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Acoustics of Anthropogenic Habitats: The Impact of Noise Pollution on Eastern Bluebirds

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COMPLIANCE PAGE

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ABSTRACT PAGE

An increasing number of habitats are affected by anthropogenic noise pollution, which is often louder, has a different frequency emphasis, and may occur over a different temporal scale, than natural noise. An increasing number of studies indicate that acoustically-communicating animals in such areas can modify their vocalizations in order to make themselves heard over the noise, but many questions still remain, including: How taxonomically widespread is vocal flexibility in response to anthropogenic noise, and do all vocally flexible species employ the same mechanisms to escape acoustic masking? Are there fitness repercussions for living, communicating, and breeding in noisy habitats? And, can particular habitat features be used to predict environmental noise levels and sound propagation characteristics? Here, I present data collected from the breeding territories of eastern bluebirds (*Sialia sialis*) to address each of these questions. My results add another species to the list of those who are able to avoid acoustic masking by modifying temporal and spectral traits of vocalizations. I also show that anthropogenic noise is associated with changes in several eastern bluebird breeding parameters. Finally, I demonstrate that both anthropogenic noise levels and sound propagation traits can be predicted by particular habitat characteristics.

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CHAPTER 1

A REVIEW OF PHYSIOLOGICAL AND BEHAVIORAL RESPONSES OF WILDLIFE TO ANTHROPOGENIC NOISE

Anthropogenic noise is an increasingly pervasive pollutant, expanding in scope and intensity commensurate with human population growth and urban development (Goines & Hagler 2007; Slabbekoorn & Ripmeester 2008). Human noise can reach sound pressure levels far exceeding those generated by natural sources of noise, and it may occur more often and in more places (Goines & Hagler 2007; Katti & Warren 2004; Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Warren et al. 2006). Although previous work has documented the affects of noise, in general, on a variety of animal taxa (Amoser & Ladich 2005; Aubin & Louventin 2002; Brumm & Todt 2002; Cui et al. 2009; de la Torre & Snowdon 2002; Kirschel et al. 2009; Morton 1975; Nemeth et al. 2001; Poesel et al. 2007; Ryan & Brenowitz 1985; Siegel & Mooney 1987; Turner et al. 2007; Witte et al. 2005), these studies have mostly focused on environmental sources of noise, or on unrealistically loud ambient noise levels in laboratory conditions (Cui et al. 2009; Siegel & Mooney 1987; Tanaka et al. 2009; Van Raaij et al. 1996). It is not surprising, then, that recent research has increasingly attempted to improve our understanding of the ways in which anthropogenic noise affects biota in the wild. In this context, birds are arguably the most studied organisms (Bermudez-Cuamatzin et al. 2009; Brumm 2004b; Fernández-Juricic et al. 2005;

Mockford & Marshall 2009; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). Of particular interest is the variety of ways in which anthropogenic noise affects bird song and avian communication; several reviews (Brumm 2006; Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Warren et al. 2006) have suggested not only how vocalizations may evolve in the presence of environmental noise, but also methods by which land managers might mitigate the impacts of sound pollution on avian populations.

In light of these recent analyses and the growing evidence for further increases in anthropogenic noise, we feel it is timely and informative to step back and review the influence of environmental noise on a broader array of traits than has recently been discussed. To this end, the following review is organized into two major sections, in which we summarize evidence and hypotheses for how environmental noise may affect both physiological and behavioral traits, respectively, and the resulting implications for individuals, populations, and entire communities. Our categories are not necessarily mutually exclusive, as physiology affects behavior, and vice versa; however, we feel this structure is useful in that it may help integrate sub-disciplines to address questions associated with the impact of noise on the behavioral ecology and evolution of animals, leading to a more comprehensive understanding of how anthropogenic noise affects wildlife populations.

1.1 The effects of environmental noise on physiological (including sensory) traits. Environmental noise appears to act as a physiological stressor in a broad range of taxa (Barber et al. 2010; Turner et al. 2007), including fish (Smith et al. 2004; Wysocki et al. 2007), amphibians (Bee 2008; Bee & Swanson 2007; Kaiser & Hammers 2009; Lengagne 2008; Parris et al. 2009; Sun & Narins 2005; Witte et al. 2005; Wollerman & Wiley 2002), birds (Chloupek et al. 2009; Hochel et al. 2002), and mammals (Frenzilli et al. 2004; Goines & Hagler 2007; Hanson 2008; Ising & Kruppa 2004; Mooney et al. 1985; Owen et al. 2004; Samson et al. 2005; Siegel & Mooney 1987; Stansfeld & Matheson 2003; Van Raaij et al. 1996). In this section, we intend to identify not only the taxonomic breadth of these effects but also the physiological range over which animals appear to be affected by environmental noise.

The impacts of environmental noise can be felt as early as the embryonic stage, by direct (though presumably muted) sound wave activity on the fetus, as well as via physiological impacts on pregnant females. For example, pregnant female rats exposed to elevated levels of environmental noise gave birth to pups that had greater fluctuating asymmetry (a morphological indicator of developmental instability (Moller & Swaddle 1997) in their parietal and long bones, as well as decreased dental calcium concentrations (Gest et al. 1986; Mooney et al. 1985; Siegel & Mooney 1987). Although the exact mechanism behind this response is not fully understood, these growth abnormalities appear to be a result of system-wide disruptions of calcium regulation caused when stress responses in the pregnant females altered activity along the adrenal-hypophoseal-parathyroid axis (Mooney et al. 1985; Siegel & Mooney 1987). Owen and colleagues (2004) conducted a long-term study evaluating daily behavioral and hormonal responses of a female captive giant panda (*Ailuropoda melanoleuca*) to fluctuations in ambient noise. They found that reproductive state was strongly related to the strength of her response: While the panda demonstrated increases in agitation behaviors and urine cortisol levels on days with louder average amplitude of ambient noise, these results were particularly pronounced during estrus and lactation. Unfortunately, because only one individual was studied, it is unclear whether these responses can be generalized. However, this anecdote raises the possibility that anthropogenic noise can cause stress responses similar to those elicited from more traditional environmental stressors (Wingfield 2003).

Research on Muscovy ducks (*Cairina* moschata) indicates that at least some avian embryos can exhibit responses to ambient noise stimuli when they are still in the egg (approximately 75% of the way through the incubation process) (Hochel et al. 2002). In fact, in several bird species (particularly Galliformes), inter-egg communication between developing embryos facilitates hatching synchrony (Vince 1966, 1973a, b; Woolf et al. 1976). The chicks can hear each other producing low-frequency clicking sounds associated with respiration (Vince & Salter 1967), and reception of this "signal" can shorten incubation time by as much as 10% (Woolf et al. 1976). The duration and rate of the clicking sounds, as well as the age of the embryo, can all affect the speed of hatching acceleration (Vince 1966, 1973a, b). It is possible that exposure to environmental noise (particularly low-frequency anthropogenic noise) might mimic this process. However, because these sounds accelerate development as well as hatching (Woolf et al. 1976) (*i.e.* produce chicks at equivalent physiological states despite having different ages) the long-term effects of such stimuli on avian populations are uncertain. In humans, on the other hand, excessive environmental noise (>85 dB) has been correlated with premature birth (Committee on Environmental Health & Pediatrics 1997).

Physiological responses to stressful levels of ambient noise have also been recorded outside the breeding process. Rainbow trout (*Oncorhynchus mykiss*) housed in tanks with 130 dB noise demonstrated higher blood glucose levels than trout in 115 dB tanks (Wysocki et al. 2007). However, it is not clear whether this is a biologically relevant level of noise for any free-living rainbow trout. Goldfish (*Carassius auratus*) exposed to even higher noise levels (approximately 160-170 dB) did not experience significant changes in glucose levels, but their cortisol levels were significantly higher than at pre-noise-exposure (Smith et al. 2004). Interestingly, this response only occurred over the short-term: Cortisol levels peaked at 10 minutes and then dropped to near-baseline levels after an hour despite the persistence of the environmental noise.

Short-term-only responses have also been documented in rats. Individuals exposed to short periods of moderately (85 dB) loud noise for three weeks displayed significant decreases in their humoral immune response (including increases in immunoglobulin levels, decreases in T-cells, and decreases in phagocytic activity) within the first week of the study, but reached an asymptote of response within three weeks of noise exposure (Van Raaij et al. 1996). In some individuals, immune responses even improved between week 1 and week 3. Responses such as those observed in both goldfish and rats suggest that habituation and/or short-term adaptation of sensory organs may help buffer individuals from auditory stressors. However, the exact mechanisms involved in decreasing physiological responses to acoustic stimuli are not fully understood; nor, to our knowledge, have any studies experimentally investigated the long-term physiological consequences of noise exposure.

Such research is made all the more challenging by the fact that exposure to acoustic stimuli can set off chemical cascades, involving the release and activity of diverse compounds in many different areas of the body, over different time frames (Frenzilli et al. 2004; Rabat et al. 2006; Samson et al. 2005). For instance, the neural activity required to process environmental noise leads to increased levels of free radicals, which are known to cause carcinogenic mutations (Samson et al. 2005). Indeed, noise-stressed rats displayed higher levels of adrenal DNA damage in comparison to control rats (Frenzilli et al. 2004). Furthermore, these physiological responses can be shaped not only by the amplitude of the original acoustic stressor, but also by the acoustic environment experienced immediately after exposure (Tanaka et al. 2009).

Though humans cannot be subjected to the same investigative conditions as most other animals, urbanization (and subsequent anthropogenic noise pollution) offers a "natural" experimental design. A number of researchers have correlated physiological, cognitive, and emotional states in humans with the presence of excessive, frequent, or sudden environmental noise (Environmental Protection Agency 1981; Goines & Hagler 2007; Ising & Kruppa 2004; Stansfeld & Matheson 2003). Like other animals, humans may experience a physiological stress response in reaction to noise (Goines & Hagler 2007). Under noisier conditions, humans show increases in adrenalin, noradrenaline, cortisol, heart rate, and vasoconstriction (Goines & Hagler 2007; Ising & Kruppa 2004; Stansfeld & Matheson 2003). When these responses occur routinely, for instance in industrial workers or individuals living near major transportation routes, they may be associated with significant health problems, such as hypertension, heart disease, and psychological disorders such as depression or feelings of aggression (Goines & Hagler 2007; Ising & Kruppa 2004; Stansfeld & Matheson 2003).

In school-age children, elevated noise levels have been associated with a decrease in intentional, incidental, and recognition memory (Lercher et al. 2003), a result that has also been found among rats (Rabat et al. 2006). Additionally, noise-stressed children displayed deficits in speech perception and reading ability (Hygge et al. 2002). Although scores of the latter improved once the noise had ceased, scores of the former did not. These results are reminiscent of those from several avian song-learning studies (Heaton & Brauth 1999; Lombardino & Nottebohm 2000; Marler et al. 1973; Phan et al. 2006; Troyer & Bottjer 2001; Zevin et al. 2004) investigating the effects of hearing impairment on memory and vocal ability. In one notable experiment, zebra finch (*Taeniopygia guttata*) juveniles were exposed to shorter- or longer-term treatments of extreme (>110 dB) environmental noise (Funabiki & Konishi 2003). Once released from the noise exposure, individuals of both groups were able to recover some of their vocal skills, but not all; in no case were noise-stressed individuals able to reproduce "normal," species-appropriate vocalizations.

Unfortunately, in studies such as these it can be difficult to assess the relative impacts of noise as a physiological stressor, a distraction, and/or a deafening agent. One study of cognitive deficits in rats has attempted to disentangle these effects (Cui et al. 2009). Rats were trained to use visual cues to locate a submerged platform in one quadrant of a circular pool. Individuals that experienced loud noise conditions during the learning phase of the experiment took longer to find the platform and spent less time in the target quadrant. A variety of corresponding neural assays indicated that these delayed responses resulted from learning deficits related to shifts in neuron structure, neurotransmitter balance, and neuronal receptor subunit expression. The cognitive and neurodevelopmental similarities between rats and humans suggest that similar mechanisms could underlie some of the effects of noise observed in humans.

Finally, hearing impairment and deafness are two of the most obvious—and most extensively documented—effects of extreme environmental noise on sensory systems (Funabiki & Konishi 2003; Goines & Hagler 2007; Heaton & Brauth 1999; Hough & Volman 2002; Ising & Kruppa 2004; Konishi 2004; Lombardino & Nottebohm 2000; Marler et al. 1973; Smith et al. 2004; Stansfeld & Matheson 2003; Wysocki et al. 2007; Zevin et al. 2004). These maladies result from damage of the cochlea and/or its related neural structures (Environmental Protection Agency 1981). Injuries may stem from single, extreme acoustic traumas (*e.g.* noises occurring beyond the pain threshold, approximately 135 dB), or from chronic exposure to dangerous levels of noise (for humans, approximately 75 dB)(Environmental Protection Agency 1981). These conditions can lead to perforated ear drums and the irreplaceable loss of hair cells.

Species that use acoustic communication tend to be highly adapted in their auditory filters (Klump 1996; Lucas et al. 2002; Lucas et al. 2007; Marler & Slabbekoorn 2004; Witte et al. 2005). Therefore, it is likely that even small hearing deficits can have notable negative effects on these animals' behaviors and life histories. However, most studies to date are clinical, evaluating changes in hearing threshold and associated vocal impairments (Funabiki & Konishi 2003; Smith et al. 2004; Tanaka et al. 2009; Wysocki et al. 2007). To our knowledge, there has been no research following hearing-impaired animals through subsequent life history stages in order to assess the long-term impacts of sensorineural damage.

Although the impact of environmental noise on hearing may be marked, it is worth noting that many of the experiments that have documented hearing loss have presented subjects with sound amplitude levels that few would be likely to experience in natural populations (Cui et al. 2009; Siegel & Mooney 1987; Tanaka et al. 2009; Van Raaij et al. 1996). In fact, this is a recurring theme in many environmental noise studies to date, causing us to question their ecological and evolutionary relevance. We encourage researchers to further explore more subtle responses of sound sensing organs to prolonged but realistic (in terms of frequency and amplitude) environmental noises.

1.2. The effects of environmental noise on behavioral traits. There are many reports of influences of environmental noise on animal behavior. Here, we have organized these behavioral effects into categories of auditory signal production/reception, mating behaviors, breeding behaviors, predator-prey interactions, and patterns of habitat use and community interactions. It is important to keep in mind that changes in multiple different categories of behavior may be concurrent (Kight & Swaddle 2007); these responses to environmental noise are not necessarily mutually exclusive. Although not comprehensive, we intend for these sections to illustrate the breadth of ways in which the behavioral ecology of animals could be influenced by ambient environmental noise.

1.2.1. Adjustment of auditory signal production and reception

A range of vocal manipulations have been recorded in response to environmental noise. Studies on birds (Bermudez-Cuamatzin et al. 2009; Brumm 2004b; Fernández-Juricic et al. 2005; Kirschel et al. 2009; Leader et al. 2008; Leader et al. 2005; Leonard & Horn 2005, 2008; Nemeth & Brumm 2009; Pytte et al. 2003; Kight, unpub. data; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006), frogs (Lengagne 2008; Parris et al. 2009; Sun & Narins 2005), and marine mammals (Foote et al. 2004; Miksis-Olds & Tyack 2009; Morisaka et al. 2005) have elucidated the variety of vocal adjustments that animals may make in order to maintain effective communication in noisy areas (Table 1). However, as these have been reviewed at length elsewhere (Brumm 2006; Katti & Warren 2004; Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Warren et al. 2006), we will not present any more details here.

