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# Effects of Traffic Noise on the Social Behavior of Tufted Titmice (*Baeolophus bicolor*).

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To the Graduate Council:

I am submitting herewith a dissertation written by Jessica Lynn Owens entitled "Effects of Traffic Noise on the Social Behavior of Tufted Titmice (*Baeolophus bicolor*).." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Experimental Psychology.

Todd M. Freeberg, Major Professor

We have read this dissertation and recommend its acceptance:

Gordon M. Burghardt, Neil Greenberg, Michael A. Olson, David A. Buehler

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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EFFECTS OF TRAFFIC NOISE ON THE SOCIAL BEHAVIOR OF TUFTED  
TITMICE (*BAEOLOPHUS BICOLOR*)

A Dissertation Presented for the Doctor of Philosophy Degree  
The University of Tennessee, Knoxville

Jessica Lynn Owens

May 2013

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In Memory of Grandpa Owens:

February 24, 1933 - November 15, 2012

*Behave yourself, wherever you are now*

For my family:

past, present and future.

two-legged and four.

## ACKNOWLEDGEMENTS

Having received a D in the third semester of my 6th grade science class, I never thought I would be here writing these words. My ability to thank each person, animal, being or item that has contributed to, assisted with, motivated, or inspired me, in the myriad of ways that they have done so, is inherently limited by language. However, this accomplishment is shared among us all, and it would not have been possible without each interaction. Having said this, I will do my best to show my gratitude in the lines to follow. I do not apologize for the length of this section as it is in no comparison to the amount of love and support given to me.

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Greg gave me the biggest surprises when he came to birthday parties, Uncle Gary and the Cleveland Indians games, Aunt Lisa always saying "...Jess" with surprise and shock and a bit of disappointment, Aunt Debbie was my stylist and Uncle Jeff my punching bag. I could not be more lucky and I thank you for all of the times and ways that you have loved and supported me over the years. No birthday or christmas gift was forgotten and the gatherings around the table, pool, fire or downstairs bars are fodder for stories for years to come.

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### Secrets of Success

- Do more to learn more, not learn more to do more.
- Great people refuse to accept failure.
- Be willing to commit to something and stick to it.
- Value relationships and stay away from those who aren't growing positively.
- Reap what you sew.
- Live on the edge and take a chance.
- Tomorrow is a result of attitudes and choices made today.

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## ABSTRACT

The presence of traffic noise and its potential effects on wildlife is a burgeoning topic of research within the fields of conservation behavior, animal behavior, ecology and wildlife management. Accumulated data from these efforts, mostly correlative and rarely experimental, suggest that traffic noise induces a myriad of species-specific changes to population dynamics, breeding behavior and acoustic structure of avian song. However, the degree of generalizability of these findings is confounded by the limited variety of behaviors studied within a relatively small sample of species. This original research provides experimental evidence of the effects of simulated and real traffic noise on previously unstudied social and vocal behavior in tufted titmice (*Baeolophus bicolor*). First, titmice were exposed to simulated traffic noise for 8 hours per day to determine whether traffic noise caused changes in social and vocal behavior as had been suggested by previous research. This stimulus, background noise mimicking the duration of exposure, amplitude and frequency parameters of traffic noise, significantly affected several aspects of social behavior. Analyses on the vocal behavior of these subjects suggest that noise only affects call use of the most vocally-productive bird, who also happens to be the most dominant group member. A second study broadcasted recordings of traffic noise to titmice for 2.5 hours per day to test for the effects of the temporary rise in background noise levels resulting from 'rush hour' on the same social behavior found to be affected in study one. Results of Study 2 corroborated those of Study 1 and indicated that characteristics of traffic noise itself influence its effects. Among the first of its kind, this research demonstrates a direct link between traffic noise and survival-relevant social and vocal behavior.

## TABLE OF CONTENTS

I.	CHAPTER 1: Introduction.....	1
	Style and scope.....	2
	History of sound, noise and acoustic disturbance.....	3
	Parameters, prevalence and problems of traffic noise.....	6
	Influential research: vocal communication in animals.....	7
	The development of interest in anthropogenic noise.....	13
	The effects of traffic noise on birds.....	18
	Opportunities for advancing the study of anthropogenic noise.....	23
	Aims of the current dissertation research.....	30
	References.....	35
	Appendices.....	60
	Appendix A: Tables.....	61
	Appendix B: Figures.....	65
II.	CHAPTER 2: Simulated traffic noise increases social behavior of tufted titmice ( <i>Baeolophus bicolor</i> ).....	70
	Disclosure statement.....	71
	Abstract.....	72
	Introduction.....	73
	Materials and methods.....	78
	Results and discussion.....	86
	Considerations, contributions and conclusions.....	92

References.....	94
Appendices.....	105
Appendix A: Tables.....	106
Appendix B: Figures.....	109
III. CHAPTER 3: Traffic noise and dominance status increase chick-a-dee call rate and complexity in tufted titmice ( <i>Baeolophus bicolor</i> ).....	114
Disclosure statement.....	115
Abstract.....	116
Introduction.....	117
Materials and methods.....	125
Results and discussion.....	133
Considerations, contributions and conclusions.....	142
References.....	144
Appendices.....	158
Appendix A: Tables.....	159
Appendix B: Figures.....	167
IV. CHAPTER 4: Rush hour traffic noise increases social behavior of tufted titmice ( <i>Baeolophus bicolor</i> ).....	172
Disclosure statement.....	173
Abstract.....	174
Introduction.....	175



Materials and methods.....	179
Results and discussion.....	186
Considerations, contributions and conclusions.....	194
References.....	195
Appendices.....	200
Appendix A: Tables.....	201
Appendix B: Figures.....	205
V. CHAPTER 5: The effects traffic noise on tufted titmouse ( <i>Baeolophus bicolor</i> ) social behavior: Contributions, considerations and conclusions.....	211
Style and Scope.....	212
Contributions and implications of the current research.....	213
Considerations for future work.....	231
Concluding remarks.....	239
References.....	241
Appendices.....	260
Appendix A: Tables.....	261
VI. VITA.....	265

**CHAPTER 1**  
INTRODUCTION

# CHAPTER 1

"...ghetto blasters, Walkman earphone seepage, elevator music, cellular phone chatter, automobile alarms, and 'boom cars.' Engulfed by what cultural critics dub 'sonic exhibitionism' from the 'audio-terrorist,' it 's easy to believe that we live in a world of unsurpassed noisiness" (Baily, 1996; Keizer, 2001; as cited in Coates, 2005, p. 640).

## I. Style and scope

Very few scientific endeavors occur in a vacuum; as such, this introduction is structured to provide a broad review of relevant literature from several perspectives. I begin by describing the historical relationship between humans and their acoustic environment. The concept of anthropogenic disturbance will be introduced and traffic noise will be identified as an anthropogenic disturbance of practical and pressing importance. The body of the introduction describes seminal work from the 1970s and 1980s that provided a basic understanding of the effects of natural noise on avian behavior and communication. The second half of the introduction follows the progression of interest in the effects of anthropogenic noise on humans to wildlife. This second half culminates in a review of the current research on traffic noise. Opportunities for advancement are identified and used to organize the rationale for the current dissertation research. This chapter ends with a concise statement of the aims, goals and methods of the dissertation research described herein. In closing, several terms that appear in this chapter have been used interchangeably within the literature. Many of these terms are defined with

specific regard to their use here (see Table I). This table is referred to following the first occurrence of any of these terms.

## **II. History of sound, noise and acoustic disturbance**

### ***A. Sound or noise ?***

Sound (Table I) includes a seemingly infinite array of quantitatively distinct combinations of auditory phenomena that play an integral role in the lives of all species. Hearing provides such rich information that is hypothesized to have evolved not for communication, but for learning about the environment (Popper & Fay, 1999; Fay & Popper, 2000). The sounds we encounter make up our acoustic scene and inform an organism about the surrounding environment (Bregman, 1990; Dooling & Popper, 2007). The relationship between sound, hearing and learning about an environment is most evident in the adjectives chosen to describe the acoustic scene of an unfamiliar place. Explorers of a new land often used adjectives with a negative connotation to describe sounds they heard. For example, the "howling wind" or "beastly calls" of animals indicates that these sounds were sources of fear. American colonists attributed a great deal of meaning to sound as they believed that God spoke through thunder and the Devil through clamoring of storms (Rath, 2003, pp. 11). Accordingly, the clearing of wild forests for settlements and hunting of local fauna for food may have also served to gain control over sounds that inflicted a sense of vulnerability. Ironically today we consider the sounds of our current settlements bothersome and annoying (Miedema & Vos, 1998) and often mask them with recordings of nature.

This frustration with the man-made acoustic environment was evident even in ancient Rome and Medieval Europe where laws limited horse and wagon travel along stone roads at

night to reduce disturbances to those sleeping (Berglund, Lindvall & Schwela, 1999). And during the industrial revolution many commented on the presence of noise within cities. In an article titled "The horseless carriage and public health," *Scientific American* (1899) believed that the introduction of the automobile into cities was a much preferred source of transportation because they were noise-less or nearly so (as cited in Coates, 2005). Rather than using the word quiet or sound-less, *Scientific American* specifically chose 'noise-less,' suggesting that automobiles did not produce any of the sounds considered to be noise in the then current acoustic environment. But what is noise? Noise (Table I) is a subjectively-defined category of sound. Dating back to the 13th century, the word noise was adapted from the Latin word *nausea* and is currently defined as an unwanted or intrusive sound, or one that interferes with the reception of another sound (Dooling & Popper, 2007; "Noise," n.d.). Although noise and sound describe the same acoustic phenomena, they represent significantly different subjective categories of the phenomenon. As such, sound and noise are often used interchangeably; here the word noise will be used only when a sound is known to have been identified as unwanted or interruptive.

### ***B. Beyond noise: sound as disturbance***

Another categorization of sound is: natural vs. unnatural. Rath (2003) considered natural sounds as those that were unintentional and not produced by humans. Natural sounds therefore included running water, wind through trees and vocal signals of non-human animals, leaving unnatural sounds to consist of all those of human origin. While this is a potentially extreme opinion that places humans at opposition with nature, Rath does hit on a current distinction in the literature: natural vs. anthropogenic. The term 'anthropogenic' (Table I) originated in 1889 from 'anthropogeny' (1839) which was derived from the Greek word *anthropogeneia* or *anthropogenes*, meaning "born of man" ("Anthropogenic," n.d.). British ecologist A. Tansley

was one of the first scientists to use the term, and did so in reference to human influences on climax plant communities (Bampton, 1999). While anthropogenic is simply an adjective referring to anything of human origin or design, it is often used in contexts where human-caused contexts negatively affect natural systems. The most common use of anthropogenic is in combination with "disturbance." Disturbance (Table I) has been defined in several ways, but for our purposes here an anthropogenic stimulus is considered to be an anthropogenic disturbance if its presence influences the normative survival, physiology, behavior or social organization of an organism. Similarly, as with sound and noise, I shall refrain from using the word disturbance to refer to a stimulus unless it has been shown to alter or interfere with any of the aforementioned systems.

The previously mentioned adjective-noun combination, "anthropogenic disturbance," has developed into its own topic of study. Anthropogenic stimuli and disturbances are evolutionarily recent and present many species with a range of novel stimuli that have only begun to be studied (Bulluck & Buehler, 2006; Brawn, Robinson, & Thompson III, 2001; King, Griffin, & DeGraaf, 1998; Klump, 1996; Slabbekoorn & Peet, 2003; Slabbekoorn & Ripmeester, 2008). Initially and extensively studied within humans, urban noise (see "urban" and "noise" in Table I), is a type of anthropogenic disturbance that has been linked to a variety of negative effects on psychological, physiological, behavioral and social processes. With regard to the impacts of anthropogenic stimuli on wildlife, there has been a surge of relevant literature within the past decade often identifying these stimuli as anthropogenic disturbances. Of specific interest here are anthropogenic stimuli of an acoustic nature, specifically traffic noise.

### III. Parameters, prevalence and problems of traffic noise

Traffic noise (Table I) is a low-frequency sound with a concentration of energy below 2 kHz that gradually decreases in power up to 4 kHz (Figure 1). These acoustic qualities are a function of traffic volume (vehicles / hour), speed of travel, size of vehicles, and pavement type. The area of land covered by roadways in the U.S. is estimated to be over 20 million acres (Evink, 2002), approximately 20% of the total land area (Forman, 2000). From 1997 to 2007 the US population increased by approximately 30%, but traffic on the roads has nearly tripled (<http://www.census.gov/compendia/statab>; <http://www.fhwa.dot.gov/ohim/tvtw/tvtpage.cfm> as cited in Barber, Crooks & Fristrup, 2009). The average moving vehicle creates enough noise to surpass the sound levels of naturally occurring ambient background noise of similar frequencies (Barber et al., 2009) at a distance of up to 1 km away (Riitters & Wickham, 2003). This means, for example, that traffic noise significantly affects the acoustic space of approximately 83% of the land area within the contiguous U.S. (Riitters & Wickham, 2003).

The term "traffic sound" could be used to define the sounds resulting from vehicular travel, but has probably rarely, if ever been spoken. It is also probably no coincidence that the phrase "traffic noise" is more commonly used, considering the known effects it has on mood (Mediema & Vos, 1998). Traffic noise and similar acoustic anthropogenic stimuli have been associated with reduced species diversity and density (Forman, Reinking & Hersperger, 2002; Reijnen & Foppen, 1994, 1995; Reijnen, Foppen, ter Braak, & Thissen, 1995; Rheindt, 2003), low pairing and breeding success (Forman & Alexander, 1998; Habib, Bayne & Boutin, 2007; Halfwerk, Holleman, Lessells & Slabbekoorn, 2011; Reijnen & Foppen, 1995) and a host of other behavioral changes in a variety of species (Borkowski et al., 2006; Bronzaft & McCarthy, 1975; Chan, Giraldo-Perez, Smith & Blumstein, 2010; Hygge et al., 2002). The most commonly

cited effect of traffic noise is that it masks sounds important for communication and creates a challenge for signalers, receivers and eavesdroppers alike (Figure 2). Traffic noise is a significant contributor to the urban acoustic scene (i.e. urban noise); however, traffic noise is not limited to urban areas, but is a variable of concern anywhere that motorized vehicles travel.

The topic of traffic noise and its potential effects, beneficial or detrimental, is a newer topic of study attracting much attention and interest. This may be because traffic noise is obvious in our own environments or because this noise is likely to continue growing in both amplitude and range of effect as the network of roads expand and extend into new habitats every day. However, regardless of the popularity of this topic, there are still plenty basic questions that need to be answered. A majority of the efforts to study the effects of traffic noise fall within a narrow focus on a few behaviors of a few species and rarely provide experimental data. While opportunities for advancement are discussed at length below, it will suffice to quickly mention that the literature review to follow will illustrate that this field could greatly benefit from asking basic questions and testing predictions from relevant hypotheses using experimental and standardized methodologies.

#### **IV. Influential Research: vocal communication in animals**

Successful species are adapted to their environments. Research on vocal signaling and perception has provided clear demonstrations of how organisms adapt to environmental challenges. But how are species responding to evolutionarily novel environments like those whose acoustic scenes are altered by the presence of traffic noise (Figure 3)? The knowledge gained from efforts to understand sound propagation, signal design and hearing in natural habitats is helpful in understanding the challenges posed by traffic noise. Additionally, because



of the inherent relationship between vocal communication, hearing, and the effects of traffic noise on the acoustic space of a habitat, this research also sheds light on why our knowledge on the effects of traffic noise are limited to so few species and behaviors. As such, these data will be discussed before our current knowledge of the effects of anthropogenic noise.

### ***A. Environmental sources of selection***

Propagation of a sound was believed to be frequency dependent, whereby higher frequencies are more susceptible than lower frequencies to environmental factors that reduce transmission distance (Konishi, 1970; Morton, 1975). While generally true, this assumption overlooks the habitat specific effects of attenuation (Table I) and degradation (Table I) (Allee, 1926; Eyring, 1946; Pridmore-Brown & Ingard, 1955; Richards & Wiley, 1980; Waser & Brown, 1986). In a forest, the shorter wavelengths of high frequency sounds are reflected off of branches and leaves while the longer wavelengths of lower frequencies travel around these structures and are, generally, only degraded and or attenuated by broad surfaces. In open habitats high frequencies are degraded by the presence of temperature gradients and wind while low-frequency sounds are attenuated by the ground.

In a seminal study, E.S. Morton (1975) measured the acoustic properties of different habitats and determined whether these habitat-specific differences predicted the acoustic structure of vocal signals produced by resident species. Pure tones and broadband noise were broadcast through open (grassland), mixed (edge) and closed (forested) habitats and re-recorded (dB / sound pressure level, SPL) at differing distances from the sound source. Excess attenuation (EA), which is calculated by subtracting the SPL recorded from the value of attenuation expected from spherical divergence (6 dB / every doubling of distance from the

sound source: Peterson & Gross, 1967), was used to describe the attenuation resulting from spherical divergence (Wiener & Keast, 1959).

Forest habitats attenuated sounds above 2.5 kHz more than expected, and less than expected on frequencies of 1.5 - 2.5 kHz. Excess attenuation within grassland and edge habitats increased as frequencies rose, as predicted. These data suggested that, regardless of habitat, vocal signals within 1.5 - 2.5 kHz are optimally designed for propagation. These data cause one to expect forest birds to produce calls of lower frequencies than those in open habitats. This prediction was supported by Morton's analysis of vocal signals from 177 different species. Additionally, forest birds also produced more tonal signals within a narrow frequency range and with little within-call variation in sound types compared to grassland species whose songs included trills and frequency modulations across a wide range of frequencies. These differences in degree of tonality and frequency range were not completely explained by the habitat-specific predictions resulting from Morton's sound propagation data. Morton speculated on three possible explanations. The first suggested that the 1.5 - 2.5 kHz optimal frequency range of forest habitats may provide enough selection pressure to result in relatively tonal, frequency constant signals; however, the same prediction would then be made for the open habitat. Tonal signals provide two benefits that may explain their prevalence in forested habitats. The first is that tonal signals do not experience much attenuation in forested habitats, as reverberation exerts stronger effects on broadband signals. Additionally, tonal signals increase propagation because they allow a signaler to package more energy and vocalize louder compared to broadband signals that have energy spread across different frequencies. It is also likely, as shown later by Lohr, Wright and Dooling (2003), that tonal signals are easier to detect in natural background noise than broadband signals.

Morton's habitat-specific predictions for sound propagation, later-named the Acoustic Adaptation Hypothesis (AAH) (Hansen, 1979), have been repeatedly supported (Eyring, 1946; Wiener & Keast, 1959) and fine-tuned to account for other important variables affecting sound transmission (Attenborough, 1988; Price, Attenborough & Heap, 1988; Bullen & Fricke, 1982; Huisman & Attenborough, 1991). Likewise, the predictions of habitat-specific acoustic signal structure have also been generally supported and extended. For example, the degree to which habitat type explains variation in the frequency structure of avian song was found to be low to moderate, ranging from 14.8 to 31.6% (Boncoraglio & Saino, 2007). These results support the conclusion of a later study that habitat type is a better predictor of acoustic variation for mammals and anurans than birds (Ey & Fischer, 2009). Admittedly the AAH is limited, as other variables, such as sexual selection, have shaped the design of vocal signals across evolutionary time (i.e. Morton, 1975; Boncoraglio & Saino, 2007; Jensen, Larsen & Attenborough, 2008). Arguably, the most salient predictions of the AAH pertain to frequency structure of acoustic signals (Blumstein & Turner, 2005).

### ***B. Influence of the receiver***

In addition to signal design, propagation is also affected by the auditory sensitivity of the receiver and the presence and type of ambient background noise (Morton, 1975). The receiver's perspective was initially addressed through research on avian hearing in the 1970s and 1980s. Much of our knowledge of the auditory perception of birds comes from psychophysical (conditioned responses) methods used to construct auditory curves (Dooling, 1982). This curve is the pattern of minimum sound pressure (dB) required for perception of a sound at different frequencies throughout an organism's hearing range. The minimum sound pressure required to hear a specific frequency is referred to as the hearing threshold. A high threshold indicates that a

sound must be produced at a higher pressure (louder) to be perceived. With that said, songbirds generally exhibit lower thresholds at higher frequencies than non-songbirds, indicating that they are better prepared to perceive higher frequency sounds (Dooling & Popper, 2007). The auditory curves of avian species suggest that many birds have similar hearing abilities, and likely share a comparable auditory space (Dooling, 1980, 1982, 1992; Dooling, Lohr & Dent, 2000). Within species, auditory sensitivity is fine-tuned to perceive the range of frequencies produced (Dooling, 1980, 1982). Detecting conspecific signals within an acoustic space shared with several heterospecifics is aided by the ability of the avian auditory system to act as band-pass filters allowing separate perceptual analyses of individual frequencies of auditory input (Manley, 1990). Taken together, these data suggest that the presence of background noise within the frequency range of auditory sensitivity or vocal production would appear to provide a large communicative challenge for signalers and receivers, alike.

### ***C. Communication in noise***

The most commonly cited effect of ambient noise on communication is masking, which is defined as the interference of detection, recognition or perception of a sound due to the presence of another sound, the latter sound being the masker. Background noise is most likely to mask signals or portions of signals that it shares a frequency range with (Dooling, 1980; Klump, 1996). Although the organization of the avian auditory system inherently emphasizes masking when signal and background noise overlap, many adaptations exist to improve communication in noise.

Signal detection (i.e. auditory sensitivity) amid background noise is defined by the critical ratio (dB) (CR), which is the ratio of a signal's power to that of the background noise (Dooling, 1982). This number indicates the power of the signal over and above the background

noise when first audible. In general, mammals and birds share the same pattern of signal detection in noise; both require an average CR of 2 - 3 dB per increase in octave (Fig 10, Dooling, 1982, p. 114; Okanoya & Dooling, 1987). Therefore, increasing the power, or amplitude, of signal frequencies overlapping background noise should improve signal detection in noise. Indeed, when songs that had previously elicited a response at playback (Brenowitz, 1982a) were broadcast with increased power (CR = 3 dB) within the range of accompanying background noise, receiver response was similar to the no-noise condition (Brenowitz, 1982b).

The challenges posed by background noise may be managed in several ways, including: producing tonal signals within a narrow frequency range (Lohr et al., 2003), exploiting the organization of the receiver's peripheral auditory system to perceive differences in directionality between the noise source and the signaler (Hine, Martin & Moore, 1994; Saberi, Dostal, Sadralodabai, Bull & Perrott, 1991; Schwartz and Gerhardt, 1989), signaling during times of reduced background noise (Cody & Brown, 1969), lengthening the duration of a signal (Dooling & Searcy, 1985), or shifting parts of the signal outside of the frequency range of the noise (Ficken, Ficken & Hailman, 1974). Although potentially adaptive, consequences may exist for modifying signals to improve transmission in a noisy habitat. For example, a signal may fail to elicit an appropriate behavioral response if any characteristic is modified by more than 2 standard deviations from the local population mean (Dabelsteen & Pedersen, 1992; Nelson, 1988, 1989; Naugler & Ratcliffe, 1992).

## **V. The development of interest in anthropogenic noise**

### ***A. Anthropogenic noise affects anthropoids***

The effects of anthropogenic noise were being investigated while Morton was exploring ecological sources of variation on communication; however, these efforts were focused on humans. The literature on the effects of anthropogenic noise on humans is overwhelming. Cited by the World Health Organization as a "Global Dilemma," (Berglund et al., 1999), the effects of urban noise are extensive. While some research has shown that noise may improve performance (Hockey, 1970) specifically for outgoing personality types (Baddeley, 1968; Davies & Hockey, 1966), the majority of work suggests otherwise. Within the human literature, an adverse effect of noise is identified as a change in the morphology or physiology of an organism that causes impairment of functional ability, or an impairment of the ability to regulate additional stress, or increases an organism's susceptibility to the negative effects of other environmental challenges (World Health Organization, 1994). Using this definition, noise has been found to affect concentration, energy levels, clarity of thought, self-confidence, mood, work capacity, social relationships and stress, physiological measures of health and sleep patterns (Berglund & Lindvall, 1995; Smith, 1989).

Among the physiological effects of noise are hearing impairment, cardiovascular disease, and chronic elevation of stress. The severity of these effects vary with exposure levels and individual susceptibility, among other variables (Berglund & Lindvall 1995; Passchier-Vermeer & Passchier, 2000; Smith, 1989). However a pattern appears to be consistent across different noise sources and effects. Initial and acute exposures elicit moderate responses that are often mediated across time following the end of exposure. In comparison, long-term exposures to even moderate sound levels (< 70 dB) increases the risk of permanent damage to several

systems. For example, it is believed that acute noise activates the autonomic system which increases blood pressure, heart rate and vasoconstriction. However there is little evidence that acute noise produces chronic effects as these physiological responses return to baseline levels quickly after exposure has ended (Berglund et al., 1999). Although the results of individual studies rarely reach significance, the culmination of evidence suggests that long-term exposure to noise may place one at higher risk for cardiovascular effects, specifically ischemic heart disease (Babisch, 2000; Berglund et al., 1999; Ising & Kruppa, 2004).

Laboratory and workplace studies indicate that noise can also act as a distraction. Bronzaft and McCarthy (1975) showed that noise from a nearby elevated train caused the scores of children on the noisy side of the school building (89 dB) to lag behind those of children on the quiet side (59 dB) by 3 to 4 months. A later study eloquently showed that not only did long term memory, reading ability and speech perception in school children decrease when a nearby airport opened, but that these same measures improved in children at a different school when a nearby airport shut down (Hygge et al., 2002).

In addition to these effects on learning, noise significantly affects mood and related behavior. "Noise annoys," while a catchy title to a song by the Buzzcocks (1978), is also a true statement. Defined as a negative feeling resulting from any context or stimulus believed to cause a negative effect on the organism (Lindvall & Radford 1973), Mediema & Vos (1998) have shown that traffic noise is the second most annoying noise compared to aircraft and railway noise. However, annoyance is just one of the negative emotions evoked by noise. Anger, disappointment, dissatisfaction, depression, anxiety, distraction, irritability and fatigue are all experienced by people exposed to noise (Job, 1993, as cited in Job, 1996; Job, 1996). Noise also reduces helping behavior (Berglund & Lindvall 1995; Page, 1977), increases aggression

(Donnerstein & Wilson, 1976), negatively affects sleeping patterns (Bluhm, Nordling & Berglund, 2004) and influences judgment (Siegel & Steele, 2011). However, identifying the root or mechanisms behind these effects are difficult because they are complex, subtle and indirect (Berglund & Lindvall, 1995).

## ***B. Anthropogenic disturbances and wildlife***

This section of the introduction will initially establish the general fact that humans and their activities are disruptive and disturbing to a range of species. The response of animals to dynamic stimuli, such as pedestrians moving through an environment, will be compared to static stimuli, like a roadway. Following this, the general effects of anthropogenic noise will be reviewed. The list of potential anthropogenic stimuli, contexts and activities that have been addressed as disturbance is extensive. As such, a limited review will be provided of those sounds that are most common and relevant to the topic of study here, including: boat noise, traffic noise, airplane and helicopter noise, industrial noise and random noise. Following this, the discussion will begin to focus. Specifically, a string of investigations referred to as 'road ecology' will be presented, as they often implied that traffic noise was responsible for certain relationships observed between roadways and animal behavior and population structures. However, while implicated, empirical support was generally lacking.

Many anthropogenic stimuli, from the mild, presence of people, to the severe, sonic booms, function as anthropogenic disturbances because they are generally disruptive to the normative behavioral patterns of many major taxa, including: amphibians (Rodriguez-Prieto & Fernández-Juricic, 2005), anurans (Eigenbrod, Hecnar & Fahrig, 2008, 2009), birds (Grubb & King, 1991; Klein, 1993; Klein, Humphrey & Percival, 1995; Stalmaster & Newman, 1978), cephalopods (Andre et al., 2011), cetaceans (Nowacek, Thorne, Johnston & Tyack, 2007), felids



(Kerley et al., 2002), fish (Blaxter & Hoss, 1981; Rucker, 1973), insects (Frings, 1959), plants (Francis, Kleist, Ortega & Cruz, 2012), primates (dela Torra, Snowdon & Bejarano, 2000), reptiles (Rudolph & Burgdorf, 1997) and ungulates (Borkowski et al., 2006). With regard to anthropogenic noise, the most heavily studied group of species is birds. Because of this focus, efforts have been made to include data from other taxa that are often under-represented in the review to follow.

The effects of noise on the physiological health of humans were presented above. Although animals were often used to determine the health risks of noise exposure on humans (see Berglund & Lindvall, 1995; Berglund et al., 1999; Smith, 1989), very few studies have addressed the physiological effects of noise exposure on wildlife even though different techniques exist (Bonier et al., 2006; Romero & Wikelski, 2002; Wingfield et al., 1997) and have been reviewed for their applicability and ease of use (Bonier, 2012; Tarlow & Blumstein, 2007). The few studies that do exist provide clear evidence that anthropogenic disturbances of different types have the ability to affect hormonal responses, but the direction of the response varies between species, sex and disturbance type. For example, white-crowned sparrows (*Zonotrichia leucophrys*) in urban habitats exhibited increased baseline corticosterone levels compared to conspecifics in rural habitats, but only for males (Bonier, et al., 2006). In contrast, urban European blackbirds (*Turdus merula*) exhibited no differences in baseline corticosterone levels when compared to their rural counterparts, but did show a significant reduction in their response to acute stressors compared to rural birds (Partecke, Schwable & Gwinner, 2006).

Arguably one of the most benign forms of human disturbance is their mere presence. These disturbances (including: standing, hiking, walking, speaking, etc) are normally dynamic and short-term, resolving as a person moves through an environment. For some species though,

brevity of exposure does not necessarily reduce disturbance. For example, the Bald Eagle (*Haliaeetus leucocephalus*) is more often flushed by our presence than by the noise created by a passing airplane (Grubb & King, 1991; Grubb, Bowerman, Geisy & Dawson, 1992). Similar avoidance and fleeing responses to the presence or passing by of people have been observed in many other species, including raptors (Andersen, Rongstad & Mytton, 1990; Stalmaster & Newman, 1978), waterbirds (Klein, et al., 1995; Riddington, Hassall, Lane, Turner & Walters, 1996), colonial gulls (Burger, 1981), ungulates (Stankowich, 2008), primates (de la Torre et al., 2000) and large carnivores (Kerley et al., 2002). However, it is important to note that several species do show signs of habituation to human activities over time (e.g. Klein et al., 1995; Schultz & Bailey, 1978), and many return to normal habitats and activities after the disturbance has ended (Andersen, Rongstad & Mytton, 1986).

One anthropogenic stimulus that is more static is a road. For many species, the simple presence of such a structure can be troublesome. One example is the "barrier effect" observed in smaller animals, specifically invertebrates, reptiles and anurans, whose movements are restricted and populations isolated by the presence of a roadway (Mader, 1984; Minton, 1968). Although the movements of animals are not necessarily restricted by the presence of a road, it can affect population dynamics for reptiles and amphibians up to 2000 m away (Findlay & Houlihan, 1997). Similarly, these same effects are noted for birds (Foppen & Reijnen, 1994; R  ty, 1979; Reijnen & Foppen, 1994; Reijnen, Foppen, Meeuwsen, 1996), large snakes (Rudolph et al., 1999) and African nocturnal primates, ungulates and carnivores (Laurance et al., 2008). Other species, presumably those who benefit from these areas, exhibit high rates of population density and diversity near roadways (Free, Gennard, Stevenson & Williams, 1975; Ward, Anderson & Petty, 2008).

Using the definitions of anthropogenic, disturbance or noise from Table I, any sound produced by a person or human-made item is an anthropogenic sound capable of becoming an anthropogenic disturbance or noise if it disturbs an organism. While the effects of noise depend on the acoustic stimulus and species in question (Radle, 1998), the most common are: physical damage to ears, stress responses, fright-flight responses, avoidance responses, changes in behavioral patterns, changes in reproductive success, changes in communicative behavior, interference with hearing and population level shifts (reviewed in Ortega, 2012). Acute noise is most commonly associated with alerted, distracted or escape behaviors, as has been observed in raptors (Grubb & King, 1991), fish (Blaxter & Hoss, 1981; Rucker, 1973), crustaceans (Chan et al., 2010) and ungulates (Borkowski et al., 2006). The presence of chronic noise has not been adequately studied, but evidence suggests that it is often associated with avoidance of areas with higher levels of noise and increases in social behavior. Bottlenose dolphins often avoid foraging in noisy areas (Nowacek et al., 2007); however, if boat activity and noise increase in their immediate presence, dolphins respond by increasing social behavior (Hastie, Wilson, Tufft & Thompson, 2006; Nowacek, Wells & Solow, 2001) and swimming speed (Nowacek et al., 2001). Similarly, killer whales (*Orcinus orca*) stop feeding and begin socializing and travelling when boat activity and noise increase in their vicinity (Williams, Lusseau & Hammond, 2006).

## **VI. The effects of traffic noise on birds**

### ***A. Road ecology and the missing empirical evidence***

A series of studies focusing specifically on the relationships between roads and birds is often cited as the impetus for current investigations into the effects of traffic noise. The first and second manuscripts resulting from this work documented the characteristics of willow warbler

(*Phylloscopus trochilus*) population structure along highly travelled road ways. This effort reported a reduction in the presence of territorial males within 200 m of the roadway and differences in dispersal behavior compared with males in similar habitats further away from roadways (Foppen & Reijnen, 1994; Reijnen & Foppen, 1994). The lower density was attributed to a lack of mature males, meaning that the proportion of young or first-year males to more than 50% higher than other quieter habitats. Further, this roadside habitat was settled by these younger males later than quieter habitats, suggesting that mature males selected the optimal habitats causing the less-experienced males to occupy less-optimal habitats. Following their first breeding season within these habitats, males dispersed to new habitats further away than those from quieter habitats (Foppen & Reijnen, 1994). The authors suggested that breeding success may influence dispersal, whereby less successful males dispersed further and more frequently than successful males.

The authors speculated that these effects may be related to the reduction of food caused by air pollution's effects on insects (Przybylski, 1979; Bolsinger & Flückinger, 1989), but suggested that it was more likely that noise, an understudied phenomenon, may be important. In an attempt to address traffic noise while controlling for the visual presence of road traffic, an analysis of the breeding density of 43 avian species with respect to distance away from the roadway revealed that: (1) 60% of study species exhibited reduced population densities near roadways, (2) noise was the best predictor of this pattern, (3) visibility of road traffic did not predict population densities and (4) species varied with respect to population patterns along roadways (Reijnen et al., 1995). Similar correlative data have been provided by others (Forman & Deblinger, 2000; Rätty, 1979; Reijnen et al., 1996; Summers, Cunnington & Fahrig, 2011). Having identified traffic noise and not visibility of traffic as the best predictor, Reijnen and

colleagues (1995) were among the first to suggest that traffic noise was the causal variable responsible for the many population and behavioral changes occurring near roads.

### ***B. Traffic noise assumed then tested***

The assumption that traffic noise was responsible for the differences in avian behavior occurring along roadways persisted for several reasons. Arguably the main reason was because of the potential for traffic noise to mask vocal communication, which for many avian species, particularly songbirds, is imperative to aspects of daily life and survival (Catchpole & Slater, 2008; Knight, 1974). Warren and colleagues (2006) identified four related arguments used to support this assumption: (1) The visual stimuli of roads and cars were not believed to be significant factors influencing density and diversity of avian populations as these measures were reduced beyond visibility of roads (Reijnen & Foppen, 1994, 1995). (2) Avian diversity was often lower in noisier habitats (Stone, 2000). (3) Birds forage in roadside habitats, but do not breed there (Forman et al., 2002). (4) Birds with higher frequency songs are more abundant near roads (Rheindt, 2003).

Several groups utilized natural experiments to test the relationships among noise, breeding success, population density and masking. One such study reported that ovenbirds (*Seiurus aurocapilla*) breeding in a habitat permeated by continuous industrial noise consisted of mostly inexperienced birds who exhibited a significant reduction in pairing success compared to conspecifics of similar male quality in habitats of similar structure and quality without noise (Habib et al., 2007). With regard to population structure, there appear to be mixed results. Whereas both density and diversity were reduced along roads (Rheindt, 2003), only a reduction in species diversity was recorded in active compared to inactive gas-well compressor sites (Francis, Ortega & Cruz, 2009).

With regard to masking, as predicted by Reijnen and colleagues (1995), birds closer to the roadway produced songs with higher dominant frequencies (Rheindt, 2003). Rheindt suggested that traffic noise may be affecting roadside avian population structure by driving away species with lower-frequency songs and attracting lower-quality males who could not hold higher quality territories. However, as suggested from early hearing studies, communication in noise may be improved by a number of mechanisms including adjustments to amplitude, frequency or temporal characteristics of signals (Dooling, 1982; Klump, 1996; Brumm & Slabbekoorn, 2005).

