such as those used in mate choice, yet other signals should be similarly affected by anthropogenic disturbance. Thus, one facet of my research examines how anthropogenic disturbance can influence parent-offspring communication. I tested whether nestling mouth coloration in Eastern bluebirds (*Sialia sialis)* was a signal of quality, and if a parents ability to discriminate among the mouth coloration of their nestlings was affected by level of human disturbance. I found that the perceived color contrast of nestling mouths against its nest was significantly correlated with nestling body condition, suggesting that it may be signal of nestling quality. Additionally, I found that the parent's ability to perceived a difference in color contrast of a nestling's mouth among nest-mates was lower in disturbed habitats, than in undisturbed habitats, showing less discriminability among nestlings in disturbed habitats. These results suggest that

parent-offspring communication can be affected by anthropogenic disturbance which may reduce a parent's ability to preferentially invest in high quality young.

Past research on anthropogenic disturbance and signaling has focused on the response of single signals, yet most organisms communicate using signals from multiple sensory systems (*i.e.*, multimodal signals). Thus, I examined how anthropogenic disturbance can simultaneously influence components of multimodal signals in Eastern bluebirds. I measured the visual and acoustic environment at different disturbance levels and related them to male plumage and song characteristics. I found that in areas with high levels of anthropogenic noise, males sing at a higher minimum frequency, presumably to avoid overlap with low frequency background noise. I also found that the visual background is altered in disturbed sites; however, plumage characteristics did not covary with the altered habitats. These results suggest that human disturbance is interfering with both visual and acoustic signals, yet only acoustic signals have responded to the changes.

Few studies on anthropogenic disturbance directly explore the explicit evolutionary mechanisms underlying the changes in signal design. Thus, in the final chapter of my dissertation, I explored how selection on traits varied across habitats with different levels of disturbance. To do this, I determined paternity of nestlings using microsatellite. Then, I determined the major factors influencing rates of extra-pair paternity (i.e., proportion of nestlings within a nest that were sired by other males), and tested whether these factors varied with disturbance

levels. I found that the minimum frequency of song, and the brightness of the male's chestnut breast are important predictors of extra-pair paternity rate across all disturbance levels. Additionally, I found an interaction between disturbance level and the minimum frequency of song in relation to extra-pair paternity. This interaction effect was due to differences in selection pressure on the minimum frequency of song in relation to habitat disturbance. Males that sing in higher minimum frequencies have lower rates of extra-pair paternity, in disturbed areas, but higher rates of extra-pair paternity in undisturbed areas. These results suggest that selection on signals vary across disturbance levels and this could drive the observed changes in the design of signals. Potential consequences of these changes include the possibility of long-term differentiation between bluebird populations living in disturbed and undisturbed habitats, and a shift in important traits across the entire species.

THE CONSEQUENCES OF ANTHROPOGENIC DISTURBANCE ON COMMUNICATION AND THE OPERATION OF SEXUAL SELECTION IN THE EASTERN BLUEBIRD (*SIALIA SIALIS*)

By

Ellen Michale Wisner
B.S. Centre College, 2006

DISSERTATION

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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CHAPTER I

INTRODUCTION

There is tremendous diversity of animal signals throughout the natural world. This diversity is hypothesized to be the product of natural selection acting on signal design. Signal design is determined by two components: strategic design, which deals with the content of the signal, and signal efficacy, which deals with the effective transmission and reception of the signal in its physical habitat (Guilford and Dawkins 1991). Natural selection on signal design often favors signals that serve as reliable indicators of need, health, or quality of the signaler, whereas natural selection on signal efficacy favors signals that are easy to detect, discern, and remember (Guilford and Dawkins 1991). Detectability is the ease with which a signal is discriminated from background noise, and selection on detectability often deals with signals that are used for long-range communication. Discriminability addresses the ability to distinguish one signal from another and to place it in a discrete category. That is, selection favors signals that allow receivers to easily differentiate among individuals in a group. Lastly, memorability addresses the receivers' ability to remember a signal. For instance, selection should favor warning signals that are memorable because both the predator and prey gain from the predator quickly learning that bearers of the signal are unpalatable (Guilford and Dawkins 1991). Hence, selection on detectability, discriminabilty, and memorability should alter signal design when the signaling environment is altered (Searcy and Nowicki 2005; Patricelli and Blickley 2006).

Several correlative studies have shown that the design of visual and acoustic signals covary with their distinct signaling environment, providing support for the hypothesis that natural selection on signal efficacy can account for signal diversity across taxa and habitats (Slabbekoorn and Smith 2002a; Podos and Nowicki 2004; Thery 2006). For example, in a comparative study of 20 bird species from both relatively dark (e.g., closed) and relatively light (e.g., open) habitats, species in darker habitats were found to have plumage richer in long-wavelengths, thus maximizing the chromatic contrast of plumage from the darker habitat (McNaught and Owens 2002). Likewise, in the little greenbul *Andropadus virens*, individuals living in habitats with higher amplitude of low frequency noise sing songs with higher minimum frequencies to avoid song-masking (Slabbekoorn and Smith 2002b). Nevertheless, testing the ideas of signaling theory experimentally has been difficult (Rowe and Skelhorn 2004).

Anthropogenic Disturbance as an Experiment

With a growing global population, the amount of human-disturbed land throughout the world is rapidly increasing (Meyer and Turner 1992; Foley et al. 2005). Moreover, anthropogenic disturbance can quickly change an organism's signaling environment, providing a unique opportunity to experimentally explore how signals evolve in response to a changing signaling environment. Many recent studies have found predictable changes in signal design in response to noise pollution across several taxa including birds, mammals, and amphibians (Table 1.1). For instance, the neotropical treefrog *Dendropsophus triangulum* acoustic call rate (i.e., signals more often) in areas that are louder due to anthropogenic noise (Kaiser and Hammers 2009). Additionally, a handful of studies have examined how human-induced eutrophication affects visual communication in fish, and how human introduction of chemicals (i.e., pesticides, fertilizers, heavy metals) can lead to disruption of chemical signaling in fish and amphibians (Table 1.1). In general, these studies provide unique insights into the role of signaling environment in signal design. However, they mainly focus on sexual signals from single modalities, and have not explored the potential mechanisms driving the changes in signal design. Here I examine how anthropogenic disturbance can influence (1) signals that function in parent-offspring communication, (2) signals in multiple sensory modalities (i.e., “multimodal signals”) and (3) selection pressures on signals.

Signal Function

Most theoretical and empirical studies of the effects of anthropogenic noise on animal signals have focused on communication between adults, especially in the context of mate choice, even though signals used for other purposes should be similarly disrupted by human disturbance (Patricelli et al. 2006; Slabbekoorn and Ripmeester 2008). For instance, nestlings signal their need to parents through begging calls, and increased noise caused by anthropogenic disturbance should interfere with these begging calls by making difficult for parents to hear their young. So far this has not been tested in the field, but some studies show that nestlings increase the amplitude of their begging calls in response to increases in ambient noise from natural causes (i.e., wind, water movement; Leonard and Horn 2005, 2008). Likewise, aposematic or warning coloration may also be affected by human disturbance. Due to studies concentrating on signals used in mate choice, we lack an overall understanding of how all types of signals can be affected by human disturbance.

Multimodal Communication

Studies on anthropogenic disturbance and signaling have also overwhelmingly addressed only the response of signals in one signaling modality, yet most species communicate in multiple sensory modalities ("multimodal signals"; reviewed in Partan and Marler 1999; Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005). Multimodal signals are used for both inter- and intraspecific communication (Candolin 2003; Hebets and Papaj 2005) and are used by a variety of taxa, including: amphibians (e.g., foot-flagging frogs, Grafe and Wanger 2007; squirrel treefrogs, Taylor et al. 2007), birds (reviewed in Hebets and Papaj 2005; cowbirds, O'Loghlen and Rothstein 2010), mammals (e.g., grey squirrels, Partan et al. 2010; primates, Slocombe et al. In Press), crustaceans (e.g., crayfish, Aquiloni et al. 2009), insects (e.g., ants, Holldobler 1999; butterflies, Papke et al. 2007; bees, Barth et al. 2008; tiger moths, Ratcliffe and Nydam 2008), and arachnids (e.g., wolf spiders, Gordon and Uetz 2011).

Two major hypotheses address the purpose of multimodal signals. The Multiple Message Hypothesis posits that the different signals provide different messages, and the Redundant Signaling Hypothesis posits that different signals redundantly provide the same message (Candolin 2003; Hebets and Papaj 2005). In both cases, signals can either be assessed sequentially or simultaneously (Candolin 2003). The interaction and function of multimodal signals may affect how they evolutionarily respond to anthropogenic disturbance. For instance, if signals are providing multiple messages, then disruption of either signal should lead to selection favoring changes in the affected signals. However, in the case of redundant signals, it is possible that disruption of one signal is compensated for by the second signal, and thus selection may not favor shifts in overall signal design. Indeed, it has been hypothesized ("efficacy backup hypothesis", Candolin 2003) that the purpose of redundant signals is to “back up” the other signal when environmental conditions limit the transmission of one of the signals. For example, males of the wolf spider *Schizocosa retrorsa* attract females with seismic and visual signals. Experimental masking of seismic signals did not alter male mating success, suggesting that females only needed one signal type to make mating decisions (Hebets and Uetz 1999). Alternatively, multimodal signals may convey different messages or have different functions. For instance, over 90% of bird species use multimodal signals (Hebets and Papaj 2005). Bird song is thought to be used primarily in long-distance communication (Catchpole and Slater 2003), while plumage coloration may be used at closer range. Thus each signal may have a different function in conspecific communication and may be assessed sequentially (Candolin 2003). Consequently, in the study of anthropogenic disturbance, it is important to study multimodal signals, as multimodal signaling theory may yield insight about why certain signals change, and others do not.

Mechanism of Selection Acting on Signal Design

Signals are used for a variety of purposes such as signal alarms, attracting mates, begging for food, and conveying social dominance (Searcy and Nowicki 2005). The functions of signals are important for both the signaler and the receiver. Thus changes in signals or signaling efficacy in response to anthropogenic disturbance may have negative effects on individuals. In signals that function in mate choice, especially those that indicate mate quality, disruptions of signals could lead to individuals being unable to accurately assess their potential mates. In cases where signals are disrupted, selection should favor signals to change. Previous work has shown that signals can change in response to communication disruption (references above), yet we know little about the explicit mechanisms that favor the change or the biological consequences of these signal changes (Rabin et al. 2003; Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). The changes in signals that have been observed in response to anthropogenic disturbance may be the result of changes in selection pressure. Potential consequences of these changes in selection pressure due to anthropogenic disturbances include the possibility of long-term differentiation between disturbed and undisturbed habitats. This may result if selection favors different traits in disturbed and undisturbed areas. Another potential consequence could be a shift in important traits across the entire species, which may result if human expansion continues and the majority of habitat for a species is affected by human disturbance.

Uncovering how human disturbance can influence communication, and determining the biological consequences of these changes, is complicated. Thus far studies have mainly focused on the response of signals of a single modality used in mate choice, and have yet to explore the biological consequences of changes in signals and signal efficacy in nature. In my research I explore 1) how human disturbance can influence parent-offspring communication, 2) how multimodal signals respond to anthropogenic disturbance, and 3) how changes in signaling efficacy caused by anthropogenic disturbance can influence the selection acting on signals and how this can affect signal design.

CHAPTER II

THE EFFECTS OF ANTHROPOGENIC DISTURBANCE ON NESTLING MOUTH COLORATION IN THE EASTERN BLUEBIRD, *SIALIA SIALIS*

SUMMARY

The perception of signals depends on the sensory parameters of the receiver and the environment in which signals are produced, transmitted, and received. Signal design should evolve in response to changes to signaling environment. Indeed, recent work suggests that signal design evolves in response to rapid changes in the signaling environment, including those induced by humans. However, little is known about how these changes are actually perceived by the intended receivers, and, more important, how these changes can potentially alter a receiver's ability to discern among signalers. Nestling birds have bright mouth coloration, which can be used by parents as indicators of health and thus to allocate resources adaptively. I examined nestling mouth coloration of Eastern bluebirds in disturbed, intermediate, and undisturbed areas and tested whether mouth coloration is a reliable signal of nestling quality, and examined how human disturbance of the visual signaling habitat can influence the utility of this signal. I found a positive association between nestling body condition and conspicuousness of mouth coloration, suggesting that mouth coloration can be used by parents to assess offspring quality and allocate resources accordingly. In addition, I found that changes in ambient light among habitats of different disturbance levels resulted in a reduction of the perceived variation among nestlings in mouth coloration (discernability). Consequently, anthropogenic induced changes in light may prevent parents from optimally allocating food based on the variation in quality among their young. The results suggest that anthropogenic disturbance can reduce the utility of signals.

INTRODUCTION:

There is a tremendous diversity of animal signals in the natural world which serve a variety of purposes including warning others of danger, attracting mates, begging for food, and signaling dominance (reviewed in Johnstone 1997; Searcy and Nowicki 2005). Understanding this diversity requires recognition that signals have two major components: 1) the content of the signal (e.g., strategic design), and 2) the physical design of the signal, which optimizes transmission and detection in its environment (e.g., efficacy Guilford and Dawkins 1991). For example, in parent-offspring communication, strategic design may be the result of evolutionary pressure on offspring to effectively communicate their need to parents, whereas signal efficacy may be a result of natural selection favoring begging signals that are easily detectable from the background. Moreover, it is critically important that receivers not only detect the signal from the background noise but also discern variation in the signal to allow discrimination (Guilford and Dawkins 1991). Changes in the signaling environment can therefore affect the efficacy, and thus the utility, of signals.

An increasing global population has caused cities to continue to expand, and more land has become influenced by human disturbance (Meyer and Turner 1992; Foley et al. 2005). Many studies have shown that human disturbance can influence the signaling environment and interfere with animal communication (reviewed in Rabin et al. 2003; Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). Most studies of the effects of anthropogenic disturbance on animal signals have focused on signaling between adults, especially signals used in mate choice, even though signals used for other purposes should be similarly disrupted by human disturbance (Patricelli et al. 2006). For instance, increased noise caused by anthropogenic disturbance could interfere with nestling begging calls, making it harder for parents to hear their young. This has not been tested in the field, yet there is some evidence that nestlings increase the amplitude of their begging calls in response to increases in ambient noise from natural causes (i.e., wind, water movement; Leonard and Horn 2005, 2008).

In addition to begging calls (Horn and Leonard 2008), nestlings often have conspicuously colored mouths that are thought to play a role in parent-offspring communication and influence parental feeding decisions (Wright and Leonard 2002; Wiebe and Slagsvold 2009). Bright mouth coloration is hypothesized to serve three non-mutually exclusive functions. First, it may make nestlings more conspicuous from the nest, allowing for more efficient feeding ("detectability hypothesis"; Kilner and Davies 1998; Heeb et al. 2003; Wiebe and Slagsvold 2009). This hypothesis is supported by the observation that species that nest in dark areas, such as cavity nesters, often have paler mouth coloration than those in open nests (Kilner and Davies 1998; Hunt et al. 2003). Second, mouth coloration may distinguish conspecific young from brood parasites ("recognition hypothesis"; Schuetz 2005). Finally, the spectral properties of nestling mouth color may signal the nestling’s overall health or condition ("quality signal hypothesis"; Kilner 1997; Wiebe and Slagsvold 2009). For example, the barn swallow *Hirundo rustica* nestling mouth coloration indicates quality and influences parental allocation of food (de Ayala et al. 2007), as parents allocate food according to the reproductive value of their young (Clutton-Brock 1991). Regardless of which hypothesis is most relevant, nestling mouth coloration is clearly important in parent-offspring communication and, if the perception of nestling mouth and flanges (i.e., the outer rim of the mouth) coloration is disrupted, it may influence the parents’ ability to feed or to selectively invest in particular offspring. The effects of human disturbance on visual begging signaling (e.g., nestling mouth coloration) have not yet been studied.

Eastern bluebirds nest in cavities, and their nestlings have bright mouth coloration that reflect both in the ultraviolet and long wavelength range. Although little is known about the function of nestling mouth coloration in Eastern bluebirds in other cavity nesting birds, bright mouth coloration serve as an important signal in parent-offspring communication (Kilner and Davies 1998; Heeb et al. 2003; Wiebe and Slagsvold 2009). Here I explore 1) the function of bright mouth color as a reliable signal of nestling condition and 2) the effects of human disturbance on the discernability of these potential signals.