It is important, however, to consider other behavioral manipulations associated with communication. For species that do not—or cannot—change parameters such as pitch, amplitude, or rate of vocalizations, it may instead be helpful to change timing and/or location of the performance. Studies in diverse habitats have demonstrated birds' ability to partition themselves both temporally and acoustically in order to maximize signal-to-noise ratios (a relationship describing the amount of energy present in a vocal signal versus the energy of all other interfering sounds) (Kirschel et al. 2009; Luther 2009; Planqué & Slabbekoorn 2008; Wiley 2006). Similar patterns have been found in response to anthropogenic noise pollution: European robins (*Erithacus rubecula*) that experienced higher levels of ambient noise during the day were more likely to sing during the quieter nighttime hours (Fuller et al. 2007), while frogs exposed to airplane traffic increased their calling efforts both during and after airplane noise, presumably to take advantage of the corresponding lull in other species' vocalizations (Sun & Narins 2005). In terms of movement responses, individuals whose territories include a busy road might spend the bulk of their time far from the traffic or might choose higher perches, which are better for transmission (Brumm & Naguib 2009). Such selective movements might be particularly useful while animals are vocalizing, allowing signalers to achieve spatial release from auditory masking (Bee 2008; Bee & Micheyl 2008).

As the above summary indicates, current research has focused mainly on the signaler—particularly, adult male signalers—despite the fact that optimal communication behavior is thought to be driven by the receiver's ability to detect and respond to signals (Wiley 2006). In the future, it will be important to explore receiver-related issues, as well. These include potential changes in hearing threshold and adjustments to spatial use of territories, including perch height selection.

Whether and how animals alter communication-associated behaviors in response to noise should depend on the value of effective communication compared to the costs of optimizing both signal production and reception. One recent study on manatees (*Trichechus manatus*) indicated that calling efforts were as dependent on behavioral state as on environmental noise conditions (Miksis-Olds & Tyack 2009). These results suggest that it may be particularly informative to quantify and compare the various costs and benefits associated with communicating in noisy environments, under different conditions and in different motivational states. Such studies would benefit from taking an experimental, rather than an observational, approach. Although the required methodologies may prove challenging, they are also likely to be rewarding, since these data are essential for fully understanding the balance between environmental acoustic pressures and animals' communication behaviors.

1.2.2. Mating behaviors

Arguably the most ecologically and evolutionarily important behaviors are those associated with mating and breeding. A negative impact of environmental noise on, for example, mate choice (Ríos-Chelén 2009), pair formation, or mate fidelity, could have profound implications for individual and population fitness.

Perhaps the most basic way in which environmental noise can interfere with breeding success is to make it more difficult for potential mates to locate one another using auditory cues. An aviary study on domestic canaries (*Serinus canaria domestica*) revealed that males are better able to discriminate conspecifics' songs against a background of multiple other singers than against a background of plain white noise (Appletants et al. 2005). This indicates that at least some animals are adapted to process only specific types of noise—in this case, short bursts of relatively pure tones. Individuals in environments with more broadband noises (such as those near moving water, in windy and vegetated areas, or near human settlements) might therefore have difficulty detecting and/or locating target vocalizations. A recent field study on ovenbirds (*Seiurus aurocapillus*) is consistent with this hypothesis. Male ovenbirds in noisy territories obtained significantly fewer pairings than males in physically similar quiet territories (Habib et al. 2007), suggesting that females were unable to hear, or pinpoint the position of, singing males.

In many species, once females have located potential mates, they evaluate male quality using auditory signals (Guerra & Morris 2002; Searcy & Andersson 1986; von Helversen et al. 2004); this is particularly true of birds, insects, and frogs. The presence of environmental noise has the potential to disrupt this process (as indicated in the previous section). Importantly, environmental noise might affect both the expression of a vocal display trait and preference for that trait. In one species of neotropical treefrog (*Hyla ebraccata*), females at noisy choruses preferred calls delivered at 3.24 kHz, while females at quieter choruses preferred calls delivered at 2.96 kHz (Wollerman & Wiley 2002). Because body size and vocal pitch are related, larger males tend to make lower-pitched noises, while smaller males make higher-pitched sounds. Thus, although female frogs would typically prefer larger males, in this case smaller males became preferable simply because their higher-pitched vocalizations made them easier to locate. Hence, environmental noise could fundamentally alter mate preferences because of noise-induced behavioral plasticity. It remains to be seen whether similar mate preference plasticity occurs in other species, but we hypothesize that “noise-dependent mate preference” may be common in species where mating occurs in noisy environments and males are capable of adjusting the pitch of their vocalizations (Leader et al. 2008; Leader et al. 2005; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006; Kight, unpub. data).

Another form of noise-dependent mate preference may occur in species where females learn preferences early in life (Bailey & Zuk 2008; Lauay et al. 2004). In such cases, environmental noise could impact mate choice at two stages: when vocal preferences are being learned as a juvenile, and when mate choice decisions are being made as an adult. As environmental noise is likely to affect multiple aspects of learning—from the fidelity of the produced sound to perception and cognitive processing of the received signal (see above)—we expect both preference and song learning to be more error-prone in noisier environments. Additionally, some vocalizations may be easier to hear or learn in particular sound environments (Slabbekoorn & den Boer-Visser 2006), so it is also possible that consistently different preferences are learned in one sound environment versus another. To our knowledge, the influence of environmental noise on preference and song learning has not been studied systematically, yet may be a common occurrence in species such as songbirds.

We have also found little research on the possible effects of environmental noise on competitive interactions over mates. Vocally-mediated competition among males, for access to females, is common in many territorial species (Collins 2004). Some species appear to assess signal-to-noise ratios to maintain physical separation between competing males and therefore enforce territorial boundaries (Lengagne 2008; Ríos-Chelén 2009). If signal-to-noise ratio is degraded by environmental noise, males in noisier sites might expend more energy in territorial display, engage in more physical disputes, and experience more intrusions, all potentially imposing significant costs on individuals. One way for both sexes to avoid problems associated with auditory signaling in noisy environments would be to utilize sensory modalities other than sound. In species that defend territories with a mix of, for example, auditory and visual displays, we would predict that a relative increase in reliance on visual displays would be beneficial in noisier environments (Badyaev et al. 2002).

Even once a mate has been secured, ambient environmental noise could continue to affect breeding and future mating. For example, female great tits (*Parus major*) are able to discriminate their mates' songs with high fidelity: Incubating females rarely responded to playback of recorded neighboring males' songs, even when those songs were very similar to those of their own mates (Blumenrath et al. 2007). This highly accurate response is postulated to strengthen pair bonds by increasing males' confidence in their mates' fidelity. If environmental noise obscures mate-mate auditory contact, reduced nesting success, weakened pair bonds, and even an increase in extra-pair copulations could result.

There is some evidence in support of the latter two hypotheses. Zebra finch females that were exposed to higher levels of white noise exhibited significant decreases in preference for their pair-bonded males compared with an extra-pair male (Swaddle & Page 2007). Presumably, this occurred because the environmental noise obscured pair-bond vocalizations (J. P. Swaddle, unpub. data). In the field, male eastern bluebirds (*Sialia sialis*) living in noisier habitats experienced a decrease of paternity with their social mate, and did not appear to make up for this loss via an increase in extra-pair paternity elsewhere (Chapter 4). Although this latter pattern is not necessarily attributable to noise alone (as noise is correlated with other environmental factors, such as disturbance), both cases point to significant post-mating costs of increased environmental noise.

1.2.3. Breeding behaviors

After a pair has successfully produced young, parent-offspring vocalizations are often important in coordinating offspring feeding, warning young of predators, and maintaining contact over distance (Marler & Slabbekoorn 2004). In two studies of tree swallow (*Tachycineta bicolor*) chick begging calls, Leonard and Horn (2005, 2008) discovered that nestlings altered the structure and rate of their vocalizations in the presence of ambient noise, and maintained the structural changes even after the noise source was removed. Furthermore, the nestlings' parents were observed to increase feeding rates in response to the vocal alterations. To our knowledge, no other information exists on the impacts of environmental noise on vocalizations of juveniles of any species or taxa, yet we would predict that parent-offspring communication would be under strong selection for high message fidelity.

Juveniles of many species—including monkeys (Rendall et al. 1996), seals (Van Opzeeland & Van Parijs 2004), wild dogs (Robbins & McCreery 2003), otters (McShane et al. 1995), and birds (Mulard & Danchin 2008)—produce calls not only to beg for food, but also to facilitate individual identification. These individually unique vocalizations are especially useful for parents and young that need to locate each other in the dark (Mulard & Danchin 2008), in large groups (Aubin & Louventin 2002), or after long absences (Aubin & Louventin 2002). Once young are mobile, but before they are completely independent, contact calls may be important for preventing separation or coordinating group movement (Marler & Slabbekoorn 2004). Although interferences with these vocalizations could lead to increases in juvenile mortality, to our knowledge no research to date has investigated this possibility.

Many avian begging calls appear to be designed to minimize location information to non-parents (Briskie et al. 1999; Madden et al. 2005; McDonald et al. 2009), suggesting that alterations in these vocalizations could potentially influence depredation rates. The adults of many bird species employ anti-predator vocalizations to encourage juveniles to cease begging (Greig-Smith

1980; Platzen & Magrath 2004; Rydén 1978; Thompson & Liebreich 1987) and/or retreat into the nest (Knight & Temple 1986) until a predator has passed. These warnings can be especially important when parents are defending against predators that hunt using phonotaxis (Norris & Møhl 1983; Sakaluk & Belwood 1984). If ambient noise masks vocalizations, it may affect such potential predators and prey equally; however, many juveniles would still be threatened by predators that cue in on heat or smell. Ambient noise might also reduce the efficacy of predator distraction displays involving distraction vocalizations (*e.g.* those in plovers (Hauser 1997)), as well as obscuring the "help" cries of juveniles (Blumstein et al. 2008). On the other hand, some species may benefit from living in noisy environments if their main predators are not equally noise-tolerant. Recent work among avian communities nesting near natural gas extraction facilities indicates that nest predation rates are lower in noisier sites due to the absence of predatory western scrub jays (*Aphelocoma californica*)(Francis et al. 2009). Whether the lack of predation is offset by some other noise-related cost (*e.g.* slower development, higher stress levels, etc.) is currently unknown.

Like predators, parasites can eavesdropping to their advantage. This includes intimate parasites, such as the yellow fly (*Ormea ochracea*) that locates its victims using phonotaxis (Walker & Wineriter 1991), and nest parasites such as the brown-headed cowbird (*Molothrus ater*), which uses auditory cues when locating potential egg-dumping sites (Clotfelter 1998). In these instances, however, ambient noise might benefit individuals by "camouflaging" them from potential parasites. However, there is an additional threat in the case of nest parasites: In nests where egg-dumping has occurred, nestlings may react to the presence of "fake" siblings by increasing their own calling efforts; presumably these chicks identify egg-dumped young because of differences in vocal characteristics (Boncoraglio & Saino 2008). Ambient noise could decrease nestlings' ability to detect these intruders. This may ultimately facilitate their being out-competed for resources by larger and/or more aggressive egg-dumped individuals.

1.2.4. Predator-prey interactions

Predator-prey interactions can be affected by noise in a variety of ways, encompassing each of the subsections listed above. Alterations in signal properties—particularly amplitude—may make signalers more obvious to predators, or easier to locate within the habitat (Bayly & Evans 2003). Similarly, if individuals choose higher or more pronounced perches in order to maximize transmission or reception (Brumm & Naguib 2009), they run the risk of increasing their exposure to aerial predators (Campos et al. 2009; Moller et al. 2006).

Not only might noise mask the approach of a predator, but it could also obscure both conspecific and heterospecific warning calls, which may be used to provide a generalized alert or to offer more specific details about the location or type of threat (Kiriazis & Slobodchikoff 2006; Lea et al. 2008). The use of warning signals may improve fitness on individual, kin, and/or group levels

(Hoogland 1996; Kiriazis & Slobodchikoff 2006; Lishak 1984); thus, widespread population consequences could result from the introduction of noise pollution. Some animals, such as the eastern chipmunk (*Tamias striatus*), use conspecific alarm calls to optimize the balance between foraging and vigilance behaviors (Baack & Switzer 2000). Without this information, animals may spend excessive amounts of time scanning for potential predators and may spend too little time foraging. This has been documented in both rats (Krebs et al. 1997) and chaffinches (*Fringilla coelebs*)(Quinn et al. 2006). Interestingly, while the rats eventually habituated to the noise stimuli in their environments, the chaffinches did not, implying that a consistent noise environment could lead to long-term selection for a different balance of behavioral strategies.

It is also informative to examine noise from a predator's perspective. As mentioned previously, many predators use auditory cues to locate prey (Sakaluk & Belwood 1984). Increases in ambient noise levels may reduce phonotactic ability simply by obscuring noise cues (Schaub et al. 2008) or by prompting potential prey to use vocalizations that may be more difficult for predators to locate (Page & Ryan 2008). Hunting might be particularly difficult for species such as bats, which use sonic cues not only for prey localization, but also navigation (Fenton & Bell 1981).

Unfortunately, predator-prey interactions in noisy environments have received scant attention (but see Fenton and Bell 1981; Francis et al. 2009), despite the fact that they likely have an important influence on population stability.

1.2.5. Habitat use and community interactions

Decreases in species-specific habitat use—as measured by abundance, density, and richness—have been correlated with increases in environmental noise (Bayne et al. 2008; Rheindt 2003; Stone 2000). The reasons behind these changes in habitat use are not fully understood. Some animals may perceive loud territories as sub-par, while others might simply be frightened off by the noise (Francis et al. 2009). Or, if auditory cues are used in habitat selection and settlement (as has been suggested for certain species of fish (Egner & Mann 2005)), then excessive levels of ambient noise may decrease the ability of migrating individuals to locate appropriate territories. Whatever the cause, redistribution could lead to increases in density within the remaining suitable habitat, leading to a rise in competition over available resources.

Alterations in species assemblages may have cascading effects on the entire ecosystem (McDonnell & Pickett 1990), as was suggested by a recent study on western scrub jays. The jays were measured at lower densities in noisier sites, indicating their preference for less acoustically disturbed habitat. Because the jays are key dispersers of pinyon pine seeds, their redistribution in the habitat in response to anthropogenic noise could lead to significant changes in habitat structure and, ultimately, habitat function (Francis et al. 2009;

Srivastava 2006). To our knowledge, this is the only research linking anthropogenic noise to changes in community relationships. In the future, more work should attempt to take the long view and explore the ways in which localized responses to noise pollution might have impacts on the entire ecosystem.

1.3 Conclusions

A decrease in human expansion is unlikely to occur in the near future, making it increasingly important to understand the implications of anthropogenic stressors, such as noise, on wildlife. We are only just beginning to understand the ways in which human noise pollution impacts physiological, sensory, and behavioral traits of wildlife. However, given the diversity of these characteristics, it is clear that future work should attempt to be as integrative as possible. It will also be important for studies to examine a variety of taxa rather than focusing efforts on urban species and lab animals, as has frequently been the case thus far. Given the number of studies on humans showing that negative impacts can result from even moderate increases in ambient noise exposure, it seems well worth the effort to conduct research across the entire anthropogenic noise gradient rather than focusing on biologically unrealistic levels of noise exposure (*e.g.* >100 db). This is especially true because, although many individuals may occasionally encounter extreme levels of sound pollution, the majority of animals do not.