### ***C. Changing vocal signals in noise***

As shown by Brenowitz (1982a,b), signal detection in noise is dependent upon the signal-to-noise ratio. Increasing the amplitude of a vocal signal in noise is referred to as the Lombard effect (Lombard, 1911; as cited in Warren et al., 2006). Common nightingales, zebra finches (*Taeniopygia guttata*) and domestic fowl (*Gallus gallus domesticus*) are able to amplify their vocal signals in the presence of high levels of broadcasted white noise (Cynx, Lewis, Tavel & Tse, 1998; Brumm & Todt, 2002; Brumm, Schmidt & Schrader, 2009). Increases in signal amplitude have also been reported for the blue-throated hummingbird (*Lampornis clemenciae*) when inhabiting areas of high levels of natural ambient noise, like running water (Pytte, Rusch & Ficken, 2003). For nightingales, amplifying signals seems to be common as those communicating in areas of high traffic noise increase the amplitude of the vocal signals compared to those vocalizing in quieter areas (Brumm, 2004).

In addition to singing louder, birds may adjust the frequency parameters of a signal to increase signal detection. Signalers may shift the frequency structure of their vocal signals out of the frequency range of background noise (Ficken et al., 1974). The little greenbull (*Andropadus*

*virens*) sings at lower frequencies in habitats with naturally occurring high-frequency background noise (Slabbekoorn & Smith, 2002). Similar trends have also been recorded in response to pre-existing anthropogenic noise for great tits (*Parus major*) (Slabbekoorn & Peet, 2003; Slabbekoorn & denBoer-Visser, 2006; Mockford & Marshall, 2009), song sparrows (Wood & Yezerinac, 2006), dark-eyed juncos (Slabbekoorn, Yeh & Hunt, 2007) and European blackbirds (Ripmeester, Kok, van Rijssel & Slabbekoorn, 2010). However, the best evidence for a noise-dependent shift in signal frequency comes from an experimental study. While supporting evidence that birds near roads sing with higher minimum frequencies, Verzijden and colleagues (2010), were the first to show that experimental exposure to highway noise causes an immediate shift in song structure to higher frequencies. Further, this shift appears to be a short-term response as songs returned to pre-exposure levels the following day (Verzijden et al., 2010).

If vocal plasticity is limited, meaning that shifting the frequency structure of vocal signals is impossible, then signalers may selectively use signals or signal components that are inherently resistant to masking because of their frequency structure. Tonal signals with limited frequency modulation are particularly resistant to environmental factors reducing propagation (Lohr et al., 2003). Great tits, although not limited by a lack of vocal plasticity, quickly responded to the experimental presentation of different types of urban background noise by switching to and singing songs outside of the noise's frequency range for longer bouts (Halfwerk & Slabbekoorn, 2009).

A third option is to adjust temporal characteristics of vocal behavior. One of the most extreme examples exists in the European Robin (*Erithacus rubecula*) which has shifted from diurnal to nocturnal singing, when noise levels are lower (Fuller, Warren & Gaston, 2007). Signaling during times of reduced background noise has also been documented in common

nightingales (Brumm, 2006), least flycatchers (*Empidonax minimus*) and red-eyed vireos (*Vireo olivaceus*) (Ficken et al., 1974) who adjust the timing of their singing to avoid acoustic interference from the songs of other nearby species. Producing signals at a higher rate (Buckstaff, 2004; Doyle et al., 2008), of longer duration (Dooling, 1979, 1980; Foote, Osborne & Hoelzel, 2004), and in a repeated bout (Brumm & Slater, 2006) have also been suggested as methods to enhance communication in noisy habitats.

## **VII. Opportunities for advancing the study of anthropogenic noise**

The effect of traffic noise on birds is one of the most well studied areas within the field of anthropogenic disturbances. Unfortunately the list of related responses, processes and mechanisms that we do not have a firm understanding of is even longer. These areas in need of research have been prioritized by several different authors (e.g. Barber et al., 2009; Dooling & Popper, 2007; Kaseloo & Tyson, 2004; Ortega, 2012; Patricelli & Blickely, 2006; Warren et al., 2006). The areas of research that I considered to be the most imperative to address were used to guide the development of this dissertation work. These research objectives are listed below and discussed in turn.

### ***A. Research Objectives***

1. Isolate traffic noise as a causal variable using experimental methods and externally-valid acoustic stimuli modeled after real world exposures

Although several studies have assumed or used correlative data to imply that anthropogenic noise is the causal factor in a myriad of relationships between anthropogenic stimuli and population structure or behavior, few have directly and experimentally tested for



such an effect. A recent study by Verzijden and colleagues (2010) is important for several reasons. First, it provided experimental evidence of a noise-dependent frequency shift in a song, and that, for the chaffinch (*Fringilla coelebs*), this is a rapid response activated within the first 10 songs produced after noise exposure begins. Second, the acoustic stimulus and the amplitude at which it was presented to the birds was authentic, mimicking real-world exposures. However, like many other efforts, the methodology used creates two additional, albeit unlikely, variables that may have influenced the results. By using recordings of traffic noise as the experimental stimulus, this study cannot completely rule out the impact of confounding variables included in recordings of traffic noise, like wind, amplitude modulation, sounds of predators, conspecifics or heterospecifics. Additionally, there is a temporal disconnect between the experimental exposure to noise used in many studies and real world exposures. Traffic noise is an almost constant sound stimulus in many habitats, not an acute stimulus. While providing important experimental evidence, the results of Verzijden and colleagues (2010) were collected from birds subjected to acute exposures to traffic noise.

It is unlikely that any effort will provide complete control over all potential secondary variables, but future research may control for some of these effects by taking different approaches and carefully considering the aspects of stimuli to be tested. For example, traffic noise is characterized by its frequency range and distribution of energy from 2 to 4 kHz. By broadcasting a sound modeled to these same acoustic parameters, one can isolate these characteristics and determine the effect without any influence from confounding variables. After such a test, using recordings of traffic noise as the experimental stimulus would not be as problematic as the responses to the two acoustic stimuli can be compared and used as controls for one another. Additionally, as many birds are subjected to some level of traffic noise for 24

hours a day, with the peak of activity during the daylight hours, it is imperative that the long-term effects be addressed and tested for. In order to conduct such a study, subjects would almost certainly need to be captive to allow continuous or long-term exposures, a context that presents potential confounds of its own. However, by sequentially ruling out different secondary confounds, future research can significantly improve the methods used to study traffic noise and the knowledge gained from such efforts.

## 2. Expand the taxonomic diversity of species used as study subjects

Our in-depth knowledge of species-specific responses to noise is limited to a few popular study subjects like the great tit (*Parus major*). One specific suggestion to remedy this problem was to sample from each of the main avian taxa (Ortega, 2012). Birds are the most heavily studied species with regard to the effect of traffic noise; expanding this suggestion beyond avian species and toward other reptiles, mammals, amphibians, etc. would also be beneficial. However, it may be more important that we ensure that research efforts are including a range of species with different life history characteristics, as they heavily influence response to disturbances (Sauvajot, Buechner, Kamradt & Schonewald, 1998).

While some may argue that specific attention should be paid to species most likely to be seriously affected by traffic noise, it cannot be stressed enough that it is also imperative to study species who appear to be doing relatively well in disturbed and undisturbed areas. By studying and comparing the behavior of both at-risk and disturbance-tolerant species we may be able to detect specific attributes that predict tolerance or intolerance. Such information is likely to assist wildlife managers in identifying and prioritizing conservation efforts for specific species.

### 3. Address the effects of noise on behavior other than communication

A majority of the work addressing the effects of anthropogenic noise on avian behavior focuses on vocal communication. This focus on communication is likely a result of the nature of the disturbance and species in question. Because traffic noise is an acoustic stimulus, logically, it is most likely to affect vocal communication and hearing. Birds, especially songbirds, are known for their use of vocal signals in maintaining social, territorial, dominance and mating relationships that are imperative to fitness (Catchpole & Slater, 2008). However, noise may also be affecting non-vocal behavior (Barber et al., 2009).

This focus on communication is limited, mostly, to the more recent avian studies. Many of the earlier studies focused on population-level behaviors and often implicated traffic noise as the variable responsible for the systematic differences in density, diversity and pairing success of avian populations near roadways. It is (almost) impossible to set up two experimental forests filled with all the avian species typical of that ecosystem and then expose one of them to traffic noise while holding the other as a control. A second, and more practical, option is to test for effects of traffic noise on behaviors that influence population demographics. Since diversity, density and mating success are directly influenced by social interactions, risk taking and communication, among other behaviors, we may gain insight into how noise affects these larger systems by testing for the effects of noise on these behaviors.

Some of the most interesting responses to noise are found in social behavior. Cetaceans generally avoid areas with higher levels of boat noise, but if noise increases in their immediate vicinity dolphins and whales have both been shown to reduce inter-individual distances while increasing vocal and non-vocal social behaviors such as synchronized breathing, production of signature whistles and group travel (Hastie et al., 2003; Buckstaff, 2004; Williams et al., 2006;

Nowacek et al., 2007). While generally unstudied in birds (see Chapter 2), lab work has shown that exposure (80 min) to high levels of background noise alters normal social behavior by eroding pair preferences in finches (Swaddle & Page, 2007). This effect may be a result of masking which has negatively affected pairing behavior in other species (Bee & Swanson, 2007) or distraction caused by the relatively sudden presence of noise (Chan et al., 2010). Following the experiment, finches were reunited with their previously established pair and mated without any further disturbances resulting from the exposure to noise (Swaddle & Page, 2007), suggesting that the effect of noise on pair preferences was short-term. Future research should further investigate the potential for traffic noise to affect social behaviors as changes to these systems may shed light on the factors influencing avian diversity and density along roadways.

#### 4. Identify the effects of noise on non-song signals and signal use

For reasons previously discussed, the study of anthropogenic noise has focused on the potential effects on avian vocal communication. For most species, song is the most common vocal signal and arguably the signal that is the most important with regard to survival (Catchpole & Slater, 2008). However, one group of songbirds bends this pattern. Birds of the Paridae family, specifically the chickadees, tits and titmice, use an extraordinarily complex call in a wide range of social, territorial, feeding, threat and travelling contexts throughout the year (Lucas & Freeberg, 2007; Krams, Krama, Freeberg, Kullberg & Lucas, 2012). It is essential to measure the effects of noise on call systems, especially if they influence survival at such a broad level, like the chick-a-dee call. The initiative has been taken, as Leonard & Horn (2008) have reported that increased levels of background noise alter the vocal behavior of nestlings, but many more studies are needed.

In the presence of noise, animals may modify their vocal signals in *at least* two ways: by adjusting the acoustic structure of the signal, and, or by changing the manner in which a signal is used (Doyle et al., 2008; Wilson & Mennhill, 2011). To date, we have accrued a large amount of evidence for the first option, suggesting that at least some species are capable of overcoming, at some level, the challenges posed to communication by noise via shifts in the frequency of vocal signals (Brumm, 2004; Brumm & Todt, 2002; Brumm et al., 2009; Halfwerk & Slabbekoorn, 2009; Mockford & Marshall, 2009; Nemeth & Brumm, 2009; Ripmeester et al., 2010; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn et al., 2007; Slabbekoorn & Peet, 2003; Wood & Yezernick, 2006). While these noise-dependent modifications are widely documented, we know very little about how the second option, call use, is used to enhance communication in noise (but see Fuller et al., 2007).

Call use can be described in a number of ways, including diurnal pattern, the function of signals in differing contexts, 'information' content (quantitative unit of entropy or uncertainty resulting from the organizational rules of a communication system describing the amount of freedom a signaler has when choosing a message, Shannon & Weaver, 1949), rate of production, and note-type composition of the signal (Doyle et al., 2008; Wilson & Mennhill, 2011). Any of these characteristics of signal use can be altered to encode different messages or to modify a signal in the presence of noise. Rarely has the effect of noise on the different measures of call use been studied; however recent data suggest that this aspect of vocal signaling is altered by the presence of noise just as frequently as the more well-studied frequency structure of vocal signals.

Although few studies address signal use, available data suggest that animals communicating in noisy channels do alter normative patterns of use, the most common being an increase in repetition of individual signal-types. For example, the common chaffinch (*Fringilla*

*coelebs*) inhabiting areas near running water have been recorded singing the same songs in longer bouts than conspecifics in quieter habitats (Brumm & Slater, 2006). Likewise, the little greenbull sings specific song-types that are outside of the range of background noise more often than those that overlap with present background noise (Slabbekoorn & Smith, 2002). Repetition of signals has also been documented when animals are in the presence of anthropogenic noise. When ship noise was louder and nearer, Humpback whales (*Megaptera novaeangliae*) repeated call-types and did so at a faster rate than when background noise levels were lower and ships further away (Doyle et al, 2008).

## 5. Document within-species variation in the response to noise

Enormous variation exists between the responses of different species to anthropogenic noise, even within the Class Aves. The range of this variation extends from thriving, as is common among urban species like great tits (Slabbekoorn & den Boer-Visser, 2006), European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*), (Marzluff, 2001), to avoidance of noisy habitats (Reijnen & Foppen, 1994, 1995; Forman et al., 2002; Rheindt, 2003). However, our knowledge about differential effects of noise between individuals of the same species is sparse. But, why would conspecifics be differently affected by noise? Geographic location, social experience, maturity, and sex are all sources of variation that may affect behavior or response to stimuli. For example, many have predicted that, as a function of their respective roles, individuals of differing dominance statuses or syndrome types behave differently in response to similar stimuli or contexts (Ekman, 1987; Ekman & Askenmo, 1984; Evans, Boudreau & Hyman, 2009; Gosling, 2001; Sih, Bell & Johnson, 2004; Waite, 1987). Indeed, dominance predicts the location of a bird within a flock (Zanette & Ratcliffe, 1994), the time it spends scanning for predators (Krams, 1998), its latency to approach a novel object or arrive at a

food source (de Leat, 1985), latency to return to normal behavioral patterns following detection of a predator (de Leat, 1985), and exploratory behavior (Fox, Ladage, Roth & Pravosudov, 2009). Intra-specific variation in behavior is clearly present along the dominance/subordination continuum, predicting the behavior of individuals in a range of contexts; subsequently, similar measures of within species variation may also predict response to noise.

## 6. Measure how long the effects of noise persist beyond exposure

To date, our knowledge of the effects of anthropogenic noise is very limited with respect to temporal properties. How much exposure is required to elicit different behavioral effects? How long do the effects of noise persist following the end of exposure? Are responses to noise short-term solutions? Do these acute responses have any long-term effects on the individual, group, species or offspring? Likewise, in the case of chronic exposure, are responses short-term or permanent and capable of affecting survival or speciation? Currently there are more questions than answers with regard to this topic. One practical context worthy of investigation is the occurrence of rush hour. In a habitat where traffic noise is omni-present, many species may habituate to the presence of traffic noise at moderate levels. However, how does a short increase in the amplitude of traffic noise affect behavior, how long do those effects last, and can birds habituate to this acute increase in noise if it happens on a regular basis?

## **VIII. Aims of the current dissertation research**

The overarching aim of this dissertation research was to provide original and primary data that would advance the study of traffic noise and its effects on wildlife. More specifically, I wanted to isolate and test traffic noise as a single, causal variable using a meaningful exposure paradigm. In choosing a study species I aimed to expand the taxonomic diversity of avian species within the traffic noise literature. The focus on socio-behavioral responses to traffic

noise was chosen because social behavior and non-song vocal signals are underrepresented within the traffic noise literature and because they are imperative to survival of the study species. And finally, this work was designed to address how individual variation may alter the effects of traffic noise on behavior and to determine how long the effects of traffic noise persist beyond exposure periods. To address these aims, I conducted two experiments. The first experiment is split into two analyses (Chapter 2 & Chapter 3). Each experiment was designed to address a subset of these goals (Table II).

The dissertation research presented herein tests for the effects of traffic noise on the social behavior of tufted titmice (*Baeolophus bicolor*). The tufted titmouse is a North American songbird common to the South-Eastern Region of the United States, including Eastern Tennessee (Grubb & Pravosudov, 1994). In addition to convenience and the species' local abundance, the titmouse was chosen as the study species because it represents an ideal study system to address questions about anthropogenic noise and social behavior. This species lives in habitats with varying levels of natural and anthropogenic noise (Grubb, 1998; Grubb & Pravosudov, 1994), indicating it has a moderate level of tolerance for disturbance. Tolerance is a life-history strategy currently under-represented within the literature on anthropogenic noise (Ortega, 2012).

One of the best predictors of a species' response to anthropogenic noise is the degree of overlap between noise and its perceptual world (Barber et al., 2009). Traffic noise exists below 4 kHz with a majority of its energy between 2 and 3 kHz (Figure 1). Tufted titmice share a similar 'optimal' hearing range with other songbirds (1.75 - 3.5 kHz), which means that like other species, titmice hear best within the lower frequency ranges that overlap with traffic noise. This aspect of titmouse hearing suggests that traffic noise is likely to be a significant presence within the acoustic environment, making it an ideal study species.



All research was conducted between the months of October and March in the years 2009 - 2010, 2010 - 2011, and 2011 - 2012. These months were chosen for logistical, methodological and ethical reasons. Logistically, wild titmice are more likely to enter walk-in treadle (potter) traps baited with seed during the overwintering months as live and natural food sources are restricted. As mentioned, this research aims to test the effects of traffic noise on social behavior; titmice are arguably more social during the winter months than spring and summer when pairs of titmice are courting, mating, and raising young (Grubb & Pravosudov, 1994). Conducting this research during the spring and summer months may interrupt or negatively affect the ability of titmice to reproduce or produce successful young. Additionally, during this period this species spends a majority of its time singing rather than producing their chick-a-dee call. In contrast, during the overwintering months pairs of titmice relax territoriality and come together with neighboring pairs of titmice and other species, including chickadee, nuthatch and woodpecker species, to form mixed-species flocks (Morse, 1970). During this time mixed-species flocks live, travel, forage, and defend their territories and members against intruders and predators (Grubb & Pravosudov, 1994; Morse, 1970; Mostrom, Curry & Lohr, 2002). The chick-a-dee call is one of the most common vocal signals produced by titmice during this time (Grubb & Pravosudov, 1994). The social structure of these flocks and the behavior of titmice have been shown to influence the success and survival of flock members (Contreras & Seiving, 2011; Dolby & Grubb, 2000; Fernández-Juricic & Kacelnick, 2004; Hetrick & Seiving, 2011; Lima & Zollner, 1996; Quinn & Cresswell, 2005). To maintain this important mixed-species social context (Grubb and Pravosudov, 1994; Mostrom et al., 2002), titmice that served as subjects in the current research were always housed with Carolina chickadees, a common associate of the titmouse in mixed-species flocks (Owens et al., 2012; Chapter 2).

Upon capture chickadees and titmice were banded with individually identifying combinations of colored leg bands and their wing-chord measurements (based on wing-chord sexing described by Thirakhupt, 1985; see also Owens & Freeberg, 2007) and approximate age were recorded. These data were used to determine suitability of a bird for inclusion in the study. I designed study flocks to mimic the social and demographic aspects of normal over-wintering flocks for both species (Grubb & Pravosudov, 1994; Mostrom et al., 2002). Each study flock was to consist of an equal number of males and females, contain 4 chickadees and 4 titmice, all adults ( $> 1$  year) that were captured from the same territory. In addition to maintaining normal social contexts, these controls were put in place to limit variation in demographic factors, like age or sex, that could influence subjects' behavior.

For both studies, it was important to take an ethological approach to address the effects of traffic noise. In an effort to balance the pros and cons of laboratory and field work, while maintaining some aspect of the birds' normal social context, data were collected while subjects were housed in large outdoor aviaries with familiar conspecifics and heterospecifics from their natural flocks. For the first experiment, subjects were assigned to a noise or control condition. Both were identical, with the exception that those subjects in the noise condition were exposed to 8 hours of simulated traffic noise / day. Simulated traffic noise was produced using Brownian noise (generated at intensity = 24 and Butterworth Low-pass filtered at 2 kHz in Cool Edit Pro v. 2.0), because it closely parallels the frequency range and spectral characteristics of actual traffic noise, while omitting confounding variables, such as wind noise, that occur in recordings of traffic noise. Data were collected using focal follows and focal point sampling. Dependent measures for this study consisted of agonistic interactions used to define study flock dominance structures, three measures of sociality, and one measure of chick-a-dee calling behavior. Social

behaviors were addressed in Chapter 2. Chick-a-dee calls were analyzed for effects of noise on information content, call rate and note-type composition. Dominance status was used to determine whether subjects of separate statuses responded differentially to noise. Chick-a-dee and dominance analyses are addressed in Chapter 3.

The second experiment was designed to address 'rush hour' (Chapter 4). Titmice were trapped and housed in the same manner as experiment one. Noise exposure in this study consisted of real traffic noise recorded from three different locations along a busy 4-lane highway. Each day subjects were exposed to 2.5 hours of traffic noise, and were observed before, during and after exposure. Dependent measures were identical to the social behavioral measures in study 1. Each aviary flock was exposed to noise and control conditions with the intention of comparing behavior using a within-subjects, repeated measures ANOVA.

Each data chapter contains a short literature review, materials and methods and a combined results and discussion section. Within the results section I present the customary  $F$  and  $p$ -value statistics, followed by partial-eta squared ( $\eta^2$ ) and observed power ( $P$ ) statistics. Partial-eta squared is a measure of effect size which describes the amount of total variation (effect + error) explained by the independent factor. This statistic allows a discussion of the statistical and biological significance of effects. The observed power statistic identifies the ability of an analysis to detect an existing effect. If an analysis returns a non-significant result and  $P \geq 0.800$ , then it is reasonable to conclude that there is no effect of the independent variable on that dependent measure. However, if an analysis returns a non-significant result and  $P \leq 0.799$  then one can not conclusively state that an effect is non-existent, as the test had a 21% chance of failing to detect an existing effect.

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## **APPENDICES**

## **APPENDIX A**

### **TABLES**

**Table I.** Definitions of terminology

Term	Definition Used Here	Reference
Anthropogenic	Of, related to, or resulting from the influence of humans on nature; referring to anything of human origin or design  *anthropogenic context, disturbance, stimuli, variable, noise	Anthropogenic. (n.d.). In Merriam-Webster's online dictionary (11 <sup>th</sup> ed.). Retrieved from <a href="http://www.merriam-webster.com/dictionary/anthropogenic">http://www.merriam-webster.com/dictionary/anthropogenic</a>
Attenuation <sup>A</sup>	Progressive decrease in signal intensity resulting from spherical spreading	Peterson & Gross, 1967; Forrest, 1994
Degradation <sup>A</sup>	Structural changes to a signal from reflection, refraction, attenuation	Morton, 1986; Bradbury & Vehrencamp, 1998
Disturbance	(1)The act of disturbing.  (2)To disturb is to interfere with, alter the position or arrangement of, or upset the natural balance of a thing or system.  *anthropogenic disturbance, acoustic disturbance	(1) Disturbance. (n.d.). In Merriam-Webster's online dictionary (11 <sup>th</sup> ed.). Retrieved from <a href="http://www.merriam-webster.com/dictionary/disturbance">http://www.merriam-webster.com/dictionary/disturbance</a>  (2) Disturb. (n.d.). In Merriam-Webster's online dictionary (11 <sup>th</sup> ed.). Retrieved from <a href="http://www.merriam-webster.com/dictionary/disiturb">http://www.merriam-webster.com/dictionary/disiturb</a>
Noise <sup>B,C</sup>	A sound that is subjectively defined as unwanted, or that interferes with another stimulus or activity.	Dooling & Popper, 2007; Noise. (n.d.). In Merriam-Webster's online dictionary (11 <sup>th</sup> ed.). Retrieved from <a href="http://www.merriam-webster.com/dictionary/noise">http://www.merriam-webster.com/dictionary/noise</a>
Sound <sup>B</sup> ,	Auditory sensations resulting from vibrations moving through air, water or other medium	Dooling & Popper, 2007
Traffic noise <sup>C</sup>	Sound resulting from vehicular travel along any path including freeways, highways, streets, trails	Dooling & Popper, 2007

**Table I. Continued**

Term	Definition Used Here	Reference
Urban	Any human built or densely populated area and rural or natural lands where roadways extend	Warren, Katti, Ermann& Brazel, 2006

—\*Examples of commonly used words including the defined term

<sup>A,B,C</sup> Terms often used interchangeably within the literature. Attempts were made to differentiate terms and specify appropriate usage within these dissertation chapters.

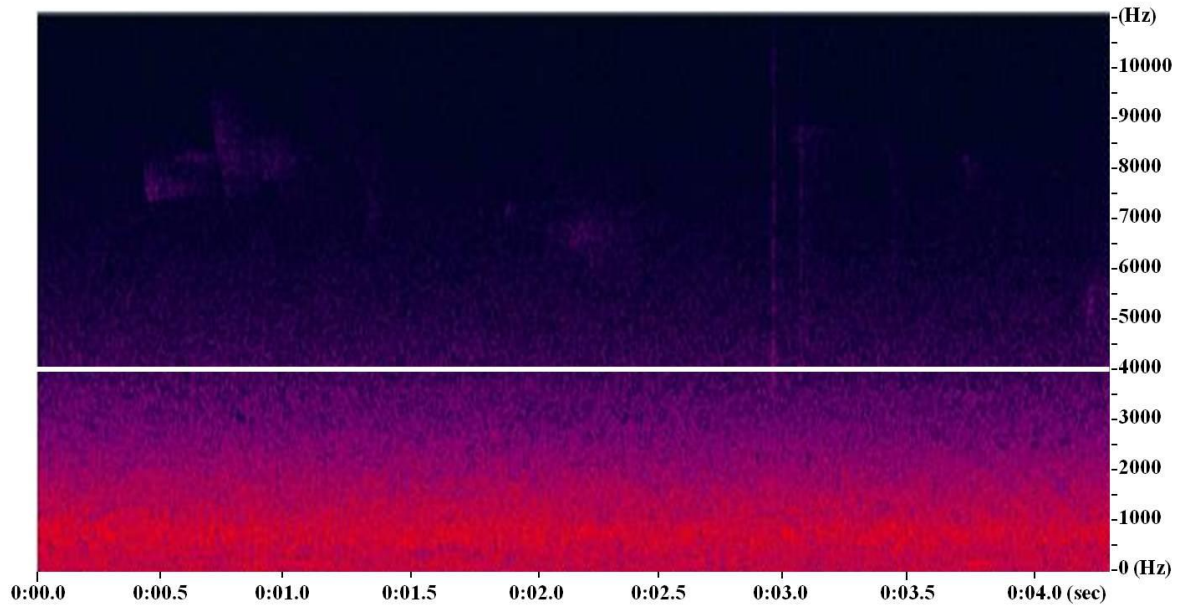


**Table II.** Design details of experiments. For experiment 1 and 2, the experimental stimulus, exposure type and dependent measures are listed. Note that experiment 1 includes two columns which represent the two analyses resulting from that experiment. Below these details the 6 aims of this research are listed in the left column. To the right of each aim is an "X" if that analysis or experiment addresses that aim.

	Experiment 1		Experiment 2
Experimental Stimulus:	Simulated Traffic Noise	Simulated Traffic Noise	Recorded Traffic Noise
Exposure Type:	Chronic	Chronic	Rush-Hour
Dependent Measures:	Social Behavior	Dominance & Call Use	Social Behavior
Chapter of Dissertation:	2	3	4
Aims			
Isolate traffic noise as causal variable; realistic exposure paradigm	X	X	
Expand taxonomic diversity	X	X	X
Effects of traffic noise on non-vocal behavior	X		X
Effects of traffic noise on non-song vocal behavior		X	
Individual variation in response to traffic noise		X	
Duration of traffic noise effects			X

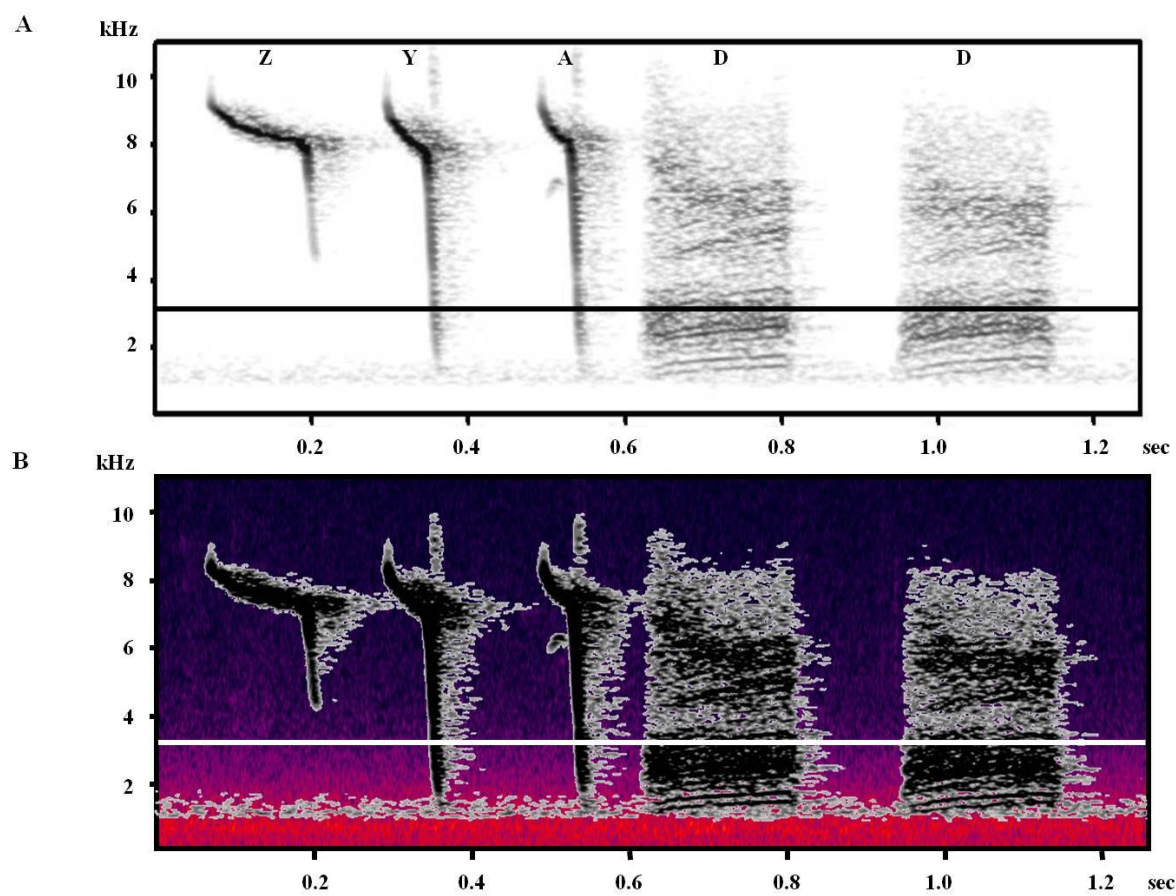
## **APPENDIX B**

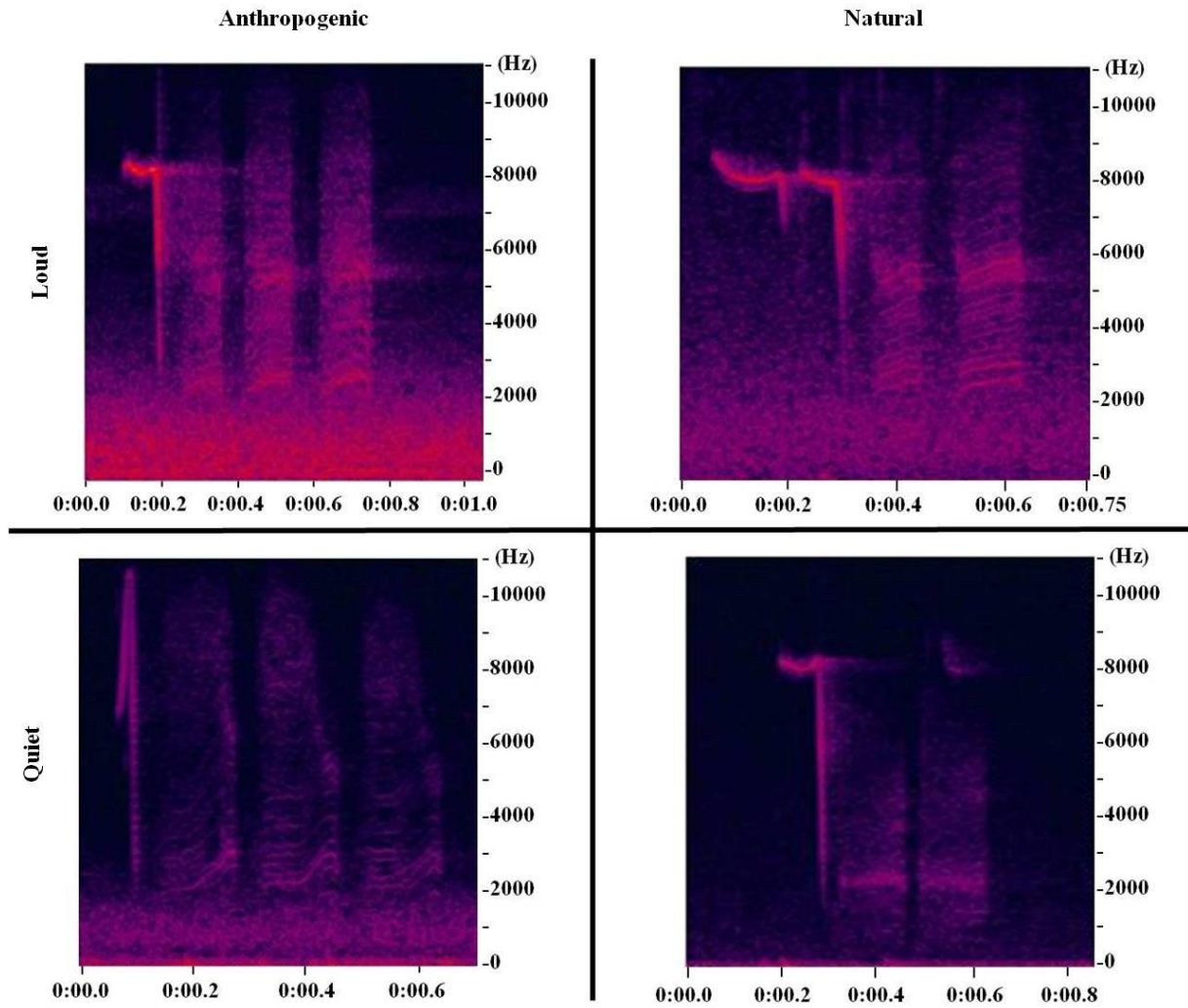
### **FIGURES**



**Figure 1.** Spectrogram of 4.5 sec of traffic noise recorded 100 m from the shoulder of a 4-lane highway ( $\bar{x} = 2043$  cars/daylight hour). Brighter colors on the spectrogram indicate higher amplitudes. The horizontal white line illustrates the upper frequency limit of traffic noise. Sound above that line is not traffic noise.

**Figure 2.** The potential problem masking causes for communication with spectrograms of a typical call produced by a tufted titmouse. Note-type composition of the call, "ZYADD," appears within the top of Figure 2A. (A) The call was recorded in a quiet habitat with minimal background noise. The black line is meant to draw attention to the concentration of energy in the last two notes of the call. (B) The call from A was cut from its original black and white spectrogram and layered on top of a spectrogram traffic noise recorded 100 m from a roadway. The white line shows the upper limits of background noise resulting from traffic noise. Note that the bright pink color indicates loud levels of low-frequency traffic noise in this habitat up to about 3 to 4 kHz. The white line mimics the black line from A. If this call had been produced in the latter habitat shown in B then the majority of those last two notes may have been masked by the traffic noise.





**Figure 3.** Diagram of four spectrograms, each showing a chick-a-dee call produced by a tufted titmouse in varying levels of traffic noise and natural background noise. Loud noise consisted of sound pressure levels  $> 70$  dB. Quiet noise was  $< 50$  dB.

## **CHAPTER 2**

### **SIMULATED TRAFFIC NOISE INCREASES SOCIAL BEHAVIOR OF TUFTED TITMICE (*BAEOLOPHUS BICOLOR*)**

This chapter is a revised version of a published manuscript:

Owens, J.L., Stec, C.L., O'Hatnick, A. (2012). The effects of extended exposure to traffic noise on parid social and risk-taking behavior. *Behavioral Processes*, 91, 61-69.

doi:10.1016/j.beproc.2012.05.010

My contributions to this work include (a) formulating the research idea, question and hypothesis, (b) training and organizing research assistants (c) designing the experiment (d) building the sound equipment and maintaining the set-up (e) obtaining and caring for subjects, (f) collecting data on social behavior, (g) organizing and conducting statistical analyses, (h) interpreting results and (i) writing of the manuscript and submission for publication. C. L. Stec assisted with husbandry and collection of approximately 25% of the social data as part of Psychology 489. A. O'Hatnick conducted a multi-stimulus presentation to assess risk-taking behavior as a continuation of earlier work by Ellen Harvey Williams.