METHODS:

Field site and field methods

I studied Eastern bluebirds at 11 sites in New York and Connecticut from April – August 2009 and 2010 (Figure 2.1). In 2009 I studied 5 sites in Central New York, and in 2010 I studied 6 sites in the Southeastern New York and 1 site in Southern Connecticut (Figure 2.1). Sites varied significantly in levels of human disturbance, density of nest-boxes, and the number of nesting adults. I used ambient noise as a measure of human disturbance (see below), and study sites ranged from quiet fields (mean Leq = 49.5 dBA) to sites near noisy roads (mean Leq = 69.8 dBA). Beginning in mid-March, each site was visited at least once a week. Boxes were checked for signs of nesting, and after the nestlings were five days old they were banded with a metal USGS band for identification, blood samples were taken, and measurements including tarsus length (mm) and mass (g) were taken for each nestling. Body condition was calculated for each nestling using the residuals from the regression of mass on tarsus length (Bize et al. 2006).

Ambient noise

Using a sound pressure level (SPL) meter (Larson-Davis 824 Sound Level Meter), I measured ambient noise for thirty seconds within each pairs’ nesting area between 0800 and 1000, during the period of highest activity in Eastern bluebirds (Gowaty and Plissner 1998). As previous studies have shown that anthropogenic noise is highest in amplitude at low frequencies and have used low frequency ambient noise as a quantitative measure of disturbance (Slabbekoorn and Ripmeester 2008), I focused on low frequency ambient noise (Leq of 0-4 kHZ) for my analyses. However, using full spectrum ambient noise (Leq of 0-20 kHz) gave qualitatively similar results. SPL measurements were averaged across each site. Based on the frequency distribution of low frequency ambient noise, sites were classified into disturbed (mean = 42.743 dBA, SE = 2.209), intermediate (mean = 33.951 dBA, SE = 0 .255), or undisturbed sites (mean = 28.246 dBA, SE=0.326) (Figure 2.2). Low frequency ambient noise (Leq 0-4) was significantly different between disturbed (D), intermediate (I) and undisturbed (U) sites (F = 28.141, d.f. = 2,8, $p < 0.001$).

Measurement of nestling mouth reflectance and nest reflectance, and ambient light

Ten scans of nest material, and three reflectance scans of each nestling’s flanges (i.e., the external rim around the mouth; Figure 2.3) and mouth were taken using an Ocean Optics USB2000 spectrophotometer (Ocean Optics In., Dunedin, FL, USA) and a Xenon flash light source (Ocean Optics PX-2; as in Uy and Stein 2007). A black anodized aluminum sheath with a 45° tip surrounded the micron fiber-optic probe. Each scan was standardized with a 97% reflecting spectralon white standard (Labsphere) and a dark current reading. CLR: Colour Analysis Program v. 1.05 (Montgomerie 2008) was used to compile raw reflectance data. The multiple scans for nest, mouth and flanges were later averaged for each individual.

To quantify the intensity and spectral properties of light illuminating nestlings, I measured the irradiance of ambient light inside each nest-box with an Ocean Optics USB 2000 spectrophotometer (Dunedin, FL) and a cosine corrected sensor (Ocean Optics CC-3-UV) pointed towards the opening of the nest box. To allow for comparisons across nests and sites, irradiance measurements were calibrated with a standard light source (LiCor 1800-02, LiCor Environmental, Lawrence, KS, USA).

Modeling nestling mouth coloration

To determine how conspicuous nestlings are from their background and how discriminable they are from each other, I modeled the contrast between nestlings and their background, and nestlings against each other, using generalized Passerine eye parameters, a Weber fraction of 0.05 and known cone densities of blue tits *Parus caeruleus* (Vorobyev and Osorio 1998; Hunt et al. 1999; Endler and Mielke 2005).

Calculation of quantum catch of each cone: In this model the quantum catch of each avian cone (i.e., ultraviolet-wavelength sensitive (UWS), short-wavelength sensitive (SWS), medium-wavelength sensitive (MWS), and long-wavelength sensitive (LWS)) in response to a color patch (i.e., area of color) is calculated by multiplying the reflectance of the color patch (i.e., mouth, gape, and nest material) by the ambient light illuminating the color patch (irradiance), and then by the spectral sensitivities of each cone. The quantum catches were then transformed using a von Kries transformation, which is calculated by dividing the quantum catch for each color patch by the quantum catch of a pure white object, which controls for color constancy (Vorobyev et al. 1998).

Calculation of chromatic contrast: To estimate the perceived conspicuousness of nestling mouth coloration against the nestling background, and the discriminability of mouth coloration among nestlings, I calculated the chromatic contrast by finding the difference between the quantum catch of each cone for the two color patches being compared (e.g., mouth vs. nest, nestling's mouth vs. another nestling's mouth), and weighting these differences by receptor noise (Vorobyev et al. 1998). The resulting measurement is Delta S (ΔS), which measures the contrast in color between the two color patches irrespective of brightness.

Calculation of achromatic contrast: To measure achromatic contrast (e.g., brightness contrast) between two patches, I calculated the quantum catch of the avian double cones in response to both color patches being compared. Double cones are a separate class of photoreceptors that are used by birds for achromatic visual tasks (e.g., pattern recognition). Because the principal and accessory members that make up the double cone contain MWS and LWS pigments (Hart and Vorobyev 2005), the spectral absorbance of double cones was approximated by combining the spectral absorbance of MWS and LWS single cones (Osorio et al. 1999). The procedure for calculating the quantum catch of double cones is the same as the calculations for single cones (see above). Achromatic contrast was then calculated as the difference in quantum catch by the double cones stimulated by two color patches factoring in neural noise (as in Loyau et al. 2007). The resulting measurement is Delta fQ (ΔfQ).

Both ΔS and ΔfQ are measured in “just noticeable differences” (jnd). Jnd’s greater than 1.0 indicate that the bird can likely distinguish the two color patches (Vorobyev and Osorio 1998; Cassey et al. 2008). This estimate is based on a Weber fraction of 0.05 which was determined from behavioral experiments on the Pekin robin, *Leiothrix lutea* that tested the ability of individuals to distinguish between different colored screens (Maier 1992).

Plotting quantum catch in tetrahedral space: Since there was a difference in the chromatic contrast of nestling mouth color in relation to disturbance level, I further explored whether it was the ambient light illuminating the nestling and/or the intrinsic color of the nestling’s mouth was responsible for the change in discriminability. Thus, I plotted the quantum catch of each cone (see above) in response to ambient light, and in response to nestling mouth reflectance in tetrahedral space using Avicol v.5 (Gomez 2006). This method uses a tetrahedral (height of 1) representation of the stimulation of each of the four avian cones, with each vertex representing one of the avian cones, and then compares them to the achromatic origin (Appendix 1, Figure A.1). This provides a measure of chroma (r), and latitudinal (ϕ) and longitudinal (θ) hue for both ambient light, as well as for nestling mouth reflectance (Appendix A, Figure A.1; for more details see Endler and Mielke 2005). Chroma measures the purity of the color, and is the distance of the color patch/ambient light from the achromatic origin. Latitudinal hue, is the angle between the y-axis and the vector from the achromatic origin to the point plotted in tetrahedral space, which describes color in the uv-color range. Longitudinal hue is the angle between the x-axis and the vector from the achromatic origin to the point plotted in tetrahedral space, which describes color in the visual color range of humans (Appendix A, Figure 2.1).

Statistical analysis

Regression analysis was used to determine whether mouth and flange color were predicted by body condition, while controlling for both site and disturbance level by entering these into the model as covariates. Additionally, I ran this regression without any covariates and obtained similar results.

To test whether if disturbance level influenced the discernability of nestling mouth coloration, I used nested ANOVAs for each of the color patches (i.e., Flanges ΔS and ΔfQ, and Mouth ΔS and ΔfQ) with disturbance level as a main effect, and site nested within disturbance level. Nested ANOVAs were also used to examine the relationship between the color properties of irradiance and mouth color, such as hue (θ and ϕ) and chroma (r) between disturbed, intermediate, and undisturbed sites. All statistical analysis were two-tailed and were conducted in SPSS Statistics 19.0 (Chicago, IL).

RESULTS:

Flanges and mouth coloration in relation to body condition

Nestling mouth and flanges reflect light in both the ultraviolet and long wavelength (Figure 2.4). There was a significant relationship between body condition and mouth ΔS ($r=0.315$, d.f.=38, $p=0.053$; Figure 2.5), but not between body condition and flanges ΔS ($r= 0.19$, d.f.=38, $p=0.213$), flanges ΔfQ ($r=-0.127$, d.f.=38, $p=0.451$), or mouth ΔfQ ($r=0.088$, d.f.=38, p=0.568). Site and disturbance level did not significantly affect any of the relationships between body condition and mouth and flanges coloration.

Discernability between nestlings and disturbance level

There was a significant relationship between disturbance level and mouth ΔS (Wald χ^2=6.169, d.f.=2,7, p=0.046), but not between disturbance level and flanges ΔS (Wald χ^2=2.228, d.f.=2,7, p=0.328), flanges ΔfQ (Wald χ^2=0.870, d.f=2,7, p=0.647), and mouth ΔfQ (Wald χ^2=0.393, d.f.=2, p=0.821) (Figure 2.6).

Irradiance and mouth reflectance in comparison to disturbance level

When examining the color properties of irradiance separately, I found that longitudinal hue (Θ; Wald χ^2=8.287, d.f.=2,7, p=0.016) and chroma (r; Wald χ^2=15.767, d.f.=2,7, p<0.001) differed significantly between sites differing in disturbance. Longitudinal hue was highest in intermediate areas (mean=0.628 radians), intermediate in undisturbed areas (mean=0.335 radians) and lowest in disturbed areas (mean = 0.070 radians), indicating that ambient light is more orange in color in disturbed areas and more yellow in undisturbed areas. Because this pattern does not coincide with the pattern found in the changes in discernability across disturbance levels, it is unlikely that the hue of irradiance is an important factor influencing discernability. However, chroma was found to be highest in undisturbed areas (mean = 0.228), intermediate in intermediate areas (mean=0.200), and lowest in disturbed areas (mean=0.162), which is consistent with the pattern I found in discriminability in nestling mouth color. Latitudinal hue (ϕ; Wald χ^2=5.091, d.f.=2,7, p=0.078) and brightness (Wald

χ^2=1.493, d.f.=2,7, p=0.496) were not significantly different between the three disturbance levels.

With respect to mouth reflectance, there was a significant difference in latitudinal hue (ϕ) between disturbance levels (Wald χ^2=6.710, d.f.=2,7, p=0.035). Intermediate sites had the highest ϕ (mean=-0.603 radians), followed by disturbed sites (mean=-0.640 radians), and then undisturbed sites (mean=-0.677 radians), suggesting that intermediate sites have the highest UV reflectance. As this is inconsistent with the pattern found in measures of discernability it is unlikely to play an important role in the differences in discernability across disturbance levels. Additionally, visual examination of the average reflectance spectra of the mouth suggests little difference in color properties across disturbance levels (Figure 2.7). The other spectral properties of nestling mouths did not vary across disturbance levels (θ, Wald χ^2=4.945, d.f.=2,7, p=0.084; r, Wald χ^2=2.123, d.f.=2,7, p=-0.346; brightness, Wald χ^2=2.225, d.f.=2, p=0.329).

DISCUSSION:

I found a relationship between nestling body condition and the perceived chromatic contrast of mouth color, suggesting that nestling mouth coloration may serve as signal of nestling quality to parents. Like many other Passerine species, Eastern bluebird nestlings have bright mouth coloration that reflects both ultraviolet and long-wavelength light (Figure 2.4). Our finding that neslting mouth color is related to body condition of nestling is consistent with the quality-signalling hypothesis, and is consistent with other studies that have found relationships between offspring quality and mouth coloration (e.g., de Ayala et al. 2007). I did not find a relationship between flanges coloration and body condition, suggesting that flanges coloration may not signal offspring quality, but may instead serve in detectability or recognition. These results are consistent with a recent study that found that mouth color in the barn swallow *Hirundo rustica* serves as an indicator to parents of nestling condition, but flanges coloration does not (de Ayala et al. 2007). However, de Ayala et al (2007) did find that nestlings with brighter flanges coloration received more food from their parents, suggesting that flanges color does serve as an important signal, perhaps as a potential target for parents.

Using generalized Passerine optical parameters and spectral data on signal and natural ambient light, I found that the perceived discriminability of nestlings' mouth coloration varied among disturbed, intermediate, and undisturbed sites. Specifically, nestling mouth color was least discriminable in disturbed habitats, followed by intermediate, and then undisturbed habitats (Figure 2.6). A visual examination of the average irradiance within each disturbance level shows that mean irradiance for disturbed habitats has lower values in 400-520 nm range than undisturbed and intermediate sites (Figure 2.8), suggesting lower chroma in blue-to-yellow light. As the second peak for nestling mouth coloration occurs at ca. 510 nm (Figure 2.4), the reduction in chroma in ambient light in disturbed areas makes the second peak of nestling mouth color less discernable in disturbed areas. Moreoever, I did not find a change in mouth color across disturbance levels that coincided with the changes in discernability among nestlings. Thus, the change in discriminability found between disturbance levels is likely due to changes in the spectral property of ambient light illuminating the nestlings, and not the intrinsic properties of mouth color. The difference in discriminability between nestlings from disturbed and undisturbed sites was 1.508 just noticable differences (jnds). Since birds can discriminate between objects that differ by greater than 1.0 jnds, the perceived difference in discernability among nestlings in disturbed and undisturbed habitats should be biologically relevant. For example, the cuckoo finch *Anomalospiza imberbis* can discriminate the eggs of conspecific brood parasites that were less than 1 jnd from their own (Spottiswoode and Stevens 2010). This provides evidence that a contrast difference of 1 jnd can be significant in discriminability in birds. Thus the decrease of 1.508 jnds may affect a parent's ability to discriminate among their young. However, as the average jnd between neslings' mouth chromatic contrast in disturbed habitats was 4.198 jnds, the difference in ambient light does not fully disrupt the ability of parents to distinguish between the nestlings within the nests but it should decrease their ability to do so.

It is hypothesized that parents preferentially feed nestlings that are in better condition since they should have a higher reproductive value to the parent (Clutton-Brock 1991; Godfray 1991, 1995). Thus, disruption of signals of quality will influence the parent's ability to effectively discriminate and preferentially allocate resources among young, which could negatively affect the reproductive success of parents. Experiments examining how decreased discriminability can influence parental feeding are needed to test how decreases in discriminability caused by anthropogenic distubances will affect optimal allocation of limited resources.

Conclusions

Previous studies find that anthropogenic disturbance can lead to changes in signaling. For instance, in many bird species, increased ambient noise is correlated with changes in song characteristics including an increased minimum frequency (reviewed in Rabin et al. 2003; Patricelli et al. 2006; Slabbekoorn and Ripmeester 2008). Additionally, comparative studies have found that bird species with darker nests often have brighter mouth coloration (Kilner and Davies 1998; Hunt et al. 2003). If the same processes are at work in microevolutionary scales, the color of nestling mouths may shift to overcome the effects of disturbance. However, this depends on the assumption that bluebirds born in disturbed areas return to disturbed areas, that a decrease in discriminability amongst nestlings decreases fitness, and that nestling mouth coloration has a strong genetic basis. Testing these critical assumptions will provide insights into the potential evolutionary response of nestling mouth color to changes in signaling environment.

CHAPTER III

THE EFFECTS OF ANTHROPOGENIC DISTURBANCE ON MULTIMODAL SIGNALS IN THE EASTERN BLUEBIRD, *SIALIA SIALIS*

SUMMARY:

Natural selection favors signals that are conspicuous and thus easily distinguished from background noise. Alterations to a signaling environment that decrease the effective transmission of a signal should therefore lead to changes in the design of these signals. Anthropogenic disturbance can cause rapid changes to the signaling environment, and recent work shows that indeed anthropogenic noise can lead to changes in acoustic signals. Most species rely on signals in more than one sensory modality ("multimodal signaling") and little is known about how multimodal signals change in response to a changing signaling environment. This chapter examines how anthropogenic disturbance can affect multimodal signals in the Eastern bluebird, *Sialia sialis*, a Passerine that uses song and plumage color in conspecific communication. I studied the song and plumage characteristics of Eastern bluebirds in disturbed, intermediate and undisturbed habitats. I found that disturbed sites have higher levels of low frequency ambient noise, and, that male bluebirds at these sites sing at a higher minimum frequency. Additionally, I found that the visual background differs between disturbed and undisturbed sites, with disturbed sites having less chromatic (i.e., less pure in color) background, and backgrounds greener in color than the yellower undisturbed sites. Although there are differences in the visual background between disturbance levels, I do not find concurrent changes in plumage characteristics. Using the spectral properties of plumage patches and the visual habitat, along with published Passerine sensory eye parameters, I modeled how males will be perceived in disturbed, intermediate, and undisturbed sites, and find that the conspicuousness of male's uv-blue color patch is lowest in disturbed habitats,

intermediate in undisturbed habitats, and highest in intermediate habitats. Therefore the results suggest that Eastern bluebirds have responded to anthropogenic changes in acoustic but not visual environment. The difference in response to changes in signaling environment may reflect differences in the functions of the signals, or differences in how plumage and song characteristics are inherited.