Likewise, it may be counterproductive to limit our studies of human habitats by thinking of them as "urban" or "rural." Though some environmental variables may neatly fall into such dichotomous classifications, noise may not. For example, we quantified ambient noise levels of eastern bluebird territories in Williamsburg, Virginia, USA (Chapters 2-4). We collected recordings from multiple contiguous territories within a site at multiple different types of site (*e.g.* a college campus, golf course, cemetery). Surprisingly, we found that even in generally quiet sites (*e.g.* cemetery) there are certain territories with noise levels comparable to those at generally louder sites (*e.g.* college campus). Thus, had we followed tradition and grouped our recordings subjectively, by site-type, we might have missed biologically relevant patterns.

In the future, geographic information systems (GIS) will be useful in creating more fine-grained, detailed analytical approaches that evaluate study locations not on a predetermined, qualitative scale, but on a quantitative level that is more representative of local conditions. It will be especially enlightening to create sound maps (Warren et al. 2006; Yepes et al. 2009), which depict the amplitude and frequency of local noise conditions in a style similar to the way topographic maps depict height above sea level. These maps are likely to redefine the way we choose study sites and design field protocols. Once we are able to examine responses along the entire range of ambient noise conditions, it will be possible to model species' responses more accurately. For example, although the presence of threshold effects of noise has also been theorized

(Hanson 2008; Smith et al. 2004), few, if any, studies have been designed to collect the data necessary to detect these asymptotic relationships. The use of sound maps may allow researchers to select an appropriate number and distribution of sites for investigating threshold trends.

Additionally, spatial data will be invaluable for exploring questions that revolve around highly mobile individuals or species. In the case of migratory birds, for instance, it will be interesting to document the differences in ambient noise levels that individuals experience as they move from natal territory to overwintering sites, and then to breeding territories. Even for more sedentary animals that disperse over shorter distances, it is important to measure the range of ambient noise they experience. Once we have achieved this level of detail, it will be much easier to evaluate the relative importance of exposure source, intensity, and duration as well as to understand whether these variables have different impacts at different life stages.

This may be well be related not just to the noises themselves, but also to the environments through which they propagate. As has been reviewed by Warren et al. (2006), a variety of landscape features will influence the way residents experience noise. Although a fair amount of attention has been paid to the ways in which natural features degrade or amplify sounds (Dabelsteen et al. 1993; Derryberry 2009; Marten & Marler 1977; Marten et al. 1977; Nemeth et al. 2001; Slabbekoorn & Smith 2002; Wiley 1991), much less is known about the effects of human-made materials, structures, and habitat arrangements.

Advances in the study of anthropogenic noise will contribute to two major objectives: (1) improved conservation and management efforts, and (2) an enriched understanding of the ways in which a single environmental variable—such as ambient noise—can place selective pressure on multiple traits (sometimes simultaneously). In terms of the former objective, future research might suggest practical solutions to noise pollution, such as an increased use of ear plugs in hazardous locations or by susceptible individuals; the erection of sound barriers to decrease sound propagation; the use of buffer areas around particularly loud sites (*e.g.* industrial areas); retrofitting noisy equipment with noise-reducing parts (Bayne et al. 2008); redesigning equipment to emit sounds at a less harmful amplitude and/or pitch (frequency); or using construction materials that tend to attenuate or absorb environmental sounds at frequencies that appear most harmful to wildlife. On a larger scale—and perhaps most important given the continuing increases in urbanization—this information can also be used by landscapers, city planners, and wildlife managers who are interested in maximizing land use while minimizing exposure to health hazards (Yepes et al. 2009).

With respect to the latter objective, many researchers have questioned whether various species of wildlife possess the means to adjust to a variety of human disturbances, including noise (Kight 2005; Kight & Swaddle 2007; Marzluff et al. 1998; Partecke & Gwinner 2007; Rabin & Greene 2002; Rabin et al. 2003). Though in many ways anthropogenic noise can be quantitatively and qualitatively compared to “natural” noise events (Katti & Warren 2004; Lugli & Fine 2003; Lugli et al. 2003; Warren et al. 2006), its intensity and pervasiveness cannot be matched by these other acoustic pressures. Anthropogenic noise research thus offers an ideal opportunity to investigate the relative strengths of short-term, within-individual responses, such as flexibility, acclimatization, and learning. When exploring these relationships, it will be important to remember that behaviors often trade-off with each other due to resource limitation, time constraints, and/or genetic correlations. When individuals alter the relative investment in one behavioral strategy versus another—by whatever mechanism—they may experience fundamentally different selection on overall behavior and life history strategies. Because environmental noise is such an omnibus factor, it is likely that it may effect shifts in entire suites of behaviors simultaneously.

Finally, conducting longer-term, population-level research will be essential for understanding species adaptations resulting from widespread individual-level responses to noise stressors. These data are particularly interesting not only because they facilitate the creation of models to predict a number of biological patterns in the future, but also because of the light they shed on the ways in which acoustic environments may have shaped evolution in the past.

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Source	**Type of species**	**Vocal adjustment in response to louder ambient noise (significant relationships and strong trends)**
Bermudez-Cuamatzin et al. 2009*	Bird	Increased min. frequency
Brumm 2004*	Bird	Increased amplitude
Brumm et al. 2004	Marmoset	Increased amplitude
Brumm et al. 2009	Bird	Increased amplitude, increased call rate, fewer complex calls
Fernandez-Juricic et al. 2005*	Bird	Increased min. frequency, fewer notes/song
Foote et al. 2004*	Whale	Increased call duration
Fuller et al. 2007*	Bird	Increased nocturnal singing
Kaiser and Hammers 2009**	Frog	Increased calling rate
Lengagne 2008*	Frog	Reduced calling rate
Leonard and Horn 2005**	Bird	Increased calling length (field only), increased amplitude (field and lab), increased frequency range (field only)
Leonard and Horn 2008**	Bird	Increased min. frequency, narrower frequency range
Miksis-Olds and Tyack 2009	Manatee	Decreased calling rate, increased duration, decreased peak frequency
Morisaka et al. 2005	Dolphin	Reduced frequency of whistles, fewer frequency modulations
Nemeth and Brumm 2009*	Bird	Higher min. frequency, reduced intersong intervals
Parris 2009*	Frog	Increased min. and dominant frequency
Pytte et al. 2003	Bird	Increased amplitude of chips
Rabin et al. 2003*	Squirrel	Shift acoustic energy to non-overlapped harmonics
Slabbekoorn and den Boer-Visser 2006*	Bird	Increased min. frequency; shorter, faster songs; atypical song types
Slabbekoorn and Peet 2003*	Bird	Higher min. frequency
Sun and Narins 2005*	Frog	Altered calling rate; changed call type
Wood and Yezerinac 2006*	Bird	Increased min. frequency; less power in overlapped frequencies

Table 1.1 Documented vocal adjustments in response to environmental (anthropogenic and non-anthropogenic) noise. These studies include observations of vocal responses to natural environmental noise (no asterisk), "naturally-occurring" human noise (*), and playbacks, including both white and anthropogenic noise (**). It is important to note that many of these studies discuss additional contributions of variables other than noise on vocal parameters (e.g. habitat structure, the presence of conspecifics, etc.); it is therefore difficult to directly compare these results. However, it is clear that certain vocal manipulations—particularly increases in minimum frequency and amplitude—are fairly ubiquitous across taxa in response to loud ambient noise.

CHAPTER 2

ACOUSTIC SPACE IS AFFECTED BY THE PRESENCE OF ANTHROPOGENIC HABITAT FEATURES

2.1 INTRODUCTION

Physical ecology plays an important role in shaping vocal signals (Brown & Handford 2000; Brumm & Naguib 2009; Marten & Marler 1977; Marten et al. 1977; Wiley 1991; Wiley & Richards 1982). This stems predominantly from the ways in which ecological conditions—including temperature, humidity, air turbulence, and the presence/absence of structures with varying acoustic properties—impact sound degradation, the process by which a signal undergoes changes while traveling from a signaler to a receiver (Morton 1975). Degradation arises as a result of attenuation (the loss of intensity of a signal, such as occurs through absorption) and scattering (changes in the path of sound waves due to reflection, refraction, and/or diffraction)(Wiley & Richards 1978). Over time, the signals that propagate most efficiently despite degradation will be favored within populations (Hauser 1997; Wiley 2006) because they will be most effective in eliciting the intended response. However, as the environment continues to change, animals should also change their vocalizations in order to maintain their suitability within a given habitat (Derryberry 2007, 2009).

A number of studies have illustrated which ecological factors have the largest impact on signal design. These include the type of habitat (generally categorized as either forest/closed or grassland/open (Brown & Handford 2000; Morton 1975; Wiley & Richards 1978)) and the height of and distance between signalers and receivers (Blumenrath & Dabelsteen 2004; Brumm & Naguib 2009; Fernández-Juricic et al. 2005; Nemeth et al. 2001). Both the presence, and spectral characteristics, of ambient noise will also influence signal design: Acoustically communicating organisms should evolve signals that reduce *masking*, the process by which a more intense sound (*e.g.* ambient noise) obscures a less intense sound (*e.g.* a song or call) occurring within the same frequency range.

The ecology of communication has, perhaps, been studied most comprehensively in birds. Studies across different species in the same habitat (Boncoraglio & Saino 2007; Lemon et al. 1981; Marten & Marler 1977; Marten et al. 1977; Ryan & Brenowitz 1985), and within species across different habitats (Dingle et al. 2008; Kirschel et al. 2009; Leader et al. 2005; Slabbekoorn & Peet 2003; Slabbekoorn et al. 2007; Wood & Yezerinac 2006), have illuminated the vocal manipulations that allow signal optimization in complex environments. Birds in closed, forested habitats consistently sing at higher frequencies (Brown & Handford 2000; Marten & Marler 1977; Marten et al. 1977), a trend that generally remains true regardless of the exact frequency characteristic (minimum, maximum, range) being measured. Frequency stratification occurs vertically, as well, with birds higher in the canopy singing at higher frequencies (Blumenrath & Dabelsteen 2004; Kirschel et al. 2009; Nemeth et al. 2001). These patterns stem from the fact that higher-frequency sounds are attenuated less by surfaces such as leaves (Forrest 1994). However, these same frequencies will also be subject to higher levels of scattering (Blumenrath &

Dabelsteen 2004; Brumm & Naguib 2009; Slabbekoorn et al. 2002; Wiley & Richards 1978). To combat this problem, birds in closed habitats also tend to produce purer tones and to space notes more widely in order to avoid signal distortion due to reverberation (Brown & Handford 2000; but see Slabbekoorn et al. 2002).

As might be expected, birds in open, grassland habitats tend to produce lower-frequency sounds, which propagate more efficiently over longer distances (Forrest 1994; Wiley 2006; Wiley & Richards 1978). Again, this pattern is seen vertically as well, with birds at lower perches using lower-frequency sounds (Brown & Handford 2000; Morton 1975; Wiley 1991). Signal degradation in open habitats occurs mainly as a result of irregular amplitude fluctuations caused by air conditions (Brown & Handford 2000; Wiley & Richards 1978). In response to this pressure, grassland birds often employ trills, or rapid repetitions of the same note (Brown & Handford 2000; Derryberry 2009; Slabbekoorn et al. 2007). Although this technique does not counter the effects of degradation, *per se*, its main benefit is the increased likelihood that at least one of the many repeated notes will be detected by a receiver.

Because birdsong can be so specifically tailored to environmental conditions, disruptions to the habitat have the potential to impact communication negatively. One disruption that has received much recent attention is human disturbance (Brumm 2004b; Habib et al. 2007; Katti & Warren 2004; Mockford & Marshall 2009; Rabin et al. 2003; Slabbekoorn & den Boer-Visser 2006; Warren et al. 2006; Wood & Yezerinac 2006). Most research to date has been focused on anthropogenic noise pollution and corresponding vocal adjustments among affected individuals and populations (Bermudez-Cuamatzin et al. 2009; Fernández-Juricic et al. 2005; Slabbekoorn & Peet 2003). However, while ambient noise is an important part of the overall ecology of disturbed birds, it is only one of the potential anthropogenic selective pressures on avian communication. As noted by Warren et al. (2006), human habitat modifications are also likely to play an important role in the evolution and plasticity of vocalizations in disturbed habitats. These modifications include habitat restructuring—razing trees, clearing scrub, building structures—and replacing "natural" materials with concrete, metal, and glass.

Despite the fact that human expansion is occurring at an unprecedented rate (Goines & Hagler 2007), little is known about sound propagation in these growing areas of anthropogenically-modified habitat. Many authors have suggested management techniques for mitigating the impacts of anthropogenic noise (Habib et al. 2007; Katti & Warren 2004; Slabbekoorn & Ripmeester 2008; Warren et al. 2006), but these proposals fail to address the possibility that physical habitat modifications may also place selective pressures on vocal parameters by altering the way sound propagates through the habitat. In order to fully understand the ways in which human habitats could be affecting avian communication, it is important to understand how sound propagates within them. Further, a comparison of "natural" and "anthropogenic" habitats is needed in order to evaluate whether there is a significant difference between these habitats, or whether sound propagation characteristics within anthropogenic areas fall within the range of those occurring in natural environments.

To meet this need, we have examined acoustic properties in breeding territories surrounding nest boxes distributed across an anthropogenic disturbance gradient in Williamsburg, Virginia, USA. These boxes are home to a variety of passerine species, most notably the eastern bluebird (*Sialia sialis*), Carolina chickadee (*Poecile carolinensis*), and house wren (*Troglodytes aedon*), which our research group has previously studied in the context of direct anthropogenic disturbance (Kight 2005; Kight & Swaddle 2007) and land use (Le Clerc et al. 2005). Each of these species emphasizes a slightly different frequency range in its songs (on average, eastern bluebird : 2-4 kHz; Carolina chickadee: 4-6 kHz; house wren: 4-8 kHz)(Gowaty & Plissner 1998; Johnson 1998; Mostrom et al. 2002). Accordingly, we elected to examine the propagation of sound at three frequencies (3, 5, and 7 kHz) in order to better interpret our results within a biological context. We examined three propagation characteristics at these three frequencies, at four different distances, in each of the four cardinal compass directions within the nest box territory. We also measured absolute noise levels at each distance in each direction. Further, we used Geographic Information Systems (GIS) to digitize high-quality maps of each territory so that we could relate propagation measurements and ambient noise levels to specific structures and materials found within the acoustic space of each habitat.

We predicted that signal persistence would be highest for lower frequency tones, over shorter distances, and in open, acoustically soft environments. We expected to find the highest levels of reverberation among lower frequency tones, over shorter distances, in more anthropogenic and acoustically hard environments. Finally, we predicted that SNR would be lowest in territories with the most anthropogenic features. Likewise, these are the environments where we also expected to find the highest levels of ambient noise.

It is our intention that the data from this work will serve two purposes. First, to illuminate whether, and how, human habitat modifications can affect the sound environment of wildlife (between 3 and 7 kHz, at least). This information is essential not only for understanding the ways in which human activities might shape further evolution of avian communication, but also for developing adequate management plans.

Second, we hope to promote the view that habitat types should be considered along a gradient, rather than in dichotomous pairs. Traditionally, both sound and disturbance research juxtapose only two types of habitat—“closed” versus “open,” for instance, or “urban” versus “rural.” While this is adequate for preliminary research projects hoping to establish the existence of patterns, further studies should examine questions on a more continuous scale, since humans manipulate habitats across the entire rural-urban gradient.