For inclusion in this dissertation, several revisions have been made to the original manuscript. The writing has been supplemented with additional literature and revised for brevity. The results and discussion have also been combined and are followed by a section on considerations, contributions and conclusions. The risk-taking aspect of the study, conducted by AOH, has been removed because this test was inconclusive with regard to the predictions of the hypotheses tested and the effects of noise. Details regarding this aspect of the study are included in the published manuscript.



## ABSTRACT

This study provides the first experimental evidence of the effects of long-term exposure to simulated traffic noise on social behavior. Subjects were wild-caught Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) that were socially housed in mixed-species flocks. Half of the 16 study flocks were exposed to 8 hours of simulated traffic noise per day, while the other half were held as controls with no exposure to noise. Data collected were nearest neighbor distance (NND), rates of perching within one meter of a flockmate and conspecific-preference for perch-mates. Analyses revealed that noise increased sociality by reducing NNDs and increasing the number of close-perches within study flocks. These behavioral responses mimic those of species in high-risk situations, such as birds in the presence of a predator.

## CHAPTER 2

### SIMULATED TRAFFIC NOISE INCREASES SOCIAL BEHAVIOR OF TUFTED TITMICE (*BAEOLOPHUS BICOLOR*)

#### I. Introduction

Anthropogenic disturbances, by definition, are generally disruptive to a range of species, including: anurans (Eigenbrod, Hecnar & Fahrig, 2008, 2009), birds (Stalmaster & Newman, 1978), carnivores (Kerley et al., 2002), cephalopods, (Andre et al., 2011), cetaceans (Nowacek, Thorne, Johnston & Tyack, 2007), insects (Frings, 1959), plants (Francis, Kleist, Ortega & Cruz, 2012), primates (de la Torre, Snowdon & Bejarano, 2000), reptiles (Rudolph & Burgdorf, 1997) and ungulates (Borkowski et al., 2006). In comparing the potential costs (i.e. expended energy vs. death / injury), one of the safest tactics is to respond to any disturbance as a potential threat (i.e. Haftorn, 2000). Indeed, many studies have documented that the response of different species to anthropogenic disturbances imitate those elicited by a predator (Beale & Monaghan, 2004; Blumstein, 2006; Frid & Dill, 2002; Gill, Sutherland & Watkinson, 1996).

Many responses to anthropogenic disturbance are variations of fleeing, alerting or anti-predator behavior (Blumstein, 2006; Frid & Dill, 2002); however, a closer look at the literature suggests that responses to acute disturbances differ drastically from responses to chronic disturbances. For example, when presented with a short sample of motor noise terrestrial hermit crabs were distracted, resulting in delayed response to an approaching predator model (Chan, Giraldo-Perez, Smith & Blumstein, 2010; see also Chan, Stahlman et al., 2010). In contrast, the presence of chronic noise from active wind-turbines caused sciurids to be hyper-alert, resulting

in higher levels of vigilance and cautious behavior in response to conspecific alarm calls (Rabin, Coss & Owings, 2006; see also Kikuchi, 2008). The results of these studies draw attention to a fundamental difference in the potential effects of anthropogenic noise. Short-term, acute or unfamiliar disturbances often cause alerting, starting or flight responses (Burger, 1981; Klein, Humphrey & Percival, 1995; Stankowich & Coss, 2009), where chronic stimuli allow for habituation and sensitization, in that alarm responses dissipate and vigilance is upregulated. One effect of habituation may be the ability to respond to stimuli in more adaptive ways. Although generally resistant to habituation (Kastelein et al., 2000; Pfeifer & Goos, 1982), animals can acclimate to acute disturbances (Bisson, Butler, Hayden, Romero & Wikelski, 2009; Maes & de Groot, 2003), as observed in white-tailed deer (*Odocoileus virginianus*) (Behrend & Lubeck, 1968), elk (*Cervus canadensis*) (Schultz & Bailey, 1978) and birds (Klein et al., 1995). This process of habituation may be a key aspect of the differential effects of acute vs. chronic noise.

This distinction has consequences for the theoretical framework used to understand the effects of anthropogenic disturbances. For example, considering that the presence of chronic noise creates hyper-vigilant subjects that were arguably 'primed' to respond to a threat, the Distracted Prey Hypothesis (Chan, Giraldo-Perez et al., 2010; Chan, Stahlman et al., 2010; Chan & Blumstein, 2011), which argues that noise distracts organisms from immediately important behavior, may be more specific to acute disturbances. In response to these data, I proposed an alternative hypothesis to explain the effects of anthropogenic noise (Owens, Stec & O'Hatnick, 2012). The 'Increased Threat Hypothesis' (ITH) is an extension of the Risk-Disturbance Hypothesis (Frid & Dill, 2002) in that it uses the assumption that disturbance is functionally analogous to predatory risk in an effort to explain how chronic noise affects behavior. Contrary to the Distracted Prey Hypothesis, the Increased Threat Hypothesis argues that chronic or

familiar noise raises the perceived level of threat within an environment or context, increasing reactive and possibly baseline levels of anti-predatory behavior.

Traffic noise is one of the most noticeable and least understood forms of chronic anthropogenic noise in urban, suburban and rural areas (Barber, Crooks & Fristrup, 2009; Forman, 2000; Riitters & Wickham, 2003). Its presence changes the acoustic space of a habitat (Bee & Swanson, 2007; Dooling, 1980; Klump, 1996) by increasing the amplitude of background noise within lower frequencies (Barber et al., 2009) and interfering with the active space of other sounds, like vocal signals (Brumm & Slabbekoorn, 2005). Thus far, experiments using traffic noise or simulated traffic noise have focused on its effects on vocal communication (Bermúdez-Cuamatzin, Ríos-Chelén & Garcia, 2011; Verzijden, Ripmeester, Ohms, Snelderwaard & Slabbekoorn, 2010). In comparison to noise and vocal behavior, we know relatively little about the effects of traffic noise on non-vocal behavior (Barber et al., 2009). In the current study I tested for the effects of simulated traffic noise on the social behavior of two North-American songbirds, the Carolina chickadee (*Poecile carolinensis*) and the tufted titmouse (*Baeolophus bicolor*) while assessing the predictions of the Increased Threat Hypothesis proposed earlier.

### ***A. Goals, expectations & predictions***

This research was designed with three goals in mind. (1) The first goal was to test for the effects of traffic noise. To avoid the potential influence of any confounding acoustic variables associated with real-world traffic noise, I chose to use simulated traffic noise as the experimental stimulus in this study. This stimulus mimicked the frequency-structure, amplitude and duration of exposure for traffic noise present within the habitat of the study species. (2) The second goal was to broaden the scope of traffic noise research by focusing on previously under-studied

behaviors and species. This aim functions to increase the usefulness of these data to applied fields like species conservation. First, increasing our knowledge of the diversity of behavioral responses to noise is likely to prove useful in noise abatement initiatives, conservation and wildlife management practices (Blumstein & Fernández-Juricic, 2010). Similarly, the second function is to broaden the range of species included in this type of research. While still new, the study of anthropogenic noise has thus far focused on a few species. To improve the diversity of species studied, Ortega (2012) suggests broadly sampling members of each taxa. Another method may be to study species from a variety of different life-history strategies (Blumstein, 2006; Sauvajot, Buechner, Kamradt & Schonewald, 1998). Similarly, I suggest that efforts should be made to study species in the center of the disturbance-tolerance continuum, as their responses may give insight to the behavioral or physiological "types" most able to cope with the introduction of a novel disturbance.

I selected Carolina chickadees and tufted titmice as the study species because they are an ideal study system. Chickadees and titmice are considered disturbance-tolerant because they are present within a range of habitats, from disturbed and undisturbed natural areas, as well as backyard feeders in urban and suburban areas and within parks (Grubb & Pravosudov, 1994; Mostrom, Curry & Lohr, 2002). As members of the Paridae family, chickadees and titmice share an extraordinarily complex social system marked by over-wintering mixed-species flocks that live, travel, forage, and defend their territories and members against intruders and predators (Ekman, 1989; Grubb & Pravosudov, 1994; Morse, 1970; Mostrom et al., 2002). Because their social structure influences the success and survival of both species (Contreras & Seiving, 2011; Dolby & Grubb, 2000; Fernández-Juricic & Kacelnick, 2004; Hetrick & Seiving, 2011; Lima & Zollner, 1996; Quinn & Cresswell, 2005) it is important to determine whether noise affects

aspects of their social lives. While there are many parallels between the behavior and life-histories of these study subjects, it is imperative to recognize any species differences that exist within their responses to disturbance. As such, I tested for any differential effects of noise between chickadees and titmice.

Finally, the third goal of this research was to assess the predictions of the Increased Threat Hypothesis with regard to the effects of chronic noise on social behavior. One method that birds use to reduce or manage threat is to join or increase the density of a social group (Elgar, Burren & Posen, 1984; Krause & Ruxton, 2002; Metcalf, 1984). These strategies have also been reported in several cetacean species (Hastie, Wilson, Tufft & Thompson, 2003; Nowacek et al., 2007; Nowacek, Wells & Solow, 2001; Williams, Lusseau & Hammond, 2006). To determine if traffic noise affects social behavior I measured nearest neighbor distance (NND), frequency of close-perch interactions and the strength of preference for conspecific close-perch partners. If long-term exposure to traffic noise increases threat as predicted by the ITH then I expected to see an increase in sociality indicated by a decrease in NND and an increase in the number of close-perches for noise subjects compared to those in control. The degree to which noise increases or decreases preferences for conspecific perch-partners will indicate whether noise increases sociality at a general level within the flock or specifically within species. Because the social lives of chickadees and titmice are so inter-connected during the over-wintering months, I predict that noise will reduce preferences for conspecifics in exchange close contact with any flockmate.

## II. Materials and methods

### *A. Research design*

This research was conducted at the University of Tennessee Forest Resources Research and Education Center (UTFRREC) from October 2009 to March 2010. During this time, study subjects are commonly involved in mixed-species flocks. Prior to their inclusion in this research, study subjects were free-living members of naturally occurring, mixed-species flocks at the UTFRREC or a North Knoxville residential area. Chickadees and titmice were obtained from these flocks using a walk-in treadle trap baited with a 1:1 mixture of safflower and black-oil sunflower seed. Birds were only eligible to be subjects if the background noise (consisting of natural and anthropogenic noise) measured at their site of capture was less than 55 dB, as measured using a General Radio Sound Pressure Level meter (1565-B series, A-weighting). This restriction was used to increase the likelihood that any effects detected here were due to the experimental exposure to noise and were not residual effects from previous experiences with anthropogenic noise.

Upon capture birds were banded with individually identifying combinations of colored leg bands and their wing-chord measurements and approximate age were recorded. These data were used to determine suitability of a bird for inclusion in the study. I designed study flocks to mimic the social and demographic aspects of normal over-wintering flocks for both species (Grubb & Pravosudov, 1994; Mostrom et al., 2002). Each study flock was to consist of 4 chickadees and 4 titmice, all adults ( $> 1$  year), captured from the same territory. For each species, we aimed to have at least one known male and one known female (based on wing-chord sexing described by Thirakhupt, 1985; see also Owens & Freeberg, 2007). Due to uncontrollable factors (higher numbers of titmice trapped than chickadees, weather, time restraints, etc), these

exact specifications were not always met. All study flocks contained 4 titmice, but due to variation in ability to trap chickadees, mixed-species study flock sizes ranged from 6 to 8 birds (Table I). Additionally, while all conspecifics within a study flock were trapped from the same location, heterospecific flockmates were occasionally obtained from nearby or distant sites (Table I). Although this variation in flock structure and composition was not planned a priori, it does mimic real-world variation in naturally occurring flocks (Grubb & Pravosudov, 1994; Mostrom et al., 2002).

Following capture, birds were transported to and housed with other subjects in large outdoor aviaries (6 m x 9 m x 3.5 m) located at the UTFRREC. Aviaries included several hanging perches, young trees, grass and an enclosed and roofed shelter area. Subjects were provided with ad lib access to a variety of fresh fruit and vegetables, live food and seed combinations. Vitamin supplemented water was also available ad libitum in several different locations within the aviaries. Background noise levels within each aviary consisted of natural and anthropogenic noise. The average SPL of this noise was similar across all four aviaries used to house subjects. For the two aviaries 550 m from the nearest roadway noise averaged 59.3 dB with a range of 48 - 82 dB. The second set of aviaries were located approximately 850 m from the nearest roadway and had an average background noise level of 54.9 dB, with a range of 49 - 65 dB. The high sound pressure levels reported (i.e. 82, 65 dB) resulted from naturally occurring noise such as wind moving through trees or falling leaves, not anthropogenic noise from surrounding roadways.

After the last subject was added to a study flock a 10-day acclimation period began, in which subjects were provided time to explore the aviary and establish social relationships with flockmates. During this time, subjects were exposed to observers, data collection practices and



equipment. The start of the acclimation phase also coincided with the beginning of experimental exposure for noise subjects. The sound stimulus used here was made from Brownian noise, which emphasizes low-frequencies, closely paralleling the frequency structure of actual traffic noise which is composed mainly of sounds below 2 kHz and 4 kHz. Using simulated traffic noise as the experimental stimulus also omits the influence of confounding acoustic variables like wind noise or animal sounds that are present in recordings of real traffic noise. I generated 4 different 60-minute sound files of Brownian noise (intensity = 24) filtered with a Butterworth Low-Pass filter (2 kHz) in Cool Edit Pro (version 2.0, Syntrillium Software, Scottsdale, Arizona). Sound files were stored as .WAV files on an iPod Nano (1st generation, Apple Inc.) and played two times each day in a randomized order. Traffic noise was broadcast through a 150-watt outdoor speaker (Bogen<sup>®</sup> Communications Inc., N.E.A.R. model A-6) located at a central position on the inside of the aviary wall about 2.5 m above the ground. This system was powered by connecting two deep-cycle, 12-volt marine batteries. Noise was broadcast during daylight hours (between 0700 - 1700 EST) for 8 hours each day (start time varied) at an average amplitude of 75 dB / SPL at 1 m from the speaker. Depending on a subject's position within the aviary and variation in the power-source or sound file, a subject was exposed to experimental noise ranging from 60 - 80 dB / SPL. Experimental exposure was modeled after characteristics of real traffic noise present in local titmouse and chickadee habitats located about 100 m from the shoulder of a 4-lane highway ( $\bar{x}$  = 2,043 vehicles / daylight hour; range = 1,176 - 2,460 vehicles / daylight hour).

Exposure to observers, equipment and data collection procedures were held constant for each study flock. Control and experimental subjects received the same treatment with exception of the presence of noise and speakers within the experimental aviaries. There was no indication

that the presence of speakers affected the distribution of subjects within the aviaries or their behavior. Subjects would often perch on or near speakers, even caching or retrieving food from the speaker. However, the presence of the observer likely had an effect on the distribution and behavior of subjects. Initial entry into an aviary appeared to be the most disruptive, as subjects often took flight, changed perch-location and vocalized. These responses were more mild following the 10-day acclimation period. Still, after entering an aviary, observers always waited 5 minutes before collecting any data. Further, when sitting in the aviaries observers minimized movements to avoid interfering with subject behavior. Following some time in captivity subjects would regularly approach and perch within a meter of an observer to call, preen, feed or forage, suggesting habituation to observer presence. Any effects of observers were balanced between experimental condition and equally present in all study flocks and should not be considered to significantly affect results presented here.

### ***B. Data collection***

Data collection began after the last day of acclimation. All data were collected between 0700 - 1700 EST and noise subjects were always observed while noise was broadcasted. Two different methods were used for collecting the data analyzed here. Nearest neighbor distance was measured using instantaneous focal point sampling. An observer would enter the aviary and wait approximately 5 minutes before collecting data. Upon locating a focal bird the observer scanned outward in a circular pattern to find and identify the closest subject. Distances between birds were estimated based on known distances between objects within the aviary. NND was recorded as ordinal data: < 30 cm, 30 cm - 1 m, 1 m, 2 m, 3 m, 4m, etc. These data were collected for each subject once per day on 10 separate days. The order in which aviaries were

observed was randomly selected each day, and within each aviary the order that subjects were observed was randomized daily.

Close-perching behavior and conspecific preference data were collected during 10-minute focal follows conducted on 10 separate days. An observer would enter the aviary and wait approximately 5 minutes before collecting data. Upon locating a focal individual the observer would begin data collection, following and narrating the focal bird's behavior in real-time. Narrations of focal follows were recorded using a Sennheiser ME-66 microphone and Fostex FR-2 digital recorder. An observer would use the words "close-perch" to identify any time that the focal bird approached a flockmate within 1 m and maintained this association for at least 1 second, or when a flockmate exhibited the same behavior toward the focal bird. Additionally, directionality of the interaction was dictated by the order in which a bird's identity preceded or followed the words close perch. For example, "red titmouse close perch focal" means that the titmouse identified as red approached the focal individual within 1 m and maintained that, or a shorter, distance for at least 1 second. The directionality and species of the bird(s) involved in these close-perch contexts allowed me to calculate the degree of conspecific preference each subject had for perch partners by subtracting the observed proportion of close perches directed at a conspecific from expected proportion of interactions directed at a conspecific (expected by chance considering overall study flock size). If the resulting difference score was a high positive number then the subject exhibited a strong preference for conspecifics. To control for any potential effects of activity on the frequency of close-perches, I also recorded the number of times a focal bird took flight. A flight was defined as a lift off, extension of the wings and a distance moved of  $\geq 1$  m. Consecutive follows for a subject were usually separated by about 12 - 24 hours to reduce the chance of observing an individual in related contexts.

However, occasionally consecutive follows were completed within the same day, in which case they were separated by a minimum of two hours. The order that aviaries and subjects within each aviary were observed was randomized each day.

### ***C. Statistical analysis***

#### **1. Controlling observer bias and testing reliability**

Due to the nature of this study, data could not be collected or analyzed blindly, but all data presented here were collected by two, independent observers (JLO and CLS). To control for any bias I may have introduced into the data when transcribing from sound files, inter-rater reliability was calculated by comparing my coding scores for close perches with chickadees, close perches with titmice and number of flights for 11 subjects to those of an independent observer using spearman's correlations. Inter-rater reliability between JLO and CLS' s independent scoring of sound files was excellent for all four variables tested: total number of close-perches ( $r_s = 0.979$ ,  $N = 106$ ,  $p \leq 0.001$ ), number of close-perches with chickadees ( $r_s = 0.935$ ,  $N = 106$ ,  $p \leq 0.001$ ), number of close-perches with titmice ( $r_s = 0.943$ ,  $N = 107$ ,  $p \leq 0.001$ ) and number of flights ( $r_s = 0.990$ ,  $N = 106$ ,  $p \leq 0.001$ ).

#### **2. Ad hoc analyses**

Prior to conducting the planned analyses testing for effects of traffic noise and species, I tested for the influence of several environmental factors that may have affected subjects' behavior, including: time of year, aviary, number of chickadees within each study flock and study flock. MANOVAs resulted in several significant main effects on dependent measures. Study flock ( $F_{(15,112)} = 5.210$ ,  $p < 0.001$ ,  $\eta^2 = 0.446$ ,  $P = 1.00$ ), time of year ( $F_{(3,112)} = 8.03$ ,  $p < 0.001$ ,  $\eta^2 = 0.188$ ,  $P = 0.989$ ), aviary ( $F_{(3,112)} = 4.65$ ,  $p = 0.004$ ,  $\eta^2 = 0.118$ ,  $P = 0.882$ ) and

number of chickadees ( $F_{(2,112)} = 5.54, p = 0.005, \eta^2 = 0.096, P = 0.844$ ) all significantly affected close perching behavior. Study flock ( $F_{(15,112)} = 3.571, p < 0.001, \eta^2 = 0.356, P = 0.999$ ) and number of chickadees ( $F_{(2,112)} = 4.109, p = 0.019, \eta^2 = 0.073, P = 0.717$ ) also affected NND. Study flock also significantly affected conspecific preference ( $F_{(15,112)} = 2.99, p = 0.001, \eta^2 = 0.317, P = 0.995$ ). However, once entered into the analysis as covariates, only study flock, time of year and number of chickadees were significant at  $p \leq 0.05$ . The influence of study flock on the dependent measures appeared to be a result of one flock. When the data were re-analyzed without the data from influential flocks, the effect of flock was reduced and the effect of noise returned. These results indicated that the influence of study flock was driven by one or two influential groups for each dependent variable. As such, variability resulting from study flock was left alone and not included in the analysis as a factor or covariate. Further analyses revealed that the other two significant covariates, time of year and number of chickadees, were significantly correlated ( $r_s = -0.589, N = 113, p \leq 0.001$ ), whereby study flocks 1 - 4 each had 4 chickadees where later flocks varied from 2 to 4 chickadees. Because time of year only affected one dependent measure, number of chickadees was included in the analysis as a covariate.

### 3. Planned analyses

I expected effect sizes to be relatively small. To increase statistical power, a GLM MANCOVA was used to quantify the effects of traffic noise on the median or mean scores for the three social measures and flights for all 113 subjects, regardless of species. Experimental condition (noise or control) was used as the fixed factor in this analysis and number of chickadees was entered as the covariate.

These 'overall effects' were then quantified for each species. MANCOVAs were conducted for titmice and chickadees separately, with experimental condition as the fixed factor

and number of chickadees as the covariate. These analyses were used to determine if the 'overall effects' detected in the first MANCOVA were present in each species. Additionally, these analyses provided insight into the biological significance of effects for each species

Information on species-specific behavior is important to conservation research. Detailed descriptions of chickadee and titmouse social behavior in the context of human disturbance are rare. As such, a third set of MANCOVAs were conducted to identify any differences in the social behavior of chickadees compared to titmice in baseline and experimental contexts. For these analyses, species was used as the fixed factor and group size as the covariate. This analysis will identify any differences in behavior related to species.

All data were analyzed at the level of the individual subject. Although this may promote some pseudoreplication, as the behavior of one subject within a study flock may influence the behavior of their flockmates, I argue that non-independence of behavior between group-mates is a central fact of real flocks. Multiple comparisons within each analysis were controlled for using the conservative Bonferroni correction. Still, the data are interpreted cautiously and with the recognition that several analyses were conducted.

Some of these data and the related residuals were non-normal, suggesting that parametric tests are inappropriate. Because some assumptions of these parametric tests could not be met, independent non-parametric Mann-Whitney  $U$  tests were conducted. Although the exact  $p$ -values vary between analyses, the overall results for significance were the same between the parametric and non-parametric tests. Therefore, only parametric test statistics are reported here. For all analyses, the effect sizes ( $\eta^2$  = partial eta squared) and observed power ( $P$ ) are reported following the customary  $F$  and  $p$ -value statistics. All analyses were conducted using SPSS v. 19.

### III. Results and discussion

Data were collected from 16 different study flocks that contained 113 subjects, 64 of which were titmice and 49 were chickadees. Study flocks were counter-balanced between the 4 aviaries and 2 experimental contexts. Information on these study flocks, including details of group size and composition, are listed in Table I. Observers accumulated approximately 11,407.83 minutes (190.13 hours) of audio recordings from focal follows. The total time that the average subject was observed during his own focal follows was 100.95 minutes.

#### *A. The effects of noise on social behavior and implications for the Increased Threat Hypothesis*

Exposure to traffic noise significantly increased sociality. Subjects in the noise condition maintained significantly smaller NNDs ( $F_{(1,112)} = 13.239, p < 0.001, \eta^2 = 0.109, P = 0.950$ ) (Figure 1A), experienced more close-perch interactions (initiated and received perches combined) ( $F_{(1,112)} = 4.192, p = 0.043, \eta^2 = 0.037, P = 0.528$ ) (Figure 1B) and exhibited significantly relaxed conspecific-preferences for close-perch partners ( $F_{(1,112)} = 9.188, p = 0.003, \eta^2 = 0.078, P = 0.852$ ) (Figure 1C). The increase in the number of close-perch interactions did not appear to be explained by an increase in activity, as noise did not significantly increase the number of flights performed by subjects ( $F_{(1,112)} = 0.698, p = 0.405, \eta^2 = 0.006, P = 0.131$ ).

The pattern of overall effects of noise on each measure was corroborated for both species; however, statistical significance varied. Noise caused titmice ( $F_{(1,63)} = 5.850, p = 0.019, \eta^2 = 0.088, P = 0.663$ ) and chickadees ( $F_{(1,48)} = 6.905, p = 0.012, \eta^2 = 0.131, P = 0.730$ ) to significantly reduce their NND (Figure 2A). However, neither chickadees ( $F_{(1,48)} = 2.288, p = 0.137, \eta^2 = 0.047, P = 0.316$ ) nor titmice ( $F_{(1,63)} = 2.183, p = 0.145, \eta^2 = 0.035, P = 0.307$ )

exhibited a significant increase in close-perch interactions as predicted by the combined analysis (Figure 2B). The effect of noise on the strength of preference for conspecific partners during focal-initiated close-perch interactions was detected for titmice ( $F_{(1,64)} = 8.436, p = 0.005, \eta^2 = 0.121, P = 0.816$ ) but not for chickadees ( $F_{(1,48)} = 1.887, p = 0.176, \eta^2 = 0.039, P = 0.270$ ) (Figure 2C). There was also no significant effect of noise on flights for chickadees ( $F_{(1,48)} = 1.098, p = 0.300, \eta^2 = 0.023, P = 0.177$ ) but or titmice ( $F_{(1,63)} = 3.691, p = 0.059, \eta^2 = 0.056, P = 0.473$ ), supporting the conclusion that flying behavior was not responsible for the effects of noise on close-perching behavior.

These results are accompanied by effect size and observed power statistics which were meant to provide additional information about of the strength of the relationship and ability of the analysis to detect an existing relationship, respectively. These values for each analysis are displayed in Table II to simplify their review. The observed power of these analyses (P) ranged from 0.131 (overall flight analysis) - 0.950 (overall NND analysis), indicating that respective analyses had approximately an 86% to 5% chance of failing to detect an existing effect for respective dependent measures. If the observed power of an analysis is  $\geq 0.800$  and one obtains nonsignificant results, it is reasonable to conclude that an effect does not exist. Considering this relationship, the low P values obtained in non-significant analyses conducted here indicate that an effect of traffic noise may exist, but that a larger sample size would be required to detect it. Although several analyses indicated support for the null-hypotheses, none of the analyses resulted in non-significant findings had a  $P \geq 0.800$ ; therefore I am unable to confidently state that noise does not affect these measures (non-significant cells in Table II).

The effect sizes ( $\eta^2$ ) of the analyses conducted here ranged from 0.006 (overall flight analysis) - 0.131 (chickadee NND analysis) (Table II). These values indicate that traffic noise



accounted for anywhere from approximately 0.6% to 13% of the overall (effect + error) variance for respective dependent measures. Although the strength of the effect of traffic noise on behavior was not large, it was statistically significant for several measures, indicated in Table X. The biological significance of these effects will be considered within the interpretation and discussion of these data.

There is a growing literature that acknowledges the similarities between behavioral responses to disturbance and predation risk (Frid & Dill, 2002), specifically those that are socially mediated via group density. I suggest that the interpretation of these results is best expressed through the perspective that disturbance and predatory threat are functionally analogous (Frid & Dill, 2002; Gill et al., 1996; Millinski, 1985). For example, birds often join flocks (Krause and Ruxton, 2002) or increase the density of social groups in response to predatory threat (Elgar et al., 1984; Metcalf, 1984; Whitfield, 1988). One of the clearest examples of this relationship comes from a study that presented a multi-modal predator stimulus (model + alarm-calls) to wild mixed-species flocks including great tits, willow tits and chaffinches. Following the presentation subjects were significantly closer to nearest neighbors regardless of whether that individual was a hetero- or conspecific (Forsman, Mönkkönen, Inkeröinen & Reunanen, 1998). These data from European relatives of the chickadee and titmouse demonstrate a clear similarity between the response of Parids to predatory threat and the effects of noise on social behavior identified here (Figure 1A, 2A). Taken together, the studies reviewed and my results provide initial, but strong, support for the Increased Threat Hypothesis.

Increased sociality is often thought to benefit group members in a number of ways, including improved predator detection, risk aversion and communication (Krause & Ruxton, 2002). The density of a group influences perceived threat, whereby closer NNDs result in less

time spent vigilant (Elgar et al., 1984; Pöysä, 1994). Even when not the primary source for aggregation, group density benefits individuals in the same way (Lindström, 1989). While not measured here, vigilance may have been reduced as a result of reduced NNDs between subjects exposed to noise. A second, and equally likely function of increasing sociality in noise may be to enhance communication (Pöysä 1994). The 'elective group size' concept (Pitcher, Magurran & Allan, 1983) maintains that the benefits of group living are in part dependent upon individuals maintaining a distance allowing continuous information exchange. Indeed, birds are known to use the behavior of flockmates as a source of information about predation risk (Bekoff, 1995; Elgar, 1989; Lindström, 1989; Pöysä, 1994). Both of our study species are information sources to members of their mixed-species flocks regarding threat related contexts (titmice: Branch & Freeberg, 2012; Dolby & Grubb, 2000; Hetrick & Seiving, 2011. chickadees: Bartmess-LeVasseur, Branch, Browning, Owens & Freeberg, 2010; Nolen & Lucas, 2009). While much of this information transfer occurs through vocal signaling, the presence and flight patterns of titmice provide information on relative safety of a context and important flock movements (Contreras & Seiving, 2011; Dolby & Grubb, 2000). As suggested by Pitcher and colleagues (1983), information transfer is dependent upon distance between signaler and receiver. Fernández-Juricic and Kowalski (2011) found a non-linear decrease in the transfer of threat-related, non-vocal, social information as distance between the signaler and receiver increased from 1 m to 35 m. For the house sparrow the optimal inter-individual distance for information transfer is within 1.2 m (Elgar et al., 1984). Given that communication is subject to different constraints according to species, habitat and weather condition (i.e. Morton, 1975), this 'optimal communication distance' is likely applicable to the species studied here as titmice and house sparrows are similarly sized (Grubb & Pravosudov, 1994; Lowther & Cink, 2006). If applicable,

then noise caused chickadees and titmice to engage in more social interactions within a space that optimizes communication (Figure 1A, B; 2A, B). While social grouping is almost definitively influenced by a number of factors, given the life-history characteristics of our study species, the noise induced amplification of social-proximity detected here appears to be, at least in part, a function of communication.

One may argue that optimizing communication would not be a likely function of increased sociality in the presence of noise because chickadees and titmice were less likely to perch near a conspecific. However, species living in mixed-species flocks readily respond to the alarm behavior of conspecifics and heterospecifics (Sullivan, 1984; Templeton & Greene, 2007). Thus, the reduction in conspecific preference detected here may be the result of the increasing importance of maintaining contact with a flockmate within that ‘optimal communication’ range. Or in other words, if a bird cannot be near a conspecific, then the next best thing may be to be near any flockmate that can provide information. In fact, this possible function of increasing sociality to improve communication is especially likely for species, like chickadees and titmice, which rely heavily on visual and vocal communication for flock cohesion, and survival.

Future research needs to address whether and how the relationships identified here transfer into natural or wild contexts. For example, the effect sizes obtained in analyses with significant findings were relatively small (range of  $\eta^2 = 0.037 - 0.131$ ), indicating that, although statistically significant, these relationships may not be biologically significant. To address this, future research should determine whether these effects exist in wild populations and if changes to normative social behavior affects survival relevant processes, like vocal or visual communication.

## ***B. Species differences in control conditions and in response to noise:***

### ***differences in degree, not kind***

No significant differences were detected for NND ( $F_{(1,54)} = 0.635, p = 0.429, \eta^2 = 0.012, P = 0.123$ ), close-perch frequency ( $F_{(1,54)} = 3.203, p = 0.079, \eta^2 = 0.058, P = 0.420$ ) or conspecific-preferences ( $F_{(1,54)} = 2.540, p = 0.117, \eta^2 = 0.047, P = 0.346$ ) between chickadees and titmice within the control (baseline) contexts (Figure 2). The small effect sizes suggest that any differences between species in a baseline context, with regard to these aspects of sociality, are relatively minor. However, because none of these analyses resulted in a  $P \geq 0.800$ , I cannot rule out the possibility that with a larger sample size, species differences may exist. Interpreting these results conservatively and strictly, these species engage in qualitatively and quantitatively similar social interactions. Although statistically non-significant, raw data reveal a pattern of increased sociality in chickadees compared to titmice; chickadees exhibit smaller NNDs, higher numbers of close-perches and weaker conspecific-preferences for perch partners.

Interestingly, the presence of noise appears to exacerbate species' differences in NND and close-perch behavior, where chickadees experience significantly more close-perches ( $F_{(1,57)} = 6.291, p = 0.015, \eta^2 = 0.103, P = 0.693$ ) and significantly smaller NNDs ( $F_{(1,57)} = 4.949, p = 0.030, \eta^2 = 0.083, P = 0.589$ ) than titmice (Figure 2A, B). As in the control context, there were no significant species differences for the effects of noise on conspecific preferences ( $F_{(1,57)} = 0.036, p = 0.850, \eta^2 = 0.001, P = 0.054$ ) (Figure 2C). Again, the same pattern exists where chickadees are consistently more social than titmice, across experimental context and across social-behavioral measures.

Taken together, these results suggest that species differences in social behavior are more of *degree* not *kind* for chickadees and titmice. It appears that chickadees may exhibit a generalized-sociability ('social butterfly' approach) compared to titmice who are more likely to engage in specific social interactions ('clique' approach). Recently it had been suggested that personality-like behavioral traits of different species or individual may affect responses and adaptability to challenges (Papouchis, Singer & Sloan, 2001; Sih, Bell & Johnson, 2004). These slight differences, observed in the raw baseline data and detected in the noise data, confirm anecdotal descriptions of the behavior and 'personality' of the two species. Titmice have regularly been referred to as dominant over, or higher-ranking than, chickadees in mixed-species flocks (Harrap & Quinn, 1995). This view is supported here, as exposure to noise had a stronger effect on the social behavior of chickadees causing them to perch closer with flockmates and to do so more often than titmice (Figure 2A, B). Admittedly, the species differences reported here are mild. Whether this is a valid result or related to potential constraints resulting from any of the many aspects of semi-natural captivity that subjects were exposed to is unknown. However, similarity should not be surprising as chickadees and titmice share several life history characteristics (Grubb & Pravosudov, 1994; Mostrom et al., 2002) and are both considered nuclear species (Morse, 1970) that provide flockmates with important information (Bartmess-LeVasseur et al., 2010; Branch & Freeberg, 2012; Dolby & Grubb, 2000; Hetrick & Seiving, 2011; Nolen & Lucas, 2009).

#### **IV. Considerations, contributions & conclusions**

Presented here is the first experimental evidence that traffic noise alters fundamentally important, species-typical, non-vocal behavior. Taken together, these data tell an interesting

story. First, the effects of noise detected here were caused by a stimulus that modeled the duration of exposure, amplitude and frequency structure of traffic noise while controlling for potential confounding variables. This is the first study to isolate, test and identify these characteristics of traffic noise as causing effects on avian behavior. Second, the presence of simulated traffic noise increased several aspects of sociality in chickadees and titmice. Equally considering the limitations and contributions of this study, I believe these results serve as strong, but not conclusive, evidence to suggest that traffic noise alters the normative social behavior of these species. However, the presence of these effects in wild birds and the biological significance of these effects remain to be addressed. And third, the similarity between the avian and Parid response to predatory threat and the response of our birds to the presence of traffic noise demonstrate support for the Increased Threat Hypothesis. If the effects identified here are present in wild birds dealing with exposure to traffic noise, the social data provide several converging lines of evidence to support the idea that the responses of chickadees and titmice to noise may function to optimize information transfer among hetero- and conspecific flockmates.

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## **APPENDICES**

## **APPENDIX A**

### **TABLES**

**Table I.** Unplanned variation in study flock size and composition across experimental condition.

Values in each cell of the first three columns represent the number of study flocks in each category of flock size (6, 7 or 8); the number of titmice in each flock was always 4, differences in flock size resulted from variation in the number of chickadees. The values in the second set of columns represent the number of study flocks where heterospecific members were captured from the same, neighboring (near) or non-neighboring (far) territories.