INTRODUCTION:

There is an astounding diversity of animal signals throughout the natural world. These signals include sexual displays, aggressive behaviors, begging signals, and alarm calls (Johnstone 1997; Searcy and Nowicki 2005). This diversity of signals is mediated by selection working on two major components of signal design: natural selection on strategic design which favors signals that serve as reliable indicators of need, health, danger, and quality, and natural selection on signal efficacy which favors signals that are easily discernable, detectable, and memorable (Guilford and Dawkins 1991). Many correlative studies have found that signal structure is related to the signaling background (Slabbekoorn and Smith 2002a; Podos and Nowicki 2004; Thery 2006). For example, in a comparative study of 20 bird species from dark (e.g., closed) and light (e.g., open) habitats, species in darker habitats were found to have plumage richer in long-wavelengths, thus maximizing their chromatic contrast with the darker habitat (McNaught and Owens 2002). Likewise, analysis of intraspecific variation in the little greenbul, *Andropadus virens*, revealed that individuals living in habitats with louder low frequency noise sing songs at a higher minimum frequencies to avoid song-masking (Slabbekoorn and Smith 2002b). Direct experiments testing how signals change in different signaling environments are rare (Rowe and Skelhorn 2004).

Changes in the environment driven by industrialization and urban development can serve as an experiment that allows us to examine how populations respond to rapid changes in signaling conditions. Recent work has shown that noise pollution can alter the design of acoustic signals in birds (Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008), frogs (Sun and Narins 2005), and mammals (Goold 1996; Miller et al. 2000; Foote et al.

2004; Schaub et al. 2008). Likewise, human-induced eutrophication in lakes can lead to significant changes in how animals communicate (Seehausen et al. 1997; Engstrom-Ost and Candolin 2007). Research on the effects of anthropogenic disturbance on communication has focused on signals used in one sensory modality. However, many species communicate using a suite of signals from multiple modalities (i.e., "multimodal signals").

Multimodal signals are used by species from a variety of taxa including: amphibians (Grafe and Wanger 2007; Taylor et al. 2007), birds (Hebets and Papaj 2005; O'Loghlen and Rothstein 2010), mammals (Partan et al. 2010; Slocombe et al. In Press), crustaceans (Aquiloni et al. 2009), insects (Holldobler 1999; Papke et al. 2007; Barth et al. 2008; Ratcliffe and Nydam 2008), and arachnids (Gordon and Uetz 2011). There are two main hypotheses explaining the function of multimodal signals: multiple messages, in which the signals convey different messages, and redundant signaling, in which the signals reinforce the same information by redundancy (Candolin 2003; Hebets and Papaj 2005). In both cases, signals can either be assessed sequentially or in unison (Candolin 2003). It is essential when studying anthropogenic disturbance on signal design to explore not just the response of a single signal, but the response of a suite of signals. Moreover, the function of a signal and the way it is assessed may influence how it responds to a change in signaling environment. Here I explore the effects of anthropogenic disturbance on the design of visual and acoustic signals in the Eastern bluebird, *Sialia sialis*.

Eastern bluebirds live in a variety of open habitats ranging from very quiet to noisy areas nest-boxes for Eastern bluebirds are often placed along busy highways and interstates (e.g., Interstate-90 in NY State). Because of this variation in nesting habitat, bluebirds are exposed to a wide range of both visual and acoustic signaling conditions. Based on past research in other species suggesting that signals can change in response to changes in signaling conditions, I predicted that changes to the visual and acoustic signaling environment would lead to changes in visual and acoustic signals in the Eastern bluebird. Since Eastern bluebirds have a low frequency song (1.5 - 3.5 kHz; Gowaty and Plissner 1998), low frequency anthropogenic noise is predicted to drive changes in frequency components of Eastern bluebirds' song including shifts in minimum frequency, peak frequency, and potentially maximum frequency. Eastern bluebird's ancestral habitat consisted of open areas including fire-maintained savannas, openings in forest with water (e.g., ponds), large openings in forests, and exposed areas of hills (Kiviat 1982 in Gowaty and Plissner 1998), whereas habitats currently range from open "natural" habitats (e.g., abandoned fields), to more heterogeneous visual habitats (e.g., areas with roads, trees, and buildings). Plumage coloration including the blue coloration of their back, rump, wings and tail, as well as the chestnut breast coloration, has been found to play an important role in the reproductive success of bluebirds (Siefferman and Hill 2003). Since plumage serves as an important signal, I predicted that the more heterogeneous visual habitat in disturbed areas may lead to changes in visual signals.

METHODS:

Field site and field methods

I studied Eastern bluebirds at 11 sites in New York and Connecticut from April – August 2009 and 2010. In 2009, I studied 5 sites in central New York, and in 2010, I studied 6 sites in southeastern New York and 1 site in southwestern Connecticut (Figure 2.1). Sites varied significantly in levels of human disturbance. I used ambient noise as a measure of human disturbance (see methods below), and my sites range from quiet fields (mean Leq = 49.5 dBA), to sights near noisy roads (mean Leq = 69.8 dBA).

Beginning in mid-March, each site was visited at least once per week. Nest-boxes were checked for signs of nesting, and surrounding areas were checked for the presences of adult bluebirds. Once a pair of bluebirds began defending a nest-box, mist nets or box traps were used to capture the breeding pair. I banded each individual with unique, plastic color bands and a metal USGS band for identification.

Ambient noise

Using a sound pressure level (SPL) meter (Larson-Davis 824 Sound Level Meter), I measured ambient noise for thirty seconds within each pairs' nesting area between 0800 and 1000, the period of highest song activity in Eastern bluebirds (Gowaty and Plissner 1998). Because I was interested in how increased anthropogenic noise could affect Eastern bluebird song, I examined ambient noise that would mask their song's known frequency range (1.5-3.5 kHz) (Gowaty and Plissner 1998). Additionally, previous studies have shown that anthropogenic noise is highest in amplitude at low frequencies, thus I focused on low frequency ambient noise (Leq of 0-4 kHz). However, using full spectrum ambient noise (Leq of 0-20 kHz) gave similar results. SPL measurements were averaged across each site. Based on the frequency distribution of low frequency ambient noise, sites were classified into disturbed (mean = 42.743 dBA, SE = 2.209), intermediate (mean = 33.951 dBA, SE = 0 .255), or undisturbed sites (mean = 28.246 dBA, SE=0.326) (Figure 2.2). Low frequency ambient noise (leq 0-4) was significantly different between disturbed (D), intermediate (I) and undisturbed (U) sites sites (F = 28.141, d.f. = 2,8, $p < 0.001$).

Song measurements

For each male, 15 minutes of continuous song was recorded using a Marantz PMD670 digital recorder (Mahwah, NJ) set to 16-bit PCM, 48 kHz sampling rate, and a Sennheiser (Old Lyme, CT) unidirectional microphone. Song files were analyzed in Raven Pro 1.3 (Cornell Lab of Ornithology, Ithaca, NY). I measured the maximum frequency (F_{max}), minimum frequency (F_{min}), peak frequency (F_{peak}), and frequency bandwidth (F_{bw}) for each song bout within a haphazardly chosen one-minute portion of each males' song (Figure 3.1). I then took the average of each song characteristics for each site.

Measurement of the visual habitat: ambient light and visual background

I measured radiance and irradiance of each male's signaling environment. Down-welling irradiance measures the intensity and spectral properties of light over 180 degrees, which characterizes the ambient light that illuminates birds and their visual background (e.g., trees, grass, etc. Endler 1993). Irradiance measurements were taken with an Ocean Optic USB 2000 (Ocean Optics, Dunedin, FL), and a cosine corrected sensor (Ocean Optics CC-3-UV) pointed upwards above each pair's nest-box. Radiance collects light that reflects over 1 sterideam degree from objects that make up the bird's visual background (Endler 1993; Leal and Fleishman 2002). In essence, this measures light that is being reflected back by objects being illuminated by the ambient light. Because the visual background is composed of many objects that vary in reflectance, I took 16 radiance measurements using a fused silica collimating lens (Ocean Optics 74-UV) in a spherical arrangement, with one measurement every 45 degrees. The 16 radiance scans were then averaged for each territory, providing a measure of the average visual background. To allow for comparison across territories and sites, radiance and irradiance measurements were calibrated using a standard light source (LiCor 1800-02, LiCor Environmental, Lawrence, KS, USA).

Measurement of plumage characteristics

I used an Ocean Optics USB2000 spectrophotometer (Ocean Optics In., Dunedin, FL, USA) and a Xenon flash light source (Ocean Optix PX-2, as in Uy and Stein 2007) to measure the plumage reflectance of each male's color patches, including the head, back, breast, belly, rump, tail, and wings. The micron fiber-optic probe was surrounded by a black anodized aluminum sheath with a 45 degree tip. Each scan was standardized with a 97% reflecting spectralon white standard (Labsphere) and a dark current reading. Three scans were taken for each patch, which were averaged for each individual.

Modeling the visual signaling environment, plumage reflectance, and the perceived conspicuous of males using avian eye parameters

To avoid making assumptions about the avian visual system, I modeled the plumage color (i.e., reflectance) of males, visual background (i.e., radiance), and ambient light (i.e., irradiance) using avian eye parameters and plotted in tetrahedral space (see below).

Since the successful transmission of signals requires individuals to be able to distinguish signals from the background, I also calculated the conspicuousness of males against their signaling background to get a non-biased measure of how anthropogenic disturbance may be changing the conspicuousness of birds. For all calculations, I used generalized higher Passerine eye parameters, a Weber fraction of 0.05 and known cone densities of blue tits *Parus caeruleus* (Vorobyev and Osorio 1998; Hunt et al. 1999; Endler and Mielke 2005).

Calculation of quantum catch of each cone: In this model the quantum catch of each of the four avian cones (i.e., ultraviolet-sensitive (UVS), shortwave-sensitive (SWS), mediumwave-sensitive (MWS), and longwave-sensitive (LWS) cones) in response to stimulation of color patches was calculated by multiplying the reflectance of the color patch (e.g., breast), by the ambient light illuminating the color patch (irradiance), and then by the spectral sensitivities of each cone. Similarly, to calculate the quantum catch of each avian cone in response to stimulation by the visual background, the radiance was multiplied by the spectral sensitivities of each cone. These quantum catches were then transformed using a von Kries transformation, which was calculated by dividing the quantum catch for each color patch by the quantum catch of a pure white object, which controls for color constancy.

Plotting quantum catch in tetrahedral space: To compare plumage color, visual background and ambient light across disturbance levels, I plotted the quantum catch of each cone (see above) in response to the signal when illuminated by white light in tetrahedral space using Avicol v.5 (Gomez 2006). This method plots the cone stimulation on a tetrahedron with a height of 1, with each vertex representing one of the four avian cones. The origin or center of the tetrahedron represents achromatic objects (Appendix 1; Figure A.1). This provides a measure of chroma (r), and latitudinal (ϕ) and longitudinal (θ) hue for ambient light, as well as plumage reflectance (Appendix A, Figure A.1; for more details see Endler and Mielke 2005). Chroma measures the purity of the color, and is the distance of the color patch/ambient light from the achromatic origin. Latitudinal hue, is the angle between the y-axis and the vector from the achromatic origin to the point plotted in tetrahedral space, which describes color in the ultraviolet range. Longitudinal hue is the angle between the x-axis and the vector from the achromatic origin to the point plotted in tetrahedral space, which describes color in the visual color range of humans (Appendix A, Figure A.1).

Calculation of chromatic contrast: To estimate the perceived conspicuousness of male plumage against the signaling background, I calculated the chromatic contrast by finding the difference between the quantum catch of each cone for the two color patches being compared (i.e., plumage reflectance and background radiance), and weighting these differences by receptor noise (Vorobyev et al. 1998). The resulting measurement is Delta S (ΔS), which measures the chromatic contrast between the two color patches irrespective of brightness.

Calculation of achromatic contrast: To measure achromatic contrast (e.g., brightness contrast) between two patches I calculated the quantum catch of the combination of avian double cones in response to both the plumage signal, and the background signal. Double cones, a separate class of photoreceptors, are used by birds for achromatic visual tasks (e.g., pattern recognition). Because the principal and accessory members that make up the double cone contain MWS and LWS pigments (Hart and Vorobyev 2005), the spectral absorbance of double cones was approximated by combining the spectral absorbance of MWS and LWS single cones (Osorio et al. 1999). The procedure for calculating the quantum catch of double cones is the same as the calculations for single cones. Achromatic contrast was then calculated as the difference in quantum catch by the double cones stimulated by the signal and the background factoring in neural noise (as in Loyau et al. 2007). The resulting measurement is Delta fQ (ΔfQ).

Both ΔS and ΔfQ are measured in "just noticeable differences" (jnd). Jnd's greater that 1.0 indicate that the bird can likely distinguish the two color patches (Vorobyev and Osorio 1998; Cassey et al. 2008). This estimate is based on a Weber fraction of 0.05 which was determined from the behavioral experiments on the Pekin robin, *Leiothrix lutea* which tested the ability of individuals to distinguish between different colored screens (Maier 1992).

Statistical analysis

To test for a relationship between low frequency ambient noise and song characteristics I calculated Pearson correlation coefficients between the average F_{min}, F_{max}, F_{peak}, and $F_{bandwidth}$ for each site, and the average low frequency ambient noise (Leq 0-4). In order to determine if the visual habitat was changing in relation to human disturbance, I compared the average brightness and spectral properties of ambient light (irradiance), and visual background (radiance) per site between habitat types (disturbed, intermediate, and undisturbed) using a one-way ANOVA. In order to determine how changes in the visual background may influence plumage coloration, I calculated Pearson correlation coefficients between background characteristics (i.e., radiance longitudinal hue and radiance chroma) that varied across sites and each of the male plumage characteristics. To determine how the perception of a visual signal is affected by anthropogenic changes in the visual environment, I used the measures of perceived plumage conspicuousness (see above) and compared them across disturbance level using an ANOVA. All statistical analyses were done using SPSS/PASW Statistics 18 (Chicago, IL). All tests of significance are two-tailed.

RESULTS:

Effects of ambient noise on song characteristics

There was a significant relationship between the amplitude of low frequency ambient noise and F_{min} (r = 0.705, d.f. = 10, p = 0.015; Figure 3.2), but not with the other song characteristics (F_{max} r = 0.281, d.f. = 10, p = 0.403; F_{peak} r = -0.137, d.f. = 10, p = 0.689; $F_{bandwidth}$ r = -0.023, d.f. = 10, p = 0.942).

Visual background in relation to disturbance

Latitudinal hue (ϕ; F = 0.697, d.f. = 2,8 p = 0.530), and brightness (F = 0.061, d.f. = 2,8, p=0.942) of the visual background (radiance scans) did not differ across sites of varying disturbance level. I did, however, find trends in the relationship between disturbance level and longitudinal hue (θ; F = 3.342, d.f. = 2,8, p = 0.096), and chroma (r; F = 3.610, df. = 2,8, p= 0.084). Undisturbed sites had an average longitudinal hue of 1.039 radians (i.e., more yellow color), intermediate sites had an average of 1.977 radians (i.e,. green/blue color) and disturbed sites had an average of 1.700 radians (i.e., more green in color). This suggests that undisturbed sites have a more yellow visual background, whereas intermediate and disturbed sites have a more green background. Chroma refers to the purity of the color, and undisturbed sites had the highest chroma (mean = 0.148 , SE = 0.004), the intermediate sites had a intermediate chroma (mean = 0.131, SE = 0.009), and the disturbed site had the lowest chroma (mean = 0.148, SE = 0.011). Finally, I found no significant differences between disturbance level and ambient light longitudinal hue (θ; F = 0.892, d.f. = 2,8, p = 0.452), latitudinal hue (ϕ; F = 0.614, d.f. = 2,8, p = 0.568), chroma (r; F = 0.806, d.f. = 2,8, p = 0.484), and brightness (F = 0.966, d.f. = 2,8, p = 0.426).

Plumage characteristics in relation to changes in visual habitat

To test if plumage coloration varied with changes in the visual environment caused by disturbance level, I compared plumage coloration to both the hue (i.e., color) and chroma (i.e., purity) of the visual background, which varied with respect to disturbance level. I found no significant correlations between the spectral properties of the visual background, and plumage in males (Table 2.1).

Modeling conspicuousness of plumage patches

Objects that differ from the visual background will be more conspicuous than those that match the visual background. Hence, to estimate perceived conspicuousness of male plumage, I calculated the perceived chromatic contrast (ΔS) and brightness contrast (ΔfQ) of each plumage color patch against the visual background. I found that the ΔS of the blue color patch was significantly different between sites of varying disturbance levels (Figure 3.3; F = 3.881, d.f. = 2,8, p = 0.06), with disturbed sites having the lowest average ΔS (mean = 21.006 jnd, SE = 3.128), the intermediate sites having the highest average ΔS (mean = 33.321 jnd, SE = 4.651), and the undisturbed sties having an intermediate average ΔS (mean = 27.0622 jnd, SE = 1.364). I did not find significant relationships between chestnut ΔS (F = 0.412, d.f. = 2,8, p = 0.676), chestnut ΔfQ (F = 0.331, d.f. = 2,8, p = 0.727), or the uv-blue patche ΔfQ (F = 0.347, d.f. = 2,8, p = 0.717) and levels of disturbance.