2.2 METHODS

2.2.1 "Study Species" and Site Description

Our study was designed to investigate the acoustic properties of territories centered around nest boxes distributed across a disturbance gradient in and near Williamsburg, Virginia, USA; more detailed geographical information can be found elsewhere (Kight 2005; Kight & Swaddle 2007; Le Clerc et al. 2005). Since 2003, we have studied three cavity-nesting species breeding in these boxes: eastern bluebirds, Carolina chickadees, and house wrens. Although the current research has no study species, *per se*, the protocols were designed with these species in mind, with the goal of examining the sound propagation results within the context of these birds' life histories and, therefore, making our results more biologically meaningful. In cases where life history differences precluded the possibility of choosing a methodology that allowed broad application to each of the "study species," we chose protocols based on the behaviors of eastern bluebirds, our primary study species.

Territories were located in a variety of sites, including parks, golf courses, campuses, cemeteries, and roadsides. Accordingly, habitat features and layouts differ greatly; there is much variation in the openness of the habitat, the number and type of anthropogenic features, and the distance to the nearest acoustically significant structure. This amount of variation is typical of our study species' territories which, historically, have been found along habitat edges and in areas undergoing rapid succession (Gowaty & Plissner 1998; Johnson 1998; Mostrom et al. 2002).

2.2.2 Sound Propagation Recordings

We conducted playback recordings at 39 nest boxes during the 2007 breeding season. All recordings were collected between 0800 and 1800 h on days with little to no wind. Recordings were collected either prior to nest box occupation or after completion of breeding, so as to minimize disturbance to the animals. Since the acoustic characteristics evaluated here are influenced by permanent physical structures in the environment, differences in collection date, relative to box occupation date, should not substantially alter our ability to interpret how sound propagation might affect resident breeding birds.

Although we originally intended to record weather conditions associated with each collected recording, we had technical problems midway through the season and were not able to resume measurement of temperature, wind speed, or humidity thereafter. However, we devised an alternative way of measuring, and therefore controlling for, variations in weather conditions (see below).

We used NCH ToneGenerator (NCH Software, Inc., Greenwood Village, CO) to create 0.1 s clips of pure tones at 3, 5, and 7 kHz. Next, we created a master playback file consisting of 10 repeats of the following sequence: 3 kHz tone, 2 s silence, 5 kHz tone, 2 s silence, 7 kHz tone, 2 s silence. Using a decibel meter (Extech Instruments Model 407727) and RavenPro 1.3 acoustic software (Cornell Lab of Ornithology, Ithaca, NY), we calibrated our recording instruments (Sennheiser ME65 directional microphone with windscreen, Marantz PMD 660 solid state recorder, Sony SRS T70 personal travel speakers, and an Apple iPod). We also determined and marked an appropriate volume setting on the iPod in order to consistently play tones at approximately 65 dB at 1 m from the speakers.

Because our focal species defend an approximately 50 m radius territory around their nest boxes, and because behaviors during the breeding season are focused around frequent nest visits, we assumed that the box location would be a fairly accurate representation of the center of the birds' acoustic space. This was therefore the point of broadcast for the sequence of pure tones, which we delivered via the speakers after mounting them at the top of a 3 m pole in order to simulate an average perch height (Gowaty & Plissner 1998). Likewise, we recorded the playback with the microphone mounted at the top of an identical pole. Recordings were collected at distances of 20, 40, 60, and 80 m from the nest. These values reflect typical distances to a nearby mate, an intruding bird, the edge of a neighbor's territory, and halfway into a neighbor's territory, respectively. We made recordings at each set of distances in each of the four cardinal compass directions, beginning at east and working clockwise through north.

Although we attempted to position the microphone as accurately as possible, we occasionally encountered environmental barriers such as trees or parked cars. In order to accommodate these structures, we allowed ourselves +/- 5 m of flexibility at each recording point. No recordings were made after encountering certain barriers, such as bodies of water, roads, or buildings that extended beyond our 80 m final distance (however, recordings were resumed in the few cases where these barriers ended before 80 m and allowed circumnavigation). Occasionally, we were also forced to abandon recording because of fences or land access restrictions. Due to these factors, all but 8 of our sites had incomplete sound propagation datasets.

We also collected near-field recordings in the center of the territory, with the speakers 3 m from the microphone. Since signal amplitude and distance were held constant across all sites, any differences among these recordings should be due to weather conditions (*e.g.* temperature and humidity). We therefore used this measure as a covariate to control for weather in further analyses (see below).

All recordings were analyzed in RavenPro 1.3 acoustic software. We quantified three values to describe environmental degradation of tones: a) **persistence**, a ratio of the strength of tone at each distance versus the 3 m reference tone; b) **reverberation**, a ratio of the strength of the "tail" (or echo) and the strength of the preceding tone; and c) signal-to-noise ratio (**SNR**), a ratio of the strength of the tone and the strength of the background noise (Blumenrath & Dabelsteen 2004; Dabelsteen et al. 1993; Slabbekoorn et al. 2007) (Figure 1). In all cases, "strength" denotes RMS amplitude that we converted into dB SPL (henceforth, dB), for easier interpretation in a real world context. Additionally, we used the values of noise, as calculated in (c), above, to investigate whether **ambient noise** was related to specific microhabitat features.

For the analyses, all recordings were bandpass filtered at values 1 kHz below and above the focal tone; in other words, a 3 kHz tone was bandpass filtered between 2 and 4 kHz. Environmental noise was evaluated across a 0.03

s selection of ambient noise preceding the focal tone by 0.05 s. This value was then used to calculate the strength of the tone itself. In order to measure the strength of the focal tone, we measured RMS amplitude within a 0.05 s recording selection taken from the middle of the 0.1 s tone. Finally, we measured the strength of the tone's reverberation within another 0.03 s selection beginning 0.03 s after the end of the tone. The two 0.03 s lengths were chosen because this is approximately the average length of a bluebird song syllable (Chapter 3); thus, this is the period of time over which a bird might have the opportunity to evaluate its acoustic environment and adjust its song accordingly, as well as the period of time after which reverberations might impact song performance (Slabbekoorn et al. 2002). The 0.05 s selection length was chosen to avoid distortions present at either end of the tone, which was not ramped.

2.2.3 Habitat Evaluation

We used ArcGIS v. 9.3.1 (ESRI, Redlands, CA) to digitize habitat according to the following categories: short impervious surface (including roads, sidewalks, and short walls < 3m in height), short vegetation (including shrubs and grass), tall impervious surface (including structures such as buildings and lamp posts > 3m), trees (forest and ornamental), and water. Because sound propagates spherically, sound waves can be attenuated or reflected by habitat features placed outside of the direct line between the broadcasting speakers and microphone. Therefore, for each directional set of recordings, we evaluated habitat within a 90° cone centered on the cardinal direction. At each recording distance, we measured the amount of each type of habitat present between the speaker and the microphone; thus, the 40, 60, and 80 m evaluations are cumulative. Furthermore, an additional 10 m of habitat was evaluated at each distance in order to account for the fact that sound travels fast enough to bounce off objects behind the microphone before being recorded. This means, for instance, that habitat values for the 20 m distance actually reflect features that occurred within 30 m of the nest box.

We used principal components analysis (PCA) to reduce the number of habitat variables included in the models. The PCA produced two principal components (PCs) with $\lambda > 1.0$, cumulatively explaining 61.4% of the variance (Table 1). PC1, which explained 35.8% of the variance, loaded strongly positively for total area of short vegetation, and strongly negatively for total area of trees. This combination of characteristics, which is common among the more "natural" territories of our three focal species, will hereafter be referred to as *total area open/grassy habitat.* PC2, which explained 28.3% of the variance, loaded strongly positive for both tall and short impervious surface. Because impervious surface is a product of human construction, we have called this variable *total area anthropogenic habitat.*

2.2.4 Statistical Analyses

We utilized an information theoretic model selection approach (Burnham & Anderson 2002) to evaluate the effects of habitat on sound propagation. For each dependent variable, a candidate set of models was determined *a priori*. Because several breeding territories were within a single, larger breeding site, all analyses included "site" as a random variable in order to avoid the effects of pseudoreplication. "Weather" was also included in all analyses in order to control for the effects of temperature and humidity on sound propagation. "Distance" was only included in models seeking to explain persistence and reverberation, since neither SNR nor ambient noise were measured in comparison to a baseline, near-field recording and thus would not be expected to change with increasing distance from the speakers. All models contained terms for habitat characteristics, as well as two-way and three-way interactions between habitat, frequency, and distance, as appropriate.

We used SPSS v. 15 (LEAD Technologies, Inc., Chicago, Illinois) to run generalized linear mixed models (GLMM) in order to determine Akaike's Information Criterion (AIC) for each model. These values were used to calculate AIC_c (which corrects AIC for small sample sizes), Δ- AIC_c (the difference between the model with the lowest AIC_c and each subsequent model), Akaike weight (an indicator of support for each model), and model likelihood. We then used model averaging (Mitchell 2008) to incorporate weighted parameter estimates from all models with Δ-AIC <4.0 (Burnham & Anderson 2002).

Prior to inclusion in statistical analyses, distributions of all variables were checked for normalcy and transformed, where appropriate. Figures illustrating the relationships between sound propagation variables and interaction terms were created by categorizing one variable in the interaction term as "high" or “low” relative to median values. This allowed us to plot values for the other interaction term across two separate x-axes (“high” or “low”) and regress sound propagation variables across these two graphs in order to determine the direction and strength of the relationship. These categories were not used in any statistical analyses, but are useful for visualizing the effects of the interaction terms.

2.3 RESULTS

We sampled the relationships between acoustics and habitat at a total of 1872 points across 39 eastern bluebird breeding territories. Considering our data from the perspective of an eastern bluebird male, whose songs occur at approximately 3 kHz and whose vocal signals are utilized to defend a territory extending 50 m in radius from his nest box, the following are the average acoustic conditions (in absolute, unitless values): Signal persistence falls between a minimum of 6.0 X 10^-5 and a maximum of 1.4 X 10^-3, with an average of 4.6 X 10^-4. The expected reverberation of a vocal signal ranges from 0 to 1.3 X 10^-3, with an average of 2.1 X 10^-4. SNR falls between 0 and 1.17, with an average of 3.4 X 10^-2. Finally, environmental noise ranges from 18.4 dB (approximately as loud as rustling leaves or a quiet conversation) to 67.4 dB (approximately as loud as a radio, or typical street noise), with an average loudness of 38.1 dB (approximately as loud as a quiet home or office).

2.3.1 Persistence and Habitat.

Two models were within 4 AIC_c units of each other and best explained the effects of environment on the persistence of tone strength (Table 2). Distance, PC1 *(total area open/grassy habitat)*, and PC2 *(total area anthropogenic habitat)* appeared in both models. In the final, averaged model, standard errors for PC2 (*total area anthropogenic habitat*) and the interaction between PC1 (*total area open/grassy habitat*) and distance both overlap with zero, indicating that these terms do not strongly explain tone persistence (Table 3).

As expected, persistence was highest at lower frequencies and shorter distances. There was a positive relationship between PC1 (*total area open/grassy habitat*) and persistence, indicating that the power of tones was better preserved in increasingly open areas with fewer obstacles in the habitat. Correspondingly, there was a slight negative relationship between persistence and PC2 (*total area anthropogenic habitat*), indicating higher attenuation in sites with more buildings and impervious surface.

The relationship between persistence and the interaction term, PC1*PC2 is visualized in Figure 2, where persistence has been regressed against PC1 (*total area open/grassy habitat*) at (a) low and (b) high levels of PC2 (*total area anthropogenic habitat*). Although the slopes of both lines are positive (albeit weakly so in Fig. 2b), the gradient is much sharper in open/grassy habitats that have fewer anthropogenic structures. In these locations, not only is the mean value of persistence much lower (PC1 at low PC2: -1.16; PC1 at high PC2: -

1.32), but there is also a larger range of persistence values (PC1 at low PC2: - 2.85 to 0.57; PC1 at high PC2: - 2.77 to 0.31).

2.3.2 Reverberation and Habitat

Three models were within 4 AIC_c units of each other and best explained the effects of environment on reverberation (Table 4). Both distance and PC1 (*total area open/grassy habitat*) appeared in all three models, while PC2 (*total area anthropogenic habitat*) appeared in two of three models. The standard error of the interaction term between PC1 and PC2 overlapped almost symmetrically with zero (Table 5), indicating that this parameter did not strongly explain the amount of reverberation recorded. It will therefore not be discussed further.

As expected, reverberation increased with increasing distance between the microphone and the sound source. Reverberation decreased in territories with more total area open/grassy habitat (PC1). However, it increased in anthropogenic habitats (PC2), which contained more vertical structures and acoustically harder surfaces.

2.3.3 SNR and Habitat

Two models were within 4 AIC_c units of each other and best explained the effects of habitat on SNR (Table 6). Both models included frequency and both habitat PCs. The standard errors of both PC2 (*total area anthropogenic habitat*) and the interaction between the two habitat types both overlapped with zero. The range of errors for the interaction term was approximately symmetrical around zero, indicating no strong support for an effect of this variable on SNR. However, the range for PC2 (*total area anthropogenic habitat*) was substantially skewed to one side, suggesting that this relationship merits further consideration.

SNR was positively related to frequency, with 7 kHz tones experiencing the most favorable SNR. SNR was also positively related to PC1 (*total area open/grassy habitat*), indicating that these territories experienced the lowest levels of ambient noise. Although PC2 (*total area anthropogenic habitat*) did not have a large effect on SNR, it is worth noting that its negative relationship to SNR is consistent with our predictions about associations between anthropogenic habitat features and noise pollution.

2.3.4 Noise and Habitat

The global model best explained the effects of habitat on ambient noise level (Table 8). All three environmental parameters were related to the amount of ambient noise we measured in nest box territories (Table 9).

As implied by the SNR results (above), lower environmental noise was recorded in territories with higher levels of open/grassy habitat (PC1), while louder noise was recorded in areas with more anthropogenic habitat (PC2). A visualization of ambient noise regressed against PC1 (*total area open/grassy habitat*) at low (Fig. 3a) and high (Fig. 3b) levels of PC2 (*total area anthropogenic habitat)* indicates that the decline in open/grassy areas with more anthropogenic habitat is more rapid than the decline in noise at sites with fewer impervious structures.

2.4 DISCUSSION

We found that both frequency and distance have significant effects on signal transmission. Given what is known about the physics of sound, these results are unsurprising. However, for management and conservation purposes, it is comforting to confirm that these expected relationships hold true in anthropogenically-modified environments, and that manmade materials and habitat configurations do produce complex or unexpected effects on acoustics. We also found that habitat type was an important predictor of all three sound propagation characteristics measured here (signal persistence, reverberation, and signal-to-noise ratio), as well as associating strongly with the absolute level of ambient noise.

Specifically, we found that persistence of tones is negatively affected by both frequency and distance, as we hypothesized. All sound waves are expected to decrease in power as they propagate through the environment, since their energy is increasingly absorbed by air (Berg & Stork 2004). This is particularly true for higher frequencies, whose waves are composed of shorter periods and are therefore more likely to be scattered and absorbed (Wiley & Richards 1978, 1982).