	Flock Size			Composition		
	6	7	8	Same	Near	Far
Control Flocks	3	3	2	2	3	3
Experimental Flocks	2	2	4	3	4	1
Total	5	5	6	5	7	4

**Table II.** Strength of the effects of traffic noise on the behavior of Carolina chickadees and tufted titmice. Dependent measures are listed in the far left and associated statistics are displayed in the cells to the right, under each analysis. Displayed in the cells are the values for effect size, partial eta squared ( $\eta^2$ ), and observed power (P) statistics obtained in each analysis. Within each cell, each of these statistics are followed by percentages. For  $\eta^2$ , the percentage represents the amount of the overall (effect + error) variance explained by traffic noise for a given dependent measure. The percentage following P represents the likelihood of that analysis to fail to detect an existing effect. Statistically significant tests are denoted by an asterisk (\*) before the  $\eta^2$  value within a cell.

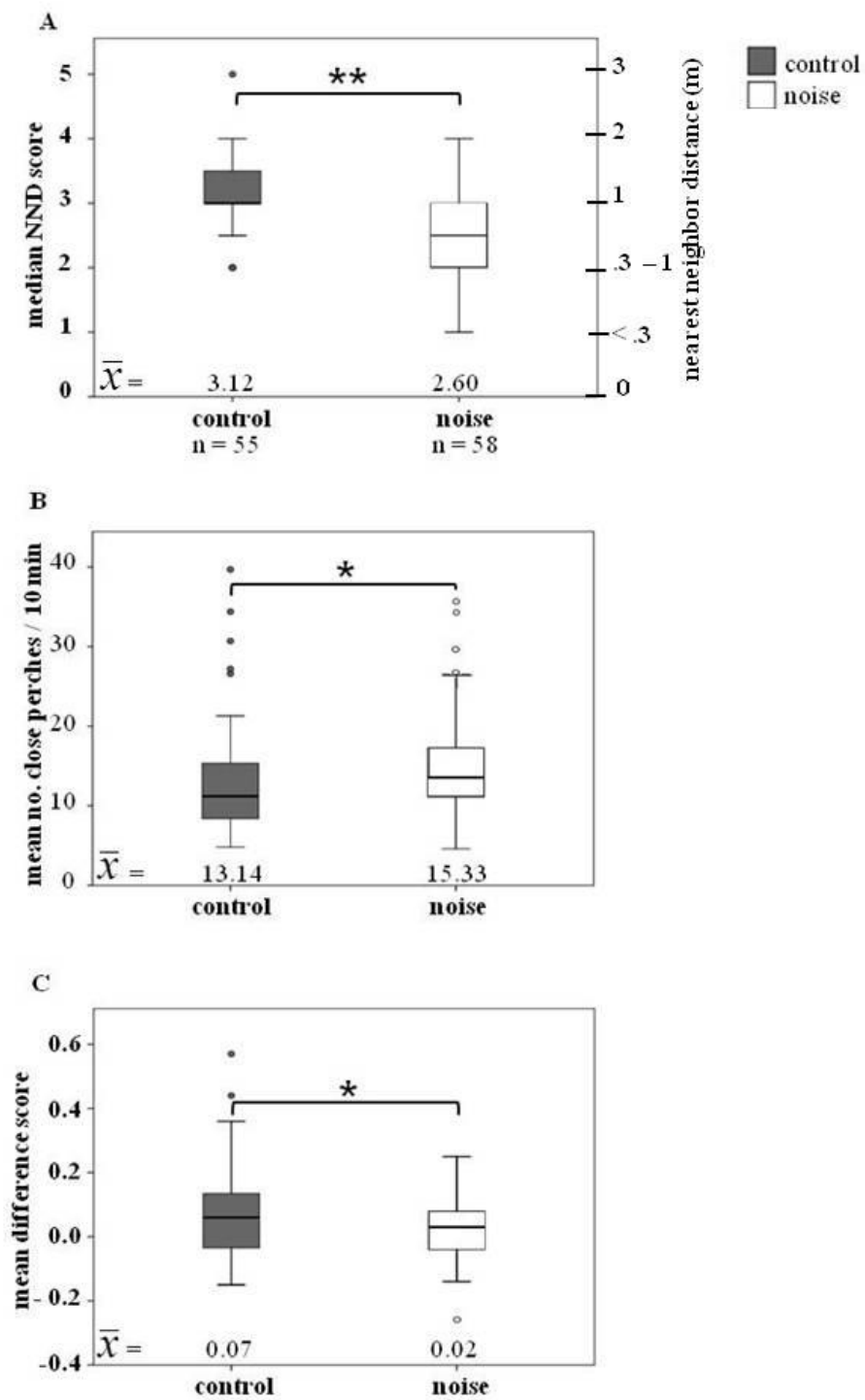
Dependent Measures	Analysis		
	Overall	Carolina Chickadee	Tufted Titmouse
NND	* $\eta^2 = 0.109$ (11%) P = 0.950 (5%)	* $\eta^2 = 0.131$ (13%) P = 0.730 (27%)	* $\eta^2 = 0.088$ (9%) P = 0.663 (34%)
Close-perch	* $\eta^2 = 0.037$ (4%) P = 0.528 (47%)	$\eta^2 = 0.047$ (5%) P = 0.316 (68%)	$\eta^2 = 0.035$ (4%) P = 0.307 (69%)
Conspecific Preference	* $\eta^2 = 0.078$ (8%) P = 0.852 (15%)	$\eta^2 = 0.039$ (4%) P = 0.270 (73%)	* $\eta^2 = 0.121$ (12%) P = 0.816 (18%)
Flight	$\eta^2 = 0.006$ (1%) P = 0.131 (87%)	$\eta^2 = 0.023$ (2%) P = 0.177 (82%)	$\eta^2 = 0.056$ (6%) P = 0.473 (53%)

## **APPENDIX B**

### **FIGURES**

**Figure 1.** Overall effects of noise on social behavior. Data displayed are medians, quartiles and data range with outliers. The sample size for noise and control groups is displayed below (A), and applies to (B) and (C). Group means are displayed within each graph. All significant comparisons are denoted by brackets; a double asterisk (\*\*) denotes significance of  $p \leq 0.001$ , and a single asterisk (\*) denotes significance of  $p \leq 0.05$ . The legend is shown to the right of (A). (A) Displayed on the left Y-axis are the median NND scores; the distances that correspond to those scores are displayed on the right Y-axis. Noise significantly decreased median NND. (B) Noise significantly increased the mean number of close-perches. (C) Noise significantly decreased conspecific difference scores.

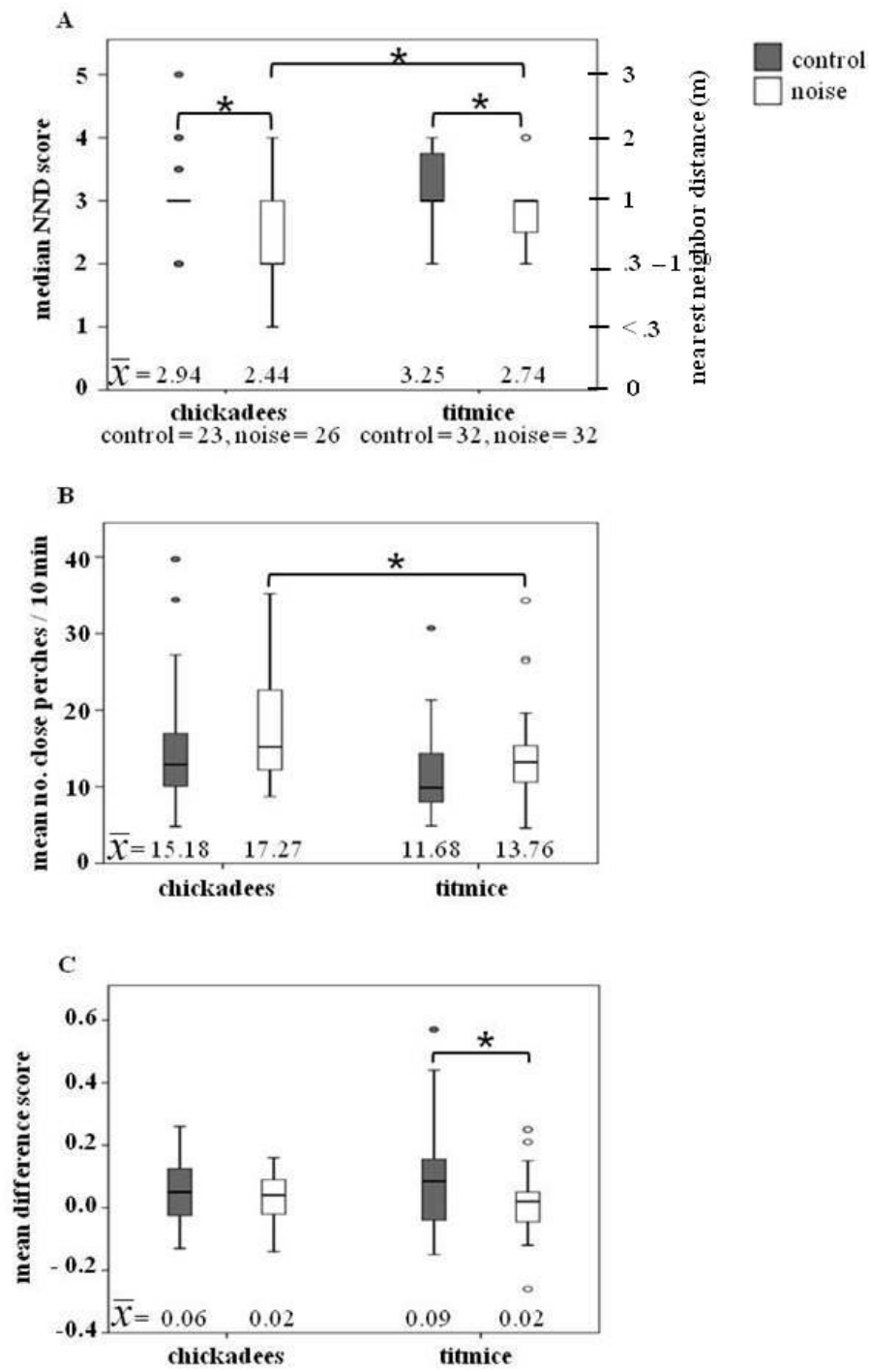
Figure 1.





**Figure 2.** Species-specific effects of noise on social behavior and species differences in social behavior within control and noise contexts. Data displayed are medians, quartiles and data range with outliers. The sample size for each group is displayed below (A), and applies to (B) and (C). Group means are displayed within graphs. All significant comparisons are denoted by brackets; a double asterisk (\*\*) denotes significance of  $p \leq 0.001$ , and a single asterisk (\*) denotes significance of  $p \leq 0.05$ . The legend is shown to the right of (A). (A) Displayed on the left Y-axis are the median NND scores; the distances that correspond to those scores are displayed on the right Y-axis. Both chickadees and titmice significantly decrease NND when exposed to noise. No significant species difference was detected in the control condition, but is present in the noise condition. (B) Noise increases the frequency of close-perches for both species as predicted by the overall effect in Figure 1B; however the effect was not statistically significant for chickadees or titmice. No significant species difference was detected the control condition; however, chickadees are involved in significantly more interactions in noise than titmice. (C) The significant reduction in conspecific preference detected in the overall analysis was only significant for titmice. No significant species differences in strength of conspecific-preference for close perch partners were detected in the control or noise condition.

Figure 2.



### **CHAPTER 3**

TRAFFIC NOISE AND DOMINANCE STATUS INCREASE CHICK-A-DEE  
RATE AND COMPLEXITY IN TUFTED TITMICE (*BAEOLOPHUS BICOLOR*)

This chapter is a revised version of a manuscript in preparation for submission for review and publication in a peer-reviewed, scientific journal:

Owens, J. L. (In Prep.) Traffic noise and dominance status influence chick-a-dee call use.

My contributions to this work include: (a) formulating the research idea, question and hypothesis, (b) training and organizing research assistants, (c) designing the experiment, (d) building the sound equipment and maintaining the set-up, (e) obtaining and caring for subjects, (f) collecting data on social behavior, (g) organizing and conducting statistical analyses, (h) interpreting results and (i) writing of the manuscript and submission for publication. C. L. Stec assisted with husbandry and approximately 25% of data collection as part of Psychology 489.

The analysis described here utilized data collected from the study described in Chapter 2 (Owens, Stec & O'Hatnick, 2012). The methods and materials section of this Chapter are abbreviated, as many details are provided in the previous Chapter.

## ABSTRACT

The Repeated Messages Hypothesis suggests that noise increases repetition and decreases 'information' in vocal signaling systems. This study tests this hypothesis by investigating the effects of traffic noise and dominance status on rates and complexity of calling in tufted titmice (*Baeolophus bicolor*). Wild-caught titmice were socially housed in semi-naturalistic aviary settings with familiar conspecifics trapped from the same home territory. Half of the sixteen study flocks were exposed to eight hours of simulated traffic noise / day, while the remaining eight were held as controls with no noise exposure. Data collected included dominance interactions, calling rates and note-type compositions of calls. Information theoretical analyses were used to analyze call complexity at two levels of uncertainty. The most dominant bird within study flocks produced calls at a greater rate and complexity than subdominant flockmates. There was also a significant interaction between noise and dominance where traffic noise increased the diversity with which note-types were used within calls, but only for the most dominant titmouse. This noise-induced increase in call complexity did not support the predictions of the Repeated Messages Hypothesis. These results suggest that not all titmice are affected by noise in the same manner. This finding emphasizes the importance of addressing the potential for individual variation to influence responses to anthropogenic disturbance.

## CHAPTER 3

### TRAFFIC NOISE AND DOMINANCE STATUS INCREASE CHICK-A-DEE RATE AND COMPLEXITY IN TUFTED TITMICE (*BAEOLOPHUS BICOLOR*)

#### I. Introduction

To avoid communicative challenges resulting from anthropogenic noise, animals may modify their vocal signals by adjusting the acoustic structure of the signal, changing the manner in which a signal is used, or both (Doyle et al., 2008; Wilson & Mennill, 2011). To date, we know that, at least some, avian species can shift the acoustic frequency of their vocal signals to avoid masking by background noise (Brumm, 2004; Brumm, Schmidt & Schrader, 2009; Brumm & Todt, 2002; Halfwerk & Slabbekoorn, 2009; Mockford & Marshall, 2009; Nemeth & Brumm, 2009; Ripmeester, Kok, van Rijssel & Slabbekoorn, 2010; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003; Slabbekoorn, Yeh & Hunt, 2007; Wood & Yezerick, 2006). In comparison, we know much less about how noise affects signal use.

Signal use can be described in a number of ways, including signaling rate, signal composition and signal complexity or 'information' content. Rate of signaling has been associated with several contexts. Dominance status is positively correlated with signaling rate in crested tits (*Lophophanes cristatus*) (Krama, Krams & Igaune, 2008; Krams, 2000) and Carolina chickadees (Williams, 2009). Variation in calling rate has also been linked to motivation and arousal (Buckstaff, 2004; Marler, Dufty & Pickert, 1986; Nowicki, 1983; Smith, 1972) and to the presence of background noise (Buckstaff, 2004; Lengagne, Aubin, Luage & Jouventin, 1999; Serrano & Terhune, 2001).

A second measure of signal use, 'information,' describes the structural complexity of a communicative system. According to Shannon & Weaver's (1949) Mathematical Theory of Communication (a.k.a. Information Theory), information is a quantitative measure of the reduction in uncertainty resulting from the organizational rules of a communication system. Information in this sense is measured in bits per unit of analysis and describes the amount of freedom a signaler has when choosing a message. By using this standardized measure of complexity, Information Theory serves as an invaluable analytic tool for analyzing and comparing structural diversity of communication systems of heterospecifics or conspecifics in differing contexts (Freeberg & Lucas, 2012; Lengagne et al., 1999; Lucas & Freeberg, 2007; McCowan, Doyle & Hanser, 2002; Turnbull & Terhune, 1993). However, this approach is not without limits; namely, information theory measures the hypothetical amount of information within a call system. Therefore, it is necessary to corroborate the results of information theory analyses empirically; Freeberg and Lucas (2012) recommend complementary analyses that test the function of different types of signal variation across different contexts, as has been carried out for chickadee species (review Lucas & Freeberg, 2007). Even in consideration of this limitation, the information theoretic approach is arguably underutilized in the conservation literature (Penteriani, 2010; see Doyle et al., 2008 for application of information theory in study of anthropogenic noise).

While individual variation and its importance in predicting behavior is widely recognized elsewhere (Ekman, 1987; Ekman & Askenmo, 1984; Evans, Boudreau & Hyman, 2009; Gosling, 2001; Sih, Bell & Johnson, 2004; Waite, 1987), our knowledge of how individual differences affect the response to noise is limited. Dominance status, one type of inter-individual variation, predicts several aspects of signal use in avian species (Dahlin, Balda & Slobodchikoff, 2005;

Krama et al., 2008; Krams, 2000; Yorzinski, Vehrencamp, Clark & McGowan, 2006). This relationship between dominance status and vocal communication (signal use) provides a unique opportunity to integrate two valuable research initiatives into the study of anthropogenic disturbances.

In the current study I tested for the effects of noise and dominance status on chick-a-dee call use in a socially and vocally complex species, the tufted titmouse (*Baeolophus bicolor*). The tufted titmouse was chosen as the study species because it represents an ideal study system to address such questions. This species lives in habitats with varying levels of natural and anthropogenic noise (Grubb, 1998; Grubb & Pravosudov, 1994), indicating it has a moderate level of tolerance for disturbance. Tolerance is a life-history strategy currently under-represented within the literature on anthropogenic noise (Ortega, 2012). As a species, titmice are typically socially dominant, exploratory and active within their over-wintering mixed-species flocks; their behavior provides information about safety and flock movements to conspecific and heterospecific flockmates (Contreras & Seiving, 2011; Grubb & Pravosudov, 1994; Hetrick & Seiving, 2011; Morse, 1970). As a result of this 'leadership' or nuclear role (Morse, 1970) within mixed-species flocks, any effects of noise on titmouse behavior may have ramifications for others within its social group (e.g. Forsman, Hjernquist, Taipale & Gustafsson, 2008). More directly associated with the aims of this study though, titmice regularly form dominance hierarchies (e.g. Brawn & Sampson, 1983; Pravosudov & Grubb, 1999; Pravosudov et al., 1999), the details of which are not well documented.

The chick-a-dee call of this and related species (the Paridae) has been heavily studied (reviews: Krams, Krama, Freeberg, Kullberg & Lucas, 2012; Lucas & Freeberg, 2007; Sturdy, Bloomfield, Charrier & Lee, 2007). This call system consists of several distinct note-types



(described for black-capped chickadees, *Poecile atricapillus*: Sturdy, Phillmore & Weisman, 2000; Carolina chickadees, *Poecile carolinensis*: Bloomfield, Phillmore, Weismann & Sturdy, 2005; mountain chickadees, *Poecile gambeli*: Bloomfield, Charrier & Sturdy, 2004; and tufted titmice, *Baeolophus bicolor*: Owens & Freeberg, 2007; Figure 1), that are reliably identified by humans and discriminated by the birds themselves (e.g. Bloomfield, Farrell & Sturdy, 2008; Bloomfield & Sturdy, 2008). For each species studied thus far, calls are composed using rule-ordered combinations of note-types, resulting in a generative and open-ended communication system (Freeberg & Lucas, 2012; Hailman, Ficken & Ficken, 1985; Lucas & Freeberg, 2007). Variation in the acoustic structure, composition and use of the chick-a-dee call is associated with a number of potential messages (reviews in Krams et al., 2012; Lucas & Freeberg, 2007; Sturdy et al., 2007), including presence and threat level of predators and predator models (Baker & Becker, 2002; Bartmess-LeVasseur, Branch, Browning, Owens & Freeberg, 2010; Courter & Ritchison, 2010; Hetrick & Sieving, 2011; Sieving, Hetrick & Avery, 2010; Soard & Richardson, 2009; Templeton, Greene & Davis 2005; Zachau & Freeberg, 2012), food (Freeberg and Lucas, 2002; Mahurin & Freeberg, 2009), individual identity (Bloomfield, et al., 2004, 2005; Charrier, Lee, Bloomfield & Sturdy, 2005; Freeberg, Lucas & Clucas, 2003; Owens & Freeberg, 2007), flock identity (Mammen & Nowicki, 1981; Nowicki, 1983), social status (Krams, 2000) and geographic variation (Freeberg, 2012).

### ***A. Goals, expectations & predictions***

Here I tested for the effects of noise and dominance status on three measures of chick-a-dee call use in the tufted titmouse. This research was designed to answer four main questions: (1) does traffic noise affect dominance relationships?; (2) does traffic noise affect chick-a-dee

call use for titmice? (3) does dominance status affect chick-a-dee call use for titmice? (4) does dominance status alter the effect of noise on chick-a-dee call use?

## 1. Does traffic noise affect dominance ?

In the presence of chronic anthropogenic disturbance, including noise, mixed-species flocks have been reported to reduce foraging niche-specialization and to share micro-habitats while converging on foraging strategies (Matthysen, Collet & Cahill, 2008). One may have expected that the increase in proximity to another individual, especially near a resource, would result in an increase in aggressive attempts to remove or block them from the resource. However, there was no mention of increased aggression or competition between flockmates at these shared foraging sites, indicating that these measures were either maintained at levels similar to flocks in undisturbed areas or that disturbance induced an increase in cooperation, or at least tolerance. This idea is supported by the finding that increased perception of predation risk supports higher rates of cooperation between competitors (Krams et al., 2009). As such, traffic noise should not increase despotism, but might be expected to exert no effect or to shift the dominance style from despotic to egalitarian (perhaps reflecting increased cooperation between flockmates).

## 2. Does traffic noise affect chick-a-dee call rate and complexity ?

The Increased Threat Hypothesis (ITH) has previously proven useful in predicting and interpreting the effects of noise on non-vocal behavior (Owens, Stec & O'Hatnick, 2012); here it is applied to vocal behavior, specifically call rate. The effects of anthropogenic disturbance have been compared to those of perceived predatory risk, whereby disturbances typically elicit behavioral responses that are qualitatively and quantitatively similar to anti-predator behaviors (Blumstein, 2006; Frid & Dill, 2002; Gill, Sutherland & Watkinson, 1996; Millinski, 1985;

Owens et al., 2012). The Increased Threat Hypothesis, derived from and similar to the Risk Disturbance Hypothesis, recognizes this functional similarity. Specifically, the ITH posits that disturbance creates behavior comparable to anti-predator responses as a result of its effects on an animal's perception of threat or risk within its environment. Additionally, the ITH provides distinct predictions depending upon the type of disturbance. Acute or unfamiliar disturbances cause alerting or flight responses (Burger, 1981; Klein, Humphrey & Percival, 1995; Stankowich & Coss, 2009), whereas chronic stimuli often cause increases in vigilance (Rabin, Coss & Owings, 2006; see also Kikuchi, 2008). Specifically, the presence of chronic noise appears to deregulate reflexive and startle-types of anti-predator behavior while upregulating (possibly through post-habituation sensitization) more adaptive forms of anti-predator behavior, like cautiousness. In effect, while the ITH assumes that disturbance increases the perceived level of threat in the environment, the predictions for how this perceived-threat affects behavior differs between chronic and acute disturbances.

With regard to the predictions for call rate, species often increase calling rate to improve signal detection in noise (Buckstaff, 2004; Doyle et al., 2008). Additionally, titmice are known to call at higher rates in threatening contexts (Bartmess-LeVasseur et al., 2010). However, most threat contexts, including the one modeled by Bartmess-LeVasseur and colleagues (2010), are acute or short-term in duration. Likewise, the noise-induced increases in call rate occur at the onset of noise or during acute exposures to noise (Buckstaff, 2004; Fischer, Hammerschmidt & Todt, 1995; Lesage, Barrette, Kingsley & Sjare, 1999; Sun & Narins, 2005). In contrast to these systems, this study utilizes a long-term exposure paradigm (8 hours / day) to model the nearly constant presence of traffic noise in local titmouse habitats near roadways. Prior to data collection, subjects had already received 10 days of exposure to experimental traffic noise.

According to the ITH, subjects' exposure to traffic noise should induce habituation to the increase in perceived threat. Indeed, as the duration of exposure to noise increases, calling rate often decreases (Fischer et al., 1995). Consequently, traffic noise is not expected to increase subjects' call rate.

In response to the presence of noise, animals often repeat note-types within a signal or repeat the same signal or signal-type (Buckstaff, 2004; Doyle et al., 2008; Halfwerk & Slabbekoorn, 2009; Turnbull & Terhune, 1993). This type of redundancy within a signaling system is hypothesized to increase communicative efficiency by increasing the likelihood that messages are accurately perceived by potential receivers (Shannon & Weaver, 1949). However, repetition, whether at the note, call, or bout level of signaling is predicted to reduce the amount of (quantitative) information capable of being transmitted (Bradbury & Vehrencamp, 1998; McCowan, et al., 2002). Previously unnamed, this hypothesis, referred to herein as the Repeated Messages Hypothesis, predicts that signaling redundancy in response to the presence of noise will decrease communicative complexity and reduce the amount of information communicated. The RMH provides two related predictions for the effects of traffic noise on signaling complexity. The first is that traffic noise should increase redundancy within the chick-a-dee call and the second is that redundancy will negatively affect the amount of information communicated in noise.

### 3. Does dominance status affect chick-a-dee call rate and complexity ?

Dominant parids are generally more vocally active than subdominants (Krama et al., 2008; Krams, 2000; Williams, 2009); titmice are expected to follow this pattern. The predictions of the Social Complexity Hypothesis (SCH) may be applied to whether dominance status, a social status, affects chick-a-dee call use. The SCH claims that the number, diversity and quality

of relationships within a social group can influence the repertoire size, complexity or diversity of vocal signals produced by members of that group (Dunbar, 1996, 2003; Freeberg, Dunbar, & Ord, 2012). The relationship between social and vocal complexity has been tested and supported using a variety of definitions and methods (i.e. Blumstein & Armitage, 1997; Freeberg, 2006; Freeberg & Lucas, 2012; McComb & Semple, 2005; Payne, Thompson & Kramer, 2003; reviews in Krams et al., 2012; Pollard & Blumstein, 2012), suggesting that the relationship is robust. According to Krams and colleagues, the greater number of social relationships within egalitarian dominance hierarchies should result in more complex vocal communication systems than the more socially restrictive despotic hierarchies. Freeberg, Dunbar and Ord (2012) extended these predictions by applying them to individuals of different social status.

Dominant parids exert control over resources and have access to preferred areas (Brawn & Sampson, 1983; Pravosudov & Grubb, 1999; Pravosudov et al., 1999; Suhonen, Alatalo, Carlson & Höglund, 1992). Titmouse dominance is expected to be linear and peck-right (Brawn & Samson, 1983), indicating that the dominant individual interacts with all flockmates, while interactions dwindle with reduction in status ending with the subordinate titmouse who avoids all flockmates (Freeberg et al., 2012). Thus dominance is indicative of a higher number of social interactions. According the SCH, a dominant titmouse should exhibit a more complex communicative system than a subordinate flockmate.

#### 4. Does dominance alter the effects of noise on chick-a-dee call use ?

This is more of an open question. In other parid species we know that the dominant individual within a flock calls at a higher rate than its flockmates (Krama et al., 2008; Krams, 2000; Williams, 2009). Producing more signals may indicate that the dominant individual is communicating, and thus providing, more information. As a species, titmice are known as

information sources within their over-wintering mixed-species flocks (Contreras & Seiving, 2011; Grubb & Pravosudov, 1994; Hetrick & Seiving, 2011; Morse, 1970). If dominant titmice follow the parid pattern of greater rates of signaling compared to lower ranked flockmates, then it is possible that chick-a-dee call use of these birds may be more affected by the presence of traffic noise than their less vocal flockmates. However, communicative challenges presented by noise are not selective. Presumably, any individual signaling in noise should adjust their signaling to avoid masking and other challenges. Subdominant subjects may also show effects of traffic noise within their signaling. The results of this study will indicate whether and how dominance status alters the effects of traffic noise on chick-a-dee call rate, complexity and note-usage.

## **II. Materials and methods**

### ***A. Research design***

To address these four questions, I used a between-subjects experimental design and exposed wild-caught titmice to simulated traffic noise (see Chapter 2 for detailed methodologies). During this time dominance interactions were observed and used to describe the dominance hierarchy of each study flock and the relative strength of dominance of each subject. Vocal behavior of titmice was also recorded. Chick-a-dee call use was assed using three measures: call rate, information content and observed proportion of note-type use in calls. All trapping, banding, wing-chord measurements, husbandry and research were completed in accordance with IACUC protocol # 1326.

This research was conducted at the University of Tennessee Forest Resources Research and Education Center (UTFRREC) from October 2009 to March 2010. Prior to their inclusion in

this research, study subjects were free-living members of naturally occurring, mixed-species flocks at the UTFRREC or a North Knoxville residential area. During these months, titmice are commonly involved in mixed-species flocks with Carolina chickadees (*Poecile carolinensis*). Titmice and chickadees were trapped using walk-in treadle (potter) traps baited with a 1:1 mix of black-oil sunflower and safflower seed. Upon capture, subjects were socially housed in large outdoor aviaries containing several live trees, grass, indoor enclosure, and several perching spots. Titmice were housed with 3 familiar conspecifics, consisting of at least one known male and one known female (wing-chord based sexing: Thirakhupt, 1985; Owens & Freeberg, 2007; Owens et al., 2012). To maintain natural social contexts (Grubb & Pravosudov, 1994; Mostrom, Curry & Lohr, 2002), aviaries also contained 2 to 4 Carolina chickadees (Owens et al., 2012; Chapter 2). Titmice (herein referred to as 'subjects') were provided 10 days of acclimation to either a "noise" or "control" condition prior to data collection. Housing, husbandry and acclimation conditions were identical between experimental and control groups with the exception that noise birds were exposed to simulated traffic noise broadcast at 75 dB / SPL @ 1m for 8 hours / day (General Radio Sound Pressure Level meter, 1565-B series, A-weighting). Experimental conditions were balanced across aviaries.

### ***B. Data collection***

Vocal and behavioral data for each subject were collected across 10, 10-minute focal follows conducted between 0700 - 1700 EST. In cases where the observer lost visual contact with the focal subject, the time of the interruption was noted and added to the end of the recorded sound file. The order that subjects were followed was randomized daily within and between study flocks. Focal follows for a subject were typically separated by at least 24 hours to ensure independence of observations. However, due to time constraints related to weather,

approximately 30% of follows were conducted on the same day, in which case they were separated by a minimum of 2 hours. During each follow, recordings were made of the observer's narrations of the focal bird's behavior using Sennheiser ME-66 microphones connected to Fostex FR-2 digital field memory recorders. Following data collection subjects and chickadees were released at their capture sites.

## 1. Chick-a-dee call data

Data were retrieved from sound files while in the spectral view (22,050 sampling rate, 16-bit resolution) of Cool Edit Pro (V. 2, Syntrillium Software, Scottsdale, AZ). For each chick-a-dee call produced, the time of its occurrence, the caller (if narrated) and note-type composition were noted. Occasionally the observer would speak over a chick-a-dee call, making it impossible to record the note-composition of the call. In these cases, the time of the call was noted to account for its presence, but no note composition was recorded. This was done to maintain accuracy when calculating chick-a-dee call rate. The note-type composition of each chick-a-dee call recorded was identified based upon the 4-note categorization of Owens & Freeberg (2007), with one additional note type category. In this prior categorization "Z" and "A" notes were described as notes that start at higher frequencies (Hz). Both are high-frequency tonal sounds, but differentiated by duration. A notes were defined as those with a tail that were  $\leq 100$  msec, and Z notes were those with or without a tail that were  $\geq 100$  msec. In later acoustic analyses it became apparent that the presence or absence of an ending tail in the Z note of Owens & Freeberg (2007) represented two different note types. Here, "Z" notes are still  $\geq 100$  ms, but the terminal end of the "Z" note ends above 4 kHz. The new note, the "Y" note, is also  $\geq 100$  ms, but its tail extends below 4 kHz (Figure 1). This split resulted in a 5-note categorization following the note-ordering rule of: Z, Y, A, D<sub>h</sub>, D.



From these data chick-a-dee call rate and composition were obtained. Calls included in the call-rate analysis were limited to those produced by a subject within their respective focal follows only. For each subject, call rate was determined by dividing the total number of calls produced by the total amount of time observed, resulting in a measure of calls per minute. This value was then multiplied by 10 to calculate average call rate per 10 minutes.

Note-type compositions of chick-a-dee calls were used to quantify signal complexity using two measures: information content and note-type use. Shannon and Weaver's formulas for uncertainty " $U$ " and the UNCERT program written by E.D. and J.P. Hailman (Hailman et al., 1985; see Freeberg, 2006; Shannon & Weaver, 1949) were used to estimate the amount of information encoded within chick-a-dee calls. ' $U_{\max}$ ' measures the ability of a call to encode information with the underlying assumption that all note-types occur with an equiprobable chance. Titmice have 5 recognized note types, "Z, Y, A, D<sub>h</sub> and D," plus a sixth which represents the silence at the end of a call. If a titmouse produces all 5 note types (plus the 6th representing the silence) the highest potential  $U_{\max} = 2.585$ .

Chick-a-dee calls eligible for this UNCERT analysis were not limited to those recorded during the caller's own focal follows, and included any call with a known producer. Because small samples of calls may bias uncertainty measures, a subject could only be included in the analysis if it produced  $\geq 20$  chick-a-dee calls of appropriate length within each level of analysis. The resulting sample allowed uncertainty to be quantified at two different levels, designated here as: " $U_{\text{note}}$ , and  $U_{\text{pair}}$  ( i.e., at least one note per call for  $U_{\text{note}}$  analyses and at least two notes per call for  $U_{\text{pair}}$  analyses described below)." ' $U_{\text{note}}$ ' measures the ability of a note to encode information with respect to its actual frequency of occurrence, and " $U_{\text{pair}}$ " measures uncertainty for ordered pairs of note-types. In general, higher uncertainty at any level of  $U$  represents greater

information / complexity due to increased diversity in the use of notes or note pairings.

Importantly, neither  $U_{\text{note}}$  nor  $U_{\text{pair}}$  were correlated with the number of calls in the sample.

To assess redundancy within chick-a-dee calls, I obtained the observed probability of occurrence for Z, Y, A and D note types and the observed probability of note-type repetition (Z to Z, Y to Y, A to A, and D to D, in a two-note sequence) from the UNCERT call sample. D<sub>h</sub> note types were not included in this analysis as they were not produced by all subjects, and the final sample size was too small. This data set was collected for each subject included in the UNCERT analysis.

## 2. Dominance data

Agonistic interactions measured here consisted of two commonly used behavioral assays of dominance (Brawn & Samson, 1983; Grubb & Pravosudov, 1994; Pravosudov & Grubb, 1999): 'supplants' and 'chases.' A supplant occurred when an initiator bird moved toward a receiver bird, by flight or bi-pedal locomotion, forcing the receiver from its perch, which was subsequently taken over by the initiator (Freeberg & Harvey, 2008). A chase consisted of an initiator bird that flew toward a receiver bird, where the receiver responded by taking flight in a direction away from the initiator, who subsequently followed the receiver's flight path closely. Supplants and chases were typically loud and obvious interactions; observers were able to narrate these interactions using all-occurrences sampling while conducting a focal follow. The number, directionality and individuals involved in agonistic interactions were recorded during focal follows, regardless of whether the focal was involved.

These data were used to quantify dominance at two levels: structure of the dominance hierarchy for each study flock and dominance status of each individual within their respective flocks. Flock level dominance hierarchies were described using linearity and steepness (Figure

2). These measures allow tests to determine whether noise affects the organization of social relationships within the group and describe the group's dominance hierarchy. Linearity describes the degree to which a hierarchy is transitive (e.g. A dominates B, C, D; B dominates C, D; C dominates D) or circular (e.g., A dominates C, D; B dominates A,D; C dominates B; D dominates C). Landau's  $h$ , with modifications for proportional wins and losses (Singh, D'Souza & Singh, 1992), was used to quantify linearity on a scale of 0 - 1. A score of 0 represents an absence of a hierarchy and 1 represents complete linearity. A hierarchy is said to be strongly linear when  $h \geq 0.90$  (Martin & Bateson, 1993).

Steepness (slope) describes the degree of difference in overall success in dominance encounters between adjacently ranked flockmates. The steepness of a hierarchy is based on a scale of 0 - 1. Differences between dominance status of flockmates are small when steepness is close to 0, indicating an egalitarian society where the results of dominance encounters are less predictable. When steepness is closer to 1, the hierarchy is more predictable, indicating a strictly despotic structure (Vervaecke, Stevens, Vandemoortele, Sigurjónsdóttir & de Vries, 2007). Steepness was calculated using normalized David's scores (normDS) from the dyadic dominance index, corrected for chance interactions ( $D_{ij}$ ) (de Vries, Stevens & Vervaecke, 2006). These scores are based on the weighted and unweighted sum of a subject's dyadic proportions of wins combined with a weighted and unweighted sum of its dyadic proportion of losses. For each study flock, subjects were plotted on the X-axis from the highest to lowest normDS value, and normDS values were plotted on the Y-axis. Simple linear regression was used to find the slope ( $R$ ) of the best fit line for each study flock.