DISCUSSION:

Ambient noise and song characteristics

As predicted, ambient noise did have an impact on the minimum frequency of male's song. Eastern bluebird songs range from 1.5 to 3.5 kHz, which overlaps with low frequency anthropogenic noise. Males in noisier habitats were found to sing at a significantly higher minimum frequency, presumably to reduce overlap with ambient noise. This result adds to the growing body of evidence showing that birds sing at a higher minimum frequency in areas with increased urban ambient noise (Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). I did not find a relationship between low frequency ambient noise and the other song variables: F_{max}, $F_{bandwidth}$, and F_{peak}. The lack of relationship between low frequency ambient noise and peak frequency of song was particularly surprising as peak frequency is the frequency at which the most energy is exerted, and is therefore often thought to be one of the most important components of song (Hu and Cardoso 2010). For Eastern bluebirds the peak frequency is 2.518 ± 0.053 kHz, which well falls within the 0-4 kHz range where human ambient noise is loudest. Additionally, in a few other species the peak frequency has shifted upwards when exposed to anthropogenic disturbance (Hu and Cardoso 2010).

Visual background and plumage characteristics

Eastern bluebirds generally live in open grassy habitats (Gowaty and Plissner 1998), but their habitat may vary in visual background and ambient light. The results show that in disturbed areas the visual background for Eastern bluebird territories is less chromatic (i.e., pure in color) than in both intermediate and undisturbed habitats. Additionally, I find that the hue or color of intermediate and disturbed habitats are shifted towards the green – blue spectrum, whereas the hue of undisturbed habitats is shifted towards the yellow spectrum. This difference is likely due to more developed habitats having many small fragmented spaces bordered by trees, roads, and buildings. Ancestral bluebird habitat, in contrast, was likely more open (Gowaty and Plissner 1998). Interestingly, I did not find a change in male plumage despite the differences in color and chroma of the visual background across levels of disturbance. One possibility for this lack of change in plumage color is that the changes in the visual habitat may not affect the overall conspicuousness of male plumage. I did find that the changes in the visual habitat do affect the conspicuousness of the uv-blue plumage coloration of males. Specifically in disturbed habitats, uv-blue plumage is significantly less conspicuous than in undisturbed and intermediate habitats. However, the conspicuousness of the chestnut coloration of the breast does not change with habitat type. The brightness of both the uv-blue and the chestnut plumage of male Eastern bluebirds have been found to be reliable predictors of reproductive success (Siefferman and Hill 2003). Considering its importance, it is surprising that plumage color did not change despite the loss of conspicuousness in disturbed sites.

One potential explanation for the different responses of plumage and song to anthropogenic disturbance is that they function differently. Multimodal signals are thought to sometimes convey information at different physical distances (Backwell and Passmore 1996; Gibson 1996; Suk and Choe 2002). This may be the case in Eastern bluebirds since song is likely used in long-range communication, and thus may be assessed before plumage characteristics are assessed (i.e., sequential assessment, Candolin 2003). If song is disrupted, females may not be able to locate males, and would not assess their plumage characteristics.

If this is the case, then selection for a higher frequency song may be stronger than that on plumage characteristics, which are likely assessed at shorter ranges.

Additionally, if song and plumage are redundant signals, the loss in conspicuousness in plumage may not greatly affect the function of the signal if song serves as a backup. Redundant signals are thought to serve as backups for signals so that in unfavorable environments the content of the signal is still received. Because, redundant signals are thought to be most useful when both signals are distinguishable (Hebets and Papaj 2005), selection should favor a change in plumage as well. Therefore, long-term studies on anthropogenic disturbance and signaling could help to illuminate how multimodal signals may respond to disruption.

Many changes in song in response to anthropogenic disturbance have been attributed to phenotypically plastic, short-term adjustments in song characteristics like frequency and timing (Patricelli and Blickley 2006; Warren et al. 2006; Wood and Yezerinac 2006). However, as song is learned, young raised in disturbed habitats are likely to learn the altered song. Thus song learning may increases the ability of a species to adjust its' song when exposed with a changing acoustic environment (Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). Since plumage coloration is inherited genetically (Paxton 2009), it likely cannot adjust to a changing signaling environment as rapidly as a learned characteristic. Thus the difference we see between response in visual and acoustic signals may be the result of a time lag in the response of visual signals to visual disruption.

Another potential explanation for the lack of change in plumage coloration in response to visual habitat alteration is that the signal content, which likely conveys an important aspect or quality of the signaler, may be more important that signal efficacy and is thus under strong stabilizing selection not to change. In Eastern bluebirds, plumage has been shown to be an important signal, and males with brighter uv-blue, and breast coloration have a higher reproductive success and provide more parental care (Siefferman and Hill 2003). This pattern suggests that plumage may be an important signal in female mate choice, and if the signal is not completely disrupted, but instead just harder to perceive, selection on signal strategic design (e.g., content) may be stronger than selection on signal efficacy (i.e., effective transmission).

To further understand how human disturbance influences multimodal communication, we need to understand how these signals are being used by conspecifics and how selection may lead to changes in these signals. Very little research has examined how human induced changes in the environment can lead to changes in selection pressures, which can lead to changes in signals. Determining the function of signals and the selection pressures on signals may allow us to figure out why some signals in some modalities change while others do not. Additionally, research focusing on the consequences of signal change is essential, as the consequences of changes in signals and signaling efficacy caused by anthropogenic disturbance remains an open question.

CHAPTER IV

THE INTERACTION BETWEEN CHANGES IN SIGNAL DESIGN AND THE OPERATION OF SEXUAL SELECTION IN RESPONSE TO ANTHROPOGENIC DISTURBANCE IN THE EASTERN BLUEBIRD, *SIALIA SIALIS*

SUMMARY:

Natural selection favors signals that are most conspicuous in the environment in which they are produced, transmitted, and received. A critical assumption of this hypothesis is that conspicuous signals enhance the fitness of the signaler. Observations of signal design rapidly changing in response to anthropogenic disturbances provide clear evidence that selection acts on signals to maximize detectability. However, with the exception of laboratory experiments, no study to date, has established selection mediating changes in signal design in response to anthropogenic disturbances. My previous work on Eastern bluebirds indicates that males sing at a higher pitch in areas with high levels of low frequency ambient noise, but I did not find a change in male plumage color in response to changes in the visual habitat resulting from anthropogenic disturbance. Here, I explored how changes in the signaling environment influence the operation of sexual selection, as measured by the proportion of young in a nest not sired by the social mate (extra-pair paternity, EPP), and how this, in turn, may drive changes in signal design. I examined the plumage and song characteristics as well as the rate of extra-pair paternity of Eastern bluebirds in disturbed, intermediate, and undisturbed areas. I found that the minimum frequency of song, and the brightness of male chestnut breast are significant predictors of EPP rate across all levels of disturbance. However, I found that rates of EPP differed with varying disturbance levels, and that the direction of sexual selection on minimum frequency of male songs varied across disturbance level, with males that have higher minimum frequency of song having a lower rate of EPP in disturbed areas but higher rates of EPP in undisturbed areas. I did not find any significant differences in selection on plumage traits or conspicuousness across different

disturbance levels. My results show that anthropogenic disturbances can have important consequences on selection acting on sexual signals (operation of sexual selection), which, in turn, can drive changes in signal design.

INTRODUCTION:

There are a tremendous variety of signals in the natural world. The design of these diverse signals is a result of selection on two major components: strategic design, which deals with the content of the signal, and signal efficacy, which deals with the efficient transmission of the signal (Guilford and Dawkins 1991). Natural selection on strategic design often favors signals that serve as reliable indicators of need, health, danger, and quality while natural selection on efficacy favors signals that are easily discernable, detectable and memorable (Guilford and Dawkins 1991). Work comparing signals to their signaling environment supports the hypothesis that signals have evolved to be conspicuous in their particular signaling environment (reviewed in Slabbekoorn and Smith 2002a; Podos and Nowicki 2004; Thery 2006). However, experimentally documenting natural selection diversifying signal design is rare (Searcy and Nowicki 2005).

Changes in the signaling environment driven by anthropogenic disturbances can serve as an experiment to determine how signal design responds to a new signaling environment (Patricelli and Blickley 2006). Recent work monitoring populations in altered habitats suggest that anthropogenic disturbances can indeed influence signal design (reviewed in Rabin et al. 2003; Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). For instance, recent work suggests that noise pollution can alter acoustic signals in several animal groups, including birds, amphibians and mammals (Table 1.1). Additionally, work on visual signaling in fish suggests that human-induced eutrophication can similarly affect visual communication (Table 1.1). These studies highlight the importance of understanding how organisms cope with a changing environment, but few have attempted to understand how selection actually acts on traits in disturbed habitats (but see Seehausen et al. 1997;

Engstrom-Ost and Candolin 2007). Here I focus on understanding how human disturbance can influence the operation of sexual selection, how this may serve as a mechanism for changes in signals, and how this may affect the evolutionary trajectory of a species.

Both the visual and acoustic signaling environment for Eastern bluebirds has been altered by human disturbance (Chapter III). Additionally, males have been demonstrated to sing at a higher minimum frequency to avoid low frequency anthropogenic noise (Chapter III). However, no change in plumage coloration was found in response to changes in the visual background. To explore how changes in signal design may result from changes in the breeding biology of Eastern bluebirds, I assayed variation in the rate of successful paternity of young in a nest for each male as a measure of sexual selection.

Eastern bluebirds are considered socially monogamous yet males and females often participate in extra-pair copulations (EPCs; Griffith et al. 2002). EPCs may allow females, especially those with low quality social mates, to choose higher quality sires (i.e., good genes) that provide genetic benefits to her offspring (reviewed in Moller and Briskie 1995; Jennions and Petrie 2000; Griffith et al. 2002; Kokko and Morrell 2005). The choice of an extra-pair mate is often mediated by sexual signals (Smith et al. 1991; Hoi and HoiLeitner 1997; Kempenaers et al. 1997), and extra-pair paternity (EPP) rate has been shown to increase the variation in reproductive success among males, thus increasing the opportunity for sexual selection (Byers et al. 2004; Albrecht et al. 2007; Dolan et al. 2007; Balenger et al. 2009). Using extra-pair paternity rate as a measure of sexual selection, I explored how anthropogenic-caused changes in signaling efficacy may influence the operation of sexual selection, and how this can lead to changes in signal design.

METHODS:

Field site and methods

I studied Eastern bluebirds at 11 sites in New York and Connecticut from April – August 2009 and 2010 (Figure 2.1). In 2009, I studied 5 sites in central New York, and in 2010 I studied 6 sites in the southern New York and 1 site in southwestern Connecticut (Figure 2.1). Sites varied significantly in levels of human disturbance and density of nestboxes, and nesting adults. My sites ranged from very quiet sites (mean Leq = 49.5 dBA), to sights near noisy highways and interstates (mean Leq = 69.8 dBA), and I used ambient noise to classify sites as disturbed, intermediate and disturbed) (See Chapter III Methods for details on measurement of ambient noise).

Throughout the breeding season, beginning in mid-March, each nest-box was visited at least once a week. Boxes were checked for signs of nesting, and areas were checked for the presence of adult bluebirds. Once a pair of bluebirds began defending a nestbox, mist nets or box traps were used to capture the breeding pair. I banded each individual with unique, plastic color bands and a metal USGS band for identification purposes and I took measurements including: mass (g), flattened wing chord length (mm), tarsus length (mm), and tail length (mm). In addition, blood samples were taken for each adult. The brachial vein of the bird was punctured using a 30G needle, and 0.2 cc of blood was collected using a microcapillary tube. Blood was then transferred to a 1.5 ml vial filled with Longmire solution (Longmire et al. 1991).

Nestboxes were visited at least once per week. After day five, one toenail of each nestling was clipped just past the vascular tissue (Busch et al. 2000) and a drop of blood was collected in a microcapillary and then transferred into a 1.5 ml vial filled with Longmire

Buffer (Longmire et al. 1991). Parents were assigned the social parents of a nest if they were observed feeding the nestlings on more than one occasion.

Additionally, GPS points were taken at each nestbox using a Garmin Etrex Legend cx (Garmin International Inc., Olathe, KS). These points were then uploaded into ArcGIS 9.1 (ESRI Corporation, Redlands, CA) for mapping and estimating the density of mating pairs at each site.

Measurement of acoustic and visual signals and signaling environment

Song characteristics and ambient noise were measured as in Chapter III. Plumage characteristics, the visual background, and ambient light was measured as in Chapter III. In addition, to determine how visual signals are perceived by conspecifics, I modeled the conspicuousness of males in their signaling habitat (details described in Chapter III).

Paternity analysis

DNA was extracted from samples stored in Longmire buffer using the Qiagen DNeasy tissue kit and then subjected to polymerase chain reaction to amplify fragments containing five microsatellite markers (Smex 1, 5, 6, 8, 12; Ferree et al. 2008). Fragments were sized on a ABI 3730xl DNA analyzer at the Cornell University Life Sciences Core Laboratory Center, and were scored using Genemapper Software 3.0 (Applied Biosystems, Foster City, CA). Cervus 3.0 (Kalinowski et al. 2010) was used to calculate genotype frequencies and to run the paternity analysis. Genotype frequencies were calculated for all of the individuals for each year, and for parentage analysis with all males at a site treated as candidate fathers.

Offspring were considered extra-pair if they mismatched at two or more loci from the social father.

Statistical analyses

To check for a field site effect, a contingency chi-square analysis was used to compare the proportion of extra-pair young (EPY) at each site. I found no significant difference across sites ($\chi^2 =$ 31.22, d.f. = 30, $0.25 < p < .5$). Since there was no site effect I excluded site from my model explaining variation in EPY. In order to analyze the probability of having an extra-pair young in a brood I used generalized linear models (GLM; R Development Core Team 2010) with binomial errors and a logit link function, to determine which variables predicted the extra-pair paternity rate. The dependent variable was the proportion of extra-pair offspring in the brood. The main effects were: nearest neighbor distance, plumage characteristics of the social father, song characteristics of the social father, and disturbance level (i.e., disturbed, intermediate, or undisturbed). Additionally, I checked for interactions between song and plumage characteristics and disturbance levels because I was interested in determining if disturbance could lead to changes in what characteristics were related to extra-pair paternity. Because I had many explanatory variables, I only included significant interactions between signals and disturbance in the final model. In order to examine if male conspicuousness was influencing extra-pair paternity rate, I used a second GLM with binomial errors and a logit link function explaining proportion of extra-pair young, with plumage conspicuousness and interactions between plumage and disturbance level as explanatory variables. I only included significant interaction terms in the final model. All test of hypotheses were two-tailed.

RESULTS:

Extra-pair paternity analysis

Cervus frequency analysis revealed that all five of the loci were in Hardy-Weinberg equilibrium and none were found to be in linkage disequilibrium. The average number of alleles for all primers and for both years was 12.4 (Table 4.1). For both 2009 and 2010, the exclusionary power of detecting extra-pair paternity with a known mother (n=227) was 0.98 at a 95% confidence interval, and the exclusionary power of detecting extra-pair paternity without a known mother (n=19) was 0.97 at a 95% confidence interval. Based on mismatches between known mother and offspring, I calculated a typing error of 0.9%. This is likely due to human error, mutation, or null alleles.

Extra-pair paternity and site differences

Paternity analysis revealed that 22 of 188 offspring (11.7 %) were the result of extra-pair paternity, and that 15 of 47 nests (31.9%) contained extra-pair young (EPY). Of the 15 nests with EPY, eleven nests had 1 EPY, one nest had 2 EPY, and three nests had 3 EPY. Site averages range from 0 - 20.6% of nestlings being EPY and from 0 – 50% of nests containing EPY. These numbers are consistent with another study of extra-pair paternity in Eastern bluebirds (Stewart et al. 2010).

Predictors of extra-pair paternity across disturbance levels

The best predictors of EPP rate were minimum frequency of song and breast brightness (Table 2). Males with a higher minimum frequency (e.g., pitch) and those with a brighter chestnut breast had a lower extra-pair paternity rate. I found no relationship between proportion of EPP and nearest neighbor distance or other plumage characteristics (Table 2).

Anthropogenic disturbance and extra-pair paternity

Extra-pair paternity rates differed significantly between disturbed and undisturbed sites, with disturbed sites having lower rates of EPP than undisturbed sites (Table 4.3). Within these sites, there were no significant relationships between plumage characteristics and disturbance level and the level of extra-pair paternity. There was, however, a significant interaction between the minimum frequency of song and disturbance level in relation to extra-pair paternity (Table 4.3). In the undisturbed habitats, the proportion of EPP young was higher for males with a higher minimum frequency song note. However, in the intermediate and disturbed sites the proportion of EPP young was lower for males with a higher minimum frequency (Figure 4.3).