The effects of habitat on persistence also fit with established theory: Tones persisted more in environments that were more open and possessed fewer vertical obstructions (habitat PC1), but attenuated more in areas that possessed more vertical anthropogenic structures. This latter effect may have occurred as a result of buildings acting as barriers to sound or the deflection of sound waves off buildings and away from the microphone.

Perhaps more interestingly, we found a relationship between tone persistence and the interaction term, PC1*PC2. At sites with less anthropogenic habitat, persistence sharply increases as the amount of open/grassy habitat increases. At sites with more anthropogenic habitat, however, the amount of persistence is fairly constant, regardless vegetation structure in the rest of the habitat. This suggests that the presence of impervious surface (both roads and buildings) will always be associated with greater amounts of attenuation, regardless of how much the rest of the habitat is open and “natural.” Furthermore, the absolute levels of persistence are consistently lower across highly anthropogenic sites, indicating that the presence of impervious surface will always be associated with decreases in signal persistence. This may pose significant difficulties to animals attempting to communicate in such habitats.

As with persistence, we made several predictions about reverberation based on our knowledge of the physics of sound. We were slightly surprised that there was no relationship between tone frequency and reverberation. This result suggests that the ratio between wavelength and the size of the obstructing habitat feature (which determines strength of reverberation) was more similar across the three frequencies than we expected.

The associations we found between reverberation and habitat structure were as predicted: Reverberation decreased in areas that were more open and had fewer trees, resulting from the fact that these sites had fewer objects off which the sound waves could reflect. On the other hand, reverberation increased in areas with more anthropogenic habitat. This is likely related to two factors: the presence of more vertical objects (buildings), and the presence of more acoustically “hard” features (impervious surface) that reflect sound waves more intensely (Warren et al. 2006). Future work will be required to differentiate between these two possibilities—a distinction that might have important management implications.

Our final two models, investigating the relationships between habitat and both SNR and noise levels, were closely related: Habitats with higher noise levels should have lower SNR, since the amplitude of our tones (the signal) was kept constant while the ambient noise levels increased. Indeed, this is the relationship we found. Across nest box territories, more open/grassy habitats had lower levels of ambient noise and, thus, higher SNR. Correspondingly, more anthropogenic habitats had higher levels of ambient noise and lower SNR. We also found that SNR improved at higher frequencies, confirming previous observations that the bulk of environmental noise (particularly anthropogenic noise) occurs at lower frequencies, and that higher frequency signals are less susceptible to acoustic masking (Brumm 2004b; Slabbekoorn & Peet 2003). Finally, we discovered that the ambient noise levels were generally highest in more anthropogenic habitats, but surprisingly similar to those recorded in more open/grassy sites.

As we saw in the relationship between persistence and this interaction term, a little seems to go a long way, as far as anthropogenic features are concerned. Even though increasing the total amount of open/grassy area rapidly decreases ambient noise levels in more anthropogenic sites, the presence of buildings and impervious surface seems to ensure that ambient noise levels will consistently be louder in less "natural" areas. Habitat appears to have a nonlinear effect on sound propagation: Small amounts of impervious surface had strong effects in relatively natural habitats, whereas the addition of more impervious surface to previously developed areas did not have large impacts on sound propagation. This suggests that mitigation plans including nature preserves and cluster developments would be beneficial to preserving the integrity of birds' acoustic space.

Another interesting implication of our data is the differential effects that these relationships between habitat and sound propagation may have on a variety of species with different song characteristics and/or territory size preferences. For instance, species singing at higher frequencies are less likely to face transmission problems stemming from low SNR, but may have more difficulties communicating in anthropogenically-altered environments where attenuation is more likely to occur. Similarly, species that maintain larger territories are likely to have evolved signals that are more persistent over longer distances and are less likely to be obscured by their own reverberations (but see Slabbekoorn and Smith 2002). Individuals of these species may therefore have a harder time signaling effectively in more anthropogenic environments, where persistence tends to be lower and reverberation tends to be higher.

Unfortunately, these life history-specific relationships make it hard to generalize and predict how the effects of habitat on sound propagation are likely to impact all the many species living across the anthropogenic disturbance gradient. This is particularly true given the amount of behavioral flexibility that has been observed in the way birds learn both song and song preferences, as well as the variety of spontaneous vocal adjustments they may make in real time in response to current environmental conditions (Bermudez-Cuamatzin et al. 2009; Brumm et al. 2009). However, our models clearly indicate that specific habitat features can be used to predict the acoustic characteristics of particular territories, and this information can, in turn, be combined with life history information in order to make educated predictions about whether/how species may be coping with the acoustic environment. Specifically, our PCA indicates that vertical and horizontal impervious surface structures tend to co-occur in the territories we studied, and that these habitat features are fairly distinct from more "natural" features such as grass and trees. Because we derived these results from data collected across a wide variety of typical suburban habitats—including cemeteries, school campuses, parks, housing developments, roadsides, and golf courses—we feel they are likely to be fairly representative of this ever-increasing type of anthropogenic area.

However, our gradient did not include extremely "rural" and "urban" areas, such as purely agrarian sites, areas with no remaining natural habitat, or areas receiving nonstop noise pollution. Additionally, because our focal sites are located on the Coastal Plain of Virginia, they had very little topographical variation. The presence of hills and mountainsides, particularly those with large amounts of exposed rock, is likely to add an interesting element to a sound propagation analysis, as would large areas of water, denser forests, and acoustically soft features > 3m in height (including ornamental plants such as tall grasses, bamboo, and ferns). Each of these latter habitat features has been underrepresented in previous work on sound propagation and signal design, let alone within an anthropogenic disturbance context. Furthermore, future work should attempt to more directly compare anthropogenic features with analogous "natural" features in order to develop a more fine-grained understanding of how specific habitat elements impact sound propagation. For instance, one interesting question might be whether trees and buildings have similar effects on signal persistence and reverberation, or whether anthropogenic materials differ sufficiently in acoustic hardness to interact significantly differently with sound waves.

A major assumption of the many recent studies on anthropogenic noise and signal design is that more urban habitats are uniformly louder than rural habitats, or in some other way offer "worse" acoustic environments. However, as our results indicate, the average amplitude of ambient noise is only marginally higher in anthropogenic habitats than in "natural" habitats, and, in fact, there is considerable overlap in the ambient noise levels observed in these two types of site. Additionally, all habitats across our anthropogenic disturbance gradient offer their own acoustic challenges: Individuals in more anthropogenic habitats may be more susceptible to lower SNR and reduced persistence of signals, but individuals in more open/grassy sites are likely to experience more reverberation. Taken together, these relationships underline the importance of evaluating sites based on their own intrinsic acoustic or structural characteristics, as opposed to assigning them to categories based on subjective assumptions.

Furthermore, these issues suggest that future research should focus not on whether anthropogenic sites have different acoustic properties than natural sites, but on the ways in which these two types of site differ. In many cases, the range of persistence, reverberation, SNR, and ambient noise levels in anthropogenic areas may encompass those found in natural areas, and acoustically communicating animals may therefore possess enough behavioral flexibility to adjust to the presence of human structures and noise sources. Anthropogenic structural modifications and noise pollution are only likely to promote “communication breakdown” where they create conditions for which individuals are not prepared—for instance, when such disturbances are introduced to species that use innate vocalizations and are therefore less capable of vocal modifications, or when they occur within species (or population) ranges that are traditionally acoustically and/or structurally homogeneous.

On the whole, our findings indicate that future study of anthropogenic acoustics can make exciting contributions to multiple fields. For instance, our work has important conservation/management implications: The observation that small amounts of impervious surface can have a disproportionately large effect on signal efficacy suggests that wildlife managers should be cautious about installing structures such as paved access roads, boardwalks, or observation huts. These results also indicate that acoustically communicating wildlife would benefit from the presence of buffers that would shield their territories from nearby anthropogenic structures. Conversely, the inclusion of buffers around new development projects in otherwise "natural" areas might help mitigate the effects of introducing anthropogenic features to the environment.

The study of anthropogenic acoustics can also make important contributions to our understanding of signal design and communication behaviors. We have shown that SNR is highest at higher frequencies. This suggests that increases in ambient noise levels may place more intense pressure on species with lower-frequency vocalizations. This could lead to a number of frequency-related song adaptations, such as preferential performance of higher-frequency notes (Bermudez-Cuamatzin et al. 2009), omission of lower-frequency portions of song elements, and upward shifts of frequency characteristics (Nemeth & Brumm 2009; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). Alternatively—or additionally—birds may alter behaviors associated with their vocal performances. We found that signaler-to-receiver distance affected both persistence and reverberation of signals. By altering perch characteristics, such as height and location within the territory, birds could improve their signal transmission. It would be particularly interesting to see whether these signal design and delivery adaptations follow divergent routes in open/grassy habitats and anthropogenic habitats. Although such processes have often been theorized after the fact (Kirschel et al. 2009; Slabbekoorn & Smith 2002; Slabbekoorn et al. 2007), they have not been investigated in real time. Anthropogenic environments can therefore be thought of as “natural experiments” that not only can yield important evolutionary insights, but also can facilitate more informed management decisions.

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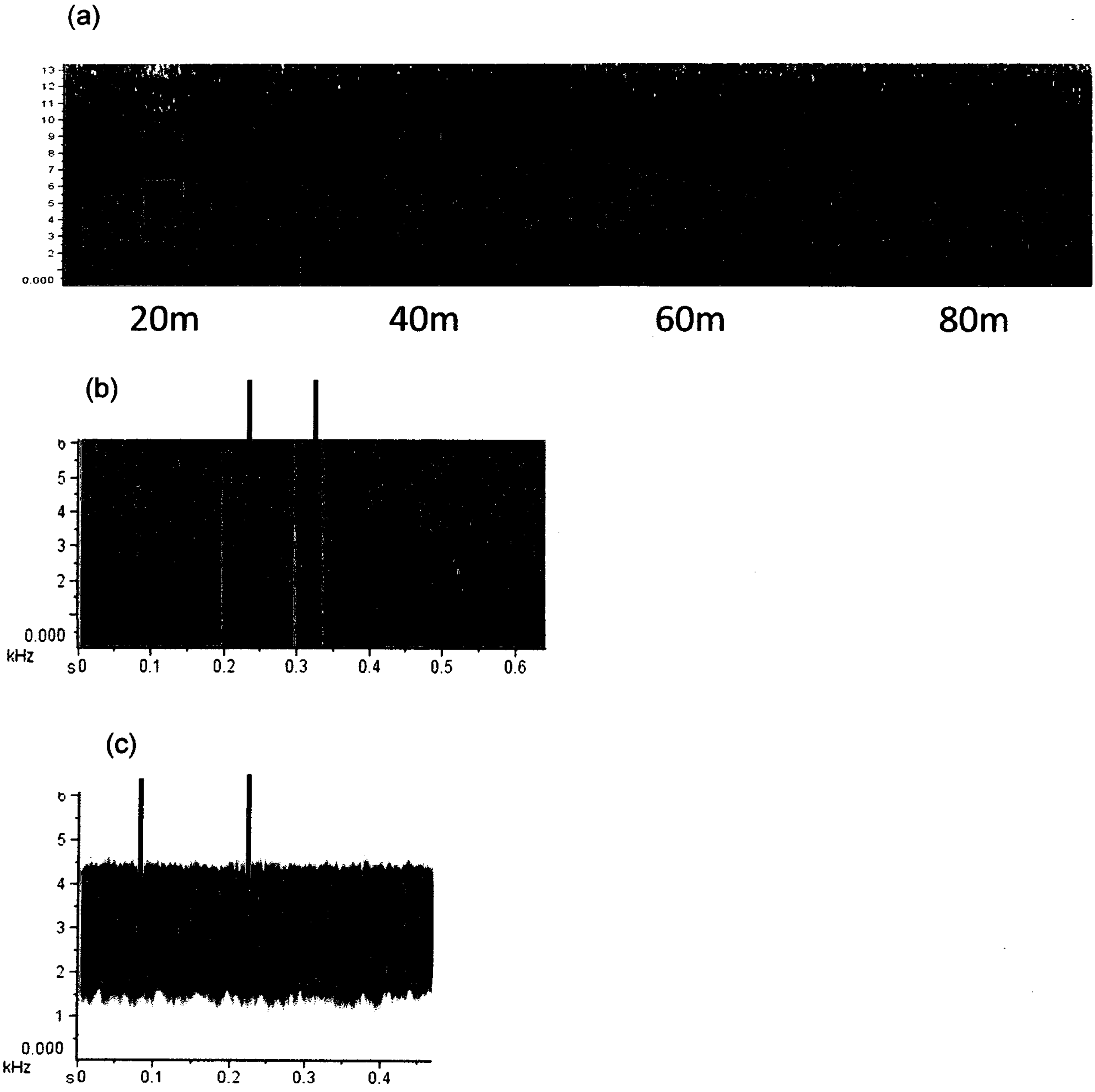

Figure 2.1. Illustrations of attenuation (a), reverberation (b; arrows denote signal (left) and tail (right)), and SNR (c; arrows denote noise (left) and signal (right)).

Variable	PC1 (35.8% of variance)	PC2 (28.3% of variance)
Short impervious surface (< 3m)	0.183	0.777
Short vegetation (grass, shrubs)	0.882	-0.352
Tall impervious surface (> 3m)	0.157	0.733
Trees (forest and ornamental)	-0.974	-0.85
Water	0.080	-0.375

Table 2.1. Loading factors for PCA of habitat features within 90 m, 90° wedges centered on each of the four cardinal directions around each territory's nest box.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Frequency, weather, distance, PC1, PC2, PC1*PC2**	**1166.2**	**0**	**0.773**	**1**
2	**Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1**	**1168.7**	**2.48**	**0.224**	**0.289**
3	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2	1177.32	11.07	0.0031	0.0040
4	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1	1184.22	17.97	9.7E-05	0.0001
5	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance	1191.06	24.81	3.2E-06	4.1E-06
6	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2	1198.51	32.26	7.7E-08	9.9E-08
7	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2	1209.58	43.33	3E-10	3.9E-10
8	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2, frequency*distance* PC2	1222.25	56.00	5.4E-13	6.9E-13
9	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2, frequency*distance* PC2, frequency*distance*PC1	1235.73	69.48	6.3E-16	8.2E-16

10	Frequency, weather, distance, PC1, PC2, PC1*PC2, distance*PC1, distance*PC2, frequency*PC1, frequency*distance, frequency*PC2, distance*PC1*PC2, frequency*distance* PC2, frequency*distance*PC1, frequency*PC1*PC22	1242.79	76.53	1.9E-17	2.4E-17

Table 2.2. Values used in linear regression models to explore effects of habitat (PC1 and PC2) on persistence of pure tones played at three different frequencies (3, 5, 7 kHz) over four different distances (20, 40, 60, 80 m).

Parameter	B	SE	95% Confidence Intervals Lower	 Upper
Weather	2.2 E -05	1.70E-05	4.97E-06	3.90
Frequency	-0.060	0.009	-0.068	-0.051
Distance	-0.017	0.0007	-0.018	-0.016
PC1 (total area open/grassy habitat)	0.081	0.047	0.035	0.128
PC2 (total area anthropogenic habitat)	-0.015	0.017	-0.033	0.002
Distance*PC1	0.0005	0.0009	-0.0005	0.001
PC1*PC2	-0.046	0.019	-0.064	-0.027

Table 2.3. Parameters included in final, averaged model explaining the relationship between tone persistence and environment.