Individual dominance statuses were represented by their respective normDSs. Parametric tests require independent variables to be ordinal or categorical; therefore, to test for an effect of

status on vocal behavior, dominance data were transformed into ordinal ranks. To achieve this, subjects within each study flock were ranked (1, 2, 3 or 4) based on their normDSs.

### ***C. Statistical analyses***

#### **1. Controlling for observer bias and assessing reliability**

Observers were not blind to experimental condition when collecting data as the experimental stimulus was audible and observers were responsible for turning the sound equipment on and off. However, potential effects of observer bias were controlled for as dominance and vocal behaviors were collected by two trained observers. Prior to the start of this study JLO and CLS independently scored the same focal follows; data collection on study subjects did not begin until independent scores reached a straight percentage agreement of 90%. After this criteria was reached, JLO and CLS independently collected data from each subject and each study flock. Of the total data collected, JLO was responsible for approximately 75%, and CLS approximately 25%.

Inter-rater reliability for note-type composition of chick-a-dee calls was calculated by comparing the scores of JLO and an independent observer, TMF, on 110 randomly selected chick-a-dee calls (approximately 17% of chick-a-dee call sample analyzed here). Reliability for scoring of chick-a-dee call note-type compositions was excellent for all categories of comparison (Cohen's Kappas: overall = 0.93, Z = 0.91, Y = 0.91, A = 0.97 & D = 0.98) except for the D<sub>h</sub> note-type ( $K = 0.50$ ). The lack of agreement for the hybrid note is likely related to small sample size. Within the sample used for reliability the D<sub>h</sub> note occurred between 2 and 4 times (depending on observer) out of 345 total notes (0.006 - 0.012% of the total sample of notes), which negatively impacts the ability to accurately assess reliability for this note-type. In a previous study the independent scores of JLO and TMF for the D<sub>h</sub> note type reached excellence

( $K = 1.00$ , Owens & Freeberg, 2007). In the case of disagreement, JLO's scores were used in the UNCERT analysis.

## 2. Ad hoc analyses

Subjects were exposed to several types of variation that may have affected their behavior, including: the time of year subjects were observed, the aviary in which subjects were housed, the number of chickadees within a study flock and the unique characteristics of each study flock.

MANOVAs were used to determine whether any of these four 'environmental' variables affected the dependent measures of chick-a-dee calling rate, slope and linearity. Statistics are displayed in Table I; analyses indicated no significant effects of these four environmental variables on subjects' behavior ( $\alpha = 0.05$ ). As such, none of these variables were included in the a priori analyses as random or independent factors or covariates.

## 3. Planned analyses

This research asks four questions. To answer the first question: does traffic noise affect dominance relationships?, dominance first needs to be quantified. Linearity and slope were calculated for each flock using the normDSs of subjects. Linearity and slope values for each flock were then entered as dependent variables into a MANOVA with noise as the independent factor.

Several analyses were required to address the remaining three questions. Differences in the size and consistency of the call rate and call complexity samples required two separate analyses. Additionally, preliminary analyses suggested that calling behavior differed between the most dominant individual compared to the rest of the subjects within a study flock. As such, for all analyses where dominance rank (1 - 4) was used as an independent variable or fixed factor, ranks were revised into 'lumped dominance ranks' (LDR), where subdominant ranks 2, 3

and 4 were lumped into one category and compared to rank 1. The first analysis consisted of using an ANOVA to test for the effects of LDR, noise and LDR\*noise on call rate. The second analysis used a MANOVA to identify the relationship(s) between noise, LDR and LDR\*noise on two measures of complexity:  $U_{note}$  and  $U_{pair}$ . And finally, the observed proportion of note-type use and note-type repetition were entered into a separate analysis of variance to corroborate significant results of the complexity analysis.

Significant interactions were tested for significance by applying simple main effects tests ( $\alpha = 0.05$ ). Residuals of all tests were normally distributed, indicating that assumptions of parametric statistics were met. For all analyses, the effect sizes ( $\eta^2 =$  partial eta squared) and observed power (P) are reported following  $F$  and  $p$ -value statistics. All statistical analyses were conducted using SPSS (v. 20).

### **III. Results and discussion**

Sixty-four titmice, divided equally into 16 study flocks of 4 titmice each, were observed for a total of 6,437 minutes (107 hours). The time the average subject was observed during its own focal follows was 100 min (range: 88.88 - 112.79 min). There was no evidence that the presence of speakers influenced the behavior of subjects as these objects were readily perched on and used as caching sites. Following acclimation, subjects often bathed and foraged on the ground near observers; these behaviors leave a bird vulnerable to predation or attack, suggesting that subjects did not perceive observers as a threat.

### ***A. Dominance hierarchies of titmice and effects of noise***

With the exception of one dyad in one flock, study flocks were fully interactive, meaning that all members of a flock experienced a dominance interaction with every other flockmate . Agonistic interactions ( $n = 790$ ,  $\bar{x} = 49$  / study flock, range: 29 - 98) were recorded from all 16 study flocks (Table II). The maximum normDS for a titmouse in this study was 3. The highest and lowest normDSs recorded were 2.834 and 0.169, respectively.

Dominance rank had a significant effect on mean normDSs ( $F_{(3,63)} = 321.23$ ,  $p \leq 0.001$ ,  $\eta^2 = 0.945$ ,  $P = 1.0$ ). Post-hoc analyses revealed that the mean normDSs of each of the four ranks were significantly different from every other rank in the following pattern: mean normDS of rank  $1 > 2 > 3 > 4$  ( $p \leq 0.05$ ). This suggests that variance between normDSs of subjects within study flocks was accurately represented by linear dominance ranks (1 - 4).

The average linearity for study flocks was  $h = 0.74$ , a relatively high value which represents a hierarchy with mostly transitive relationships. However, linearity ranged from  $h = 0.26$ , representing circular dominance relationships, to  $h = 1.0$ , a completely transitive dominance hierarchy. This range in linearity indicates that dominance reversals were common within some of the study flocks. Variation in linearity was distributed across experimental conditions (see discussion below), eliminating the presence of noise as a potential explanatory variable.

Simple linear regression was used to find the steepness of each flock's dominance hierarchy. The slope was significant for 15 of 16 flocks (Table II). These data corroborate the earlier test and present strong evidence supporting the conclusion that titmice within a flock occupy statistically different dominance statuses. From this slope analysis, titmice appear

despotic, as 8 of the 16 study flocks reached the maximum slope possible and no flock had a slope lower than 0.84 (Table II).

Noise did not affect linearity ( $F_{(1,15)} = 0.603, p = 0.450, \eta^2 = 0.041, P = 0.112$ ) or slope ( $F_{(1,15)} = 2.167, p = 0.163, \eta^2 = 0.134, P = 0.279$ ) of dominance hierarchies in this study. Additionally, there was no effect of noise on subjects' mean normDSs ( $F_{(1,63)} = 0.0, p = 0.988, \eta^2 = 0.0, P = 0.05$ ), suggesting that noise did not alter the degree or strength of dominance displayed in titmice within these study flocks. For these analyses I must accept the null-hypothesis that traffic noise does not affect dominance; however, because the observed power of each test to detect an effect is well below  $P \geq 0.800$ , this conclusion is not definite. Regardless of variation in geographic location, time of year, context and methodology used, previous studies on titmouse dominance consistently indicate a generally linear, despotic, peck-right dominance hierarchy (Brawn & Samson, 1983; Grubb, 1998; Grubb & Pravosudov, 1994; Pravosudov & Grubb, 1999; Waite, 1987; Waite & Grubb, 1987). If noise does not affect the organization of flock-level dominance or the strength of individual dominance status, then my results combined with previous research may be indicative of the stability of this social system.

Although there is general agreement between the structure of flock-level dominance hierarchies detected here and in previous work, there is minimal agreement between the dominance-determining traits of titmice in previous work and the traits of dominant subjects within this study (Table III). Dominance status is usually contributed to the presence of dominance-determining traits (Prior Attributes Hypothesis, see Chase, Tovey, Spangler-Martin & Manfredonia, 2002) like age, sex, seniority, size and fat-reserves for titmice (Grubb & Pravosudov, 1994; Pravosudov et al., 1999). Accordingly, previous work suggests that male titmice should be dominant over females and that within sex, the larger, older bird dominates the



smaller, younger bird (Grubb & Pravosudov, 1994; Pravosudov et al., 1999). On the contrary, of the 16 dominant subjects in my study, 7 were male, 4 were female and 5 were of unknown sex (Table III). Similar distributions were noted for ranks 2, 3 and 4, indicating that sex was not a significant factor in determining dominance status. Here subjects were sexed using wing-chord measurements (female  $\leq 77$  mm, male  $\geq 80$  mm; Owens & Freeberg, 2007; Thirakupt, 1985). No other measure of subjects' sizes were recorded. Because of the relationship between size and sex, using the wing chord measurements to predict dominance status would be redundant. Table III shows that the smallest subjects achieved the highest dominance within 25% of the study flocks. The order of arrival to a site or seniority of a titmouse within a territory positively correlates with dominance (Grubb & Pravosudov, 1994). However it is unlikely that seniority affected dominance of subjects as most titmice were released into the aviaries with conspecifics; 55 of 64 titmice were placed into an aviary at the same time as one of its study-flockmates. Additionally, there was no pattern of an effect of noise on who became dominant. Therefore, what factors determined who became the most, second, third and least dominant individual in study flocks is beyond the scope of these data. However, even with this unexpected variation in the individual characteristics of each rank, it was interesting that the overall structure of dominance hierarchies remained stable when compared to previous research.

Dominance determining traits do not appear to explain the variation in subject dominance statuses. The Social Dynamic Hypothesis (SDH) appears to be more applicable to these data. The SDH states that the dominance status attained by an individual may be a function of the unique interactions between the individual's syndrome, personality, phenotype or genotype with that of the other individuals within the group rather than the list of their dominance-determining traits (Chase et al., 2002). The results obtained here suggest support for the Social Dynamics

approach, in that the combination of specific individuals and their related characteristics (syndromes, activity levels, sociality, etc) may be influencing titmouse dominance.

### ***B. Effects of noise and dominance on chick-a-dee call rate***

A total of 16,792 chick-a-dee calls was recorded during this study. The signaler was identified for 5,718 of those calls. Of the 64 titmice in this study, 60 were identified as callers (those that produced at least one call). The production of calls varied between individuals; from 0 to 723 calls per subject. This distribution is highly non-normal (Kolmogorov-Smirnov = 2.363,  $p < 0.001$ ), indicating that members of a flock do not produce calls equally.

To obtain the most accurate call rate for each subject, the only calls included in this analysis were those produced by a subject during that subject's focal follows. Using this criterion, 1,917 chick-a-dee calls, produced by 47 subjects ( $\bar{x} = 40.79$  calls / caller, range: 1 - 240 calls) were included in the call rate analysis. To avoid over-estimating the call rate of 'the average' titmouse, the 17 subjects that were never identified as producing a call within their focal follows (call rate = 0) were included in this analysis (adjusted  $\bar{x}$ , including non-callers = 29.95 calls/subject, range: 0 - 240 calls). Significant main effects of dominance status ( $F_{(1,63)} = 47.63$ ,  $p \leq 0.001$ ,  $\eta^2 = 0.44$ ,  $P = 1.0$ ) and noise ( $F_{(1,63)} = 13.23$ ,  $p = 0.001$ ,  $\eta^2 = 0.18$ ,  $P = 0.95$ ) were detected for call rate. However, a significant interaction between dominance and noise was detected ( $F_{(3,63)} = 14.14$ ,  $p < 0.001$ ,  $\eta^2 = 0.19$ ,  $P = 0.96$ ), whereby traffic noise increased call rate, but only for the most dominant subjects (call rate of LDR1 > LDR2 at  $p \leq 0.05$  for simple main effects) (Figure 3).

This interaction of dominance and traffic noise on call rate, to my knowledge, has not previously been identified. If, as I suspect, the main effect of traffic noise to increase call rate is an artifact of the Noise\*LDR interaction, then the differential response of the dominant bird to

the presence of noise compared to the lack of response of the subdominants indicates a fundamental difference in the communication strategies of titmice of differing dominance status. First considering what is generally known about call rate and then separately assessing the effects of noise and the effects of dominance on this measure of call use may assist in the interpretation of the interaction effect.

Generally, increases in call rate are associated with increases in arousal and are elicited at the onset of noise (Buckstaff, 2004; Fischer et al., 1995). With extended exposure to noise, calling rates usually subside (Fischer et al., 1995). However, the persistence of greater calling rates during chronic noise are not unheard of; during longer bouts of high background noise, king penguins have been reported to produce signals at greater rates, perhaps to improve signal detection by conspecifics (Lengagne et al., 1999). My original interpretation of the ITH resulted in the prediction that if traffic noise increased perceived threat, and subjects habituated to its presence, that traffic noise should not exert an effect on subjects' call rate. However, that prediction was made without consideration of the influence of dominance on calling behavior for titmice.

The main effect of dominance on call rate detected here is a statistically strong finding ( $\eta^2 = 0.44$ ). Dominance status accounted for 44% of the variation in calling rate of titmice. This result both supports the predictions of the Social Complexity Hypothesis, as outlined by Krams and colleagues (2012) and Freeberg and colleagues (2012), and indicates that, like other parids, the dominant tufted titmouse is the most vocal member of the group (Krama et al., 2008; Krams, 2000; Williams, 2009). What biological significance is represented by increased rates of signaling? In the absence of noise, increased rates of signaling may function to communicate arousal (Clay, Smith & Blumstein, 2012; Marler et al., 1986; Nowicki, 1983) or dominance

status of the signaler (Krama et al., 2008; Krams, 2000; Williams, 2009). Interestingly, arousal is affected both by the onset of anthropogenic noise and is predicted to be increased by the presence of chronic noise, hence providing insight into the meaning of the Noise\*LDR interaction.

The presence of chronic anthropogenic noise has been linked with increased levels of cautious and vigilant behavior, indicating a level of arousal that primes individuals to respond to threat contexts in more adaptive ways than their counterparts in non-noisy habitats (Rabin et al., 2006). Much as the vocal and non-vocal behavior of the titmouse provides information on relative safety and flock movements as the dominant, nuclear species within its mixed-species flocks (Contreras & Seiving, 2011; Grubb & Pravosudov, 1994; Hetrick & Seiving, 2011; Morse, 1970), the dominant titmouse may be the greatest source of information for conspecific and heterospecific flockmates. As predicted by the ITH, titmice may have very well habituated to the presence of traffic noise, an idea that is supported by the lack of an increase in call rate in subdominant flock members. Considering the social function of the chick-a-dee call (reviews in, Krams et al., 2012; Lucas & Freeberg, 2007) and greater degree of sociality in response to traffic noise (Owens et al., 2012) and other threat-inducing stimuli (Krams et al., 2009; Matthysen et al., 2008), dominant titmice may be increasing call rate as a means to ensure the transfer of important information.

### ***C. Effects of noise and dominance on chick-a-dee call complexity***

Uncertainty values produced by the UNCERT analysis are presented in Table IV according to level of analysis and experimental context. Of the 29 birds eligible for the UNCERT analysis, 11 were ranked dominant and 18 subdominant (10 at rank 2, 4 at rank 3, 4 at rank 4). In opposition to the predictions of the RMH, the complexity MANOVA detected no

significant main effect of noise on note-encoding capacity at either  $U_{\text{note}}$  ( $F_{(1,28)} = 1.046$ ,  $p = 0.316$ ,  $\eta^2 = 0.040$ ,  $P = 0.166$ ) or  $U_{\text{pair}}$  ( $F_{(1,28)} = 0.024$ ,  $p = 0.879$ ,  $\eta^2 = 0.001$ ,  $P = 0.024$ ) within this call sample. While there was no significant effect of dominance status on call complexity at  $U_{\text{note}}$  ( $F_{(1,28)} = 0.590$ ,  $p = 0.628$ ,  $\eta^2 = 0.078$ ,  $P = 0.151$ ), there was a significant effect of dominance on information at the level of  $U_{\text{pair}}$  ( $F_{(1,28)} = 6.481$ ,  $p = 0.017$ ,  $\eta^2 = 0.206$ ,  $P = 0.687$ ). Specifically, dominant subjects produced more complex calls at the level of ordered pairs of notes than subdominant subjects. This difference in complexity between birds of different social status suggests that dominant birds are less likely to repeat the note-type that occurred first in an ordered pair, whereas subdominants are more likely to repeat note-types. However, this prediction was not upheld by the analysis of observed note-type repetition. There was no significant difference in note-type repetition for Z ( $F_{(1,28)} = 2.77$ ,  $p = 0.107$ ,  $\eta^2 = 0.09$ ,  $P = 0.36$ ), Y ( $F_{(1,28)} = 0.60$ ,  $p = 0.44$ ,  $\eta^2 = 0.02$ ,  $P = 0.12$ ), A ( $F_{(1,28)} = 0.48$ ,  $p = 0.49$ ,  $\eta^2 = 0.02$ ,  $P = 0.10$ ), or D notes ( $F_{(1,28)} = 0.16$ ,  $p = 0.69$ ,  $\eta^2 = 0.01$ ,  $P = 0.07$ ), indicating that this dominance-related increase in complexity may be less specific to note-type repetition and more indicative of the ability of the first note within an ordered pair to reduce uncertainty about the remainder of the call.

A significant interaction between noise and dominance on call complexity was detected at  $U_{\text{note}}$  ( $F_{(1,28)} = 4.472$ ,  $p = 0.045$ ,  $\eta^2 = 0.152$ ,  $P = 0.529$ ), but not  $U_{\text{pair}}$  ( $F_{(1,28)} = 0.062$ ,  $p = 0.806$ ,  $\eta^2 = 0.002$ ,  $P = 0.057$ ). Simple effects tests revealed that noise increased call complexity at the level of note-type use, but only for the most dominant bird (Figure 4; this interaction was significant at  $\alpha = 0.08$  for the main effects test). An increase in complexity at this level suggests that noise is causing dominant titmice to produce note-types in a less restricted or repetitive manner than subdominant titmice. However, this prediction was not supported by the note-type

use analysis. There was no evidence of a significant interaction effect on note-type use, as Z, A and D notes were all produced at statistically similar probabilities between noise and control contexts and between LDR 1 and LDR 2 (@  $p > 0.05$ ). However, the note-use analysis did detect an interaction effect on the Y note-type, that was in the opposite direction predicted by the MANOVA analysis. The Y note was produced significantly more by dominant birds in noise than in the control context ( $F_{(3,28)} = 3.52$ ,  $p = 0.03$ ,  $\eta^2 = 0.30$ ,  $P = 0.71$ ). As was concluded for the effect of dominance on note-type repetition, the interaction between noise and dominance at the level of note use was less specific to the proportion of use than a note-type's ability to predict something about the rest of the call.

There was no overall trend for noise to reduce signaling complexity, at the level of note-type use or repetition, as predicted by the RMH. In fact, dominance, and a noise\*dominance interaction both increased signaling complexity. The latter finding directly contradicts the prediction of the RMP that this redundancy should limited the amount of information able to be encoded while signaling in the presence of noise (Bradbury & Vehrencamp, 1998; McCowan, et al., 2002). One potential explanation for this finding may be related to the chick-a-dee call itself. The variation in note-type use and signal structure of the chick-a-dee call has been associated with different messages or levels of motivation (Hailman et al., 1985; Freeberg, 2012; Mahurin & Freeberg, 2009; Smith, 1972). Therefore, as noted by previous authors, this relationship between message and signal composition indicates that modifying the composition of the chick-a-dee call (i.e. note-type use and repetition) to improve communication is unlikely. In fact, repetition and related decreases in complexity that have been previously detected existed within comparatively simple signaling systems. In these systems the repetition of a syllable within a signal or repetition of a signal-type is not thought to encode different messages or intensity of a

message, like the chick-a-dee call. Therefore, these results indicate that noise may exert differential effects on communication systems depending on their inherent level of structural complexity.

#### **IV. Considerations, contributions & conclusions**

This study provides insight into the interaction between individual variation and the effects of disturbance. The dominance structure of study flocks reported here supports previous findings regarding linearity and steepness of titmouse dominance hierarchies (Brawn & Samson, 1983; Grubb, 1998; Grubb & Pravosudov, 1994; Pravosudov & Grubb, 1999; Waite, 1987; Waite & Grubb, 1987). However, dominance status of individuals was not associated with any of the dominance-determining characteristics identified in the previous literature, such as size, age or sex. Due to the differences in detailed observation of repeated interactions over an extended period of time between this and previous work, I feel confident in stating that the data presented here on flock-level and individual dominance accurately represents the *range* of dominance behavior in this population. Whether the greater variation in degree of linearity across flocks detected here in comparison to other studies is an effect of aviary conditions, the duration and intensity with which observations were made or is a specific attribute of the specific individuals in each flock or this population of titmice cannot be stated conclusively. However, as discussed, the variation does indicate support for the Social Dynamics Hypothesis.

This work demonstrates previously unknown effects of traffic noise on the vocal behavior of a socially complex avian species. While dominance and vocal production are linked in several other parid species, this is the first time this relationship has been identified for titmice. Additionally, the size of this effect was quite strong. The large discrepancy in calling rate

between flockmates of higher and lower status was exacerbated by the presence of noise, whereby noise increased call rate, but only for the most dominant bird. This result indicates a potentially important distinction in the communicative roles of dominant and subdominant titmice that deserves further investigation. Additionally, the interaction between dominance and noise on call rate was interesting and required a reinterpretation of the Increased Threat Hypothesis, specifically with regard to the presence of individual variation within call production, the roles of different titmice in communication and the structural characteristics of the chick-a-dee call itself.

And finally, as dominant subjects' call rates increased in noise, so too did the complexity of their vocal signals. These data directly contradict the findings of previous research and the RMH (Bradbury & Vehrencamp, 1998; Doyle et al., 2008; McCowan et al., 2002). Differences in the structural organization of the chick-a-dee call, compared to the signaling systems addressed in this previous research may explain the lack of more robust support for this hypothesis.

These findings indicate an even deeper propensity than may have been previously recognized for individual variation to affect behavior and for the effects of disturbance to interact with specific details of a species' life history or behavior to create differential effects. These effects incur consequences for conservation research, and draw attention to the importance of in-depth knowledge of species-specific behavior and responses to disturbance when designing management or conservation policies.



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## **APPENDICES**

## **APPENDIX A**

### **TABLES**



**Table I.** Nonsignificant effects of environmental variables on dependent measures. MANOVAs were used to test for potential effects of study flock, number of chickadees within each study flock, time of year and aviary. There were 16 flocks. The number of chickadees within a study flock ranged from 2 to 4. Time of year was divided into 4 categories that coincided with the four study groups: late fall, early winter, late winter, early spring. Subjects were housed in 4 different aviaries.

Variables	Dependent Measures		
	Chick-a-dee call rate	Linearity ( <i>h</i> )	Slope
Study Flock	$F_{(15,63)} = 0.36, p = 0.98$ $\eta^2 = 0.10, P = .19$	$^A F_{(1,15)} = 0.03, p = 0.96$ $\eta^2 = 0.00, P = .05$	$^A F_{(1,15)} = 0.05, p = 0.83$ $\eta^2 = 0.00, P = .06$
No. chickadees	$F_{(2,63)} = 0.04, p = 0.96$ $\eta^2 = 0.00, P = .06$	$F_{(2,15)} = 0.42, p = 0.67$ $\eta^2 = 0.09, P = .10$	$F_{(2,15)} = 0.17, p = 0.85$ $\eta^2 = 0.04, P = .07$
Time of year	$F_{(3,63)} = 0.04, p = 0.99$ $\eta^2 = 0.00, P = .06$	$*F_{(3,15)} = 3.50, p = 0.06$ $\eta^2 = 0.54, P = .58$	$F_{(3,15)} = 1.09, p = 0.40$ $\eta^2 = 0.27, P = .21$
Aviary	$F_{(3,63)} = 0.35, p = 0.79$ $\eta^2 = 0.02, P = .11$	$F_{(3,15)} = 1.40, p = 0.31$ $\eta^2 = 0.32, P = .26$	$F_{(3,15)} = 1.31, p = 0.33$ $\eta^2 = 0.30, P = .24$

\* This analysis resulted in a trend indicating that linearity of titmouse dominance hierarchies may vary across seasons. The potential for seasonal variation in linearity is supported by the large effect size and observed power statistics.

<sup>A</sup> Flock could not be used as an independent variable in analyses for linearity and slope because there was only one data point for each flock, as linearity and slope are flock level measures. Degrees of freedom and other statistics for linearity and slope were obtained from between-subjects tests with flock was as a covariate.

**Table II.** Details of study flock dominance hierarchies. Study flocks are listed on the far left of the table. To the right of each flock are several values that describe the structure of its respective dominance hierarchy. Significance of slope values are indicated by a single asterisk (\*) for  $p \leq 0.05$ , and a double asterisk (\*\*) if  $p \leq 0.001$ . Flocks highlighted gray are control flocks. As is stated in text, there was no significant effect of traffic noise on linearity or slope of study flock dominance hierarchies.

Study Flock	No. Agonistic Interactions	Linearity ( $h$ )	Slope	R <sup>2</sup>
1	74	0.92	1.00	1.00**
2	50	0.50	0.969	0.94*
3	74	0.59	0.969	0.94*
4	40	1.00	0.998	1.00*
5	34	0.72	0.963	0.93*
6	39	0.88	0.996	0.99*
7	85	0.87	0.999	1.00**
8	36	1.00	0.999	1.00**
9	98	0.49	0.844	0.71 ( $p = .16$ )
10	30	0.26	0.975	0.95*
11	45	0.77	0.981	0.96*
12	60	0.48	0.987	0.97*
13	29	0.91	0.978	0.96*
14	29	0.80	0.996	0.99*

**Table II. Continued**

	No. Agonistic Interactions	Linearity ( $h$ )	Slope	$R^2$
Study Flock				
<sup>A</sup> 15	36	0.64	0.949	0.90*
16	31	0.97	0.998	1.00*

<sup>A</sup> flock with an unknown dyadic relationship, corrected for using Singh et al., 2003

**Table III.** Dominance ranks and associated characteristics of subjects. As is stated in text, the dominance status achieved by subjects is not predicted by any of the previously identified dominance determining characteristics for titmice. Additionally, there was no significant effect of traffic noise on dominance status or degree of dominance between flockmates. Control flocks are highlighted gray.

	Subject ID	Ordinal Dominance Rank	normDS	Sex	Wing Chord	Entry Order
Study Flock 1	ccsx	3	1.058	?	78.00	1
	sxcg	2	1.94	♀	75.00	1
	dmsx	1	2.757	♂	80.00	1
	sxgg	4	0.203	?	78.50	4
Study Flock 2	ggsx	4	0.66	♀	75.00	1
	mxsg	3	0.979	♂	85.00	1
	xsbb	2	2.041	?	78.50	1
	sxmd	1	2.319	♀	76.50	1
Study Flock 3	wwsx	4	0.675	♂	80.50	1
	sxcc	3	0.839	♀	76.50	1
	rgsx	2	1.854	♀	75.50	1
	sxpp	1	2.632	?	79.50	1
Study Flock 4	wgsx	3	1.167	♀	76.00	1
	sxbc	4	0.169	?	77.50	1
	sxrg	2	1.952	♂	81.00	1
	mbsx	1	2.712	♀	76.00	1
Study Flock 5	rrsx	1	2.744	?	78.00	1
	sxod	4	0.657	♀	76.00	1
	sxwm	2	1.543	♂	82.00	1
	dbsx	3	1.056	?	78.00	4
Study Flock 6	brsx	2	2.002	♀	77.00	1
	sxgw	1	2.625	♂	80.00	1
	spdx	3	1.019	♂	80.00	1
	gbsx	4	0.345	?	78.00	4

**Table III. Continued**

	Subject ID	Ordinal Dominance Rank	normDS	Sex	Wing Chord	Entry Order
Study Flock 7	sxcd	2	1.876	♂	81.00	1
	sxww	3	1.077	♂	81.50	1
	sxdm	1	2.834	♀	77.00	1
	blsx	4	0.213	♀	76.00	1
Study Flock 8	sxdw	1	2.654	♂	80.50	1
	pwsx	2	1.873	♂	80.50	1
	sxol	3	1.186	♀	76.00	4
	oxos	4	0.287	♀	77.00	4
Study Flock 9	lbsx	3	1.131	♀	73.50	1
	sxrd	4	0.915	?	78.00	1
	xxsp	1	2.778	?	79.00	1
	gosx	2	1.167	♂	80.00	1
Study Flock 10	dpsx	3	1.27	♀	75.50	1
	sgxx	1	2.325	♂	80.00	1
	crsx	4	0.862	♀	76.00	1
	xxsw	2	1.542	♂	80.00	4
Study Flock 11	grsx	1	2.619	♂	80.00	1
	owsx	3	1.393	♂	80.50	1
	sxor	4	0.249	?	78.50	1
	sxmb	2	1.739	♀	75.00	4
Study Flock 12	sxpo	1	2.483	♀	75.00	1
	ogsx	2	1.65	♂	82.00	1
	sxlc	4	0.531	♀	76.50	1
	rdsx	3	1.336	♂	81.00	4
Study Flock 13	cbsx	3	0.858	♂	81.00	1
	sxwo	1	2.729	?	78.00	1
	sxdg	2	1.833	?	78.50	1
	lcsx	4	0.58	♀	77.00	1
Study Flock 14	sxbg	3	1.25	?	77.50	1
	ddsx	2	1.88	♀	75.00	1
	odsx	4	0.351	♀	76.00	1
	wxsm	1	2.519	♂	81.00	4

**Table III. Continued**

	Subject ID	Ordinal Dominance Rank	normDS	Sex	Wing Chord	Entry Order
Study Flock 15	mwsx	2	1.466	♀	74.50	1
	sxgm	1	2.369	♂	83.00	1
	orsx	3	1.45	?	79.00	3
	0band	4	0.715	?	78.00	4
Study Flock 16	wmsx	3	1.208	♂	80.00	1
	sxbm	4	0.338	♀	77.00	1
	sxop	1	2.588	?	78.00	1
	rbsx	2	1.867	♂	80.00	4

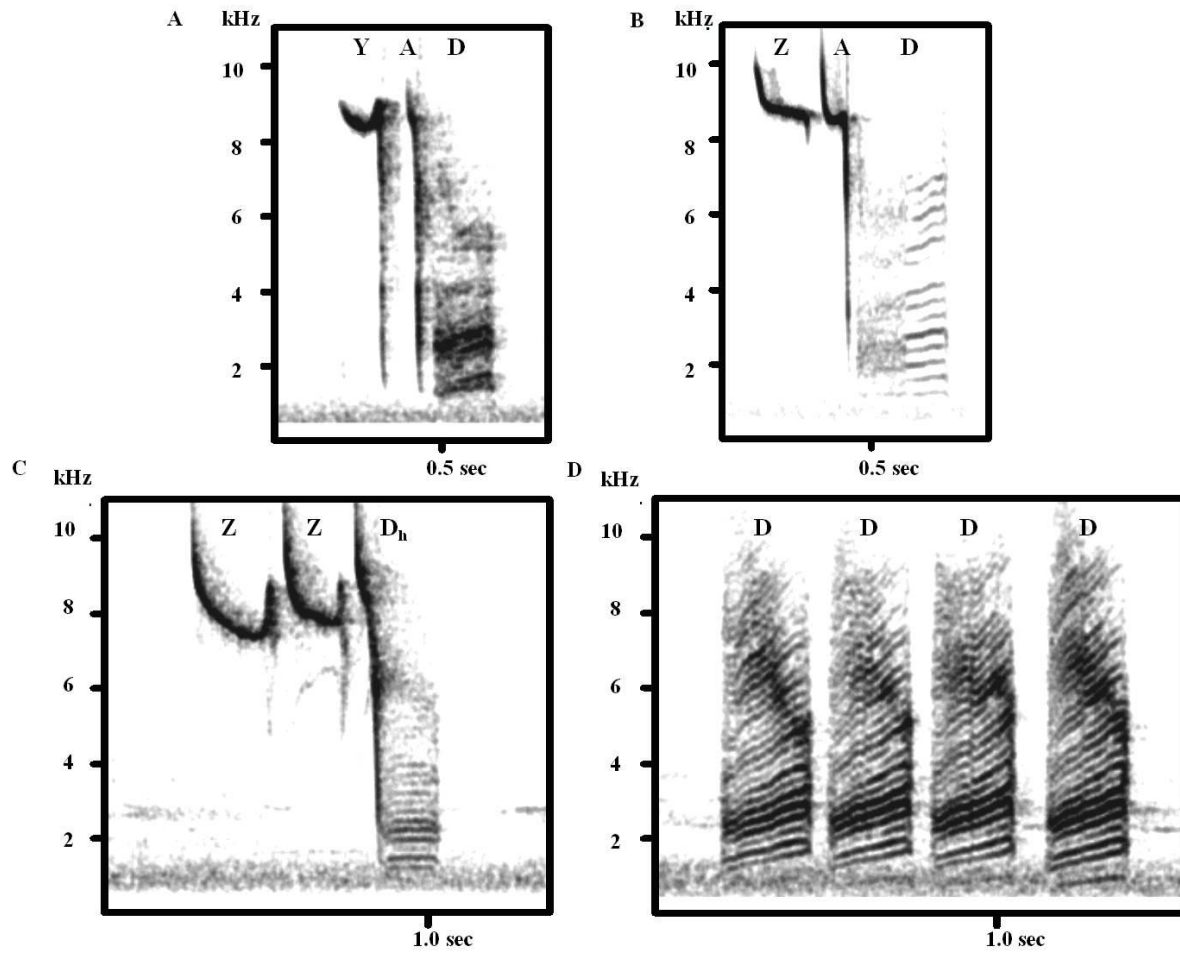
**Table IV.** Mean uncertainty values (bits / unit) produced by the UNCERT analysis. Values are displayed by each level of analysis for comparison with the results of the complexity analysis and  $U_{max}$  provided in text. Within each level of  $U$ , mean uncertainty values are listed for the most dominant subject (LDR = 1) and the subdominant subjects (LDR = 2). Additionally, values are displayed for in three categories across the top of the table: for all titmice, for titmice exposed to noise and for titmice in control conditions.