Visual Conspicuousness and extra-pair paternity

There were no significant relationships between the conspicuousness of male plumage and extra-pair paternity rate (Table 4.4). Additionally, there wertr no significant interactions between male plumage characteristics and extra-pair paternity across disturbance levels.

DISCUSSION:

Human disturbance, extra-pair paternity and selection on signals

The results show that sexual selection on the minimum frequency of song differs between disturbed and undisturbed habitats. In undisturbed habitats, I found a positive relationship between minimum frequency of song and extra-pair paternity rate (undisturbed r = 347.8 ± 299.7). Comparative studies have found that the frequency of song that birds sing at is related to their body mass, with birds with a larger mass singing at a lower frequency (Ryan and Brenowitz 1985). Thus low frequency song may serve as an indicator of male condition. So in undisturbed habitats, selection may favor lower frequency songs because they serve as a quality indicator. In contrast to undisturbed habitats, in intermediate and disturbed habitats, I found a negative relationship between minimum frequency of song and EPP rate (disturbed r = -146.4 ± 140.8; intermediate r = -424.2 ± 168.6; Figure 4.1), suggesting that males with a higher minimum frequency were less likely to be cuckolded than those with a lower minimum frequency. In these sites, the songs of males that sing at a low pitch may be masked by anthropogenic noise, and hence are not as attractive to females. This change in phenotypic selection between habitat types suggest that selection against songs with low minimum frequency may have resulted in the changes that we see in minimum frequency of song in response to anthropogenic noise, thus providing a putative link between the selective mechanism and observed changes in signal design mediated by urbanization.

Additionally, extra-pair paternity rate was found to be higher in undisturbed sites, than in disturbed sites (p = 0.012; Table 4.3). This could be explained if birds in undisturbed habitat have closer neighbors, but nearest neighbor distance was not a predictor of EPP rate. Alternatively, disturbed habitats tend to be more fragmented, whereas undisturbed habitats are more open. Thus, there may be fewer opportunities for extra-pair matings in disturbed areas because there are more barriers (e.g., tree, buildings, etc.) that isolate breeding pairs.

This different in EPP rate shows that the intensity of sexual selection is greater in undisturbed than disturbed habitats.

Overall predictors of extra-pair paternity

In addition to differences in selection on low frequency ambient noise, several signals that predicted rates of EPP across sites regardless of level of disturbance were identified. I found that males with a brighter chestnut breast and those with a higher minimum frequency of song were subject to lower levels of extra-pair paternity across all disturbance levels. However, the relationship observed between EPP and low frequency song across disturbance sites, is the result of the strong relationship between the two in intermediate and disturbed areas, and not in undisturbed (Figure 4.1). Previous research has shown a relationship between breast color and brightness with male provisioning rate, first egg date, and fledgling mass (Siefferman and Hill 2003). Thus my results, in combination with this previous research, suggest that breast coloration may serve as an honest indicator of male quality and may increase male reproductive success through lowered EPP.

In addition, previous studies of Eastern bluebirds show that males with hue shifted more towards uv-blue range sire more offspring (Siefferman and Hill 2003). Yet, I found no relationship between extra-pair paternity rate and uv-blue plumage characteristics. This result suggests that female may rely on different characteristics when choosing a social mate, versus when soliciting extra-pair matings. These results support and add to work suggesting that plumage coloration plays an important role in sexual selection in Eastern bluebirds and other bird species (Siefferman and Hill 2003).

Conclusions

The selection for higher minimum frequency of song in intermediate and disturbed habitats provides a mechanism for previous results showing an upward shift in pitch in response to low frequency anthropogenic noise. The lack of change in selection pressure on plumage characteristics across disturbance levels, is consistent with the lack of change in plumage characteristics in response to anthropogenic-caused changes in the visual signaling environment. Although the visual habitat did change due to anthropogenic disturbance, it does not affect the conspicuousness of breast coloration, which I found to be a good predictor of EPP rate. Whereas I found that the anthropogenic-caused visual habitat changes reduces the conspicuousness of uv-blue plumage. Since uv-blue plumage was not an important predictor of EPP rate, there may not be selection on the signal to change in a changing visual environment, as it may not convey important information. Thus, the lack of difference in selection pressure on plumage characteristics between disturbance levels is consistent with any observed changes I found in plumage characteristics in response to anthropogenic changes in the visual signaling environment.

Persistent differences in the direction of sexual selection between disturbed and undisturbed habitats provide the potential for population divergence between birds living in the two habitat types. For example, populations of dark-eyed junco that stopped migrating in the 1980s show considerable morphological differentiation from populations that remain migratory (Rasner et al. 2004; Yeh and Price 2004), indicating that populations can differentiate in a relatively short time period. Because most Passerine songs are thought to be learned, if birds that are born in noisy habitats learn songs from their fathers, they too will have higher minimum frequency of songs (Slabbekoorn and Ripmeester 2008). If habitat imprinting occurs, in which individuals return to habitats similar to those in which they were raised, then population divergence between the different habitat types with respect to song may occur (reviewed in Davis and Stamps 2004; Slabbekoorn and Ripmeester 2008). If the pressures causing the changes (i.e., ambient noise) are consistent, the direction of selection will likely remain consistent over time. Therefore it is possible that populations may diverge over time (Slabbekoorn et al. 2010). More research on habitat imprinting, specifically in anthropogenic habitats, is necessary to determine if this is a possibility.

Alternatively if humans continue to expand and alter natural habitats, it may limit the amount of land that is undisturbed, which could lead to selection in all areas for a higher minimum frequency of song. Thus one would expect that over time, as ambient noise continues to increase, Eastern bluebirds would continue to increase the minimum frequency of their song. This research is unique in that it shows that human disturbance cannot only lead to a change in signal design, but also provides a potential mechanism for that change. Continued research on how anthropogenic disturbance influences signals and selection on signal, and the consequences of these changes are needed to gain a fuller understanding of how humans are affecting communication and the breeding biology of birds.

APPENDIX A

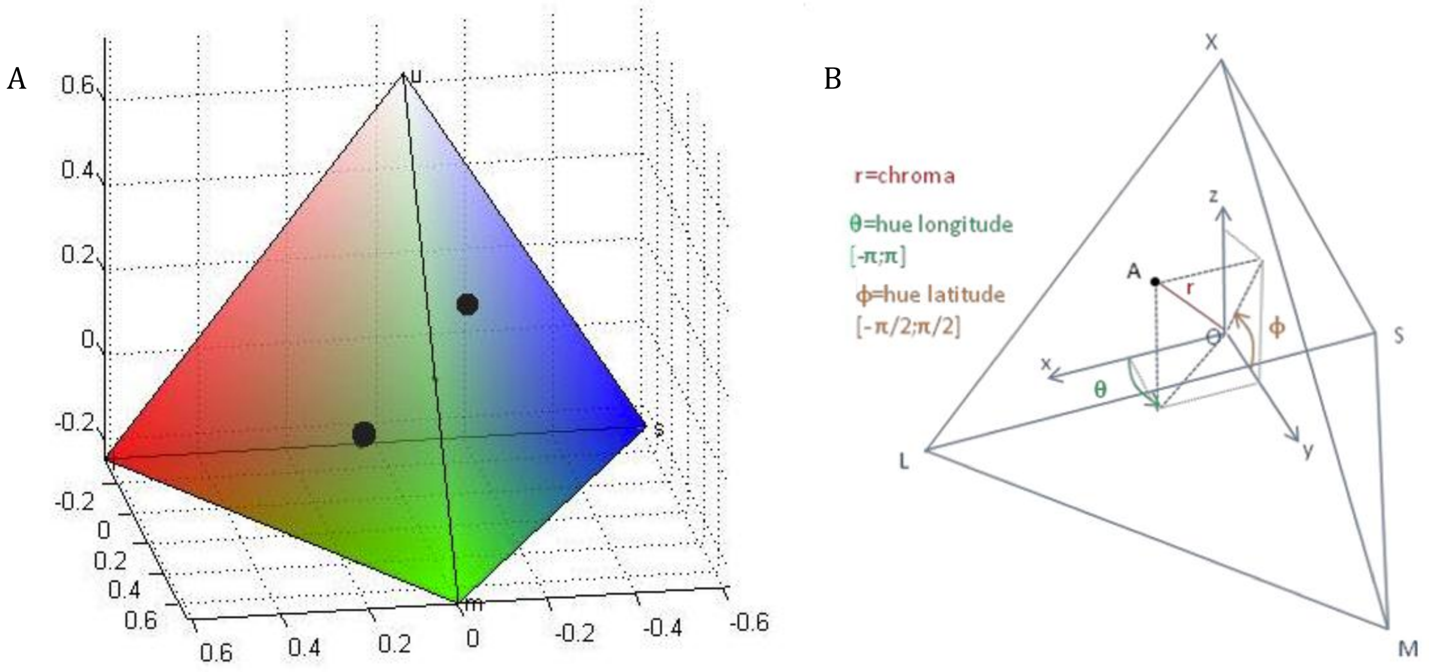


Figure 1: (A) tetrahedral plot of an Eastern bluebirds’ chestnut breast reflectance (point on left), and uv-blue patch reflectance (point on right), (B) measurements extracted from AVICOL (figure from Gomez 2006).

Table 1.1: Known changes in signals and signaling efficacy in response to anthropogenic disturbance.

Mode	Taxa	Cause	Effect	Study
Acoustic	Birds	Urban Ambient Noise	Increased pitch in higher noise	(Multiple species, Rheindt 2003; Great tit, Slabbekoorn and Peet 2003; House finch, Fernandez-Juricic et al. 2005; Song sparrow, Wood and Yezerinac 2006)
			Increased amplitude in higher noise	(Nightengales, Brumm 2004)
			Changes in timing in signaling	(Blue, and great tits, Bergen and Abs 1997; Robins, Fuller et al. 2007)
			Increased level of vocal activity	(Serins, Díaz et al. 2011)
	Amphibians	Airplane Noise	Call suppression during noise	(anurans, Sun and Narins 2005)
		Road Noise	Increased pitch in higher noise	(Brown tree frog, Parris et al. 2009)
			Increased signaling rate	(Neotropical treefrog, Kaiser and Hammers 2009)
	Mammals	Boat Noise and Sonar	Increase duration of signal	(Humpback whales, Miller et al. 2000; Killer whales, Foote et al. 2004)
			Signal more often	(Beluga whales, Lesage et al. 1999)
			Increase frequency to avoid noise	(Beluga whale, Lesage et al. 1999; Right whale, Parks et al. 2007)
			Decrease	(Bottlenose dolphins,

			duration of signal	Buckstaff 2004; Dugongs, Sakamoto et al. 2006)
			Increase amplitude of signal	(Beluga whale, Scheifele et al. 2005; Right whales, Parks et al. 2011)
		Road noise	Frequency shift to avoid urban noise	(Ground squirrel, Rabin et al. 2003)
Visual	Fish	Human-induced eutrophication	Increased display activity in hazy water	(Sticklebacks, Engstrom-Ost and Candolin 2007)
			No longer use signal	(Cichlids, Seehausen et al. 1997)
	Birds	Decreased availability of carotenoid-rich (i.e., caterpillars) food source as a result of air pollution levels	Paler coloration	(Great tit, Eeva et al. 1998)
Chemical	Fish	Heavy metals and pesticides	Impairs response to signal	(Chinook salmon, Scholz et al. 2000; Pikeminnow, Beyers and Farmer 2001)
		Fertilizers	Impairs response to signal	(Swordtail, Fisher et al. 2006)

Table 3.1: Correlation between male plumage and radiance characteristics across sites of varying disturbance levels, d.f.=10.

	UV-Blue Brilliance	UV-Blue Theta	UV-Blue Phi	UV-Blue Chroma	Chestnut Brilliance	Chestnut Theta	Chestnut Phi	Chestnut Chroma
Radiance Hue (theta)	r=-0.254 p=0.479	r=0.303 p=0.895	r=-0.134 p=0.711	r=0.514 p=0.128	r=-0.437 p=0.207	r=-0.262 p=0.465	r=-0.467 p=0.174	r=0.195 p=0.590
Radiance Chroma (r)	r=-0.196 p=0.587	r=0.199 p=0.581	r=-0.007 p=0.984	r=0.254 p=0.128	r=-0.145 p=0.690	r=0.400 p=0.252	r=-0.409 p=0.240	r=-0.101 p=0.782

Table 4.1**:** Five microsatellite loci used in paternity analysis, primer sequences, number of alleles, observed heterozygosity, and the probability of exclusion. All five loci are in Hardy-Weinberg equilibrium.

Locus	Sequence (5’→ 3’)	No. of Alleles 2009, 2010	Heterozygosity observed 2009, 2010	Probability of exclusion 2009, 2010
Smex1	F:AAGTGCATTCTCTGAAGAAAAG R:GTTTCTCCAAAGTTGTCAGTTTATCACA	12, 11	0.558, 0.698	0.481, 0.555
Smex5	F:CACAGCACCTCCTCTCCTA R:GTTTCTTCAGCAACAGGGATTCAC	21, 14	0.756, 0.750	0.639, 0.587
Smex6	F:GAAGCTAACGTAACCAATCTG R:GTTTGTTCAGCACCAACATATACAGAAG	15, 16	0.811, 0.841	0.777, 0.776
Smex8	F:AGCATCACCCACTCACTCACT R:GTTTGTACCACGGGGATTCCTATTATG	7, 8	0.719, 0.777	0.558, 0.595
Smex12	F:GGATGAGAAGGGGGACAT R:GTTCTTGGGCTGACTTGTTGATG	9, 11	0.860, 0.811	0.707, 0.690

Table 4.2: Coefficient of variation of plumage and song characteristics across disturbance levels.

Variable	F-value	d.f.	p-value
UV-blue brightness	0.113	2, 8	0.894
UV-blue longitudinal hue (theta)	0.559	2, 8	0.559
UV-blue latitudinal hue (phi)	0.085	2, 8	0.920
UV-blue chroma (r)	2.485	2, 8	0.108
Chest brightness	2.752	2, 8	0.123
Chest longitudinal hue (theta)	0.670	2, 8	0.538
Chest latitudinal hue (phi)	2.485	2, 8	0.145
Chest chroma (r)	0.542	2, 8	0.602
Fmin	0.507	2, 8	0.620
Fmax	0.010	2, 8	0.990
Fpeak	1.064	2, 8	0.389

Table 4.3: Results of GLM model testing factors explaining proportion of extra-pair young. This model has an AIC = 68.991, and explains 71% of the total variance. Significant relationships ($p<0.05$) are marked with an *.

Factor	**Estimate**	**Standard Error**	**Z-value**	**P-Value**
Disturbed v. Intermediate	-22.637	17.871	-1.267	0.205
Disturbed v. Undisturbed	-72.661	28.962	-2.509	0.012*
Minimum Frequency	-0.024	0.010	-2.284	0.022*
Maximum Frequency	-0.006	0.005	-1.056	0.291
Peak Frequency	-0.005	0.008	-0.613	0.540
Nearest Neighbor	0.003	0.002	1.231	0.218
UV-Blue Brightness	-2.958	13.197	-0.224	0.822
Chestnut Brightness	-59.872	29.159	-2.053	0.040*
UV-Blue Chroma (r)	-14.751	20.665	-0.714	0.475
Chestnut Chroma (r)	-45.974	43.802	-1.050	0.294
UV-Blue longitudinal hue (Θ)	42.922	33.648	1.276	0.202
UV-Blue latitudinal hue (ϕ)	-5.651	11.884	-0.476	0.634
Chestnut longitudinal hue (Θ)	13.870	13.057	1.062	0.288
Chestnut latitudinal hue (ϕ)	18.490	19.025	0.972	0.331
Disturbed (D v. I) X Minimum Frequency	0.014	0.011	1.266	0.206
Disturbed (D v. U) X Minimum Frequency	0.043	0.018	2.452	0.014*

Table 4.4: Results of GLM model testing plumage conspicuousness explaining proportion of extra-pair young. This model has an AIC = 109.89 and explains 5.5% of the total variance. Significant relationships ($p<0.05$) are marked with an *.