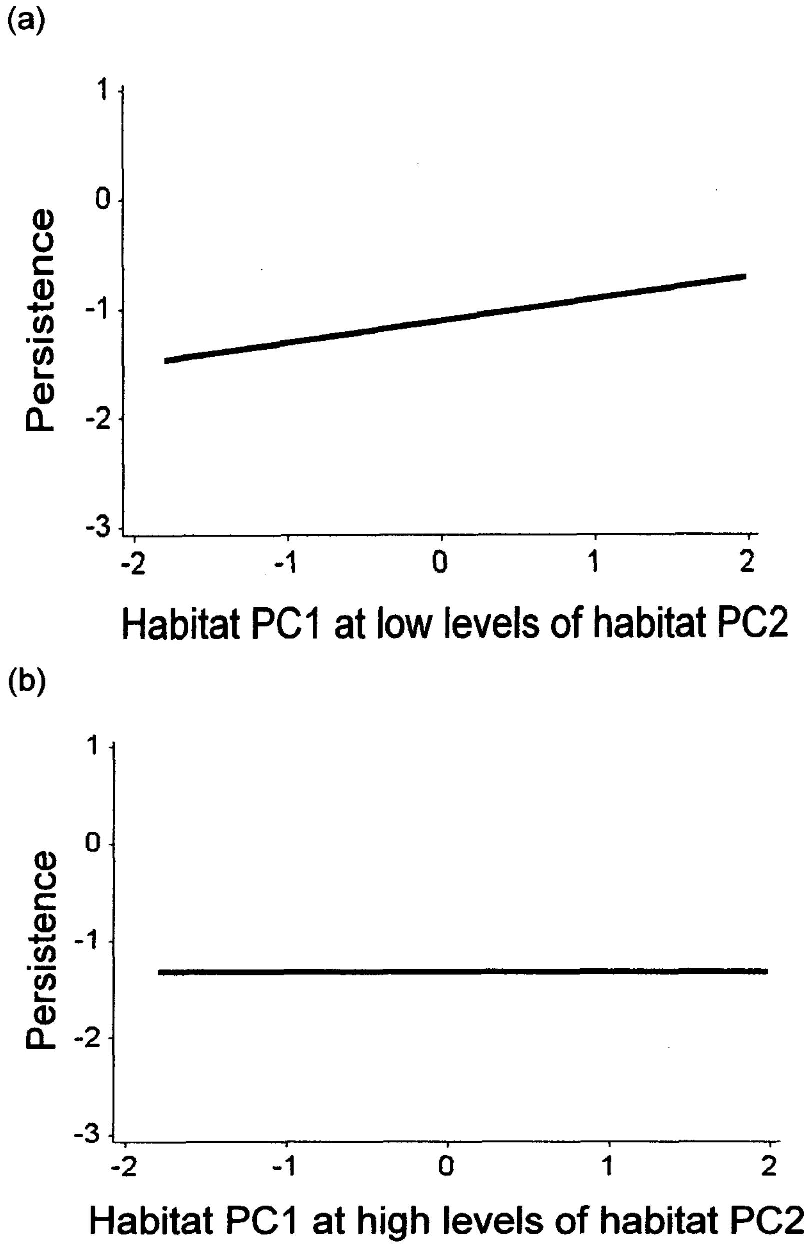

Figure 2.2. Visualization of the different interactions between persistence and habitat PC1 (open, grassy areas) at low (a) and high (b) levels of habitat PC2 (anthropogenic areas). While persistence increases rapidly with PC1 in less anthropogenic sites, there is almost no fluctuation of persistence with PC1 across more anthropogenic sites.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Weather, distance, PC1**	**1993.6**	**0**	**0.4340**	**1**
2	**Weather, distance, PC1, PC2**	**1993.7**	**0.08**	**0.417**	**0.961**
3	**Weather, distance, PC1, PC2, PC1*PC2**	**1995.8**	**2.15**	**0.148**	**0.341**
4	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1	2005.76	12.13	0.0010	0.0023
5	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency	2012.41	18.79	3.6E-05	8.3E-05
6	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1	2017.15	23.53	3.4E-06	7.8E-06
7	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2	2022.84	29.21	2E-07	4.5E-07
8	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2	2034.73	40.99	5.4E-10	1.3E-09
9	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2	2045.73	52.11	2.1E-12	4.8E-12
10	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance	2058.18	64.55	4.2E-15	9.6E-15
11	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance, frequency*distance*PC2	2070.65	77.02	8.2E-18	1.9E-17

12	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance, frequency*distance*PC2, frequency*PC1*PC2	2076.76	83.13	3.9E-19	8.9E-19
13	Weather, distance, PC1, PC2, PC1*PC2, distance*PC1, frequency, frequency*PC1, frequency*PC2, distance*PC2, distance*PC1*PC2, frequency*distance, frequency*distance*PC2, frequency*PC1*PC2, frequency*distance*PC1	2089.70	96.07	6E-22	1.4E-21

Table 2.4. Values used in linear regression models to explore effects of habitat (PC1 and PC2) on reverberation of pure tones played at three different frequencies (3, 5, 7 kHz) over four different distances (20, 40, 60, 80 m).

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
Weather	0.00007	0.004	-0.004	0.004
Distance	0.006	0.004	-0.002	0.010
PC1 (total area open/grassy habitat)	-0.167	0.147	-0.314	-0.021
PC2 (total area anthropogenic habitat)	0.030	0.030	0.0003	0.060
PC1*PC2	0.008	0.068	-0.06	0.076

Table 2.5. Parameters included in final, averaged model explaining the relationship between reverberation and environment.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Frequency, weather, PC1, PC2**	**4057.3**	**0**	**0.793**	**1**
2	**Frequency, weather, PC1, PC2, PC1*PC2**	**4060.3**	**2.97**	**0.180**	**0.227**
3	Frequency, weather, PC1, PC2, frequency*PC1, PC1*PC2	4064.3	7.03	0.024	0.030
4	Frequency, weather, PC1, PC2, frequency*PC1, frequency*PC2, PC1*PC2	4068.7	11.4	0.0026	0.0033
5	Frequency, weather, PC1, PC2, frequency*PC1, frequency*PC2, PC1*PC2, frequency*PC1*PC2	4072.7	15.4	0.0004	0.0005

Table 2.6. Values used in linear regression models to explore effects of habitat (PC1 and PC2) on SNR of pure tones played at three different frequencies (3, 5, 7 kHz) over four different distances (20, 40, 60, 80 m). Distance was not included as a covariate in this model because SNR was calculated using paired signal and noise recordings taken at each distance, and was therefore distance-independent.

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
Weather	-0.0003	0.172	-0.173	-0.172
Frequency	0.528	0.248	0.280	0.775
PC1 (total area open/grassy habitat)	0.578	0.079	0.499	0.657
PC2 (total area anthropogenic habitat)	-0.396	0.426	-0.822	0.031
PC1*PC2	-0.005	0.016	-0.021	0.011

Table 2.7. Parameters included in final, averaged model explaining the relationship between SNR and environment.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Weather, PC1, PC2, PC1*PC2**	**6756.98**	**0**	**0.99347**	**1**
2	Weather, PC1, PC2	6767.27	10.29	0.0058	0.0058
3	Weather, PC1	6771.38	14.40	0.0007	0.0008
4	Weather, PC2	6783.99	27.01	1.4E-06	1.4E-06

Table 2.8. Values used in linear regression models to explore effects of habitat (PC1 and PC2) on ambient noise levels in eastern bluebird breeding territories.

Parameter	B	SE	95% Confidence intervals Lower	 Upper
Weather	0.0005	0.094	-0.093	0.094
PC1 (total area open/grassy habitat)	-1.75	0.381	-1.56	-0.079
PC2 (total area anthropogenic habitat)	1.04	0.338	0.709	1.38
PC1*PC2	-1.17	0.375	-1.55	-0.797

Table 2.9. Parameters included in final (global) model explaining the relationship between environment and ambient noise levels.

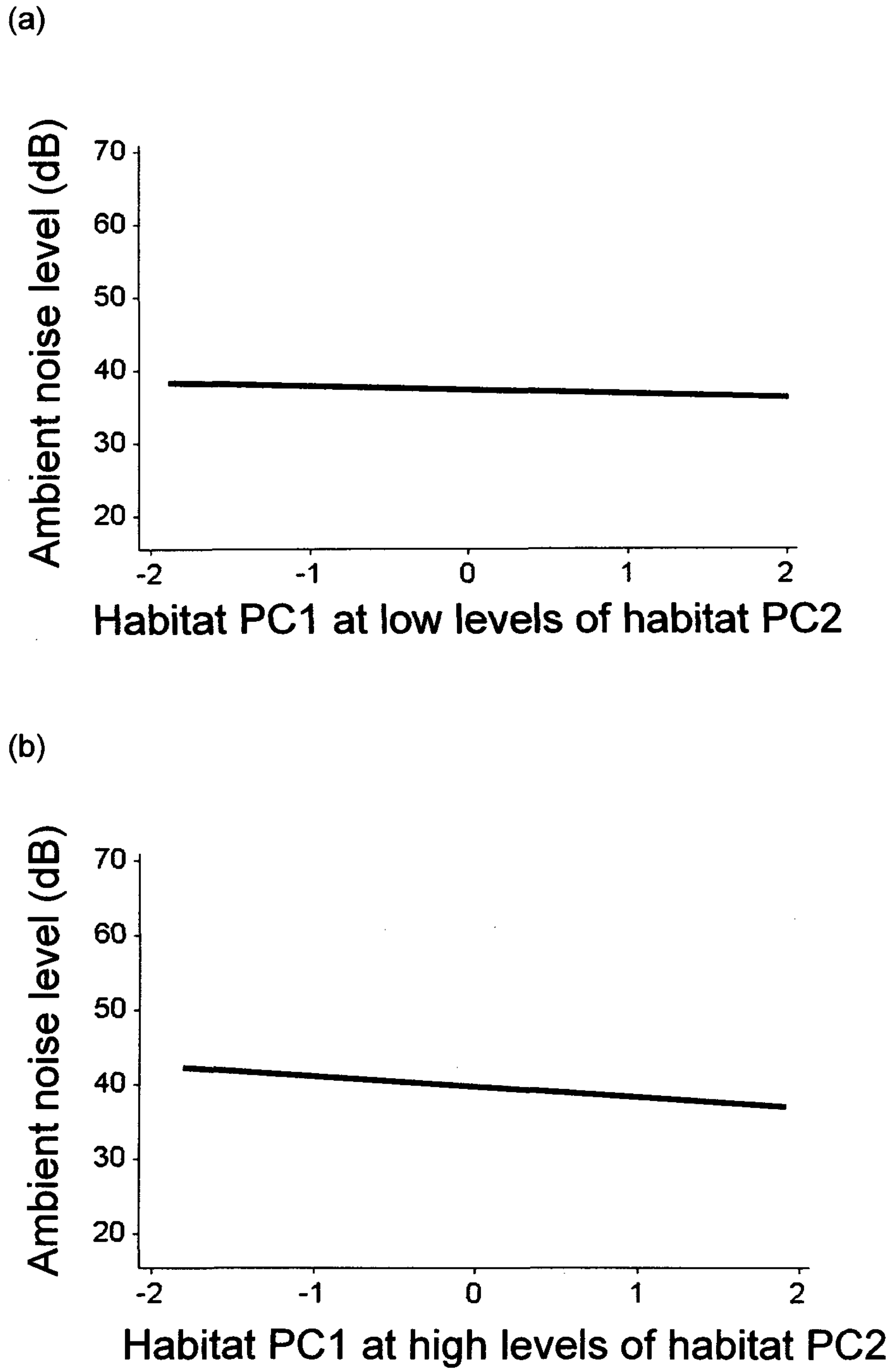

Figure 2.3. Visualization of the different interactions between ambient noise level and habitat PC1 (open, grassy areas) at low (a) and high (b) levels of habitat PC2 (anthropogenic areas). Although the range of ambient noise levels is similar across all sites (18.7 – 67.4 dB at low levels of PC2; 18.4 – 62.0 dB at high levels of PC2), there is a more rapid decrease in noise as PC1 increases at more anthropogenic sites.

CHAPTER 3

CAN YOU HEAR ME NOW? RELATIONSHIPS BETWEEN ANTHROPOGENIC DISTURBANCES, MALE SONG, AND FITNESS IN THE EASTERN BLUEBIRD (*SIALIA SIALIS*)

3.1 INTRODUCTION

Human activities have a variety of negative impacts on wildlife. Both the disturbance events themselves and the changes they bring to nearby habitat have been linked to alterations in species assemblages (Blair 1996; Chace & Walsh 2006; Loss et al. 2009; Opdam & Wiens 2002; Schueck et al. 2001), reductions in resource availability (Gill et al. 2001; Markovchick-Nicholls et al. 2007), fluctuations in predator-prey (Berger 2007) and parasite-host (McKenzie 2007; Urban 2006) relationships, changes to behavioral time budgets (Bouton et al. 2005; Burger & Gochfeld 1991; de la Torre et al. 2000; Delaney et al. 1999; Gutzwiller 1994; Kight 2005; Kight & Swaddle 2007; Knight & Cole 1995a, b; Nisbet 2000; Pease et al. 2005; Stolen 2003; Thomas et al. 2003; Yarmoloy et al. 1988), and decreases in various measures of breeding success (Arroyo & Razin 2006; Blackmer et al. 2004; Ellenberg et al. 2007).

One increasingly popular avenue of research has explored the impact of anthropogenic noise disturbances on the vocalizations of a variety of wildlife species (Barber et al. 2010; Bee & Swanson 2007; Bermudez-Cuamatzin et al. 2009; Brumm 2004b; Fernández-Juricic et al. 2005; Francis et al. 2009; Fuller et al. 2007; Habib et al. 2007; Katti & Warren 2004; Leader et al. 2005; Leonard & Horn 2005, 2008; Miksis-Olds & Tyack 2009; Mockford & Marshall 2009; Nemeth & Brumm 2009; Parris & Scneider 2008; Parris et al. 2009; Patricelli & Blickley

2006; Rabin & Greene 2002; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Slabbekoorn & Ripmeester 2008; Swaddle & Page 2007; Warren et al. 2006; Wood & Yezerinac 2006). This work has quantified the spectral characteristics of noise pollution in both terrestrial (Brumm 2004b) and aquatic (Madsen et al. 2006) environments, as well as pinpointing which activities are responsible for the bulk of anthropogenic ambient noise (Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Warren et al. 2006). One reason anthropogenic noise has attracted so much attention is the concern about its potential to mask vocalizations. Masking occurs when high-amplitude sounds (*e.g.* car traffic) obscure lower-amplitude sounds (*e.g.* bird song) within the same frequency bandwidth (Nemeth & Brumm 2009; Rabin & Greene 2002; Rabin et al. 2003; Rheindt 2003). Although anthropogenic noise has been shown to mask the vocalizations of species in several taxa, the widest variety of behavioral responses has been documented in birds. European robins (*Erithacus rubecula*), for instance, increased the amount of time they spent singing at night (Fuller et al. 2007), when anthropogenic noise was least potent. Great tits (*Parus major*)(Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003), European blackbirds (*Turdus merula*), (Nemeth & Brumm 2009), house finches (*Carpodacus mexicanus*)(Bermudez-Cuamatzin et al. 2009; Fernández-Juricic et al. 2005), and song sparrows (*Melospiza melodia*) (Wood & Yezerinac 2006) have all been shown to increase the minimum frequency of their songs above the bandwidth of ambient noise. Common nightingales (*Luscinia megarhynchos*), on the other hand, continue singing in the same frequency bandwidth, but increase their amplitude in order to improve their signal-to-noise ratio (SNR)(Brumm 2004b).