	All Subjects (N= 29)			Noise (n = 15)			Control (n = 14)		
	min	max	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$
$U_{note}$	0.51	1.96	1.56	0.51	1.96	1.6	0.67	1.85	1.52
LDR 1 n = 11	0.67	1.96	1.66	1.53	1.96	1.87	0.67	1.79	1.41
LDR 2 n = 18	0.51	1.89	1.51	0.51	1.89	1.43	1.02	1.85	1.59
$U_{pair}$	0.00	0.83	0.33	0.00	0.81	0.33	0.00	0.83	0.33
LDR 1 n = 11	0.01	0.83	0.46	0.15	0.81	0.45	0.01	0.83	0.48
LDR 2 n = 18	0.00	0.67	0.24	0.00	0.67	0.25	0.00	0.42	0.24

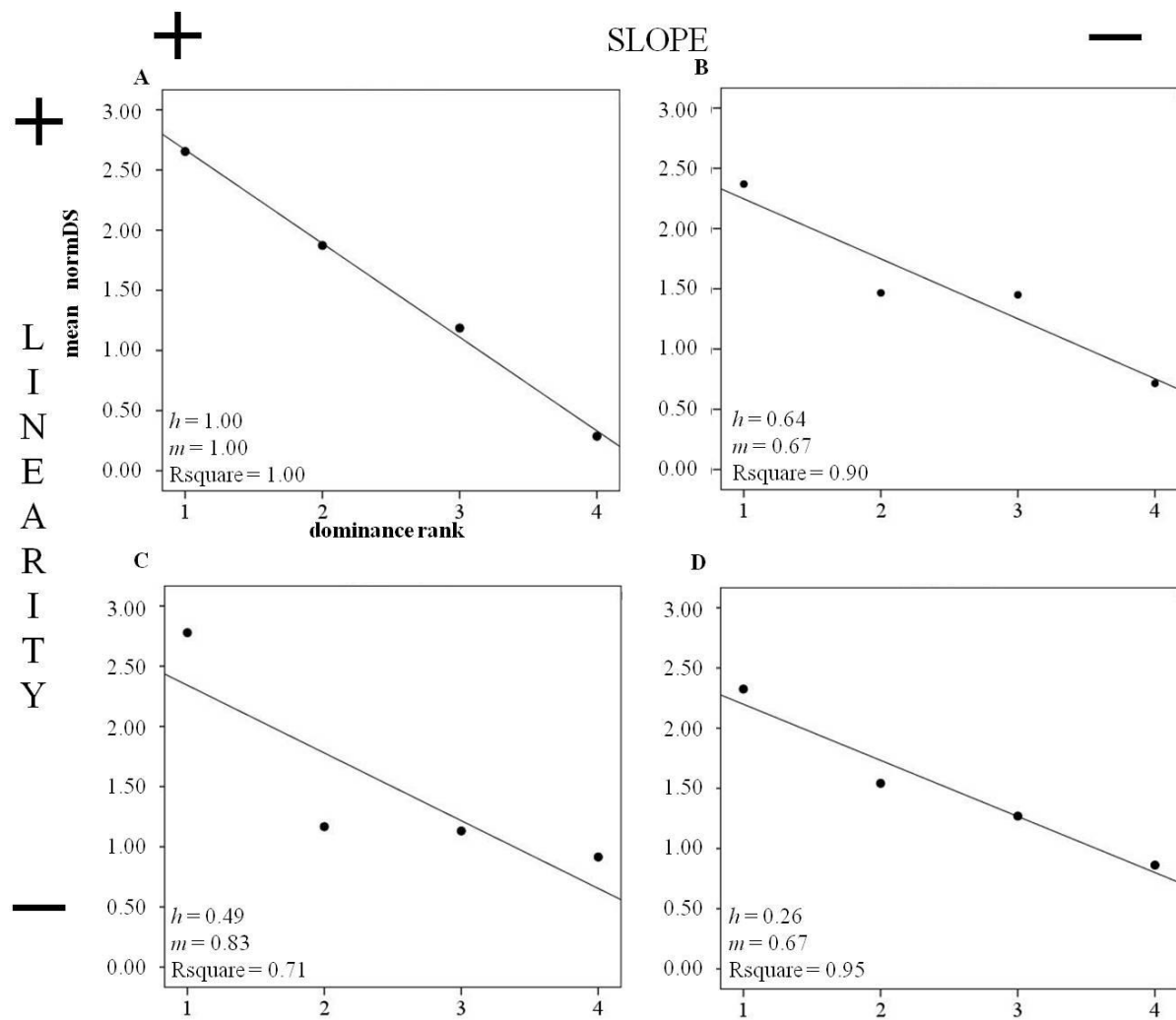
## **APPENDIX B**

### **FIGURES**

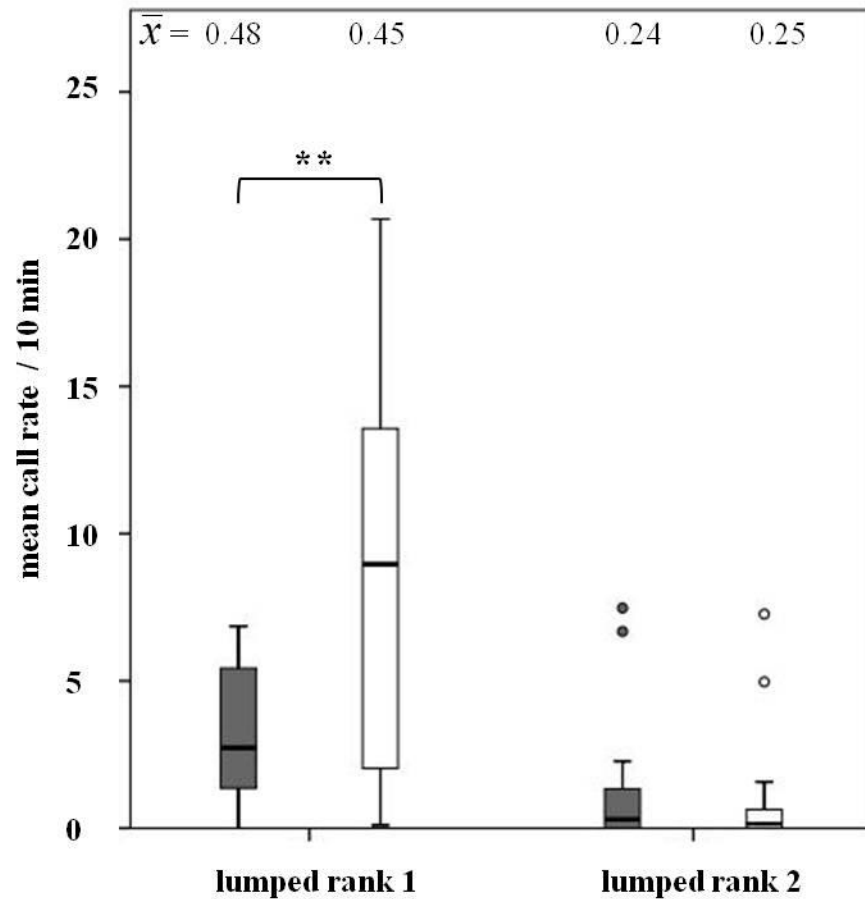




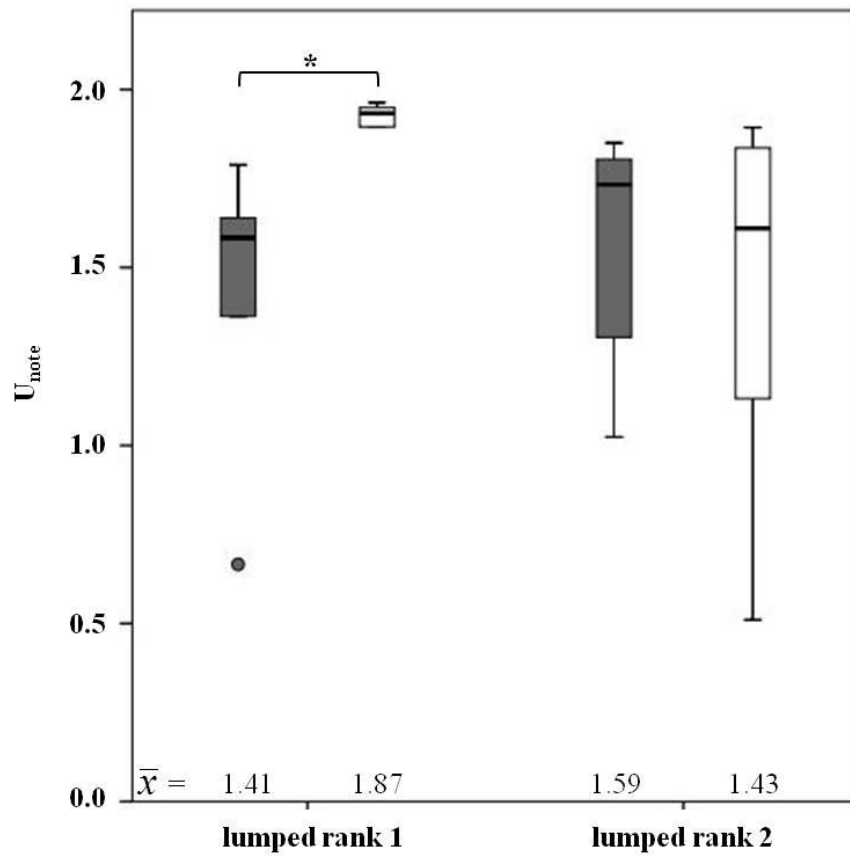
**Figure 1.** Spectrograms of four different chick-a-dee calls of tufted titmice. Panels A - D illustrate calls of different note-type compositions. All five note-types, Z, Y, A, D<sub>h</sub> and D are represented.



**Figure 2.** Visual representations of titmouse dominance hierarchies of varying degrees of linearity and steepness.



**Figure 3.** Noise and dominance interact to affect chick-a-dee call rate. Data displayed are medians, quartiles and data range with outliers. Due to lack of room at the bottom of the graph, group means are displayed above respective boxplots within graphs. Significant comparisons are denoted by brackets; a double asterisk (\*\*) denotes significance of  $p \leq 0.01$ . Control birds are shown in gray.



**Figure 4.** Noise and dominance interact to affect uncertainty. Data displayed are medians, quartiles and data range with outliers. Group means are displayed below respective boxplots within graphs. Significant comparisons are denoted by brackets; a single asterisk (\*) denotes significance of  $p = 0.08$ . Subjects in the control condition are shown in gray.

## **CHAPTER 4**

### **RUSH HOUR TRAFFIC NOISE INCREASES SOCIAL BEHAVIOR OF TUFTED TITMICE (*BAEOLOPHUS BICOLOR*)**

This chapter is a revised version of a manuscript in preparation for submission for review and publication in a peer-reviewed, scientific journal:

Owens, J. L. (In Prep.). The effects of rush hour traffic noise on the social behavior of tufted titmice (*Baeolophus bicolor*).

My contributions to this work include (a) formulating the research idea, question and hypothesis, (b) designing the experiment, (c) building sound equipment and maintaining set-up, (d) training and organizing research assistants, (e) obtaining and caring for subjects, (f) collecting data on social behavior, (g) organizing and conducting statistical analyses, (h) interpreting results and (i) writing of the manuscript and submission for publication. Michael Koszela, Ryan Moseley and Christy Whitt served as field research assistants for Fall 2010 and Spring 2011 on a volunteer basis or as part of Psychology 489. During the fall semester these students assisted with recording traffic noise and trapping subjects. During the spring semester students conducted field research.

## ABSTRACT

Recent experimental work has contributed to our understand of the ability of avian species to respond to anthropogenic noise in short-term experimental presentations. However we have little knowledge of how anthropogenic noise as experienced by species in the real-world affects behavior. Rush-hour traffic is a regularly repeated change in traffic patterns and corresponding noise levels. This study used experimental exposure to different variants of recorded traffic noise to create temporary increases in noise levels that modeled rush hour. This exposure paradigm was used to test for the effects of 'rush hour' on the social behavior of tufted titmice (*Baeolophus bicolor*). According to the Increased Threat Hypothesis, rush hour traffic should increase subjects' social behavior, which was quantified using three measures: nearest neighbor distances (NND), the number of close-proximity perches and preference for conspecific perch-partners. Subjects' flight behavior was quantified to control for potential effects of activity on social behavior. Data were collected during four exposure periods: pre-experimental exposure (PRE), first hour of experimental exposure (START), second hour of experimental exposure (END) and post-experimental exposure to experimental traffic noise (POST). Rush hour traffic noise significantly increased sociality for two of the three social behaviors, supporting the predictions of the Increased Threat Hypothesis. In addition to the specific effects of rush hour on each of the dependent measures, important differences between the effects of chronically and temporarily increased levels of traffic noise are identified and discussed. These findings indicate that the effects of traffic noise on social behavior and activity are influenced by characteristics of traffic noise itself.

## CHAPTER 4

### RUSH HOUR TRAFFIC NOISE INCREASES SOCIAL BEHAVIOR OF TUFTED TITMICE (*BAEOLOPHUS BICOLOR*)

#### I. Introduction

The study of anthropogenic noise has benefited from a recent surge of experimental work clarifying our understanding of the effects of anthropogenic disturbance on a range of behaviors. Many of these recent efforts have utilized active and inactive gas well compressor sites to study the effects of chronic anthropogenic noise while controlling for confounding variables (Francis, Kleist, Davidson, Ortega & Cruz, 2012; Kight & Swaddle, 2007; Lackey, Morrison, Loman, Collier & Wilkins, 2012; Ortega & Francis, 2012; Swaddle, Kight, Perera, Davila-Reyes & Sikora, 2012). While many sources of anthropogenic noise are constant (e.g. urban noise, traffic noise), experimental acoustic stimuli used in studies of urban and traffic noise are often of significantly shorter durations than the real-world noise sources they were intended to represent (e.g. Bermúdez-Cuamatzin, Ríos-Chelén, Gil & Garcia, 2010; Brumm, Schmidt & Schrader, 2009; Halfwerk & Slabbekoorn, 2009; Verzijden, Ripmeester, Ohms, Snelderwaard & Slabbekoorn, 2010). Findings of these studies included birds producing signals at a louder amplitude (Brumm et al., 2009), shifting the acoustic frequency above that of the masking sound (Verzijden et al., 2010), producing signals of a longer duration (Bermúdez-Cuamatzin et al., 2010) and switching to signal types that are less susceptible to masking (Halfwerk & Slabbekoorn, 2009). However, the validity of these findings is questionable as the experimental acoustic stimuli used in these studies were less than 10 minutes long (Brumm et al., 2009;



Halfwerk & Slabbekoorn, 2009) and data collection quotas were often met before the entire stimulus was broadcast (Bermúdez-Cuamatzin et al., 2010; Brumm et al., 2009; Verzijden et al., 2010). One rationale for conducting this study was to address traffic noise as it exists in the real world.

### ***A. Goals, expectations & predictions***

Anthropogenic noise is not static, but is rather variable in pattern and amplitude. Rush-hour is a common source of variation, marked by a regularly occurring period of increased traffic density and increased traffic noise. Modeling rush-hour-like increases in traffic noise provides an ethologically meaningful experimental procedure from which one can address variation in traffic noise. This study uses this system to determine how the tufted titmouse (*Baeolophus bicolor*) responds to the presence of and variation within traffic noise. Tufted titmice are an ideal species for such a study as titmice are disturbance-tolerant birds (Grubb, 1998; Grubb & Pravosudov, 1994), and are a species with a currently under-represented life-history strategy within the literature on anthropogenic noise (Ortega, 2012). Although a majority of research focuses on the vocal responses of birds to noise (review Ortega, 2012), other behavioral patterns that may be affected have received less attention (Blickely & Patricelli, 2012; Owens, Stec & O'Hatnick, 2012). Here we focus on three measures of social behavior and one measure of activity.

To model 'rush hour' I combined pre-existing environmental conditions and experimental methods. Wild-caught tufted titmice housed in aviaries were continuously exposed to background levels of traffic noise emanating from roads out of visual range. For 150 minutes each day subjects were exposed to variants of traffic noise at sound levels comparable to those detected in titmouse habitats during times of increased traffic density. For comparative purposes

with a previous study (Owens et al., 2012), behavior was quantified using four dependent variables: nearest neighbor distance (NND), number of close-perches, number of flights and strength of conspecific preference for close-perch partners. These data were collected before, during and after experimental exposures to compare the effects of 'normal' levels of traffic noise and 'rush-hour' levels of traffic noise and to identify how transitions between the two contexts affect social behavior.

A previous study has demonstrated that long-term exposure to simulated traffic noise increases rates and quality of close-proximity social behavior for titmice (Owens et al., 2012). Based upon this earlier study with titmice, I expected exposure to rush hour traffic noise to increase affiliative social behavior of titmice by reducing nearest neighbor distances, increasing the number of close-perches and relaxing normative preferences for conspecific perch-mates (Owens et al., 2012). Additionally, recent theoretical advancements in the study of anthropogenic disturbance provide potential explanatory hypotheses applicable to traffic noise.

The Distracted Prey Hypothesis (DPH) states that noise interrupts attentional processes, effectively distracting animals from engaging in immediately important behaviors and possibly leaving them vulnerable to predation or other threats (Chan & Blumstein, 2011; Chan, Giraldo-Perez, Smith & Blumstein, 2010; Chan, Stahlman et al., 2010). This hypothesis was developed across two different studies measuring the latency of terrestrial hermit crabs (*Coenobita clypeatus*) to exhibit anti-predatory behavior in response to different threatening stimuli while exposed to noise. In the second study authors replicated the findings of the first study (Chan, Giraldo-Perez et al., 2010) and determined that longer and louder noise increased distraction, causing significantly longer latencies to hide than shorter and quieter noises (Chan, Stahlman et

al., 2010). However, the stimuli used in the short and long context 10 sec and 90 sec, respectively. Compared to chronic noise, 90 sec is still relatively short term exposure.

While not stated by the DPH or its authors, this hypothesis is most likely applicable to acoustic disturbances that are novel, acute or short-term. For example, the predictions of the DPH do not support the behavioral response of ground squirrels to alarm signals produced in habitats where noise levels are chronically elevated by the presence of wind-turbines; in fact, these species exhibited increased rates of vigilance and cautious behavior that resulted in more efficient responses to alarm signals (Rabin, Coss & Owings, 2006). In response to this discrepancy between theory and the observed effects of chronic noise, I proposed an alternative hypothesis, the Increased Threat Hypothesis (ITH) (Owens et al., 2012). The ITH is an extension of the Risk-Disturbance Hypothesis (Frid & Dill, 2002). Both hypotheses recognize the functional similarity between predatory and disturbance stimuli and predict responses based on the level of perceived threat resulting from the stimuli in question. Specifically, the ITH posits that disturbance creates behavior comparable to anti-predator responses as a result of its effects on an animal's perception of threat or risk within its environment. Where the two differ is in regard to the specificity of predictions for stimuli of different durations or levels of familiarity and predictability. The ITH provides distinct predictions depending upon the type of disturbance.

Rush-hour is a common phenomenon resulting from morning and afternoon commutes related to specific patterns in human behavior; as a common and patterned occurrence, rush-hour is likely a familiar stimulus within natural habitats. According to the ITH, familiarity is linked with the processes of habituation and sensitization, which result in adaptive responses to noise rather than startle or fear responses (i.e. Bowles, 1995). One adaptive strategy that birds use to

reduce or manage threat is to join or increase the density of a social group (Elgar, Burren & Posen, 1984; Krause & Ruxton, 2002; Metcalf, 1984). If rush-hour increases threat as predicted by the ITH then I expect to see an increase in sociality indicated by a decrease in NND and an increase in the number of close-perches while traffic noise is being broadcasted.

## **II. Materials and methods**

### ***A. Research design***

Here, experimental exposure to traffic noise was used to test for the effects of 'rush hour' on the social behavior of titmice. Study flocks were continuously exposed to ambient traffic noise. The two aviaries used here are located approximately 550 m from Pellissippi Parkway (Oak Ridge, Tennessee) and have an average background noise level of 59.3 dB / SPL (range: 48 - 82 dB; General Radio Sound Pressure Level meter, 1565-B series, A-weighting). The majority of background noise (48 - 65 dB) consisted of traffic noise from surrounding highways, roads, trails and access points to industrial sites. The constant din of traffic noise within the aviaries was comparable to the lower-amplitude traffic noise present in road-effect zone habitats during non-rush-hours.

Rush-hour is a regularly occurring period of increased traffic density that causes periods of louder-than-normal traffic noise. To model 'rush hour' I broadcasted recordings of traffic noise at sound levels comparable to those detected in titmouse habitats during times of increased traffic density. Traffic noise was recorded equally from three sites along a 7,000 meter stretch of Pellissippi Parkway, a busy, four-lane highways bordering the UTFRREC. The same protocol was used for recording at the three different sites: between 800 - 1400 EST, an omni-directional Sennheiser Me-62 microphone and Fostex FR-2 digital audio recorder were set up 15 - 20 m

from the shoulder of the Parkway to record traffic noise (sampling rate = 22.5 kHz). While recording, observers collected information on sound pressure levels (SPL) at the recording site and the amount of traffic on the road. At 15 min intervals, an observer flipped a coin to determine the order in which the A- and C-weighting measures of SPL were recorded (General Radio Sound Pressure Level meter, 1565-B series). The mean SPL across sites and days of recording was 71.48 dB (range: 61.45 - 82.36 dB). The average SPL is likely a low estimate of actual SPL as passing of any large or loud vehicles was difficult to measure in the short amount of time they were present. As such, most measurements were made during constant traffic noise from smaller vehicles like cars. The second observer would use the same 15 min intervals to count the number of vehicles passing the recording site. For 60 sec the observer would count the vehicles heading North, and then switch to counting the traffic heading South; a coin was flipped to determine which direction would be counted first at each interval. The mean traffic load across sites and days of recording (North and South combined) was 2,037 cars / hour, with a range of 1,176 - 2,460 cars / hour.

Prior to use in this study, traffic noise sound files were edited using Cool Edit Pro. (22,050 sampling rate, 16-bit resolution; V. 2, Syntrillium Software, Scottsdale, AZ). Each sample of traffic noise included different patterns of sound and varied in sound pressure level and amplitude. It was important to retain this variation, but very loud noises (passing of an 18-wheel semi-truck or group of motorcycles) made some alteration necessary in order to avoid distortion during playback. While volume could not be standardized due to the dynamic characteristics of sound pressure over time and between recording sites, sound files were normalized so that the average amplitude at playback was approximately 75 dB / SPL at 1 meter from the speaker (Bermúdez-Cuamatzin et al., 2011). Due to the design of the study, another

concern was the response of subjects to the sudden increase in background noise caused by the onset of experimental exposures. To reduce this effect each sample of traffic noise was altered so that the amplitude at playback started at 50 dB and increased to 75 dB over the first 15 minutes of exposure. The same adjustment was made to the last 15 minutes of a file where the amplitude was slowly reduced from 75 dB to 50 dB before ending. Following any editing, all 18 recordings were stored as .WAV files on an iPod Nano (6<sup>th</sup> generation, Apple Inc.). At playback, .wav files were amplified with a Visonik amplifier before being broadcast through a 150-watt speaker (Bogen<sup>®</sup> Communications Inc., N.E.A.R. outdoor speaker, model A-6). Each aviary was equipped with a speaker positioned about 2.5 m above the ground. The ipod, amplifier and speaker system were powered by two, inter-connected deep-cycle, 12 Volt Marine Batteries. A roof-mounted solar panel connected to the battery system continuously (re-) charged the batteries. Recording, editing and system set-up were completed in October 2010.

During the months of October thru March of 2010 - 2011 and 2011 - 2012 subjects were collected following the methods of Owens, Stec and O'Hatnick (2012). During these months, titmice are commonly involved in mixed-species flocks with Carolina chickadees (*Poecile carolinensis*). To maintain natural social contexts (Grubb and Pravosudov, 1994; Mostrom, Curry & Lohr, 2002), titmice that served as subjects were housed with 4 Carolina chickadees for the duration of the study (Owens et al., 2012; Chapter 2). Titmice and chickadees were trapped using walk-in treadle (potter) traps baited with a 1:1 mix of black-oil sunflower and safflower seed. Both species were captured from sites with low to moderate levels of background noise (40 - 50 dB). Because previous exposure may affect the response of birds to experimental playbacks (Lackey et al., 2012), traffic noise was not a major contributor to background noise at any site of capture. Following capture, birds were banded with individually identifying colored

leg bands and placed into aviaries with familiar hetero- and conspecifics. Study flocks were formed with the goal of including an equal number of male (2) and female (2) subjects captured from the same site. For tufted titmice, the focal study species, sex-ratio requirements were met for all study flocks and capture-site requirements were met for 7 of 8 study flocks. This discrepancy was due to difficulty catching a second female as the fourth subject for flock 7. This subject had to be captured from a territory adjacent to that of the other three titmice included in study flock 7. Subjects and chickadees were housed in large outdoor aviaries (6 m x 9 m x 3.5 m) equipped with several hanging perches, young trees, grass and an enclosed shelter and continuous access to a variety of fresh fruits, vegetables, live food, seed and vitamin supplemented water. Subjects were allowed to acclimate to aviary and experimental conditions for at least 10 days prior to data collection.

Data were collected during 4, one-hour periods (Figure 1 A). Data were collected before and after the experimental exposure periods and are collectively referred to as 'non-exposure' periods. While non-exposure periods did not include experimental exposure, ambient traffic noise from nearby roads was audible at moderate levels. Non-exposure periods are referred to as 'pre-exposure' (PRE) and 'post-exposure' (POST). The 150-min experimental exposure to traffic noise was separated into two 'experimental exposure' periods. Following the 15-min period of increasing amplitude, the first 60 min of full-amplitude traffic noise is referred to as 'start-exposure' (START), as observations of subjects' behavior were occurring at the onset and initial hour of exposure to experimental presentations of traffic noise. The second 60 minutes of the exposure period is referred to as 'end-exposure' (END) as observations of subjects' behavior were occurring after an extended period of exposure and at the end of experimental exposure to traffic noise.

Data were collected for each subject on 10 separate days. The order in which aviaries were observed was determined by flipping a coin each day; however, randomization was abandoned near the end of data collection for each flock to ensure that each flock was equally sampled in pre and post periods. Likewise, the order that subjects within each aviary were observed was randomized. All data were collected between 0800 - 1600 EST, with the restriction that data were never collected during either of the 15-min periods of amplitude-transition.

Nearest neighbor distance was measured using instantaneous focal point sampling in each of the four periods (Figure 1 B). The first NND data point was collected following husbandry duties, directly before the beginning of the PRE period. The second and third NND data points were collected during START and END exposure periods, respectively. The last NND data point was collected at the end of the day, approximately an hour after experimental exposure had ended, following the POST period. At each of these collection points an observer would enter the aviary and wait approximately 5 min before collecting data. Upon locating a focal bird the observer scanned outward in a circular pattern to find and identify the closest subject. Distances between birds were determined using markers denoting 1 meter distances throughout the aviary. NND was recorded as ordinal data: < 30 cm, 30 cm - 1 m, 1 m, 2 m, 3 m, 4m, etc.

Close-perch, preference and flight data were collected using 10-min focal follows conducted during each of the four trials (Figure 1 C). Data collection did not begin until approximately 5 min after the observer entered the aviary. Upon locating a focal individual, the observer would begin data collection, following and narrating the focal bird's behavior in real-time. Narrations of focal follows were recorded using a directional Sennheiser ME-66



microphone and Fostex FR-2 digital recorder. The words "close-perch" were used to identify any time that the focal bird approached a flockmate within 1 m and maintained this association for at least 1 sec, or when a flockmate exhibited the same behavior toward the focal bird. Additionally, directionality of the interaction was dictated by the order in which a bird's identity preceded or followed the words close perch. The directionality and species of the bird(s) involved in close-perch interactions were used to calculate perch-partner preferences. In the study flocks the expected proportion of close-perches a titmouse would direct at another titmouse was 0.43 (3 other titmice in a flock of 7 birds, excluding the focal:  $3/7 = 0.43$ ). Therefore, if an individual's difference score was a high positive number then the subject exhibited a strong preference for conspecifics. To control for any potential effects of activity on the frequency of close-perches, I also recorded the number of times a focal bird took flight. A flight was defined as a lift off, extension of the wings and a distance moved of  $\geq 1$  m.

Data were collected from 32 titmice constituting 8 different study flocks. Flocks were studied in groups of two; flocks 1 - 4 were studied in 2010 - 2011 and flocks 5 - 8 were studied in 2011 - 2012. A speaker system malfunction, localized to one aviary, occurred on day 8 of data collection for the second group of study flocks. Unable to identify the technical issue, a new speaker, of the same make and model, was ordered and the wiring from the amplifier to the speaker was replaced for that aviary. The interruption in exposure to traffic noise for that aviary resulted in 7 days of data for Flock 4. Days of data collection for study flocks ranged from 7 to 10 days.

## ***B. Statistical analysis***

### **1. Controlling for observer bias and assessing reliability**

Traffic noise and associated measures of sound pressure level (dB SPL) and traffic-count data were recorded by six different combinations of 4 observers. All behavioral data were collected and coded by one observer, JLO. Spearman's correlations were used to test the agreement between the scores of JLO and two independent scorers, SB and TF, on total number of close perches, number of directed close perches, number of close perches with titmice and number of flights (Table I).

### **2. Ad hoc analyses**

Subjects were exposed to several types of variation that may have affected their behavior, including: the time of year subjects were observed, the aviary in which subjects were housed and the unique characteristics of each study flock. MANOVAs were used to determine whether any of these three 'environmental' variables affected the dependent measures. Analyses indicated several significant relationships between environmental variables and dependent measures. To control for these effects, aviary, time of year and flock are included as random factors in the planned analysis.

### **3. Planned analyses**

Linear Mixed Model Analyses of Variance with random effects were used to analyze the 10 day average of NND, close-perch (initiated and received perches combined), conspecific preference and flight data for each subject. Period was entered into the model as a repeated fixed factor with four levels (PRE, START, END and POST). Subject ID, flock, aviary and time of

year were included in the model as random factors. The inclusion of random factors was supported by significant Wald Z tests (at  $p < 0.05$ ).

The Mixed Model menu in SPSS (v. 20) does not allow the calculation of effect sizes ( $\eta^2$  = partial eta squared) or observed power (P). To obtain these measures for main effects tests, I ran a GLM multivariate ANOVA with trial as the fixed factor and flock, aviary, time of year and subject ID as covariates. Although the exact numbers varied, this analysis returned the same results as the mixed model. The effect size and observed power statistics from this MANOVA are presented following the "F" and  $p$ -value statistics from the mixed model analysis.

If a main effect of period was detected, individual linear mixed model analyses were used as post-hoc tests to identify significant differences between exposure periods. Sequential Bonferroni adjustments, a rather conservative method of controlling for multiple-comparisons, were applied but did not result in the rejection of any of the significant relationships identified. All between-level differences were identified using  $\alpha < 0.05$ . Residuals of mixed models were normally distributed ( $p > 0.05$ ), indicating that assumptions of parametric tests were met. All analyses, including inter-rater reliability, were conducted using SPSS v. 20.

### **III. Results and discussion**

#### ***A. Effects of exposure period on titmouse social behavior and activity***

The effects of exposure period on NND, close-perch, preference for conspecific close-perch partners and flight were tested using linear mixed model analyses. The final mixed model detected no effect of exposure period on conspecific preference ( $F_{(3, 93)} = 0.43, p = 0.74, \eta^2 = 0.01, P = 0.10$ ). Significant effects were identified for the three other dependent measures.

The final model for NND revealed a significant effect of period ( $F_{(3, 93)} = 14.10, p < 0.01, \eta^2 = 0.16, P = 0.99$ ) which accounted for 16% of the variation in this measure. Post-hoc tests revealed a significant difference between experimental exposure and non-exposure trials; NNDs were significantly smaller in START and END compared to PRE and POST (PRE, POST > START, END;  $p < 0.05$ ; Figure 2). There was no significant difference between the two experimental exposure periods, indicating that the effects of rush hour were uniform across the duration of exposure. Likewise, NND values were statistically equivalent between the two non-exposure periods.

The significant effect of period on close-perching behavior ( $F_{(3, 93)} = 35.04, p < 0.0, \eta^2 = 0.23, P = 1.0$ ) was defined by significant differences for all six of the possible comparisons between the four periods (START > END > PRE > POST;  $p < 0.05$ ; Figure 3). Experimental exposure to traffic noise caused a significant increase in the number of close-perches experienced in both START and END periods. However, the strength of this effect was related to the duration of exposure to noise, as subjects' close perching behavior was significantly higher during the first hour of exposure to traffic noise compared to the last hour of exposure. A similar pattern was detected for PRE and POST within the non-exposure periods. Following experimental exposure, the number of close-perches experienced during the POST period was not only significantly lower than the values of both experimental exposure periods, but was also significantly lower than the value obtained for the PRE period.

Flight behavior was also significantly affected by exposure period ( $F_{(3, 93)} = 15.36, p < 0.01, \eta^2 = 0.14, P = 0.96$ ; Figure 4). The pattern of relationships between the four periods and flight are different from those identified for both NND and close-perches. Post-hoc analyses resulted in significant effects for 5 of the 6 comparisons (START > PRE, END > POST;  $p <$

0.05). Experimental exposure to traffic noise increased the number of flights, but only during the onset of, and initial exposure to, noise. Following the first hour of experimental exposure, flight behavior returned to baseline levels obtained during the PRE period. Following this, flight behavior in the POST period was significantly reduced compared to the three other periods. Flights were analyzed to control for any potential effects of activity on close-perching behavior. The effect of noise on flight subsides over time, whereas noise continues to effect close-perching behavior beyond initial exposure. The lack of an increase in flights during the END period indicates that the effects of traffic noise on close-perch behavior are likely independent of the effects of noise on flight.

This study indicates that temporary increases in traffic noise levels affect the dependent measures in different ways. Specifically, the analysis revealed a pattern of effects related to PRE, START, END and POST exposure periods that differ between the three dependent variables. This pattern of effects is illustrated in Figure 5, which provides a visual representation of the effects of the different exposure periods on NND, close-perching and flight.

### ***B. Increased Threat Hypothesis applied to the effects of rush hour***

Rush-hour traffic and the associated increase in traffic noise levels is a common phenomenon resulting from patterns of human behavior. The Increased Threat Hypothesis predicted that the short-term experimental exposure to traffic noise in the current study would cause a significant increase in the social behavior of subjects. Two of the findings support this prediction, as evidenced by the significant reduction in nearest neighbor distances and increase in the number of close perches in both START and END periods. There was no effect of rush hour traffic noise on conspecific preference detected in this study, which would suggest that, contrary to the ITH, traffic noise does not influence this aspect of social behavior. However, the ability of

that analysis to detect an existing effect was approximately 10%. Previous research has shown that exposure to chronic traffic noise significantly reduces preferences of titmice for conspecific close-perch partners (Owens et al., 2012). The lack of an effect on preference may be a result of acuteness of the rush hour traffic noise stimuli itself. This latter explanation is most plausible as the previous study detected relaxed social preferences in response to 8 hour durations of increased traffic noise levels that occurred each day for several weeks.

The similar effects caused by seemingly opposite stimuli, short-term and long-term traffic noise, likely result from the shared characteristic of these two stimuli: familiarity. In the current study, rush hour was made a familiar stimulus during the acclimation period where subjects were exposed to temporarily increased levels of traffic noise for 10 days. In addition to this exposure, the presence and behavior of the observer was another reliable predictor of when background noise levels would increase and decrease each day. This is not a confound of the study as the predictability of rush hour within the aviary context is comparable to the predictability of rush-hour traffic in natural habitats. The results presented here provide support for the predictions of the ITH for temporarily increased levels of traffic noise. This support indicates that familiarity with a disturbance stimulus influences the effects of that stimulus. Here rush hour traffic noise, a familiar short-term stimulus, caused increases in social behavior indicative of an increased level of perceived threat. These findings confirm the validity of the distinction this hypothesis makes between anthropogenic noise stimuli of differing degrees of familiarity.

### ***C. Differential effects of temporarily vs. chronically elevated levels of traffic noise: implications for future research***

One rationale for conducting this study was to address traffic noise as it exists in the real world rather than as a stimulus separate from its ecological context. The context or variant of

traffic noise modeled here was rush-hour traffic noise, represented by a temporary increase in traffic noise levels. A previous study (Owens et al., 2012) used a long-term experimental exposure to model the increased levels of traffic noise chronically present in a typical titmouse habitat about 100 m away from the road. There are several methodological similarities between this and the chronic noise study that allow a comparison of the effects between temporary and chronically elevated traffic noise levels. Both chronic and rush hour experimental stimuli were broadcast at an average amplitude of 75 dB / SPL @ 1 meter, using the same equipment. Control conditions in the chronic study consisted of the same low to moderate levels of background traffic noise levels present in the PRE and END periods of the current study. Also, both studies collected the same four dependent measures from subjects of the same species, captured from the same population while they were held captive for comparable amounts of time (chronic  $\bar{x}$  : 35 days; rush hour  $\bar{x}$  : 33.75 days) in the same semi-naturalistic outdoor aviaries. The findings of these two studies facilitate a discussion of the effects of temporary (rush hour) vs. chronically (roadside habitat) elevated levels of traffic noise. In Table II each of the four dependant measures are listed; mean values for each measure appear in that row under the different types of experimental (chronic, START, END) and control (control, PRE, POST) conditions. While several of the current findings confirm those of Owens and colleagues (2012), there are important differences. Because of the consistency in subject pool, methodology and dependent measures between these two studies, differences in effects and behavioral rates are unlikely to derive from factors outside of the experimental stimuli tested.

NND was similarly affected by chronic and rush-hour traffic noise in that both significantly reduced NND. The consistency of effect between chronic and temporarily-increased levels of traffic noise indicates that NND is equally sensitive to the presence of traffic

noise, regardless of the duration of its presence. Additionally, the NND values for experimental and control conditions between this and the chronic study are similar (Table II), indicating additional support for the conclusion that NND is equally responsive to temporary and chronically loud traffic noise.

Close-perching behavior was affected by noise in both the rush-hour traffic noise study as well as the chronic noise study, although there were some notable differences between the two studies. First, across experimental and control conditions, close-perching was approximately three-times more common in the rush hour study than the chronic study (Table II). Close perching rates of titmice exposed to chronic traffic noise averaged around 15 close-perches / 10 minutes, while control birds experienced about 13 close-perches / 10 minutes (Owens et al., 2012). These values are significantly lower than those of titmice in the rush hour study, where subjects experienced an average of 35, 45, 41 and 27 close-perches / 10 minutes in the PRE, START, END and POST periods, respectively. Second, the strength of the effect of rush hour traffic noise on close perching behavior ( $\eta^2 = 0.230$ ) was about 6 times stronger than the effect of chronic traffic noise ( $\eta^2 = 0.037$ ). Third, close-perching was differentially affected by the two types of traffic noise. In general, chronic traffic noise increased the number of close-perches experienced by titmice in comparison to control titmice. Similarly, rush hour traffic noise also significantly increased close-perching behavior; however, the effect was weaker in the END period, the second hour of exposure to rush hour traffic noise, than in the START period.