Factor	**Estimate**	**Standard Error**	**Z value**	**P-Value**
Chestnut Breast ΔS	-0.013	0.034	-0.387	0.699
Chestnut Breast ΔfQ	-0.064	0.052	-1.226	0.220
Rump ΔS	-0.047	0.032	-1.480	0.139
Rump ΔfQ	0.054	0.047	1.153	0.249

Figure legends

Fig. 2.1	Map of sites studied in 2009 and 2010. Sites 1-4 were classified as undisturbed, sites 5-7 were classified as intermediate, and sites 8-11 were classified as disturbed
Fig. 2.2	Low frequency ambient noise across sites. Sites correspond with sites number in Fig. 2.1
Fig. 2.3	Nestling mouth and flanges
Fig. 2.4	Mean (± S.D.) nestling mouth and flanges reflectance in Eastern bluebird nestlings
Fig. 2.5	Regression of mouth chromatic contrast on body condition (R=0.315, d.f.=38, p=0.05)
Fig. 2.6	Mean (± S.E.) discernability (just noticeable differeneces) of nestlings' gapes among nestlings across habitat types
Fig. 2.7	The average mouth reflectance for each disturbance level
Fig. 2.8	The average brightness-corrected irradiance for each disturbance level
Fig. 3.1	A typical Eastern bluebird song
Fig. 3.2	Regression between minimum frequency of song and low frequency ambient noise across 11 sites (r = 0.705, p = 0.015). Error bars represent standard error
Fig. 3.3	Average chromatic contrast of uv-blue coloration across habitat type. Error bars represent standard error
Fig. 4.1	The relationships between minimum frequency and extra-pair paternity across the three sites (A = undisturbed; B = intermediate; C = disturbed). A trendline has been added to show the general pattern

Figure 2.1

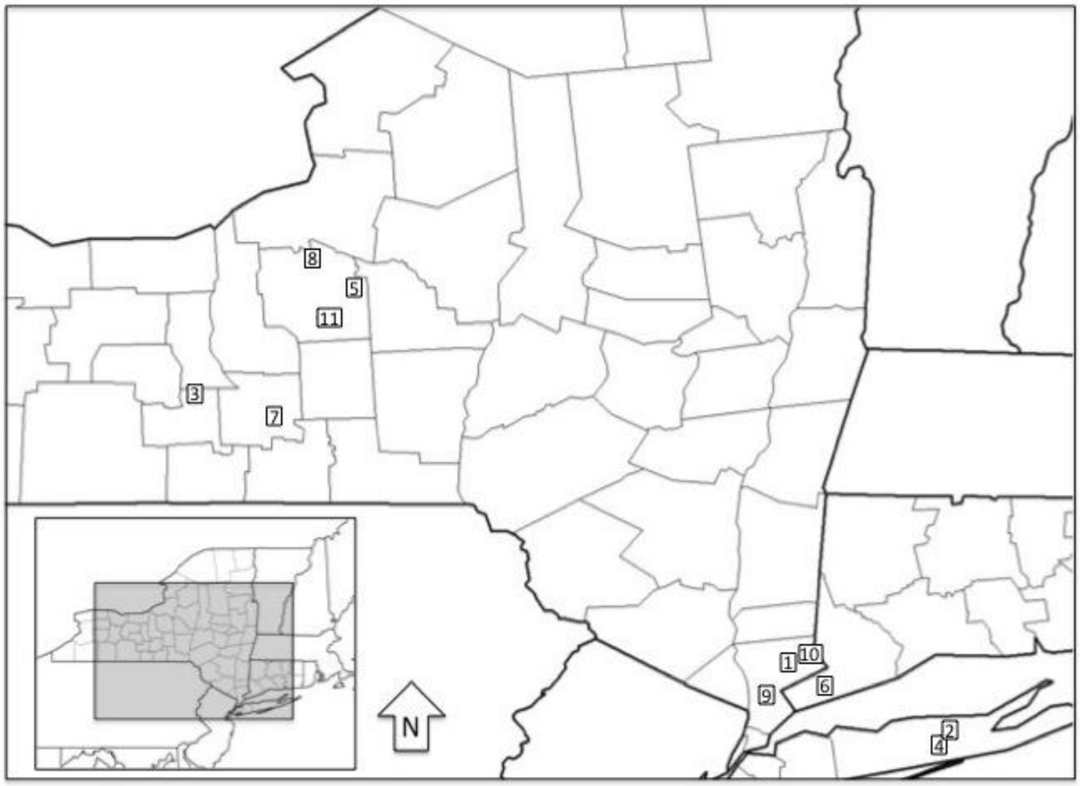


Figure 2.2

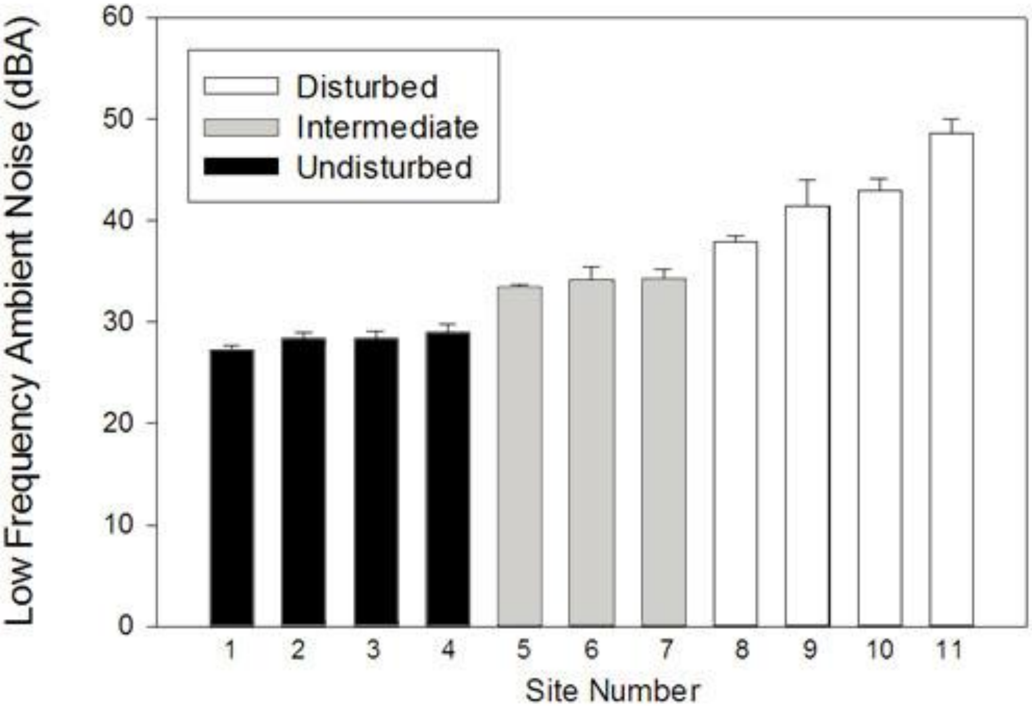

Low Frequency Ambient Noise (dBA)
0
10
20
30
40
50
60
Disturbed
Intermediate
Undisturbed
1
2
3
4
5
6
7
8
9
10
11
Site Number

Figure 2.3

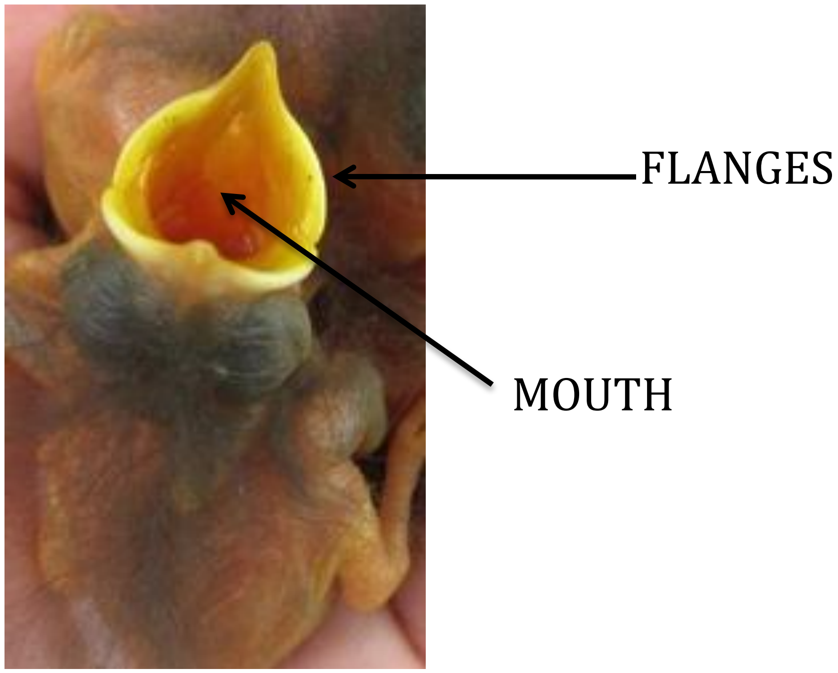


Figure 2.4

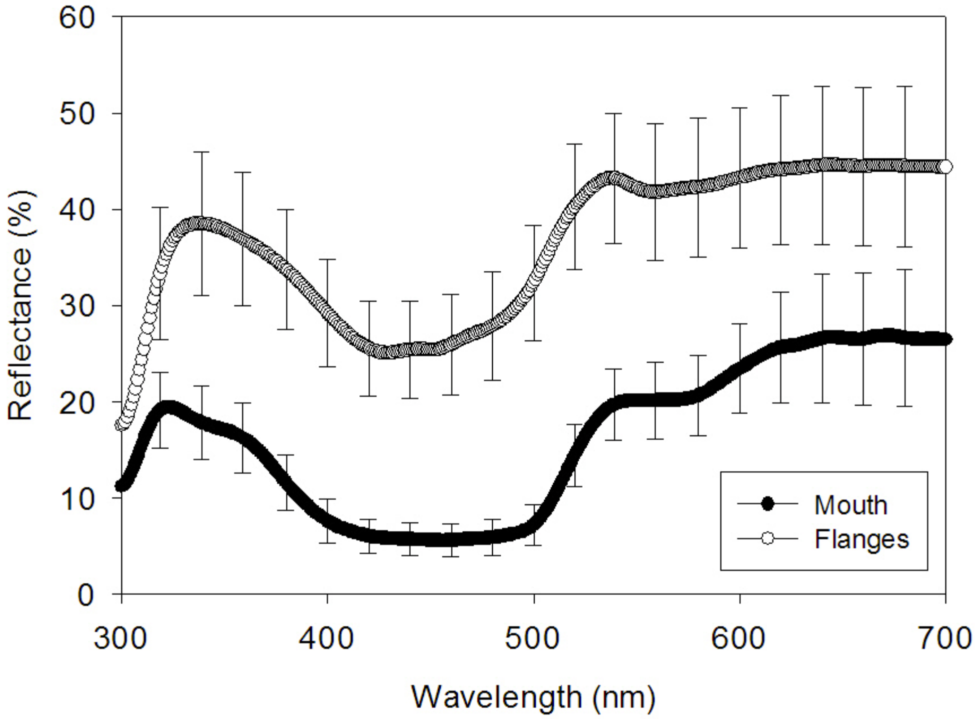

60
50
40
30
20
10
0
Reflectance (%)
300
400
500
600
700
Wavelength (nm)
● Mouth
○ Flanges

Figure 2.5

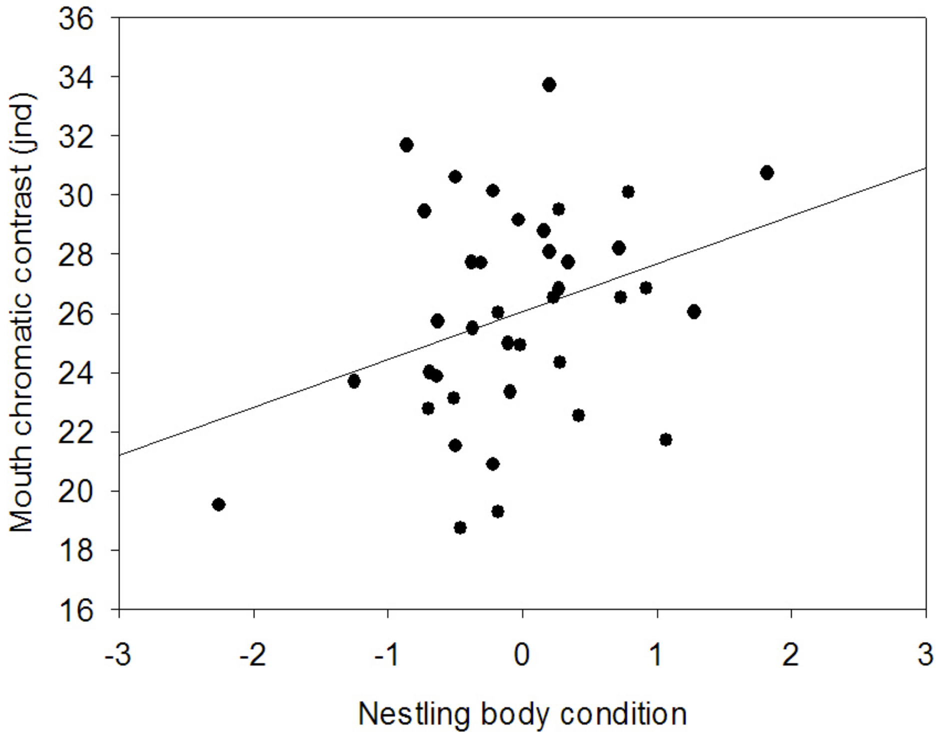

Mouth chromatic contrast (jnd)
36
34
32
30
28
26
24
22
20
18
16
-3
-2
-1
0
1
2
3
Nestling body condition

Figure 2.6

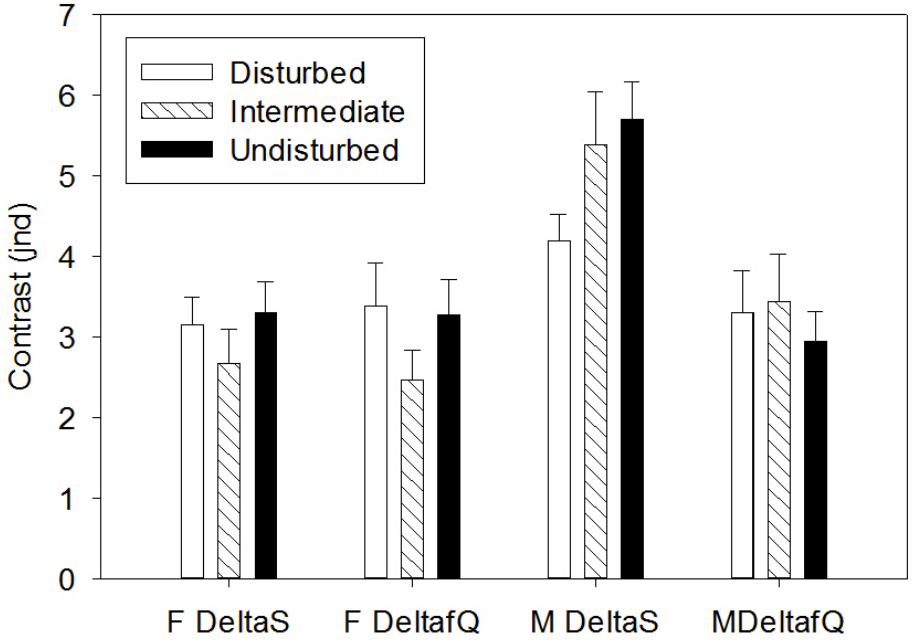
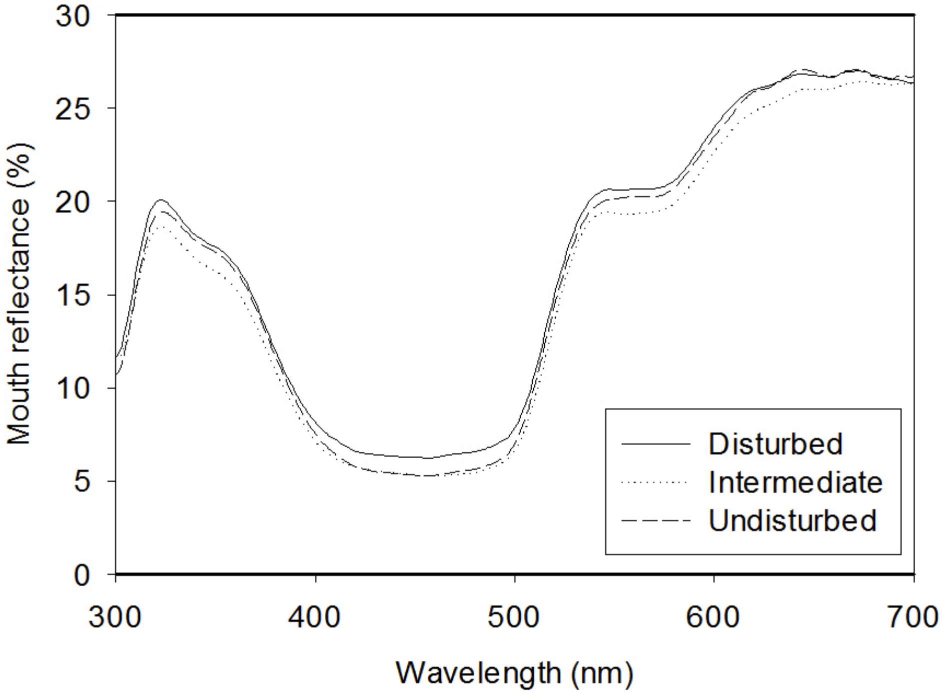