Birds may also adjust the composition of their songs in response to ambient noise. Although it has been suggested that more repetitions of syllables or song types might increase the likelihood of transmission (Brown & Handford 2000; Brumm & Slater 2006a; Morton 1975), this has not yet been observed in the wild. Instead, both song sparrows and house finches decreased number of notes per song in noisy environments, while great tits changed the length, pacing, and number of syllables in their songs (Fernández-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). Because these modifications may give the birds a chance to draw breath and/or rest muscles between performances, they have been interpreted by some as evidence of an energetic cost to singing in noisy environments (Fernández-Juricic et al. 2005; Ward et al. 2003).

Noise pollution is not the only way in which humans may interfere with avian communication. The alteration of habitat structure and the introduction of new materials with different acoustic properties can affect signal propagation (Forrest 1994; Katti & Warren 2004; Leader et al. 2008; Leader et al. 2005; Morton 1975; Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Warren et al. 2006; Wiley & Richards 1978). Specifically, anthropogenic habitat modifications may add new sources of reverberation (*e.g.* buildings), remove objects formerly responsible for attenuation (*e.g.* trees), and reduce the number of perches available for optimal song-delivery height (Dabelsteen et al. 1993;

Nemeth et al. 2001). Even if the total number, placement, and proximity of habitat structures remains approximately the same, humans may replace natural materials such as wood and foliage with metal, glass, and cement—all of which may alter the amount of reverberation and attenuation of ambient noises (Forrest 1994; Warren et al. 2006).

The importance of ecology in shaping avian vocalizations has often been demonstrated (Boncoraglio & Saino 2007; Derryberry 2007, 2009; Kirschel et al. 2009; Klump 1996; Kroodmsa et al. 1999; Marten & Marler 1977; Marten et al. 1977; Wiley & Richards 1978), and the acoustic adaptation hypothesis predicts consistent temporal and spectral differences between the songs of birds in closed and open habitats (Boncoraglio & Saino 2007; Leader et al. 2005; Morton 1975). Thus, one would expect that the recent ecological modifications associated with urbanization and increased human expansion could have serious impacts on signal efficacy. Although several hypotheses have been advanced regarding the potential relationships between anthropogenic habitat features and bird song (Katti & Warren 2004; Warren et al. 2006), they have not yet received much attention. The three existing studies have failed to link the presence of particular habitat structures or materials with variations in song (Fernández-Juricic et al. 2005; Leader et al. 2005; Slabbekoorn et al. 2007). Furthermore, this research did not take into consideration the fact that habitat features and ambient noise levels may be related (Bayne et al. 2008; Habib et al. 2007; Nemeth & Brumm 2009), which makes it difficult to assess the exact cause of avian song modifications.

Because song is a vital component of avian life histories (Marler & Slabbekoorn 2004), changes to a bird's acoustic space could have substantial life history consequences. If birds fail to modify their songs in response to anthropogenic disturbances, their signals may be less effective and they therefore may have difficulty defending territories or procuring mates. Conversely, vocal adjustments may facilitate signal transmission but change the meaning/interpretation of the signal, resulting in a breakdown of communication. Although studies have associated human noise with decreases in avian abundance and diversity (Bautista et al. 2004; Bayne et al. 2008; Rheindt 2003), it is currently unknown whether these reductions are related to avoidance of, or reduced breeding success in, noisy territories (or both). Indeed, no studies have directly measured the potential fitness costs associated with living in noisy environments (but see Bayne et al. 2008; Habib et al. 2007).

Here, we present the results of a study investigating whether, and how, song parameters of a breeding songbird varied with levels of both auditory and physical disturbance by humans. We examined male eastern bluebirds (*Sialia sialis*) breeding in nest boxes across an anthropogenic disturbance gradient. Each male defended a roughly circular territory extending approximately 50 m from his nest box. We measured the ambient noise conditions within each of those territories, both in terms of the average noise conditions, and the amount of variation in ambient noise conditions. Correspondingly, we collected song recordings from each resident male in order to measure both among-male and within-male variation in song parameters in association with ambient noise. We also measured habitat structure and composition (using Geographic Information Systems, GIS) so that we could relate physical features to both ambient noise levels and male song parameters. Finally, we examined several fitness metrics in order to determine whether they could be explained by environmental noise, habitat structure, and male song (a potential proxy for male quality (Buchanan et al. 2003; Gil et al. 2006; MacDonald et al. 2006; Nowicki et al. 2000; Nowicki et al. 1998; Searcy et al. 2004; Seddon et al. 2004; Spencer et al. 2003, 2004; Stewart & MacDougall-Shackleton 2008)). To our knowledge, this is the first study in which song parameters of a single species have been explored in response to each of the two principal types of anthropogenic acoustic disturbance (*i.e.,* direct noise and habitat structure), as well as the first to examine the fitness correlates of these acoustic factors.

3.2 METHODS

3.2.1 Study species and site description

We studied breeding eastern bluebirds (*Sialia sialis*) occupying nest boxes across a disturbance gradient in Williamsburg, Virginia, USA. The 60 territories examined here are part of a 400-box network that has been studied since 2003 (Kight 2005; Kight & Swaddle 2007; Le Clerc et al. 2005). Previous work indicates that territories do not vary significantly in feeding resources, and that there is little systematic variation in the relative size and body condition of breeding adults (Burdge 2009; Hubbard 2008; Le Clerc et al. 2005; JP Swaddle, unpub. data). However, we have documented differences in the proximity, amount, and type of anthropogenic disturbance at each site (Kight 2005; Kight & Swaddle 2007), indicating that the boxes sampled here reflect a variety of anthropogenic ambient noise conditions.

Eastern bluebirds are particularly interesting to study in an ambient noise context because they are known to nest in close proximity to humans (Gowaty & Plissner 1998) and to be fairly tolerant of a variety of human disturbances (Kight 2005; Kight & Swaddle 2007). Perhaps more importantly, their vocalizations occur almost exclusively within the 2-4 kHz range, while anthropogenic noise occurs most prominently in the 1-3 kHz range (Gowaty & Plissner 1998; Huntsman & Ritchison 2002; Slabbekoorn & Peet 2003). In addition to this bandwidth overlap, bluebirds have low-volume songs (Huntsman & Ritchison 2002), which makes them particularly susceptible to masking by noise pollution.

3.2.2 Male song and ambient noise recordings

Recordings of singing male eastern bluebirds were collected during the breeding seasons of 2007 and 2008. Because 2007 males were given unique leg band combinations, we were able to identify any repeat singers in 2008 and avoid possible pseudoreplication. In our area, male eastern bluebirds sing sporadically throughout the day, beginning as early as 0600 and singing as late as 1800. Preliminary observations indicated no obvious quantitative differences in songs performed at different times of day; thus, samples for each male were collected at random throughout this vocally active period. All recordings were collected by CRK during the nest-building phase of the breeding season; once eggs were laid, all bluebird males stopped singing until their chicks were fledged (personal observation).

Rather than record spontaneous song performances for each male, we used playback to stimulate vocal performances. This has two advantages. First, although male bluebirds use a song display while courting females, our population appears to do so early in the breeding season and perhaps even during the winter, prior to claiming nest boxes and settling down on particular territories (personal observation). During this time it is harder to identify individuals because they are more skittish and often fly away before leg bands can be observed. Additionally, many males sing outside of their eventual territories. By recording them later in the season, we achieve a measure of the ambient noise conditions in the location where they are a) singing to defend territories from rival males, b) courting females for second and third nesting attempts, and c) singing to communicate with juveniles. The second advantage to using playback is creating standardization across sites. Spontaneous song may have been provoked by any number of events, and may be directed at any number of receivers; each of these variables is known to influence song characteristics (Marler & Slabbekoorn 2004). By using a standardized playback, we increased the likelihood that all males will be using a similar type of song and/or song delivery.

We created a single stimulus song for playback, constructed of song samples obtained from the Borror Acoustic Laboratory. Each sample was originally recorded from a single bird from another state (Ohio), several decades prior. Thus, the stimulus should have been equally unfamiliar to all males in our population. We broadcast the song using an Apple iPod connected to a set of Sony SRS T70 personal travel speakers. The playback was approximately 4 minutes long, but was paused at whatever point the focal male began singing. If the male stopped singing before the recording quota was met (see below), CRK resumed a broadcast of the stimulus. However, if the male refused to sing after two full repeats of the playback, the recording attempt was abandoned for that day.

The recording procedure was as follows: Upon arrival at the territory, CRK proceeded directly to the nest box and began broadcasting the playback recording. Once the focal male began singing, the playback was paused and CRK began recording the territorial male using a Sennheiser ME65 directional microphone with windscreen, and a Marantz PMD660 solid state recorder. Recordings continued for as long as the male would sing, with one minute being a minimum recording length. Although qualitative variables, such as syllable and song type (not examined in this paper) were seen to change over time, quantitative variables such as those examined here remained fairly constant (Kight, unpub. data). Thus, we feel comfortable that even the shortest recordings are representative of each male's typical singing effort.

Many males changed perches as they sang, typically making a gradual circuit around the nest box. As the males moved, CRK adjusted the direction of the microphone and recorded the new height and distance of each perch. These values were used to assess the actual distance to each male so that all amplitude values (see below) reflect the calculated loudness 1 m from the singing bird.

For each male, we selected two songs for further analysis. These were the vocal performances occurring when environmental noise was lowest and highest (Figure 1). Recordings were visualized and analyzed using RavenPro 1.3 acoustic software (Cornell Laboratory of Ornithology, Ithaca, NY). Although the majority of males sang within the typical bluebird range, a few males were slightly higher or lower. Thus, while most songs were bandpass filtered between 2 and 4 kHz prior to analysis, some required a lower (900 Hz) or higher (6000 Hz) cutoff. Regardless of this numerical difference, there is still consistency, in that each male's song is examined only with respect to the environmental noise conditions that are likely to affect it. Furthermore, in all cases, the focal environmental noise characteristics (see below) remained the same regardless of the bandwidth values—in other words, noise characteristics were not strongly affected by sounds less than 1 kHz or more than 4 kHz. For each song, we measured the following characteristics: overall song length, internote interval, total number of song elements, internote distance, minimum frequency, maximum frequency, peak frequency (frequency with the greatest power, hereafter discussed as "emphasis"), frequency range, and average amplitude (converted from RMS amplitude to dB in order to be more easily interpretable). These parameters were chosen because they had previously been identified as avian song traits likely to be adjusted in response to ambient noise (Bermudez-

Cuamatzin et al. 2009; Fernández-Juricic et al. 2005; Slabbekoorn & Peet 2003; Slabbekoorn et al. 2007; Wood & Yezerinac 2006).

We used PCA to reduce the variables to a more manageable number and to account for the natural correlations among our song metrics. The analysis returned 4 PC's with $\lambda > 1$, explaining a total of 78.2% of the variance (Table 1). PC1 (32.3% of variance) loaded positively for song length and number of song elements, negatively for minimum frequency but positively for both maximum frequency and frequency range. This PC describes songs that are longer because they include more elements (as opposed to longer internote intervals) and have expanded frequency ranges due to shifts at either end of the frequency spectrum. Hereafter, we will refer to this PC as *longer songs/expanded frequency range.* The second PC (18.2% of variance) loaded negatively for song length and number of song elements, but did not load strongly for any other song parameters. We have named this PC *shorter songs*. PC3 (15.2% of variance) loaded positively for internote distance and negatively for peak frequency. This indicates songs with a *slower pace/lower emphasis.* Finally, the fourth PC (12.5% of variance) loaded negatively for amplitude, and slightly negatively for peak frequency. Hereafter, we will call this PC *quieter/lower emphasis.*

Male song recordings also provided data used to evaluate acoustic characteristics of the ambient noise conditions within each territory during the vocal performance. We measured amplitude (dB, converted from RMS amplitude) and peak frequency of environmental noise in 0.05 s samples directly before each song. The amplitude values were also used to separate signal from noise when evaluating male song amplitude. As with male song characteristics, we used PCA to condense variables. The analysis yielded a single principal component (PC) explaining 51.2% of the variance (Table 2). This PC loaded negatively for dB of noise and positively for peak frequency, indicating that quieter ambient noise tended to have a higher frequency emphasis, while louder ambient noises tended to have a lower frequency emphasis. This is the same relationship we have previously found across our bluebird territories (Chapter 2). Henceforth, we will refer to this PC as *Decreased Noise PC.*

We also compared power spectra for both male song and environmental noise in order to calculate signal-to-noise ratio (SNR). We extracted spectral data for environmental noise from a "spectrogram slice" occurring halfway through the 0.05 s ambient noise clip, and we extracted spectral data for male song by examining a spectrogram slice positioned halfway through the second note of the focal song. The latter criterion was chosen because some males introduce their songs with an uncharacteristically loud call note, and some songs were only two notes long. Thus, focusing on the second note allowed us to standardize our protocol across all males. Prior to evaluating spectral curves of male songs, we isolated amplitude values of the signal from the overall signal+noise spectra using the equation of Brumm et al. (2009). We then measured the total area under each curve and calculated SNR by subtracting the total area of the noise curve from the total area of the signal curve (Figure 3.2).

3.2.3 Habitat evaluation

We quantified the habitat of breeding male bluebirds using ArcGIS v. 9.3.1 (ESRI, Redlands, CA, USA). Each active territory was estimated to encompass a 50 m radius centered on the nest box. This has previously been estimated as the area that breeding bluebirds will defend (Gowaty & Plissner 1998). We classified habitat as belonging to one of four categories: short impervious surface, short vegetation, tall impervious surface, or trees. We measured the total area of each of these categories for each territory, and then condensed our dataset using PCA. The analysis produced two PCs explaining a total of 83.4% of the variance (Table 3.3). PC1 (48.2% of variance) loaded negatively for short vegetation but positively for the other three variables. This is consistent with more anthropogenic habitats, which incorporate impervious surface in the form of sidewalks, roads, and buildings, and which include many ornamental trees. We will therefore refer to this PC as *anthropogenic habitat*. The second PC (35.2% of variance) loaded negatively for short impervious surface and tall impervious surface, but positively for trees. This is consistent with much more unmanaged, forested habitats, and we will henceforth call this PC *natural habitat*.

3.2.4 Breeding and demographic data

The methods we used for monitoring nest boxes and collecting breeding data have previously been described elsewhere (Kight 2005; Kight & Swaddle 2007; Le Clerc et al. 2005). Briefly, we monitored nest boxes throughout the breeding seasons of 2007 and 2008, from March through August. Boxes were visited every 2-3 days during egg laying so that we could accurately gauge clutch initiation date (CID). Once chicks hatched, boxes were visited every 3-4 days so that chicks could be weighed, measured, and banded with both a numbered aluminum United States Fish and Wildlife Service band and a unique combination of three plastic color bands.

Three fitness variables were calculated at each nest box: a brood growth index (residuals of wing length regressed against age, averaged within broods) and a brood condition index (residuals of body mass regressed against wing length, averaged within broods), as well as overall productivity (total number of chicks successfully fledged from each box). We used principal components analysis (PCA) to condense this dataset. The analysis produced two PCs explaining 77.2% of the variance (Table 3.4). The first PC (43.4% of variance) loaded negatively for brood condition but positively for brood growth and will henceforth be called *faster growth/poorer condition*. The second PC (33.8 % of variance) loaded somewhat positively for brood growth, but negatively for productivity. We have called this PC *fewer chicks/faster growth*.