Flying behavior is also suggestive of differential effects of rush hour and chronic noise. Subjects' flying behavior was not significantly affected by chronic traffic noise; although a trend for titmice to increase flights was detected ( $F_{(1,63)} = 3.691$ ,  $p = 0.059$ ,  $\eta^2 = 0.056$ ,  $P = 0.473$ ; Owens et al., 2012). However, rush hour traffic noise did significantly increase flying behavior,



but only in the START exposure. This effect of rush hour traffic noise disappeared in the second hour of experimental exposure, resulting in comparable values in the PRE and END periods.

This finding, coupled with the lack of an effect of chronic noise on flying behavior, suggests that flying may be initially responsive to increased levels of traffic noise, but that this responsiveness declines as the duration of the increased noise levels lengthens. Additionally, rush hour subjects were generally more active, producing more flights in experimental and control contexts than chronic subjects (Table II). The greater rates of close-perching and flying behaviors of rush hour subjects compared to chronic subjects regardless of condition indicate that subjects in this study were more physically active than in the first study. It is possible that the short-term exposure to traffic noise in this study created a higher level of general arousal than the chronic noise.

Preference for conspecific close-perch partners was the only dependent variable for which the results obtained here do not corroborate the effects of traffic noise obtained in the chronic noise study. Preferences were significantly reduced by chronic traffic noise, but were not affected by rush hour traffic noise in either the START or END exposures, nor did preferences significantly shift between PRE and POST exposures (Table II). Additionally, like the NND values, the strength of conspecific preferences (values) are comparable between the control condition of the chronic study and all exposure periods of the rush hour study (Table II). The lack of an effect of rush hour traffic noise on preference indicates that conspecific preferences may not be responsive to short-term increases in noise levels.

Taken together the findings of these two studies indicate that the effects of traffic noise on social behavior and activity are dependent upon the relative duration of increased levels of traffic noise. There were higher rates of flying and close-perching behavior in rush hour subjects than chronic subjects. This suggests that flying and close-perching behavior are more reactive to

temporary increases in traffic noise levels than they are to chronically louder traffic noise. The similarity in reactivity between these two measures is likely associated with the fact that flying is inherently related to close-perching behavior as measured in both studies. Alternatively, the effects of rush hour and chronic noise on NND and the NND values for the two subject sets were comparable, indicating that for this measure of social behavior, the duration of loud traffic noise is not as influential as the presence of loud traffic noise itself.

These differences may have implications for methods used to study traffic noise and other anthropogenic disturbances. In attempts to determine how birds manage communicating in noisy habitats several previous studies have tested for the effects of traffic or urban noise on vocal behavior by exposing birds to recordings or simulated noise. Findings of these studies included birds producing signals at a louder amplitude (Brumm et al., 2009), shifting the acoustic frequency above that of the masking sound (Verzijden et al., 2010), producing signals of a longer duration (Bermúdez-Cuamatzin et al., 2010) and switching to signal types that are less susceptible to masking (Halfwerk & Slabbekoorn, 2009). However, the experimental acoustic stimuli used in these studies were less than 10 minutes long (Brumm et al., 2009; Halfwerk & Slabbekoorn, 2009) and data collection quotas were often met before the entire stimulus was broadcast (Bermúdez-Cuamatzin et al., 2010; Brumm et al., 2009; Verzijden et al., 2010). These stimuli are of significantly shorter durations than the real-world noise sources they were intended to represent. Using short-duration or acute stimuli to determine the effects of disturbance or other stimuli that are chronic, such as traffic noise, is likely to overestimate the intensity of response (Lima & Bedkenoff, 1999). This is evidenced by the stronger effect sizes and greater rates of close perching and flying behavior obtained in this study compared to the chronic noise study.

#### **IV. Considerations, contributions & conclusions**

This study investigated the effects of traffic noise in a real-world context. Here I modeled the temporary increase in traffic noise levels associated with rush hour traffic with experimental playbacks of different variants of traffic noise. Exposure to rush hour noise increased sociality by reducing NND and increasing the number of close perches experienced by subjects. These results advance our understanding of the effects of anthropogenic noise by providing insight into how variation in the duration and level of traffic noise affects behavior. Additionally, the findings of the current study corroborate the results of previous experimental work reporting increased sociality in response to exposure to chronic traffic noise. Finally, these results extend the application of and support for the Increased Threat Hypothesis. Future studies should continue to address the effects of different ecologically-relevant variants of anthropogenic disturbance on animals, to enhance our understanding and ability to combat these challenges.

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## **APPENDICES**

## **APPENDIX A**

### **TABLES**

**Table I.** Inter-rater reliability between JLO and two independent observers. Displayed below are the Spearman's correlations ( $r^2$ ) of SB and TF scores on total number of close perches, number of directed close perches, number of close perches with titmice and number of flights with those of JLO. Agreement was tested between JLO and SB and JLO and TF on two different subsets of data files. Each subset included 6 files, totaling 12 data files. Cumulatively, inter-rater reliability was calculated for approximately 6% of the total number of data files.

Agreement between JO and SB was high for 3 of the 4 measures. Agreement between JO and TF was not calculated for number of flights, but was high for 3 of 3 close-perching measures. Significant correlations are indicated by an asterisk (\*) indicating  $p < .05$ .

Dependent measures	Independent Observer	
	SB	TF
Close-perches	0.83*	0.99*
Directed close-perches	0.93*	0.99*
Close perches with titmice	0.15	0.99*
Flights	0.89*	n/a

**Table II.** Rates of behavior and effects observed in two studies testing the effects of traffic noise on social behavior and activity of tufted titmice. Listed below are four dependant measures and their average values. Experimental and control columns include three different sub-headings that represent the conditions included in the current and a previous study (i.e. Owens, Stec & O'Hatnick, 2012). Owens and colleagues (2012) tested for the effects of chronically elevated traffic noise levels on these four behavioral measures using a between subjects design. The column headings for that previous work are "Chronic" and "Control." For the current research there are two experimental and control sub-headings. Experimental exposure to rush hour traffic noise consists of "START" and "END" subheadings and control exposure consisted of "PRE" and "POST" subheadings. This table is designed to allow comparison of behavioral rates observed in each of these two studies and the effects of temporary (rush hour) vs. chronically (roadside habitat) elevated levels of traffic noise. Within each of these columns the average value for each of the four dependent measures is listed. Significant effects of rush hour traffic noise on these measures were presented in the text. The effects of chronic traffic noise on titmouse behavior are described using abbreviations for experimental (E) and control (C) conditions. These effect statements are listed under the values of each dependent measure in the "Chronic" column. Significant effects of chronic traffic noise exposure are denoted by an asterisk (\*). Data on chronic traffic noise were found in Owens, Stec & O'Hatnick, 2012.

**Table II. Continued**

	Experimental			Control		
	Chronic	START	END	Control	PRE	POST
NND	2.78 E < C*	2.37	2.41	3.20	2.98	2.95
Close-perches	13.76 E > C <sup>A</sup>	45.19	41.33	11.68	35.38	27.32
Conspecific preference	0.02 E < C*	0.08	0.08	0.09	0.08	0.05
Flights	45.8 E > C <sup>B</sup>	57.87	49.80	38.34	52.40	41.91

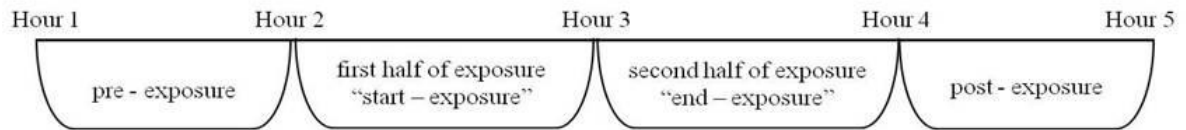
<sup>A</sup>The overall analysis, which combined data for Carolina chickadees and tufted titmice, had a higher value of observed power to detect the small effect (i.e.  $\eta^2 = .037$ ) of noise on close-perching behavior ( $F_{(1,112)} = 4.192$ ,  $p = 0.043$ ,  $\eta^2 = 0.037$ ,  $P = 0.528$ ). The statistical analysis for titmice exhibited low statistical power (i.e.  $P = 0.307$ ) to detect the small effect of chronic traffic noise (i.e.  $\eta^2 = 0.035$ ) on close-perching behavior for titmice ( $F_{(1,63)} = 2.183$ ,  $p = 0.145$ ,  $\eta^2 = 0.035$ ,  $P = .307$ ).

<sup>B</sup>The combined species analysis did not detect any effect of traffic noise on flying behavior, but the species-specific test identified a trend for titmice ( $F_{(1,63)} = 3.691$ ,  $p = 0.059$ ,  $\eta^2 = 0.056$ ,  $P = 0.473$ ).

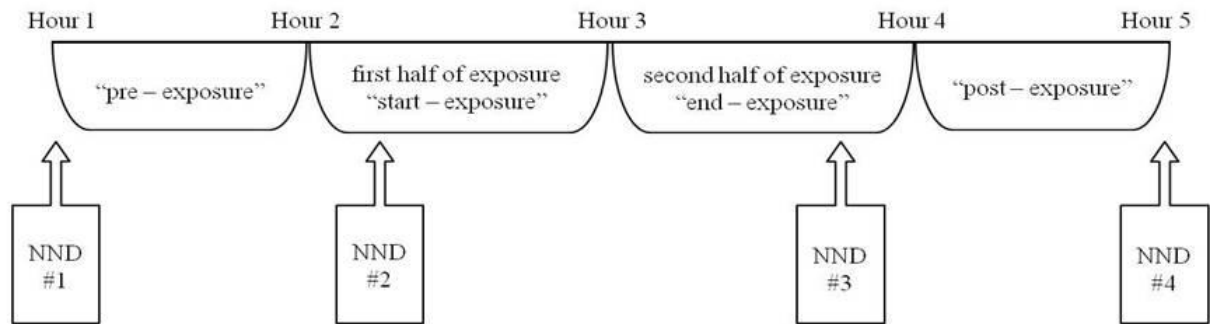
## **APPENDIX B**

### **FIGURES**

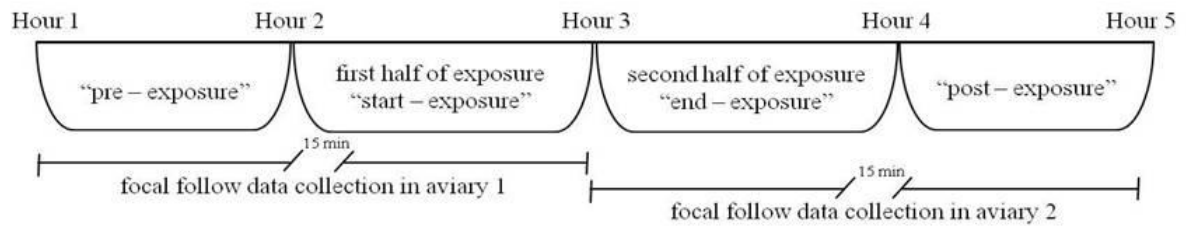
**A**



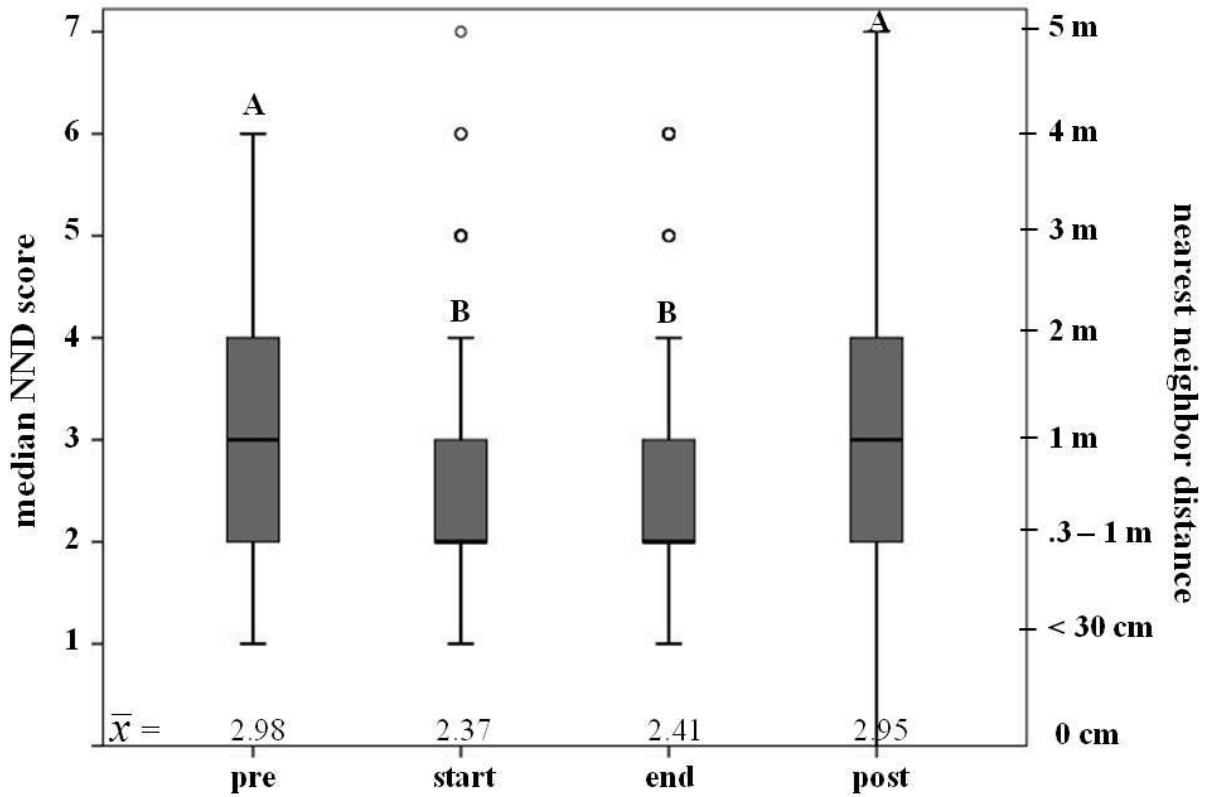
**B**



**C**

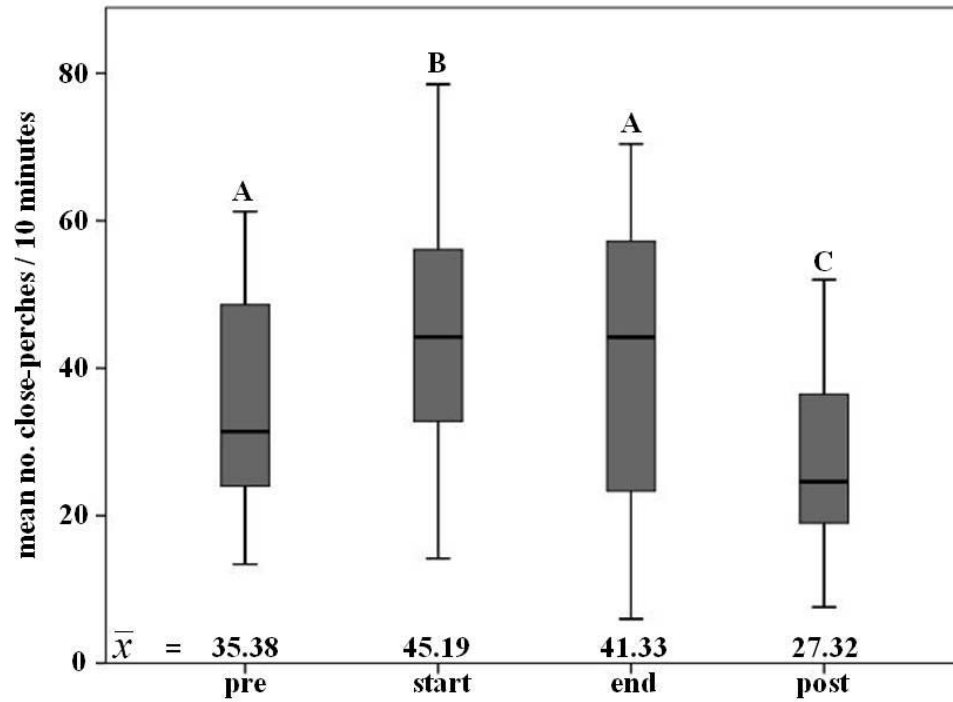


**Figure 1.** Research design and data-collection timeline

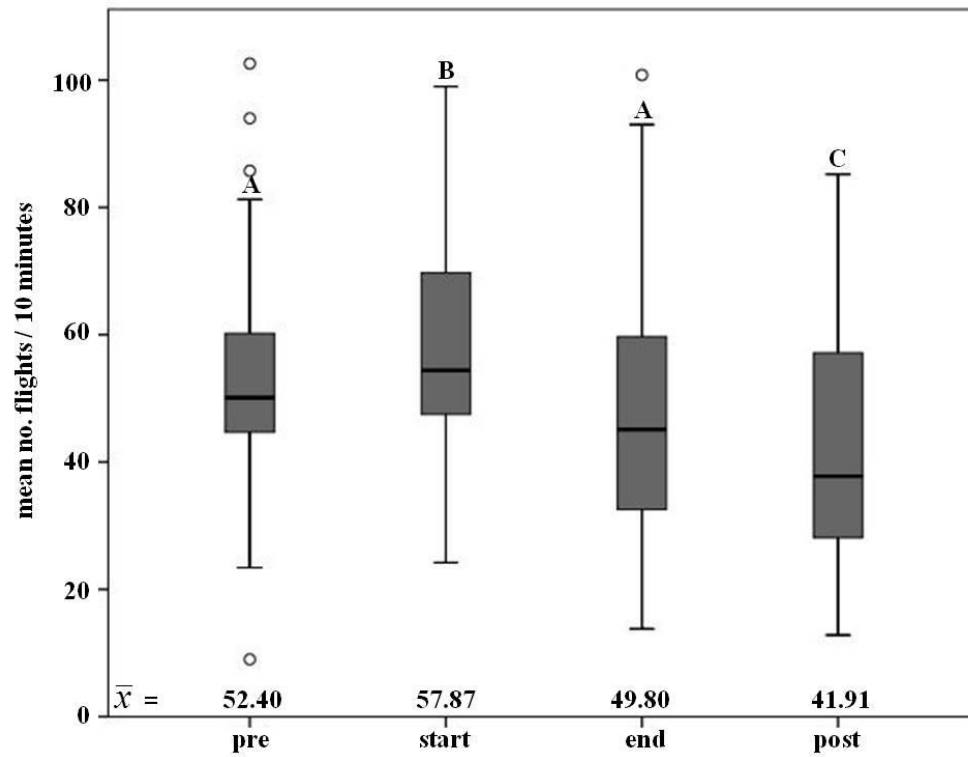


**Figure 2.** Effects of exposure period on nearest neighbor distance. NND data were collected as ordinal data: < 30 cm, 30 cm to 1 m, 1 m, 2 m, 3 m, 4 m, etc., represented as NND scores beginning with 1 (NND < 30 cm) and extending to 7 (NND = 5 m). NND scores and distances are displayed on opposing Y-axes. Boxplots display medians of NND scores (1 - 7), quartiles and data range with outliers. Mean NND scores are displayed below respective boxplots within graphs. All significant comparisons are denoted by letter assignments, and are significant at  $p \leq 0.05$ .

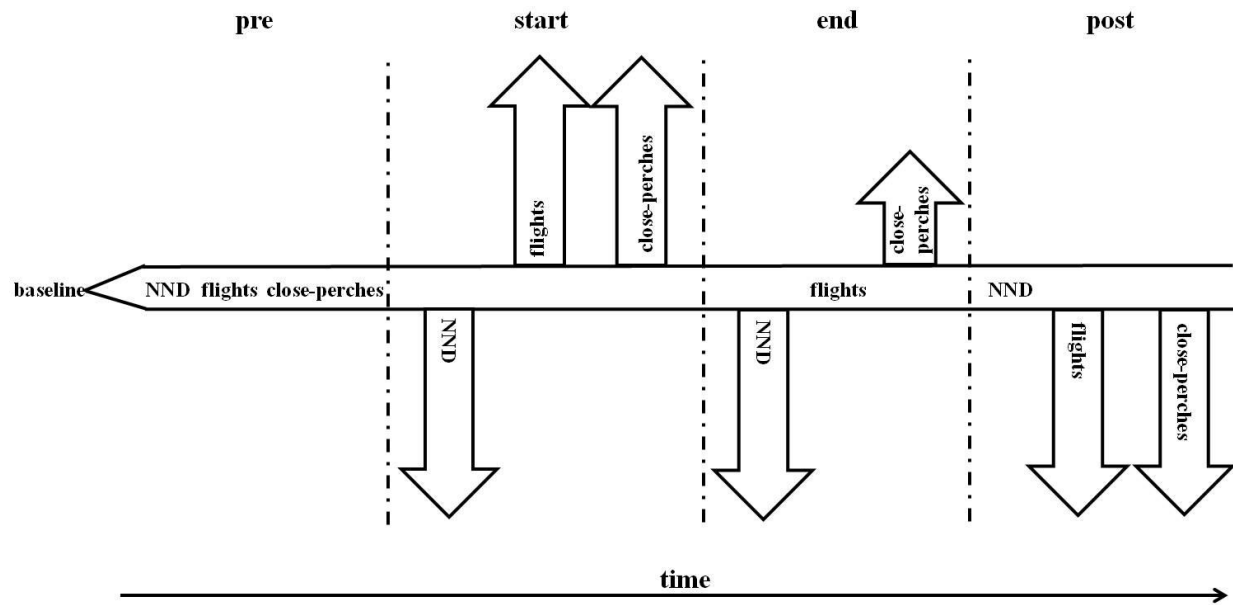




**Figure 3.** Effects of exposure period on close-perching behavior. Data displayed are medians, quartiles and data range with outliers. Group means are displayed below respective boxplots within graphs. All significant comparisons are denoted by letter assignments, and are significant at  $p \leq 0.05$ .



**Figure 4.** Effects of exposure period on flying behavior. Data displayed are medians, quartiles and data range with outliers. Group means are displayed below respective boxplots within graphs. All significant comparisons are denoted by letter assignments, and are significant at  $p \leq 0.05$ .



**Figure 5.** Diagram of effects of traffic noise on flights, NND and close-perches across exposure periods.

## **CHAPTER 5**

THE EFFECTS OF TRAFFIC NOISE ON TUFTED TITMOUSE

*(BAEOLOPHUS BICOLOR)* SOCIAL BEHAVIOR:

CONTRIBUTIONS, CONSIDERATIONS AND CONCLUSIONS

## **CHAPTER 5**

### **THE EFFECTS OF TRAFFIC NOISE ON TUFTED TITMOUSE**

#### **(*BAEOLOPHUS BICOLOR*) SOCIAL BEHAVIOR:**

### **CONTRIBUTIONS, CONSIDERATIONS AND CONCLUSIONS**

#### **I. Style and scope**

This concluding chapter focuses on developing a discussion of the contributions, considerations and conclusions of the findings of this research. This chapter begins with a summary of the results of this dissertation work, organized in point-by-point review of how the research addressed each of the knowledge gaps identified in the introduction chapter. Within each of these sub-sections these results are discussed and interpreted with regard to their importance to the study of anthropogenic noise. Following this section I suggest three approaches or considerations that should be incorporated into future research efforts. These suggestions include utilizing the perception and preferences of an organism to better understand the effects of disturbance, using physiological measures to verify, support and clarify behavioral responses to disturbance and the importance of cross-discipline efforts in organizing scientific efforts with conservation needs. This chapter concludes with a summary of the main quantitative and theoretical findings and final remarks about their significance to the study of anthropogenic disturbances.

## II. Contributions and implications of the current research

The over-arching objective of this research was to broaden the study of the effects of traffic noise on avian species. The areas of research that I considered to be the most imperative to address were used to guide the development of this dissertation work. Several opportunities for advancement were identified in Chapter 1, including the need to (1) isolate traffic noise as a causal variable using experimental methods (Blickely & Patricelli, 2010; Environmental Protection Agency, 1980; Ortega, 2012; Slabbekoorn & Halfwerk, 2009; Warren, Katti, Ermann & Brazel, 2006), (2) expand the diversity of species studied (Blumstein & Fernández-Juricic, 2010; Ortega, 2012), (3) address the effects of noise on non-vocal behavior (Barber, Crooks & Fristrup, 2009; Ortega, 2012), (4) identify the effects of noise on non-song vocal signals and signal use (Ortega, 2012), (5) measure individual variation in response to noise (i.e. Evans, Boudreau & Hyman, 2010) and (6) explore the effects of real-world variation in traffic noise on behavior (Environmental Protection Agency, 1980). Two experiments, conducted between 2009 and 2012, addressed these points with innovative methodologies, and contributed original data and results to the primary traffic noise literature (Chapter 1, Table II). The results of these experiments are summarized in Table I.

### *A. Establishing causality with ecologically relevant stimuli and study designs*

As described in Chapter 1, the development of interest in the effects of anthropogenic noise, and traffic noise specifically, was based on several correlational studies and natural experiments suggesting links between traffic noise and avian population structure, reproductive efforts and vocal behavior (i.e. Foppen & Reijnen, 1994; Forman & Deblinger, 2000; Francis, Ortega & Cruz, 2009; Habib, Bayne, & Boutin., 2007; Hu & Cardoso, 2009; Reijnen & Foppen, 1994; Reijnen, Foppen & Meeuwsen, 1996; Rheindt, 2003; Summers, Cunnington & Fahrig,

2011). Several recent efforts have since provided experimental evidence of the effects of anthropogenic noise on these same measures. In these studies, the types of noise stimuli (i.e. Brumm, Schmidt & Schrader, 2009; Halfwerk & Slabbekoorn, 2009) or the duration of exposure to the noise stimulus used to collect data (Bermúdez-Cuamatzin, Ríos-Chelén, Gil & Garcia, 2010; Brumm et al 2009; Halfwerk & Slabbekoorn, 2009, Verzijden, Ripmeester, Ohms, Snelderwaard & Slabbekoorn, 2010) likely affected the results. In other studies, the use of short exposures to stimuli that are naturally chronic or familiar (i.e. Bermúdez-Cuamatzin et al., 2010; Brumm et al 2009; Halfwerk & Slabbekoorn, 2009, Verzijden et al., 2010), is likely to overestimate the intensity of response (Lima & Bedkenoff, 1999). Obtaining true measures of the effects of disturbance are essential, and thus require more ethologically valid methodologies to be used in future research.

Although preliminary experimental efforts had been published, well-controlled experimental evidence of the effects of anthropogenic noise were still lacking from the literature as recently as July 2012 (Ortega, 2012). This observation echoes similar recent and long-standing requests for such data (Blickely & Patricelli, 2010; Environmental Protection Agency, 1980; Slabbekoorn & Halfwerk, 2009; Warren et al., 2006). My dissertation research utilized noise stimuli and exposure paradigms that closely modeled real world sources of traffic noise.

In the first study, chickadees and titmice were exposed to Brownian noise modified to match the frequency structure and playback amplitude of local traffic noise. The effects of simulated traffic noise on social and vocal behavior found in Study 1 (Chapters 2 & 3) confirmed the significant influence of the frequency structure of traffic noise while controlling for potentially confounding variables like wind, insect or other noises associated with roadside habitats or recordings of traffic noise. The results obtained in Study 1 were generally

corroborated in Study 2 (Chapter 4), which used experimental exposure to recordings of real traffic noise and a within-subjects design to determine the short-term changes that might take place in individuals exposed to temporarily increased levels of traffic noise.

In addition to establishing causality, I aimed to test for the effects of traffic noise using more ecologically meaningful exposure paradigms as had been suggested in previously unaddressed recommendations of the Environmental Protection Agency (1980). My dissertation research is distinct from previous experimental efforts (Bermúdez-Cuamatzin et al., 2010; Brumm et al., 2009; Verzijden et al., 2010) in that it addressed the effects of chronic exposures to traffic noise, such as those occurring in habitats along moderate to heavily travelled highways and roads. Study 1 was the first to utilize a long-term exposure paradigm, which more closely models the presence of traffic noise in natural habitats than short-term or acute exposures used in previous studies (Bermúdez-Cuamatzin et al., 2010; Brumm et al 2009; Halfwerk & Slabbekoorn, 2009, Verzijden et al., 2010). Study 2 was the first to model real-world variation in traffic noise patterns. This study combined experimental and naturalistic methods to model the increased levels of traffic noise associated with rush hour traffic. Subjects were maintained in aviaries with that consisted of mild to moderate levels of traffic noise emanating from a busy highway about 1,000 m away. To model rush hour, recorded traffic noise was broadcast at for 150 minutes, each day. This experimental exposure was louder than background levels of traffic noise, but was comparable to the amplitude of simulated traffic noise used in Study 1. Study 2 provided corroborative and novel findings. First, the effects of exposure to traffic noise in Study 2 were comparable to those obtained in Study 1. Second, the results of Study 2 indicated that titmice were able to respond to sudden onsets of increases in traffic noise, that the effects of temporarily increased levels of traffic noise do not persist beyond the end of exposure and that



duration and familiarity of the acoustic disturbance affects how disturbance influences behavior. Compared to previous research, this research may have reduced the possibility of over-estimating the behavioral response to traffic noise. Further, this research speaks to the importance of carefully considering the stimuli and methods used to study the effects of anthropogenic noise.

### ***B. Expanding the diversity of species studied within the noise literature***

The study of anthropogenic noise could benefit from sampling study species from a more broad taxonomic distribution, including reptiles, amphibians, mammals, etc. However, here I focus specifically on the importance of increasing diversity of avian species studied within the traffic noise literature and related consequences of limited diversity. As the study of anthropogenic noise is relatively new, the variety and number of avian species that have been studied is inherently limited. However, others have already recognized that achieving a diverse literature is important (Ortega, 2012), as a limited sample of study species constrains our ability to draw general conclusions about responses to disturbance (Blumstein & Fernández-Juricic, 2010). Likewise, our ability to understand, predict and manage the effects of disturbance is dependent upon the totality of our knowledge (Blumstein, 2006; Blumstein, Fernandez-Juricic, Zollner & Garity, 2005; Cunnington & Fahrig, 2012; Knight & Cole, 1995; Lackey, Morrison, Loman, Collier & Wilkins, 2012; Ricklefs & Wikelski, 2002; Sauvajot, Buechner, Kamradt & Schonewald, 1998).

'Diversity' may refer to any of several different levels of subject demography or variability. In a general sense, diversity is a function of the amount of variation among individuals or a population (McShea & Brandon, 2012). Those variables of interest within the anthropogenic noise literature include the number of species studied, and include considerations

of variety in: relatedness between species (Ortega, 2012), behavioral types within a species (Carrete & Tella, 2011; Evans et al., 2010; Réale, Reader, Sol, McDougall, P. T. & Dingemanse, 2007) life-history strategies (Blumstein, 2006), experience with disturbance (Lackey et al., 2012) and learning strategies (Ríos-Chelén, Slabberia, Barbosa, Garcia & Gil, 2012). These sources of variation are important as they have been found to affect responsiveness to disturbance and they carry distinct costs and benefits, which may relate to different fitness consequences in anthropogenic habitats (Blumstein & Fernandez-Juricic, 2010). For example, Ricklefs and Wikelski (2002) identify life history characteristics as behavioral, physiological and anatomical adaptations affecting behavioral and phenotypic responsiveness to environmental variation or disturbance. Therefore, behavioral traits should vary between species with different life-histories characteristics (Blumstein, 2006). And, in turn, knowledge of a species' life history characteristics should allow for general predictions of behavior. Indeed, recent research indicates that species attracted to disturbance and that therefore have a disturbance-philic life-history strategy (i.e., those typically found in urban or disturbed habitats), may be evolutionarily pre-adapted to these environments (i.e. Blumstein, 2006).

Recent research indicates that disturbance-philic species, like the great tit (*Parus major*) and house finch (*Carpodacus mexicanus*), are significantly different in their ability to respond to disturbance than other species that are disturbance-phobic (Blumstein, 2006). Additionally, there is evidence that this dichotomy also exists within conspecifics; in species that inhabit urban and undisturbed natural habitats (forests, grasslands, etc.), recent meta-analyses indicate that the individuals located within the urban or disturbed areas are more bold, aggressive and less reactive than conspecifics in natural habitats (Carrete & Tella, 2011; Evans et al., 2010). These findings indicate that urban invaders are not individuals from specifically qualified species, but

are more likely to be qualified individuals from species that exhibit a considerable amount of behavioral plasticity. Therefore, our understanding of disturbance is limited by the diversity and variety of species studied.

The consequence of a literature base with limited subject diversity is constrained generalizability. A current situation within the study of urban noise illustrates this constraint. Recent experiments indicate that birds are able to modify their vocal behavior in response to noise within minutes of its onset (Bermúdez-Cuamatzin et al., 2011; Halfwerk & Slabbekoorn, 2009). Such vocal and behavioral plasticity is likely to provide an advantage for birds dealing with the communicative challenges presented by noise. However, there is little variation between the subjects used in this work (i.e. the great tit and urban house finch), as both species are attracted to disturbance and are commonly found in urban habitats (Badyaev, Belloni & Hill, 2012; Slabbekoorn & den Boer-Visser, 2006). Because both species that have exhibited the ability to modify vocal behavior in response to the sudden onset of noise share these specific qualities, the possibility for behavioral and vocal plasticity, as exhibited here, to be a general avian response to acoustic disturbance is an open question. As such, further study is needed before determinations about generality of this ability are made at the species to species, or even population to population levels.

Much of the traffic (urban) noise literature focuses on a few European species, namely the great tit (i.e. Halfwerk & Slabbekoorn, 2009; Slabbekoorn & Peet, 2003; Slabbekoorn & Ripmeester, 2008). As discussed above, the great tit is a successful urban species typically found in both anthropogenic and natural areas (Slabbekoorn & Ripmeester, 2008). In comparison with its European relative, the tufted titmouse is a disturbance tolerant songbird commonly found in wooded, suburban and park-like habitats (Grubb, 1998; Grubb & Pravosudov, 1994). The great

tit is also better studied than the titmouse, especially within the noise literature. By choosing the tufted titmouse as the study subject for the current research, I was able to provide fundamental information on a species and life-history strategy previously unstudied within the traffic noise literature. Additionally, because the great tit and tufted titmice are related species, both of which are on the tolerant end of the response to disturbance continuum, choosing the titmouse as my focal species also provides information that may be useful in comparative analyses.

To summarize the importance of considering different sources of diversity in generalizing between similar species, I have used the 'evolutionary ecology of fear' paradigm developed by Blumstein (2006) to construct an initial comparative evaluation of the response of tufted titmice and great tits to noise. While considerations of using behavior to infer subjective states is discussed later in this Chapter, an important assumption of this paradigm is that reactivity or responsiveness to a 'threatening' stimulus, like a predator model, is considered to be an indicator of perceived threat or fear. This paradigm asserts that reactivity has coevolved with some life-history traits including body size, diet and sociality (Blumstein, 2006). For example, larger species exhibit higher flight initiation (Blumstein et al., 2004) and alerting distances (Blumstein et al., 2005) in response to threatening stimuli when compared to smaller species. In Table II, five different life-history traits are listed: diet, body size, sociality, competitiveness and body condition. For tufted titmice and great tits each of these traits is described using data available from the literature (Great tit: Beits, 1955; Gosler, 1996; Hinde, 1952; Jablonski & Lee, 2002; Krebs, MacRoberts & Cullen, 1972; Sasvari, 1992; Tinbergen & Dietz, 1994. tufted titmouse: Dolby & Grubb, 1998; Grubb & Pravosudov, 1994; Morse, 1970, 1974; Pravosudov et al., 1999). Using these data, a prediction of increased or decreased reactivity is made for each trait for each species (Table II). Both species exhibit similar diets, body size and sociality, resulting

in similar predictions for reactivity for these three traits. However, there are distinct differences between these species; tufted titmice are more likely to be dominant to conspecifics in overwintering mixed species flocks (Grubb & Pravosudov, 1994; Morse, 1970; Dolby & Grubb, 1998; Pravosudov et al., 1999) than are great tits (Jablonski & Lee, 2002; Sasvari, 1992). This difference in dominance status affects the predictions of reactivity for sociality and body condition of each species. Dominant species within mixed-species flocks have preferential access to resources, which reduces competitive interactions and risk-taking behavior required to obtain food and avoid predation (Brawn & Sampson, 1983; Pravosudov & Grubb, 1999; Pravosudov et al., 1999; Suhonen, Alatalo, Carlson & Höglund, 1992). Therefore, as the more dominant species, titmice generally engage in less risk-taking behavior and are predicted to be more reactive to disturbance than great tits. Similarly, the more dominant titmouse retains access to higher quality food sources and is predicted to exhibit better body condition (Pravosudov et al., 1999) than great tits. Higher quality body condition is indicative of less risk-taking and thus a higher degree of reactivity than great tits (Blumstein, 2006). Based on the accumulated trait-specific predictions, tufted titmice are predicted to be more reactive to disturbance, noise or predation threat than great tits. These predictions have yet to be directly assessed, and to my knowledge, the effects of noise on social behavior of the great tit have yet to be studied. But my dissertation research supports the idea of the 'reactive titmouse' as traffic noise altered normative social behaviors in a manner similar to a perceived threat would modify social behavior.