Contrast (jnd)
0
1
2
3
4
5
6
7
Disturbed
Intermediate
Undisturbed
F DeltaS
F DeltafQ
M DeltaS
MDeltafQ

Figure 2.7



Mouth reflectance (%)
30
25
20
15
10
5
0
300
400
500
600
700
Wavelength (nm)
Disturbed
Intermediate
Undisturbed

Figure 2.8

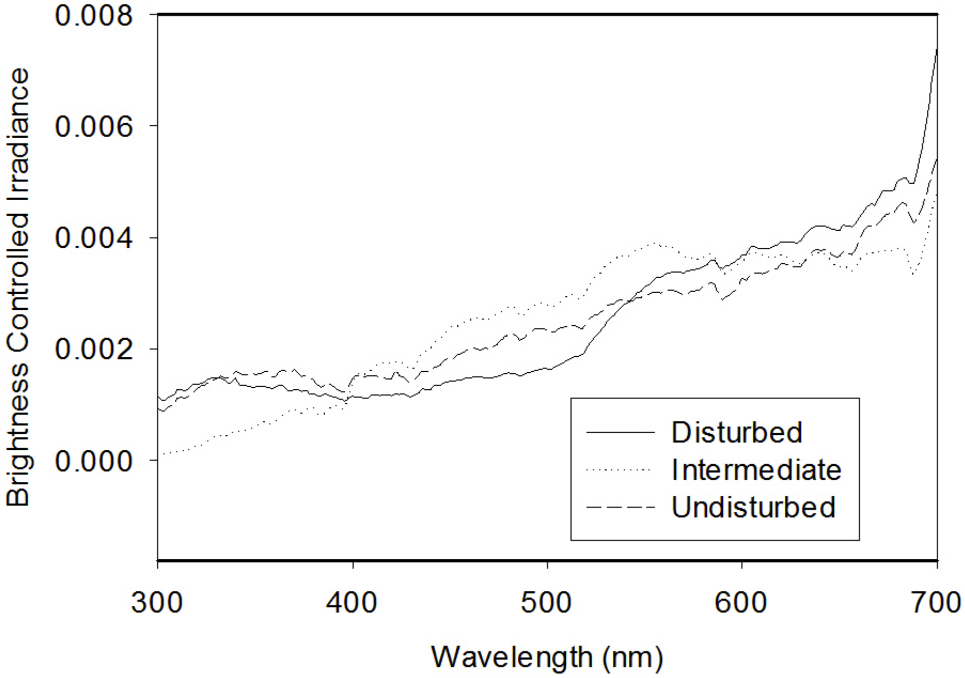

Brightness Controlled Irradiance
0.008
0.006
0.004
0.002
0.000
300
400
500
600
700
Wavelength (nm)
Disturbed
Intermediate
Undisturbed

Figure 3.1

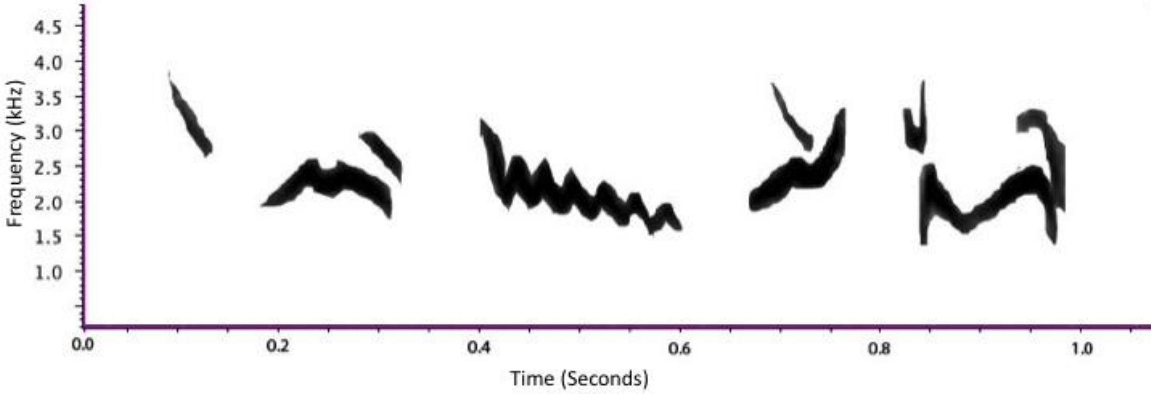

4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Frequency (kHz)
0.0
0.2
0.4
0.6
0.8
1.0
Time (Seconds)

Figure 3.2

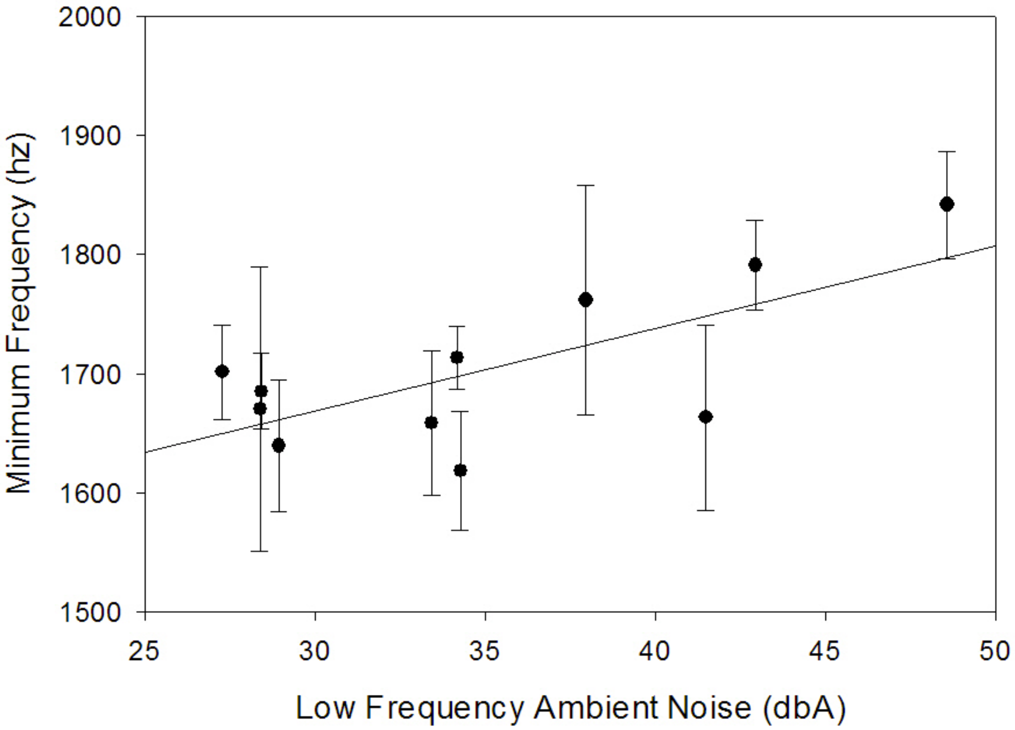

2000
1900
1800
1700
1600
1500
Minimum Frequency (hz)
25
30
35
40
45
50
Low Frequency Ambient Noise (dbA)

Figure 3.3

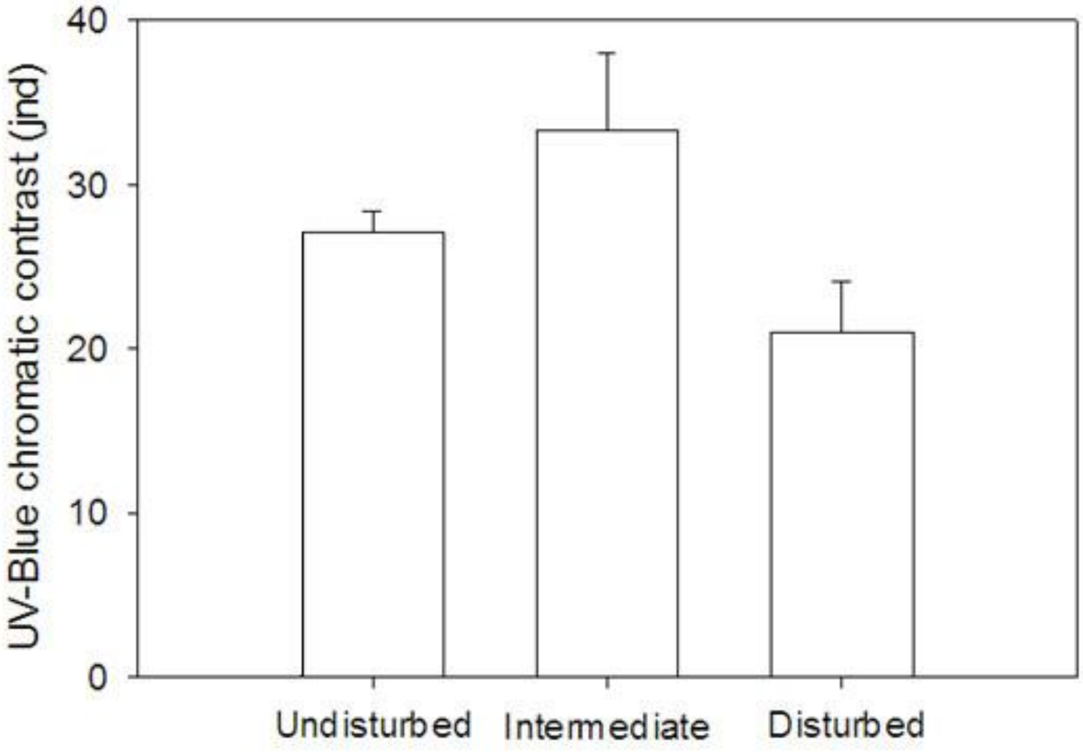
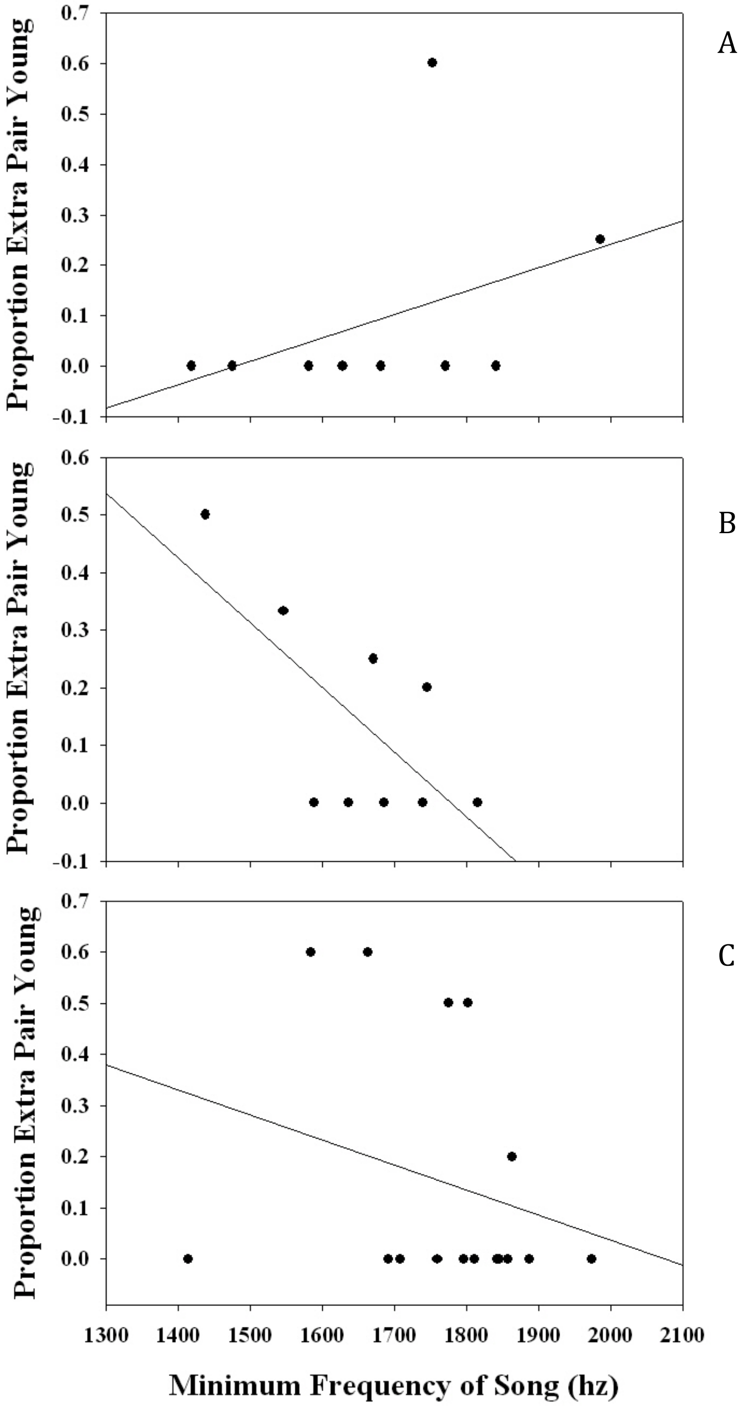

UV-Blue chromatic contrast (jnd)
40
30
20
10
0
Undisturbed
Intermediate
Disturbed

Figure 4.1


A
B
C
Proportion Extra Pair Young
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
1300
1400
1500
1600
1700
1800
1900
2000
2100
Minimum Frequency of Song (hz)

REFERENCES:

Albrecht, T., J. Schnitzer, J. Kreisinger, A. Exnerova, J. Bryja, and P. Munclinger. 2007. Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines. Behavioral Ecology 18:477-486.

Aquiloni, L., A. Massolo, and F. Gherardi. 2009. Sex identification in female crayfish is bimodal. Naturwissenschaften 96:103-110.

Backwell, P. R. Y., and N. I. Passmore. 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes.* Behavioral Ecology and Sociobiology 38:407-416.

Balenger, S. L., L. S. Johnson, H. L. Mays, and B. S. Masters. 2009. Extra-pair paternity in the socially monogamous mountain bluebird *Sialia currucoides* and its effect on the potential for sexual selection. Journal of Avian Biology 40:173-180.

Barth, F. G., M. Hrncir, and S. Jarau. 2008. Signals and cues in the recruitment behavior of stingless bees (*Meliponini*). Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 194:313-327.

Bergen, F., and M. Abs. 1997. Etho-ecological study of the singing activity of the blue tit (*Parus caeruleus*), great iit (*Parus major*) and chaffinch (*Fringilla coelebs*). Journal Fur Ornithologie 138:451-467.

Beyers, D. W., and M. S. Farmer. 2001. Effects of copper on olfaction of Colorado pikeminnow. Environmental Toxicology and Chemistry 20:907-912.

Bize, P., R. Piault, B. Moureau, and P. Heeb. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. Proceedings of the Royal Society B-Biological Sciences 273:2063-2068.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434-440.

Buckstaff, K. C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus,* in Sarasota Bay, Florida. Marine Mammal Science 20:709-725.

Busch, J. D., M. P. Miller, E. H. Paxton, M. K. Sogge, and P. Keim. 2000. Genetic variation in the endangered southwestern willow flycatcher. Auk 117:586-595.

Byers, B. E., H. L. Mays, I. R. K. Stewart, and D. F. Westneat. 2004. Extrapair paternity increases variability in male reproductive success in the chestnut-sided warbler (Dendroica pensylvanica), a socially monogamous songbird. Auk 121:788-795.

Candolin, U. 2003. The use of multiple cues in mate choice. Biological Reviews 78:575-595.

Cassey, P., M. Honza, T. Grim, and M. E. Hauber. 2008. The modelling of avian visual perception predicts behavioural rejection responses to foreign egg colours. Biology Letters 4:515-517.

Catchpole, C. K., and P. Slater. 2003. Bird song: biological themes & variations. Cambridge University Press, Cambridge.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton.

Davis, J. M., and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. Trends in Ecology & Evolution 19:411-416.

de Ayala, R. M., N. Saino, A. P. Moller, and C. Anselmi. 2007. Mouth coloration of nestlings covaries with offspring quality and influences parental feeding behavior. Behavioral Ecology 18:526-534.

Dolan, A. C., M. T. Murphy, L. J. Redmond, K. Sexton, and D. Duffield. 2007. Extrapair paternity and the opportunity for sexual selection in a socially monogamous passerine. Behavioral Ecology 18:985-993.

Díaz, M., A. Parra, and C. Gallardo. 2011. Serins respond to anthropogenic noise by increasing vocal activity. Behavioral Ecology.

Eeva, T., E. Lehikoinen, and M. Ronka. 1998. Air pollution fades the plumage of the Great Tit. Functional Ecology 12:607-612.

Endler, J. A. 1993. The color of light in forests and its implications. Ecological Monographs 63:1-27.

Endler, J. A., and P. W. Mielke. 2005. Comparing entire colour patterns as birds see them. Biological Journal of the Linnean Society 86:405-431.

Engstrom-Ost, J., and U. Candolin. 2007. Human-induced water turbidity alters selection on sexual displays in sticklebacks. Behavioral Ecology 18:393-398.

Fernandez-Juricic, E., R. Poston, K. De Colilbus, T. Morgan, B. Bastian, C. Martin, K. Jones, and R. Treminio. 2005. Microhabitat selection and singing behavior patterns of male house finches *(Carpodacus mexicanus)* in urban parks in a heavily urbanized landscape in the Western U.S. Urban Habitats 3:49-69.

Ferree, E. D., J. L. Dickinson, D. Kleiber, C. A. Stern, J. Haydock, M. T. Stanback, V. Schmidt, L. Eisenberg, and C. Stolzenburg. 2008. Development and cross-species testing of western bluebird (*Sialia mexicana*) microsatellite primers. Molecular Ecology Resources 8:1348-1350.

Fisher, H. S., B. B. M. Wong, and G. G. Rosenthal. 2006. Alteration of the chemical environment disrupts communication in a freshwater fish. Proceedings of the Royal Society B-Biological Sciences 273:1187-1193.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309:570-574.

Foote, A. D., R. W. Osborne, and A. R. Hoelzel. 2004. Environment: Whale-call response to masking boat noise. Nature 428:910-910.

Fuller, R. A., P. H. Warren, and K. J. Gaston. 2007. Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3:368-370.

Gibson, R. M. 1996. Female choice in sage grouse: The roles of attraction and active comparison. Behavioral Ecology and Sociobiology 39:55-59.

Godfray, H. C. J. 1991. Signaling of need by offspring to their parents. Nature 352:328-330.

Godfray, H. C. J. 1995. Signaling of need between parents and young - parent-offspring conflict and sibling rivalry. American Naturalist 146:1-24.

Gomez, D. 2006. AVICOL, a program to analyze spectrometric data. Free program available from the author at dodogomez@yahoo.fr.

Goold, J. C. 1996. Acoustic assessment of populations of common dolphin Delphinus delphis in conjunction with seismic surveying. Journal of the Marine Biological Association of the United Kingdom 76:811-820.

Gordon, S. D., and G. W. Uetz. 2011. Multimodal communication of wolf spiders on different substrates: evidence for behavioural plasticity. Animal Behaviour 81:367-375.

Gowaty, P. A., and J. H. Plissner. 1998. Eastern bluebird, *Sialia sialis in* A. Poole, and G. Gill, eds. Birds of North America. The Birds of North America, Inc., Philadelphia, PA.

Grafe, T. U., and T. C. Wanger. 2007. Multimodal signaling in male and female foot-flagging frogs *Staurois guttatus (Ranidae)*: An alerting function of calling. Ethology 113:772-781.

Griffith, S. C., I. P. F. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: A review of interspecific variation and adaptive function. Molecular Ecology 11:2195-2212.

Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. Animal Behaviour 42:1-14.

Hart, N. S., and M. Vorobyev. 2005. Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 191:381-392.

Hebets, E. A., and D. R. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57:197-214.

Hebets, E. A., and G. W. Uetz. 1999. Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus *Schizocosa* (*Araneae : Lycosidae)*. Animal Behaviour 57:865-872.

Heeb, P., T. Schwander, and S. Faoro. 2003. Nestling detectability affects parental feeding preferences in a cavity-nesting bird. Animal Behaviour 66:637-642.

Hoi, H., and M. HoiLeitner. 1997. An alternative route to coloniality in the bearded tit: Females pursue extra-pair fertilizations. Behavioral Ecology 8:113-119.

Holldobler, B. 1999. Multimodal signals in ant communication. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 184:129-141.

Horn, A. G., and M. L. Leonard. 2008. Acoustic interactions in broods of nestling birds (Tachycineta bicolor). Journal of Comparative Psychology 122:298-304.

Hu, Y., and G. C. Cardoso. 2010. Which birds adjust the frequency of vocalizations in urban noise? Animal Behaviour 79:863-867.

Hunt, S., I. C. Cuthill, A. T. D. Bennett, and R. Griffiths. 1999. Preferences for ultraviolet partners in the blue tit. Animal Behaviour 58:809-815.

Hunt, S., R. M. Kilner, N. E. Langmore, and A. T. D. Bennett. 2003. Conspicuous, ultraviolet-rich mouth colours in begging chicks. Proceedings of the Royal Society of London Series B-Biological Sciences 270:S25-S28.

Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. Biological Reviews 75:21-64.

Johnstone, R. A. 1997. The Evolution of Animal Signals. Pp. 155 *in* J. R. Krebs, and N. B. Davies, eds. Behavioral Ecology: An Evolutionary Approach. Blackwell Publishing, Oxford.

Kaiser, K., and J. L. Hammers. 2009. The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, Dendropsophus triangulum. Behaviour 146:1053-1069.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2010. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 19:1512-1512.

Kempenaers, B., G. R. Verheyren, and A. A. Dhondt. 1997. Extrapair paternity in the blue tit (Parus caeruleus): female choice, male characteristics, and offspring quality. Behavioral Ecology 8:481-492.

Kilner, R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. Proceedings of the Royal Society of London Series B-Biological Sciences 264:963-968.

Kilner, R., and N. B. Davies. 1998. Nestling mouth colour: ecological correlates of a begging signal. Animal Behaviour 56:705-712.

Kokko, H., and L. J. Morrell. 2005. Mate guarding, male attractiveness, and paternity under social monogamy. Behavioral Ecology 16:724-731.

Leal, M., and L. J. Fleishman. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. Proceedings of the Royal Society of London Series B-Biological Sciences 269:351-359.

Leonard, M. L., and A. G. Horn. 2005. Ambient noise and the design of begging signals. Proceedings of the Royal Society B-Biological Sciences 272:651-656.

Leonard, M. L., and A. G. Horn. 2008. Does ambient noise affect growth and begging call structure in nestling birds? Behavioral Ecology 19:502-507.

Lesage, V., C. Barrette, M. C. S. Kingsley, and B. Sjare. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. Marine Mammal Science 15:65-84.

Longmire, J. L., R. E. Ambrose, N. C. Brown, T. J. Cade, T. Maechtle, W. S. Seegar, F. P. Ward, and C. M. White. 1991. Use of sex-linked minisatellite fragments to investigate genetic differentiation and migration of North American populations of the peregrine falcon (*Falco peregriuns*). *in* T. Burke, G. Dolf, A. Jeffreys, and R. Wolff, eds. DNA Fingerprinting: Approaches and Applications. Birkhauser Press, Brasil, Switzerland.

Loyau, A., D. Gomez, B. T. Moureau, M. Thery, N. S. Hart, M. Saint Jalme, A. T. D. Bennett, and G. Sorci. 2007. Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. Behavioral Ecology 18:1123-1131.

Maier, E. J. 1992. Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix-lutea*. Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology 170:709-714.

McNaught, M. K., and I. P. F. Owens. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? Journal of Evolutionary Biology 15:505-514.

Meyer, W. B., and B. L. Turner. 1992. Human-population growth and global land-use cover change. Annual Review of Ecology and Systematics 23:39-61.

Miller, P. J. O., N. Biassoni, A. Samuels, and P. L. Tyack. 2000. Whale songs lengthen in response to sonar. Nature 405:903-903.

Moller, A. P., and J. V. Briskie. 1995. EXTRA-PAIR PATERNITY, SPERM COMPETITION AND THE EVOLUTION OF TESTIS SIZE IN BIRDS. Behavioral Ecology and Sociobiology 36:357-365.

Montgomerie, R. 2008. CLR, version 1.05. Queen's University, Kingston, Canada. (available at http://post.queense.ca/~mont/color/analyze.html).

O'Loghlen, A. L., and S. I. Rothstein. 2010. Multimodal signalling in a songbird: male audiovisual displays vary significantly by social context in brown-headed cowbirds. Animal Behaviour 79:1285-1292.

Osorio, D., A. Miklosi, and Z. Gonda. 1999. Visual ecology and perception of coloration patterns by domestic chicks. Evolutionary Ecology 13:673-689.

Papke, R. S., D. J. Kemp, and R. L. Rutowski. 2007. Multimodal signalling: structural ultraviolet reflectance predicts male mating success better than pheromones in the butterfly Colias eurytheme L. (Pieridae) (vol 73, pg 47, 2007). Animal Behaviour 73:1083-1083.

Parks, S. E., C. W. Clark, and P. L. Tyack. 2007. Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. Journal of the Acoustical Society of America 122:3725-3731.

Parks, S. E., M. Johnson, D. Nowacek, and P. L. Tyack. 2011. Individual right whales call louder in increased environmental noise. Biology Letters 7:33-35.

Parris, K. M., M. Velik-Lord, and J. M. A. North. 2009. Frogs Call at a Higher Pitch in Traffic Noise. Ecology and Society 14.

Partan, S., and P. Marler. 1999. Behavior - Communication goes multimodal. Science 283:1272-1273.

Partan, S. R., A. G. Fulmer, M. A. M. Gounard, and J. E. Redmond. 2010. Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. Current Zoology 56:313-326.

Partan, S. R., and P. Marler. 2005. Issues in the classification of multimodal communication signals. American Naturalist 166:231-245.

Patricelli, G. L., and J. L. Blickley. 2006. Avian communication in urban noise: Causes and consequences of vocal adjustment. Auk 123:639-649.

Patricelli, G. L., J. A. C. Uy, and G. Borgia. 2006. Interactive signaling during mate choice in the Satin Bowerbird: an experimental test using robotic females. Journal of Ornithology 147:12-12.

Paxton, E. H. 2009. The utility of plumage coloration for taxonomic and ecological studies. The Open Ornithology Journal 2:17-23.

Podos, J., and S. Nowicki. 2004. Beaks, adaptation, and vocal evolution in Darwin's finches. Bioscience 54:501-510.

R Development Core Team. 2010. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabin, L. A., B. McCowan, S. L. Hooper, and D. J. Owings. 2003. Anthropogenic Noise and its Effect on Animal Communication: An Interface Between Comparative

Psycology and Conservation Biology. International Journal of Comparitive Psychology 16:172.

Rasner, C. A., P. Yeh, L. S. Eggert, K. E. Hunt, D. S. Woodruff, and T. D. Price. 2004. Genetic and morphological evolution following a founder event in the dark-eyed junco, Junco hyemalis thurberi. Molecular Ecology 13:671-681.

Ratcliffe, J. M., and M. L. Nydam. 2008. Multimodal warning signals for a multiple predator world. Nature 455:96-U59.

Rheindt, F. E. 2003. The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? Journal Fur Ornithologie 144:295-306.

Rowe, C., and J. Skelhorn. 2004. Avian psychology and communication. Proceedings of the Royal Society of London Series B-Biological Sciences 271:1435-1442.

Ryan, M. J., and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126:87-100.

Sakamoto, S., K. Ichikawa, T. Akamatsu, T. Shinke, N. Arai, T. Hara, and K. Adulyanukosol. 2006. Effect of ship sound on vocal behavior of dugongs. Proceedings of the 3rd International Symposium on SEASTAR2000 and Asian Bio-logging Science:60-75.

Schaub, A., J. Ostwald, and B. M. Siemers. 2008. Foraging bats avoid noise. Journal of Experimental Biology 211:3174-3180.

Scheifele, P. M., S. Andrew, R. A. Cooper, M. Darre, F. E. Musiek, and L. Max. 2005. Indication of a Lombard vocal response in the St. Lawrence River beluga. Journal of the Acoustical Society of America 117:1486-1492.

Scholz, N. L., N. K. Truelove, B. L. French, B. A. Berejikian, T. P. Quinn, E. Casillas, and T. K. Collier. 2000. Diazinon disrupts antipredator and homing behaviors in chinook salmon (Oncorhynchus tshawytscha). Canadian Journal of Fisheries and Aquatic Sciences 57:1911-1918.

Schuetz, J. G. 2005. Low survival of parasite chicks may result from their imperfect adaptation to hosts rather than expression of defenses against parasitism. Evolution 59:2017-2024.

Searcy, W. A., and S. Nowicki. 2005. The evolution of animal communication. Princeton University Press, Princeton (NJ).

Seehausen, O., J. J. M. vanAlphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808-1811.

Siefferman, L., and G. E. Hill. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. Behavioral Ecology 14:855-861.

Slabbekoorn, H., N. Bouton, I. van Opzeeland, A. Coers, C. ten Cate, and A. N. Popper. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends in Ecology & Evolution 25:419-427.

Slabbekoorn, H., and M. Peet. 2003. Ecology: Birds sing at a higher pitch in urban noise - Great tits hit the high notes to ensure that their mating calls are heard above the city's din. Nature 424:267-267.

Slabbekoorn, H., and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular ecology 17:72-83.

Slabbekoorn, H., and T. B. Smith. 2002a. Bird song, ecology and speciation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 357:493-503.

Slabbekoorn, H., and T. B. Smith. 2002b. Habitat-dependent song divergence in the little greenbul: An analysis of environmental selection pressures on acoustic signals. Evolution 56:1849-1858.

Slocombe, K. E., B. M. Waller, and K. Liebal. In Press. The language void: the need for multimodality in primate communication research. Animal Behaviour.

Smith, H. G., R. Montgomerie, T. Poldmaa, B. N. White, and P. T. Boag. 1991. DNA fingerprinting reveals relation between tail ornaments and cuckoldry in barn swallows, *Hirundo rustica.* Behavioral Ecology 2:90-98.

Spottiswoode, C. N., and M. Stevens. 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. Proceedings of the National Academy of Sciences of the United States of America 107:8672-8676.

Stewart, S. L. M., D. F. Westneat, and G. Ritchison. 2010. Extra-pair paternity in eastern bluebirds: effects of manipulated density and natural patterns of breeding synchrony. Behavioral Ecology and Sociobiology 64:463-473.

Suk, H. Y., and J. C. Choe. 2002. Females prefer males with larger first dorsal fins in the common freshwater goby. Journal of Fish Biology 61:899-914.

Sun, J. W. C., and P. A. Narins. 2005. Anthropogenic sounds differentially affect amphibian call rate. Biological Conservation 121:419-427.

Taylor, R. C., B. W. Buchanan, and J. L. Doherty. 2007. Sexual selection in the squirrel treefrog *Hyla squirella*: the role of multimodal cue assessment in female choice. Animal Behaviour 74:1753-1763.

Thery, M. 2006. Effects of light environment on color communication *in* G. E. Hill, and K. J. McGraw, eds. Bird Coloration. Harvard University Press, Cambridge, MA.

Uy, J. A. C., and A. C. Stein. 2007. Variable visual habitats may influence the spread of colourful plumage across an avian hybrid zone. Journal of Evolutionary Biology 20:1847-1858.

Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. Proceedings of the Royal Society of London Series B-Biological Sciences 265:351-358.

Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 183:621-633.

Warren, P. S., M. Katti, M. Ermann, and A. Brazel. 2006. Urban bioacoustics: it's not just noise. Animal Behaviour 71:491-502.

Wiebe, K. L., and T. Slagsvold. 2009. Mouth coloration in nestling birds: increasing detection or signalling quality? Animal Behaviour 78:1413-1420.

Wood, W. E., and S. M. Yezerinac. 2006. Song sparrow (Melospiza melodia) song varies with urban noise. Auk 123:650-659.

Wright, J., and M. L. Leonard. 2002. The Evolution of Begging: Competition, Cooperation and Communication. Kluwer Academic Press, Dordrecht.

Yeh, P. J., and T. D. Price. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. American Naturalist 164:531-542.

VITA

NAME OF AUTHOR: Ellen Michale Wisner

PLACE OF BIRTH: Dothan, Alabama

DATE OF BIRTH: May 8, 1984

PRIOR SCHOOLS ATTENDED:

Centre College, Danville, Kentucky

DEGREES AWARDED:

Bachelor of Science in Biology, 2006, Centre College

AWARDS AND FELLOWSHIPS:

2010 Sigma-Xi Grants-in-Aid of Research

2010 American Ornithologists' Union Travel Grant

2010 Travel Grant, Graduate Student Organization, Syracuse University

2010 Travel Grant, Department of Biology, Syracuse University

APPOINTMENTS AND SERVICES:

2010-2011 Graduate Representative, Graduate Education Recruitment Committee, Department of Biology, Syracuse University

2009-2011 Teaching Mentor, Syracuse University

2009-2010 President, Biology Graduate Student Organization, Syracuse University

2008-2009 Vice President, Biology Graduate Student Organization, Syracuse University

2007-2008 Biology Representative, Graduate Student Organization, Syracuse University

PROFESSIONAL EXPERIENCE

2006-2011 Teaching Assistant, Department of Biology, Syracuse University