While studying a diverse set of species is imperative, careful selection of focal species is needed. Rather than sampling study species at random from the taxonomic record, several suggestions have been made. Equal representation from different taxa (Ortega, 2012), life-history types (Blumstein, 2006) and behavioral types (Réale et al., 2007) are all plausible

methods to increasing diversity. Additionally, several of these sources of variation are associated with different predictions regarding the ability of a species to respond to disturbance, making for stronger tests of hypotheses. By studying closely related species with varying degrees of disturbance tolerance or different life history traits, these predictions may be directly or indirectly assessed. Regardless of the method, by studying and comparing the behavior of a range of species we will be better equipped to generalize between species and identify specific attributes that predict tolerance or intolerance for disturbance.

### ***C. Noise affects non-vocal behavior, too: a unified theoretical approach and a behavioral framework for studying anthropogenic disturbance***

A modified version of Chapter 2 published earlier this year in *Behavioural Processes* was the first account of the effects of traffic noise on the social behavior of a songbird (Owens, Stec & O'Hatnick, 2012). In Study 1, exposure to simulated traffic noise significantly reduced nearest neighbor distance (NND), increased the number of close-perch interactions and relaxed conspecific preferences for close-perch partners. Using recordings of traffic noise as the experimental stimulus and a within-subjects experimental design, Study 2 generally corroborated the results of the first study with increased statistical power. These data are among the first of their kind in the noise literature. The implications of anthropogenic noise altering normative social behavior may be far reaching and creates a wealth of potential experimental and observational studies for future research efforts, which will be discussed later. Of the most interest to me is the development of our understanding of disturbance and explanatory hypotheses that have accompanied the study of behavior. The effects of traffic noise on social behavior recorded here mimic socially-derived anti-predator behavior of birds. Although these data are among the first of their kind, the parallels between anti-predator behavior and response

to anthropogenic disturbance have long been recognized (Blumstein, 2006; Frid & Dill, 2002; Gill, Sutherland & Watkinson, 1996; Lima, 1998a; Lima & Dill, 1990).

## 1. Anti-predator behavior

Anti-predator behavior has been heavily studied in mammals and birds (i.e. Caro, 2005; Lima 1998a, b; Lima & Bedkenoff, 1999; Lima & Dill, 1990). The 'fight or flight' response was identified by Cannon (1929) as the physiological reactions to stimuli that induce fear, pain or even anger. Fight or flight consists of increased heart rate and respiration, increased blood flow, blood sugar and body temperature and reduced blood flow to the skin and digestive organs, all of which prepare an organism to either physically fight, or flee from, a threat (Gabrielsen & Smith, 1995; Mayes, 1979). As such, fight or flight is also referred to as 'active defense' and is considered an anti-predator or anti-threat behavioral response (Gabrielsen & Smith, 1995). Of course, organisms may also hide, become still or death-feign in the face of a threat, all of which are considered 'passive defense' strategies.

In addition to these more familiar anti-predatory behaviors, social behavior can also serve as an anti-predator strategy (Krause & Ruxton, 2002). Birds often join flocks (Krause and Ruxton, 2002) or increase the density of social groups in response to predatory threat (Elgar, Burren & Posen, 1984; Metcalf, 1984; Whitfield, 1988). Many different theories provide potential explanations for the advantages of social behavior in the predatory context. The 'Many Eyes Theory' suggests that as group size increases, individuals are able to spend less time being vigilant without increasing their susceptibility to predation (Treherne & Foster, 1980). Another potential advantage of social grouping in the presence of a predatory threat is described by the 'Predator Confusion Theory,' which suggests that prey individuals are more difficult to single-out and attack within larger groups (Fels, Rhisiart & Vollrath, 1995). However the advantages are

achieved, it is clear that sociality, social grouping, and increasing the density of those groups can serve to reduce perceived and actual predation risk.

## 2. Similarities of behavioral responses to predator and disturbance stimuli

The behaviors of fight, flight, vigilance and social grouping are also common responses to anthropogenic disturbances (reviews: Blumstein, 2006; Frid & Dill, 2002; Knight & Gutzwiller, 1995). There is a positive relationship between frequency of human-disturbance and aggression toward humans in red-tailed hawks (Knight, Andersen, Bechard. & Marr, 1989), red-winged blackbirds, American robins and American goldfinches (Knight & Temple, 1986a,b). In addition to fighting, many avian species, including raptors (Stalmaster & Newman, 1978; Andersen, Rongstad & Mytton, 1990), waterbirds (Klein, Humphrey & Percival, 1995; Riddington, Hassall, Lane, Turner & Walters, 1996) and colonial gulls (Burger, 1981), flee in response to anthropogenic disturbances. Other species exhibit more passive responses to disturbance; for example, the presence of noise increases vigilance in the chaffinch (*Fringilla coelebs*) (Quinn, Whittingham, Butler & Cresswell, 2006).

From this short review, the similarities between responses to predators or threatening stimuli and the responses to disturbance are evident. Indeed, many studies have documented that the response of different species to anthropogenic disturbances imitate those elicited by a predator (Beale & Monaghan, 2004; Berger, Daneke, Johnson & Berwick, 1983; Blumstein, 2006; Frid & Dill, 2002; Gill et al., 1996). But beyond these general similarities, there is another reason as to why disturbance and predatory threat are functionally analogous; responses to predation risk (Lima, 1998a; Lima & Dill, 1990) and disturbance stimuli (Brattstrom & Bondello, 1983; Steidl & Anthony, 1996) both divert time and energy away from other immediately important behaviors (Frid & Dill, 2002).



There also appears to be a similarity between the factors that influence anti-predator behavior and those that influence response to disturbance (Lima 1998a). Frid and Dill (2002) list four factors that influence anti-predator behavior: structure of the environment, social context, predator behavior and predation risk. For example, individuals in the central position of a social group or in a larger social group tend to spend less time being vigilant for predators, allowing them more time to feed (Krause & Ruxton, 2002). Likewise, a predator's approach and targeting behavior influence whether grouped house finches fly to nearby cover or fly away from nearby cover to avoid the trajectory of the oncoming predator (Lima & Bedkenoff, 2011). Similar factors influence responses to disturbance stimuli (Knight & Cole; 1995). For example, like the qualities of the predators approach affect fleeing behavior, a fast moving snow-mobile or human will elicit stronger alarm or flight responses (Burger, 1981) compared to a slow moving or slow approaching disturbance. Parallels can be drawn between the influential aspects of predatory and disturbance stimuli. For example, predator abundance and frequency and magnitude of disturbance: animals are less likely to spend time in habitats where predators are abundant or predation risk is higher, likewise, animals often avoid areas that are heavily disturbed. If avoidance of an area is impossible, as it may contain a particular resource, then vigilance is often increased, in both the habitat with more predators and the habitat that is more disturbed (Blumstein & Fernández-Juricic, 2010). The same similarities could be described for habitat structure and disturbance type or social group and context. Both types of influence may be summarized or thought of generally by 'intensity'; one may expect that the responsiveness to a disturbance or predatory stimuli will be positively correlated with the intensity and directness of that disturbance or predatory stimuli.

The relationship between disturbance and predatory stimuli is not inherently obvious; several criticisms of this comparison have been considered (review in Frid & Dill, 2002). The first argues that disturbance stimuli are not analogous to predator risk because of the difference in the amount of time each stimulus has been present over evolutionary time. Prey have evolved predator-specific anti-predator behaviors, but anthropogenic disturbances are evolutionarily novel. This is true. However, recent research has provided evidence suggesting that species attracted to disturbed habitats, like cities, may possess certain qualities or experiences that have pre-adapted them to these types of environments. For example, species that have evolved in habitats with naturally occurring levels of low-frequency noise, like the little greenbul (Slabbekoorn & Smith, 2002) may be better able to respond to anthropogenic disturbances that are qualitatively similar (i.e. Bermúdez-Cuamatzin et al., 2011; Halfwerk & Slabbekoorn, 2009).

Frid and Dill (2002) present a second argument against the functional analogy between disturbance and predatory stimuli; that anti-predator responses serve to avoid severe injury or mortality, and, contrary to 'predation,' disturbance does not necessarily cause mortality. It is important to point out that predation risk or the presence of a predator do not necessarily result in mortality either (Lima, 1998a). Although disturbance is arguably less of a direct lethal-threat than predatory threat, the response to predatory and disturbance stimuli are both the result of the same decision processes based on costs and benefits (Frid & Dill, 2002). Making the decision to engage in anti-predator behavior in either context is a decision to abort immediately important behaviors, like foraging or parental care, to reduce the probability of death (Abrams, 1993; Hugie & Dill, 1994; review in Lima, 1998b). It is a considerably safer strategy to overestimate danger than to underestimate danger, as the consequence of reactivity is energy loss compared to injury or death (Bouskila & Blumstein, 1992). This idea has recently been described as the

'Better Safe Than Sorry' principle (Haftorn, 2000; Zachau & Freeberg, 2012) and is represented in the early work of Dill (1974a, b), where anti-predator responses were generalized from predatory stimuli to two different types of ambiguous predatory models.

### 3. Developing a framework for studying anthropogenic disturbance

The parallels between responses to predatory and disturbance stimuli have created a synthesis between the conservation and anti-predation literature. Frid and Dill (2002) suggested that responses to disturbance should vary based on the same economic principles of cost and benefit associated with predatory contexts and the Predation Risk Theory (Berger et al., 1983; Gill & Sutherland, 2000; Gill et al., 1996). These principles were used to develop the 'Risk-Disturbance Hypothesis,' which predicts that the specific characteristics of a disturbance affect an organism's response to that disturbance, in much the same way that the characteristics of a predatory context affect an organism's response. The main consideration here is the level of perceived threat resulting from the disturbance or predatory stimuli.

The Increased Threat Hypothesis (ITH), proposed and supported in the current dissertation research, was proposed as a sub-hypothesis of the Risk Disturbance Hypothesis (RDH). Both hypotheses recognize the functional similarity between predatory and disturbance stimuli and predict responses based on the level of perceived threat resulting from the stimuli in question. Additionally, both hypotheses suggest that disturbance creates behavior comparable to anti-predator responses as a result of the effects of the disturbance on an animal's perception of threat or risk within its environment. Where the ITH is distinct is in regard to predictions based on durations or levels of familiarity and predictability of acoustic disturbance stimuli. The RDH is likely to make predictions that are similar to those of the ITH, but I am unaware of any RDH statements regarding the familiarity or predictability of noise.

Acute or unfamiliar disturbances cause alerting or flight responses (Burger, 1981; Klein et al., 1995; Stankowich & Coss, 2009), where chronic stimuli often cause increases in vigilance (Rabin, Coss & Owings, 2006; see also Kikuchi, 2008). Specifically, the presence of chronic noise appears to deregulate reflexive and startle-types of anti-predator behavior while upregulating (possibly through post-habituation sensitization) more adaptive forms of anti-predator behavior, like cautiousness. In effect, while the ITH assumes that disturbance increases the perceived level of threat in the environment, the predictions for how this perceived threat affects behavior differ between chronic (familiar) and acute (unfamiliar) sub-types. These predictions of the ITH are supported by classic work by Lima and Bedkenoff (1999) indicating that anti-predator responses should be most intense to brief and infrequent high-risk contexts, with intensity and reactivity decreasing as high-risk contexts become more familiar or are less-risky.

Predatory threat is a significant evolutionary force that influences behavior of all organisms (Lima & Dill, 1990). The functional similarities between predatory threat and disturbance stimuli have resulted in a predation-disturbance framework that is likely to provide heuristic benefits to the study of predator-prey relationships and the study of anthropogenic disturbance (Frid & Dill, 2002). Using the predation risk theory and relevant literature on anti-predatory behavior will enhance the design, generalizability and conservation value of future research by focusing experimental questions, hypotheses and predictions.

#### ***D. Noise discriminates and contradicts theoretical predictions for vocal signal use***

The many sources of individual variation (including temperament, dominance status, or disturbance tolerance) and their influence on behavior are widely recognized (Ekman, 1987; Ekman & Askenmo, 1984; Evans et al., 2009; Gosling, 2001; Sih, Bell & Johnson, 2004; Waite, 1987). A recent review has synthesized the variation in terminology used to describe five traits of 'temperament,' also referred to as 'behavioral syndromes,' 'behavioral profiles' and 'non-human personality' (Réale et al., 2007):

1. shy - bold: response to risky or threatening contexts
2. exploration - avoidance: response to novel, non-threatening contexts
3. activity: quantity of movement in familiar and safe contexts
4. aggressiveness: degree of aggression in interactions with conspecifics
5. sociability: degree of sociability in interactions with conspecifics

These five temperament traits are distinct concepts, meaning that a bold individual is not necessarily the most active or exploratory. In fact, for titmice, dominance is associated with exploration but not boldness (Hill, 1986; Sullivan, 1985; Waite, 1987; Waite & Grubb, 1987).

These five traits may act separately or interact to affect the response of individuals to disturbance. For example, urban-dwelling song sparrows (*Melospiza melodia*) exhibit significantly bolder behavior toward humans and are more aggressive in response to playbacks of conspecifics at territory boundaries, than are sparrows living in rural habitats (Evans et al., 2009). However, the correlation between dominance and aggression for song sparrows regardless of habitat type was not detected within urban sparrows (Evans et al., 2009). In addition to temperament traits, differences in life history characteristics (Blumstein, 2006),

behavioral plasticity (Carrete & Tella, 2011) and tolerance for variation (Bonier, Martin & Wingfield, 2007) and learning (Rios-Chelen et al., 2012) have all been shown to affect the response to disturbance.

The frequency with which individual differences are identified as influencing some aspect of behavior or response to stimuli suggests that these sources of variation should be more often considered by researchers. Although it is impossible to simultaneously address all sources of individual variation, knowledge of species-specific behavior and characteristics should provide insight into which measures of variation may be important for one's study species or research question (Frid & Dill, 2002). Using the current dissertation research as an example, observations of vocal and social behavior of tufted titmice across many contexts and over the course of several years indicated to me that, like other parid species (Krama, Krams & Igaune 2008; Krams, 2000; Williams, 2009), there may be a relationship between dominance and vocal behavior. This educated guess based on knowledge of species-typical behavior resulted in identifying a significant interaction of dominance and traffic noise on titmouse behavior.

The presence of noise within a communication channel necessitates a certain degree of redundancy and repetition within a signal to ensure accurate transmission (Buckstaff, 2004; Doyle et al., 2008; Freeberg, 2012; Hailman, Ficken & Ficken, 1985; Lengagne, Aubin, Luage & Jouventin, 1999; Mahurin & Freeberg, 2009; Serrano & Terhune, 2001; Smith, 1972; Wiley & Richards, 1982). This idea is formalized by the Repeated Messages Hypothesis which predicts that messages will have greater redundancy in noise, and that the presence of redundancy limits the amount of information capable of being encoded while signaling in the presence of noise (Bradbury & Vehrencamp, 1998; Doyle et al., 2008; McCowan, Doyle & Hanser, 2002). This study produced two results relevant to these predictions. First, the presence of traffic noise failed

to reduce complexity at any level of communication as predicted by the Repeated Messages Hypothesis. And second, a significant interaction between noise and dominance resulted in an increase in chick-a-dee-call complexity for the most dominant titmouse within each study flock. This interaction effect indicates that noise affects some titmice and the noise-induced increase in call complexity explicitly contradicts the predictions of the Repeated Messages Hypothesis.

This contradiction is not entirely surprising when the characteristics of the chick-a-dee call are compared to those of other signaling systems. Specifically, where repetition of a syllable serves as an effective strategy of increasing signal detection without changing the meaning of that signal (Lengagne et al., 1999; Wiley & Richards, 1982), variation in the use and repetition of note-types within the chick-a-dee call is associated with different messages and meanings (Hailman et al., 1985; Freeberg, 2012; Mahurin & Freeberg, 2009; Smith, 1972). As such, it is unlikely that species using the chick-a-dee call can improve signal detection by modifying the note-type composition, without potentially modifying the meaning, of a call (Freeberg, Lucas & Clucas, 2003). Instead, as was detected here, increasing signal rate or reducing NND may be better options to reduce masking of vocal communication by noise. These data suggest that more complex communication systems, like the chick-a-dee call, may limit a signaler's ability to improve signal detection by altering signal length use of note-types. However, many other options are available for titmice and chickadees to improve signal detection in the presence of noise, such as signaling at a higher rate (Buckstaff, 2004; Doyle et al., 2008) or shifting call frequencies beyond those of the masking noise (Proppe et al., 2012; Verzijden et al., 2010).

### ***E. Exploring the effects of real-world variation in traffic noise on behavior***

Study 2 (Chapter 4) included experimental exposure to traffic noise that was modeled after the occurrence of rush hour traffic. Rush hour consists of a period of increased traffic

activity that results in increased levels of traffic noise which is common and repeated across days. The regularity and predictability of this pattern associated with rush hour traffic promotes habituation to this stimulus (Masini, Day & Campeau, 2008). As a result of these characteristics, the Increased Threat Hypothesis, and possibly the Risk Disturbance Hypothesis, predicted that rush hour noise would cause similar effects on social behavior as chronic noise from Study 1. In support of the ITH, the results obtained in this study were generally comparable with those of Study 1; rush hour traffic noise increased sociality of titmice by reducing NNDs and increasing the number of close perches.

This study also addressed two general expectations based on previous research. The first, was that, like the great tit and house finch, tufted titmice should exhibit the ability to respond to the abrupt increase in traffic noise resulting from rush hour noise (Bermúdez-Cuamatzin et al., 2011; Halfwerk & Slabbekoorn, 2009). The shifts in flight, NND and close perching behavior caused by the onset of rush hour traffic noise indicate that titmice are indeed able to quickly respond to abrupt changes in background levels of traffic noise. The second expectation was that effects of rush hour traffic noise on behavior may extend beyond the experimental exposure, as was reported for frequency-shifted song in great tits (Slabbekoorn & Peet, 2003). However, this study did not detect any persisting effects of rush hour traffic noise on social behavior or activity levels of titmice.

### **III. Considerations for future work**

This section of the discussion provides three suggestions for future research that may advance the scientific and applied study of anthropogenic noise. These suggestions include the importance of considering the perspective of an organism when studying its response to



disturbance; moving toward establishing a link between behavior and physiological responses to disturbance; and using the knowledge gained from scientific inquiry to improve conservation efforts and using conservation needs to guide scientific investigations. In creating this list I took an interdisciplinary approach, and reviewed several different fields of study searching for suggestions that have not already been repeated in previous manuscripts. This is by no means an exhaustive list of considerations for future work, but represents a different perspective on how to make the study of anthropogenic disturbance a more comprehensive and cross-disciplinary effort. The rationale of the potential importance behind these factors has been discussed in classic and recent manuscripts; here I apply them to the study of anthropogenic disturbance and noise.

***A. Umwelt; using perception and preferences to determine species' needs***

"We do no longer ask the animal 'How does the outer world push you around?', we now ask it  
`What do you perceive of the outer world, and what is your response?'"

(von Uexküll, 2001, pg. 117)

Aspects of an animal's environment are perceived according to their relative significance (von Uexküll, 2001), meaning that perception is subjective and specific to each individual. The German biologist, von Uexküll (1909), originally developed and defined this concept of 'an animal's perceptual world or environment' in his native language as "Umwelt" (Burghardt, 1985). The occurrence of a stimulus within an animal's perceptual sphere is filtered through its specific perspective and elicits a response that ultimately leads to continuation of life or death (Sagan, 2010). When this process is repeated, the environment stimulates chains of events that influence survival.

Within the wording of the Increased Threat Hypothesis and the Risk Disturbance Hypothesis, perceived levels of threat or states of fear have been implicated when discussing factors affecting the response of species or an individual to predatory and disturbance stimuli (Frid & Dill, 2002; Lima & Dill, 1990; Lima & Bedkenoff, 2011; Owens et al., 2012). Because of the influence of perception on responsiveness, the study of anthropogenic noise and other disturbances should address this 'perception' linkage between animals and the environment. The study of predator-prey relationships and anti-predatory behavior, which I and others have argued is fundamental to our understanding of anthropogenic disturbances, has benefitted greatly from addressing perception. In developing an understanding of predator-prey relationships, the perspective of the prey has become essential to identifying the factors responsible for how anti-predator behaviors manifest in specific contexts. Pioneering work has shown that birds' perception of characteristics specific to the predator, predator's targeting behavior and habitat influence decision making in predatory contexts (Evans, Evans & Marler, 1993; Frid & Dill, 2002; Krams, Krama, Freeberg, Kullberg & Lucas, 2012; Lima & Dill, 1990; Lima & Bedkenoff, 2011; Quin & Cresswell, 2005; Templeton, Green & Davis, 2005). This work has proven useful in explaining variation in anti-predator behavior between species. Future work on perceptual differences will likely elucidate how safety in numbers, and other anti-predatory hypotheses, function to reduce predatory threat.

Within the study of anthropogenic disturbance, the conservation behavior perspective uses a species' or individual's perception or preferences to address conservation concerns (Blumstein & Fernández-Juricic, 2010). To this end, several methods, including simultaneous and sequential choice tests, can be used to learn the preferences of another species or individual out of a number of different choices. These tests or tasks can be utilized to determine which

aspects of a habitat are most important to a species that is losing quality habitat, or to test for the effects of noise on social preferences or mate-choice. Swaddle and Page (2007) have used a three-choice test to provide experimental evidence that high levels of noise (80 dB) alters normal social behavior by eroding pair preferences in female zebra finches (*Taeniopygia guttata*). These methods can also be applied outside of the laboratory context. In the current research, preferences for social partners were assessed based on a bird's close-perching choices during natural interactions between study flockmates. Although these data were collected in the more controlled environment of a semi-naturalistic aviary, similar data could be collected during naturalistic observations.

Measuring preferences may also prove useful in testing predictions from hypotheses related to the effects of anthropogenic disturbance. For example, the Increased Threat Hypothesis predicts that the effects of familiar disturbances increase the perceived level of threat within an environment or context. An example of how to directly test the predictions of the ITH involves measuring the amount of time spent interacting with preferred versus neutral flockmates or food items in contexts of disturbance versus predation-risk. Small changes to different aspects of these tasks provide an organized way to test the influence of different factors on decision making behavior in the presence of anthropogenic noise or other disturbances.

### ***B. Linking behavior and physiology***

Currently, the degree of threat perceived by animals confronted with anthropogenic noise is largely being interpreted from similarities in behavioral responses to predatory and disturbance stimuli. However, physiological responses could also provide a rich source of information about how an organism reacts to its environment (Ricklefs & Wickelski, 2002). Predatory stimuli elicit behavioral responses, such as the fight or flight response, which are associated with

physiological changes. Specifically, the hypothalamic-pituitary-adrenal (HPA) axis is activated causing changes in glucocorticoids, like corticosterone (CORT), indicative of physiological and even emotional stress (Sapolsky, Romero & Munck, 2000). Activation of the HPA axis is an adaptive response to acute environmental stressors (Astheimer, Buttemer & Wingfield, 1995; Boonstra, McColl & Karels, 2001) that functions to return the organism to a homeostatic state (Sapolsky et al. 2000; Wingfield et al. 1998). However, long term activation of the stress response, as in the case of chronic stressors, is often associated with detrimental physiological effects (Sapolsky et al., 2000). To my knowledge, the effect of traffic noise, specifically, on baseline or reactive corticosterone levels in birds has not yet been quantified; however, this potential future study would provide a physiological mechanism for the effects of traffic noise on behavior.

Few studies have addressed the physiological effects of noise exposure on wildlife, even though different techniques exist (Bonier et al., 2006; Romero & Wikelski, 2002; Wingfield et al., 1997) and have been reviewed for their applicability and ease of use (Tarlow & Blumstein, 2007; Bonier, 2012). The few studies that do exist provide clear evidence that anthropogenic disturbances of different types have the ability to affect hormonal responses. For example, white-crowned sparrows (*Zonotrichia leucophrys*) in urban habitats exhibited increased baseline corticosterone levels compared to conspecifics in rural habitats, but only for males (Bonier, et al., 2006). In contrast, urban European blackbirds (*Turdus merula*) exhibited no differences in baseline corticosterone levels when compared to their rural counterparts, but did show a significant reduction in their physiological response to acute stressors compared to rural birds (Partecke, Schwable & Gwinner, 2006). Similar sources of variation have been observed in other studies on avian species (Bonier et al., 2006; Fokidis, Orchinik & Deviche, 2009).

Although there are hormonal differences between birds in urban and rural habitats (review Bonier, 2012), these effects are both species and sex-specific (Fokidis et al., 2009; Bonier, 2006). One important consideration is that each of these studies was conducted using subjects from an urban habitat which includes a variety of different anthropogenic factors. While ethologically valid, these studies are unable to identify specific effects of any particular aspect of the urban environment, like traffic noise.

***C. Using scientific curiosity to affect conservation policy, organizing scientific endeavors by conservation needs***

When studying the effects of anthropogenic disturbance on behavioral processes, it is important to interpret data in not just scientific and theoretical terms, but to contribute to the conservation literature. Oftentimes the effects of anthropogenic disturbance on behavior are often important to wildlife managers compiling lists of reasonable concerns to use in preparing management strategies, species action plans and conservation policies (Blumstein & Fernández-Juricic, 2010; Bowles, 1995). The likelihood of successfully translating scientific knowledge of disturbance effects into conservation policies is related to the ability of that information to provide useful predictions of the effects of potential management policies (Blumstein & Fernández-Juricic, 2010). Acknowledging the importance of this relationship, many authors have encouraged interdisciplinary cooperation to advance scientific and conservation endeavors (Blumstein, 2010; Blumstein & Fernández-Juricic, 2004, 2010; Bonier, 2012; Chan & Blumstein, 2011; Ortega, 2012; Rabin, McCowan, Hooper & Owings, 2003; Ricklefs & Wikelski, 2002).

Anthropogenic disturbances have traditionally been studied from the field of conservation biology, which considers an event, natural or anthropogenic, to be of concern only if it

negatively affects survival of an individual, group, community, population, species, or ecosystem (Groom, Meffe & Carroll, 2006; Primack, 1993; Soulé & Wilcox, 1980). Although conservation biology is an integrative field of study, like most other fields, this perspective has a specific focus; conservation or wildlife biologists receive training in wildlife management and are experts in the behavior of particular species (Blumstein & Fernández-Juricic, 2010). This focus may develop out of necessity of the manner in which conservation legislature is designed and delegated to scientists within the U.S. Fish and Wildlife Service. For example, once a species is listed as endangered, USFWS scientists must develop a recovery plan aimed at resolving current conservation issues causing endangerment so that the species can be unlisted (Environmental Protection Agency, 1980). As such, a majority of the conservation literature focuses on measures of survival or the efficacy of different management techniques. Surprisingly, only recently has there been discussion of inter-disciplinary efforts between conservation biology and related fields to enhance the efficacy and success of conservation efforts. Due to different agendas and perspectives, one field may possess information that is useful to the other. For example, knowing the factors that influence mate or nest preferences or the inclination for infanticide is likely to increase efficacy of captive breeding programs. Additionally, if conservation biologists, ecologists, physiologists and behaviorists all interested in a similar species coordinate research efforts according to the needs of their colleagues, resulting progress in each of the subfields is likely to be more streamlined and comprehensive.

Developed from the fields of animal behavior and behavioral ecology, the emerging field of conservation behavior was introduced as a complementary approach to conservation biology (Blumstein & Fernández-Juricic, 2010). As the terminology suggests, the field of conservation behavior recognizes that behavior is the interface between individuals and the environment and

uses our knowledge of behavior to identify how disturbance affects ecological or social structures that are important to species' normative behavioral patterns. Conservation behavior has a distinct and complementary use compared to conservation biology. Because conservation behavior does not directly address survival, it is not useful in determining whether an anthropogenic factor is a conservation concern. Identifying conservation issues is the function of conservation biology. However, once an event has been identified as a conservation concern (i.e. negatively affects survival), conservation behavior may be used to provide insight on how a conservation concern may be causing negative effects on survival through its effects on behavior (Blumstein & Fernández-Juricic, 2010).

My dissertation research provides preliminary insight into the effects of traffic noise on birds, and identifies several important questions to guide future research. Before I can state that the behavioral responses to noise reported here are adaptive or effective at mediating the challenges presented by traffic noise, it is important to quantify their effects on communication, predator detection and evasion in addition to mating success. Further, this study was conducted during the overwintering months when the two study species are less territorial and more gregarious than during the spring and summer months. Future work should consider seasonal variations in sociality and their potential consequences. Does the increased sociality reported here extend into the breeding season and if so, what effects does it have on pairing, mating and territory defense. It is also important to recognize that the effects of traffic noise reported here are limited in their application to different species. All of the responses to traffic noise presented are dependent upon behavioral plasticity, suggesting that highly stereotypic species may be more at risk from anthropogenic noise.

#### **IV. Concluding remarks**

The completion of this dissertation research has provided innovative methodologies, novel data and theoretical considerations that carry implications for the study of anthropogenic disturbances. First, this research developed and used acoustic stimuli and experimental exposure methods that closely modeled the real-world problem of traffic noise. This approach limited the influence of extraneous and confounding factors that affect responsiveness to disturbance. As such, the results obtained here, while constrained by the aviary setting, are suggested to be more representative of the behavioral responses to traffic noise.

Second, this research has succeeded in establishing causality between traffic noise and several measures of social and vocal behavior in the tufted titmouse. The observed increase in titmouse sociality in response to traffic noise is interesting for several reasons. This response of the titmouse provides insight into the possible function of social proximity in response to noise. As sources of information to flockmates within their over-wintering mixed species flocks and as a species whose daily survival depends on successful vocal communication, it is likely that one function of increased sociality for titmice is to enhance the reception of vocal signals between flockmates. It is apparent from the combined effects of traffic noise and dominance status on the structure and use of the chick-a-dee call that titmice are likely to adjust their vocal behavior in response to acoustic disturbances. Future efforts should determine if these increases in call rate and complexity provide any communicative benefit to callers or receivers. Additionally, the effects of noise on the chick-a-dee call contradicted the predictions of the leading explanatory hypothesis; which introduces many interesting questions. Is this an artifact of the unusual complexity of the chick-a-dee call or sociality of the Paridae family, and, if so, does sociality influence other responses to anthropogenic disturbance?



The third point of interest is an extension of the quantitative and theoretical findings. Birds commonly use social strategies, such as flocking, as a form of anti-predator behavior. Per current themes in the predator-prey and anthropogenic literature, noise was predicted to increase the level of perceived threat, causing titmice to engage in more densely-packed social groups. This functional similarity between predatory and disturbance stimuli suggested in the Risk-Disturbance Hypothesis, and the overarching Predation-Risk Theory, was supported here as the behavioral response to traffic noise provided support for several predictions of the Increased Threat Hypothesis. Using this predation-disturbance framework and relevant literature will enhance the design, generalizability and conservation value of future research by focusing experimental questions, hypotheses and predictions. Also, this functional similarity between predatory threat and disturbance stimuli is inherently interesting and may be indicative of a more basic connection between these two types of stimuli. Predatory threat evokes physiological responses indicative of fear, which is often mediated by socially-derived anti-predator behavior. Using the results obtained here and the predation-disturbance framework, this same relationship likely exists for anthropogenic disturbance. The pattern of fear inducing stimulus followed by social behavior is reminiscent of the classic work from social psychology (Harlow, 1958; Schachter, 1959) describing the importance of social stimuli in relieving fear or anxiety. The description of this relationship between sociality and fear sparks curiosity on the possibility that the processes linking predatory and disturbance stimuli may be even more basic than previously thought. This link with social psychology and fear alleviation speaks to the fundamental importance of the perspective provided by predation risk theory in studying anthropogenic disturbances.

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## **APPENDICES**

## **APPENDIX A**

### **TABLES**

**Table I.** Summary of main findings from experiments 1 and 2, Chapters 2 - 4. For experiment 1 and 2, the experimental stimulus, exposure type and the chapter of the dissertation where these data can be found. Note that experiment 1 includes two columns which represent the two analyses resulting from that experiment. Below these details the dependent measures from each study are listed. To the right of these measures, in the cells below each analysis, is a quick reference representation of the main findings. Within each cell, there is an arrow indicating in which direction noise altered the dependent measure. For example, the first dependent measure is NND, to the right of this measure is a cell with a downward facing arrow. This indicates that exposure to chronic, simulated traffic noise reduces NND. Under the arrow the partial-eta squared value is displayed. For this same cell, this effect of chronic noise on NND had an effect size of approximately 11%.

**Table I. Continued**

	Experiment 1		Experiment 2
Experimental Stimulus:	Simulated Traffic Noise	Simulated Traffic Noise	Recorded Traffic Noise
Exposure Type:	Chronic	Chronic	Rush-Hour
Chapter of Dissertation:	2	3	4
Dependent Measures			
NND	$\downarrow$ $\eta^2 = .109$		$\downarrow$ $\eta^2 = .160$
No. Close Perches	$\uparrow$ $\eta^2 = .037$		$\uparrow$ $\eta^2 = .230$
Conspecific Preference	$\downarrow$ $\eta^2 = .078$		no effect
No. Flight	no effect		$\uparrow$ at start, $\downarrow$ after 1 hr $\eta^2 = .140$
Chick-a-dee Call Rate		$\uparrow$ for dominant $\eta^2 = .190$	
$U_{note}$		$\uparrow$ for dominant $\eta^2 = .152$	
$U_{pair}$		no effect	



**Table II.** Predictions of reactivity associated with life-history characteristics. Predictions of reactivity and underlying logic were obtained from Blumstein (2006). Diet, body size, sociality, competitiveness and body condition are described for each species within the over-wintering months. Trait descriptions are estimates for the average individual of each species (i.e. values are representative of the population mean for each characteristic). References for sources used to obtain descriptions of traits are denoted by superscript numbers which are associated with 'in-text' citations below the table. Arrows are used to represent direction of predicted reactivity. An arrow pointing up represents heightened reactivity. An arrow pointing down represents suppressed reactivity. Abbreviations include: O (omnivorous) and MSF (mixed-species flock).

	tufted titmouse ( <i>Baeolophus bicolor</i> )		great tit ( <i>Parus major</i> )	
	description	reactivity	description	reactivity
diet	seed, nuts, live, O <sup>1</sup>	↑	seed, nuts, live, O <sup>6</sup>	↑
body size	18 - 25 g, small <sup>1</sup>	↓	15 - 20 g, small <sup>7</sup>	↓
sociality	flocking common <sup>1,2</sup>	↓	flocking common <sup>8,9</sup>	↓
competitiveness	dominant to heterospecifics <sup>1,2, 3,4</sup>	↑	varies with msf composition; subdominant <sup>10, 11</sup>	↓
body condition	low fat reserves <sup>4, 5</sup> good condition	↑	moderate <sup>5, 12</sup>	↓

<sup>1</sup>Grubb & Pravosudov, 1994

<sup>2</sup>Morse, 1970

<sup>3</sup>Dolby & Grubb, 1998

<sup>4</sup>Pravosudov et al., 1999

<sup>5</sup>Morse, 1974

<sup>6</sup>Beits, 1955

<sup>7</sup>Tinbergen & Dietz, 1994

<sup>8</sup>Hinde, 1952

<sup>9</sup>Krebs, MacRoberts & Cullen, 1972

<sup>10</sup>Jablonski & Lee, 2002

<sup>11</sup>Sasvari, 1992

<sup>12</sup>Gosler, 1996

## **VITA**

Jessica Lynn Owens was born in Massillon, Ohio as the first of three daughters to parents Lynn L. Roman and Doug A. Owens. After graduation from Perry High School in 2001, Jessica was accepted at Mount Union College in Alliance, Ohio. There she majored in Psychology and minored in Biology. While at Mount Union, Jessica used her summers for specialized study in animal behavior and marine mammal research at Duke University Marine Laboratory and the National Aquarium in Baltimore, MD. Following her Junior year, Jessica was awarded a National Science Foundation Grant to study serial pattern learning with Stephen Fountain at Kent State University. Her senior year was spent investigating the effects of enriched environment on rats' recoveries following a medial-frontal cortex contusion. This research was partially supported by a Psi Chi Undergraduate Research Grant awarded to Jessica. Following graduation from Mount Union College, Jessica began her graduate career in the Experimental Psychology program at The University of Tennessee, Knoxville. Under the direction of Todd M. Freeberg, she studied several aspects of social and vocal behavior of the tufted titmouse, focusing on the effects of traffic noise on the social behavior of this species.