Because male song characteristics are often influenced by male body size (Brumm 2004b; Marler & Slabbekoorn 2004), we also attempted to capture and measure as many males as possible in order to control for size (using wing length, mm) in all song analyses. To this end, we employed trap doors (placed in nest boxes during the brood care phase of the breeding season) and mist nets. Despite our efforts, 21 males evaded capture. Rather than exclude them from our analyses, we estimated their sizes using regressions of body size against song characteristics measured from the 39 other males who were both recorded and measured. We generated multiple size estimates by regressing body size against each frequency and amplitude parameter, then using the resulting regression equation to extrapolate independent measures of each unmeasured male's size. These individual extrapolations were then averaged in order to yield one final body size estimate for each unmeasured male.

3.2.5 Statistical Analyses

We utilized an information theoretic model selection approach, employing Aikaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham & Anderson 2002), to answer the following questions:

- *Do ambient noise levels predict male song parameters?* To investigate the relationships between male song and environmental noise, we calculated values for all males/territories by averaging across the high and low recordings. For these and all following analyses, we created generalized linear mixed models (GLMM) in SPSS v. 15 (LEAD Technologies Inc., Chicago, IL, USA). We predicted that in louder sites, males would sing louder songs with a higher frequency emphasis (including higher minimum, peak, and maximum frequencies). We suspected that males might compensate for potential energetic demands of these song adjustments (Fernández-Juricic et al. 2005) by increasing internote intervals, decreasing the number of song elements, and decreasing overall song length.

- *Do changes in male song parameters correspond to changes in ambient noise?* We measured change by subtracting values of "high" recordings from those of "low" recordings of both male song and environmental noise. Thus, negative values represent instances where acoustic parameters were higher in "low" settings than "high" settings. During "low noise" conditions, we expected that most males would have song characteristics like those of birds in overall quieter sites (above). However, we expected these same males to make "real time" adjustments to ambient noise conditions, such that during "high noise," their song characteristics would resemble those of songs sung in overall louder sites (above).
- *Do habitat features predict ambient noise characteristics?* For a subset of 25 of our 60 sites, we were able to examine relationships between ambient noise and habitat structure. Because the GLMMs for this analysis, as well as the following analyses, involved multiple covariates, we used model averaging (Mitchell 2008) to incorporate weighted parameter estimates from all models with Δ-AICc < 4. We predicted that noise would be louder in areas with more impervious surface.
- *Do habitat features predict male song parameters?* For a subset of 22 of our 60 sites, we examined relationships between habitat structure and male song parameters. We expected that songs in sites with more vertical features and/or acoustically hard surfaces would be tailored to avoid reverberation from these structures—for instance, that internote intervals would be longer, and that frequency characteristics would be higher

pitched. Conversely, we predicted that songs from more open sites and areas with softer acoustic surfaces would have more notes and higher pitched frequency characteristics.

- *Do male song parameters predict breeding success?* For a subset of 15 of our 60 sites, we explored the relationship between male song parameters and fitness. We predicted that males would seem more appealing to females, and thus have higher breeding success, if they had higher SNR and sang lower-frequency, higher-amplitude, more complex (*e.g.* greater frequency range, more elements, greater length) songs.

All analyses included the (random) variable "year" in order to control for potential annual variations in male song, environmental noise, or breeding success. Analyses with male song parameters included the variable "male size" to control for potential morphological impacts on song. Analyses investigating relationships with fitness parameters included clutch initiation date (CID) in order to control for seasonal variation in breeding success, which we have previously documented in our population (Duerr et al., manuscript in preparation).

Prior to inclusion in statistical analyses, variable distributions were checked for normality and transformed, where appropriate. Data are represented as means ± standard error.

3.3 RESULTS

We collected song recordings from 60 eastern bluebird males during the breeding seasons of 2007 (28 males) and 2008 (32 males). On average, we found that song parameters of our focal birds were similar to those reportedly previously in the only other study of eastern bluebird song (Huntsman & Ritchison 2002). Songs lasted for approximately 0.710 ± 0.178 s (range = 0.280 to 1.178 s) and comprised an average of 3.37 ± 0.932 elements (range = 2 to 6) that were 0.062 ± 0.043 s apart (range = 0 to 0.426 s). The average minimum frequency for songs was 1574.1 ± 213.5 (range = 996.6 to 2055.6), while the average maximum frequency was 4045.6 ± 598.4 (range = 3052.1 to 5889.1). Male bluebird songs contained frequency modulations averaging changes of 2471.5 ± 694.3 Hz (range = 1322 to 4360.2 Hz). The peak frequency of their songs, 2488.6 ± 317.1 (range = 1378.1 to 3445.3), fell very near the midpoint of their frequency range. The average power of a male bluebird song, extrapolated to 1 m from the singing bird, was 51.99 ± 21.74 dB (range = 40.33 to 87.93 dB). Male spectral curves were, on average, larger than environmental noise curves (574.1 ± 315.5), but there was considerable variation in whether the power of male songs exceeded that of noise, and, if so, by how much (range = -387.05 to 1409.63).

3.3.1 Do ambient noise levels predict male song parameters?

Higher levels of *Decreased Noise PC* tended to be associated with a decrease in song PC1 (*longer songs/expanded frequency range*) (B = -0.199, SE = 0.134); in other words, birds in louder environments tended to sing longer songs that had larger frequency ranges. Models for PC2 (*shorter songs*) and PC3 (*slower pace/lower emphasis*) did not find any strong relationships between male song and environmental noise (PC2: B = 0.0079, SE = 0.129; PC3: B = -0.042, SE = 0.133). However, song PC4 (*quieter/lower emphasis*) was positively related to environmental noise, indicating that males in noisier environments sang, on average, louder songs with higher peak frequencies (B = 0.260, SE = 0.125). This apparent match between amplitude of song and environmental noise was further confirmed by the absence of a relationship between environmental noise and SNR (B = -28.9, SE = 42.1).

3.3.2 Do changes in male song parameters correspond to changes in ambient noise?

Changes in environmental noise conditions were not strongly related to changes in any of the first three male song PCs (PC1: B = 0.170, SE = 0.143; PC2: B = -0.045, SE = 0.147; PC3: B = 0.034, SE = 0.155). However, there was a strong tendency towards a positive relationship between song PC4 (*quieter/lower emphasis*) and *Decreased Noise PC* increased (B = 0.253, SE = 0.140). In other words, when ambient noise levels became louder and had a lower frequency emphasis, male songs also became louder, and had a higher frequency emphasis. Correspondingly, changes in SNR were strongly negatively related to changes in environmental noise (B = -149.9, SE = 49.8): As environmental noise increased in amplitude and decreased in frequency emphasis, bluebirds' SNR improved.

3.3.3 Do habitat features predict ambient noise characteristics?

In model sets for both average *Decreased Noise PC* and variation in *Decreased Noise PC* at each site, all models fell within 4 AIC_c units of the best model and, accordingly, were included in the final, averaged model (Table 3.5). Habitat PC1 (*anthropogenic habitat*) and PC2 (*natural habitat*) both appeared in three of the top four models in each dataset. However, the SE for all variables in both averaged models were fairly symmetrical around zero, suggesting that habitat structure does not have a strong influence on either the average amount of noise a territory receives, or the amount of variation in ambient noise conditions within a territory (Table 3.6).

3.3.4 Do habitat features predict male song parameters?

In the model sets for each of the four male song PCs, all models were within 4 AIC_c units of the best model and were therefore included in the final, averaged model (Table 3.7). Habitat PC1 (*anthropogenic habitat*) and PC2 (*natural habitat*) both occurred in three of the four models for each of the male song PCs. In most cases, the SE for all terms overlapped with zero, indicating little support for a strong relationship between habitat features and male song parameters (Table 3.8).

However, the one notable exception was the emphatic negative relationship between habitat PC1 (*anthropogenic habitat*) and SNR (Table 3.8). This indicates that males singing in more anthropogenic areas have poorer SNR. In order to further explore this trend, we created another model where *Decreased Noise PC* was included as a control and found that the relationship remained strong (B = -121.8, SE = 57.59).

There were three interesting trends that may also be worth further attention. Habitat PC1 was negatively related to song PC1 (*longer songs/expanded frequency range*) and positively related to both song PC3 (*slower pace/lower emphasis*) and song PC4 (*quieter/lower emphasis*) (Table 3.8). However, once *Decreased Noise PC* was entered as an additional covariate in models for each of these dependent variables, the trends disappeared (PC1: B = -0.053, SE = 0.162; PC3: B = 0.164, SE = 0.119; PC4: B = 0.122, SE = 0.130). Although this implies that the relationships were not driven strictly by an influence of habitat features *per se*, it may be worth investigating them in the future with a larger sample size.

3.3.5 Do acoustic parameters predict breeding success?

There were 21 models within 4 AIC_c units of the minimal model explaining variations in breeding PC1 *faster growth/poorer condition* (Table 3.9). The most common terms appearing in the models were male song PCs. Environmental noise appeared in approximately three quarters of the models, while the habitat PCs appeared in approximately half. The SE of all terms overlapped with zero

(Table 3.10); however, there are two interesting trends worth noting. Both song PC1 *longer songs/expanded frequency range* (B = -0.532, SE = 0.327) and song PC2 *quieter/lower emphasis* (B = -0.186, SE = 0.256) were negatively related to breeding PC1 *faster growth/poorer condition*. Biologically, this means that broods in the best condition have fathers who sing longer songs with more frequency modulation, as well as quieter songs with a lower peak frequency. On the other hand, broods with the highest growth rate have fathers who sing shorter songs with less frequency modulation, and louder songs with a higher peak frequency.

There were 28 models within 4 AIC_c units of the minimal model explaining variations in breeding PC2 *fewer chicks/faster growth* (Table 3.11). The most common terms appearing in the models were male song PCs, particularly PCs 2-4. As with the models for breeding PC1, environmental noise appeared in approximately three quarters of the models, while the habitat PCs appeared in approximately half. Again, the SE of all terms overlapped fairly symmetrically with zero (Table 3.12), indicating that male song was not a strong predictor of breeding PC.

3.4 DISCUSSION

Here, we present evidence that male eastern bluebirds are able to vocally compensate for the presence of anthropogenic noise in their acoustic space, and appear to do so without suffering any decreases in breeding success. For this species, at least, individuals appear sufficiently behaviorally plastic to cope with anthropogenic factors, which helps explain why these birds readily nest along a disturbance gradient.

Recent studies on noise and communication have shown that several other species employ some of the same vocal modifications reported here. Amplitude adjustment in response to environmental conditions has previously been documented for both bird song (Brumm 2004b; Brumm & Slater 2006b) and bird calls (Brumm et al. 2009; Pytte et al. 2003). This is arguably the easiest way to maintain signal-to-noise ratios in the face of fluctuating environmental conditions. Because this vocal modification, also known as the Lombard effect, appears to be fairly common in the animal kingdom (Bee 2008; Bee & Micheyl 2008; Bermudez-Cuamatzin et al. 2009; Brumm 2004a; Brumm & Todt 2002), we were unsurprised to observe it in our focal birds. Not only did we demonstrate that males in noisier territories sing, on average, louder songs, but we also found that changes in the amplitude of environmental noise corresponded to changes in male song amplitude. This implies that male bluebirds are capable of making vocal adjustments to ambient noise conditions in real time, rather than expending energy to maintain an unnecessarily high-amplitude song at all times.

We also show that songs in noisy environments have a higher peak frequency and an overall expanded frequency range, compared to those in quieter areas. This was another anticipated result, since frequency shifts appear to be a common mechanism for escaping masking by ambient noises (Bermudez-Cuamatzin et al. 2009; Fernández-Juricic et al. 2005; Leonard & Horn 2005, 2008; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet

2003; Wood & Yezerinac 2006). However, it has been debated whether this modification arises simply as a side effect of the Lombard effect (Bermudez-Cuamatzin et al. 2009). Because male song PC4 *quieter/lower emphasis* included both these amplitude and frequency characteristics, it is not possible for us to determine whether they are truly separate responses or co-occur due to the physiology of song production. Regardless, male bluebirds certainly would reduce acoustic masking by raising their peak frequencies out of the bandwidth dominated by ambient noise, and by shifting their entire vocal performance to a higher frequency bandwidth.

Previous studies debate the energetic costs of song and song modifications (Fernández-Juricic et al. 2005; Gil & Gahr 2002; Oberweger & Goller 2001; Parker et al. 2006; Patricelli & Blickley 2006; Ward et al. 2003). Songs at higher amplitudes and frequencies may consume more energy, given that they require more muscle control and respiratory stamina (Cardoso et al. 2006; Fernández-Juricic et al. 2005; Hoese et al. 2000; Oberweger & Goller 2001; Ward et al. 2003). If this is the case, it is surprising that we report males singing longer songs (with more elements) in the same noisy territories where they are also singing louder, higher-frequency songs. This result is contrary to one reported for male house finches (Fernández-Juricic et al. 2005), but consistent with one seen in nestling tree swallows (*Tachycineta bicolor*) (Leonard & Horn 2005). Clearly, more work is needed to determine how much energetic and physiological pressure is imposed by noisy conditions. Our results suggest that certain song parameters may not be as costly as once theorized (at least for male eastern bluebirds), or that it is ultimately more costly for birds to have their vocalizations obscured than to sing complicated, loud, and/or high frequency songs.

Unlike most previous anthropogenic noise studies (Fernández-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006), we measured not only among-male, but also within-male differences in responses to changing environmental noise levels (but see Bermudez-Cuamatzin et al. 2009). We found that the male eastern bluebirds were able not only to sustain, but even to improve their SNR in response to rising ambient noise levels, by increasing the amplitude and peak frequency of their own songs. This was the only song characteristic that strongly related to ambient noise regardless of whether we looked at averaged values or within-male variation in values (across the "low" and "high" recordings). Song length and total frequency range, on the other hand, were higher in territories with louder average ambient noise levels, but were not shifted "on the fly" when individual males experienced temporary increases in background noise levels. This suggests that, while amplitude and peak frequency are adjusted in real time in response to fluctuating ambient noise conditions, song length and total frequency range are *consistently* greater in noisier sites. Unfortunately, our data do not enable us to determine the mechanism behind this trend, which could result from differential song-learning, post-dispersal song modification, or preferential use of noisy sites by males who happen to sing longer, more frequency-modulated songs.

One common criticism of anthropogenic noise research is that most studies do not consider the fact that noisy areas have many correlates that may be responsible for driving the observed vocal trends (Bayne et al. 2008; Habib et al. 2007). For instance, increases in anthropogenic noise generally occur in habitats with more anthropogenic structures and activities. To address this issue, we investigated whether the presence of particular habitat features could be used to predict ambient noise levels. Surprisingly, we did not find any significant relations, or even any strong trends. Absolute noise levels, as well as fluctuations in noise levels, were similar across territories regardless of how "natural" or "anthropogenic" they were. In a separate study involving a larger-scale analysis of sound propagation in territories across the anthropogenic noise gradient, we found a related unexpected result, indicating that many "natural" territories had louder and more variable noise conditions (Chapter 2).

Just as ambient noise may have habitat structure correlates, so too may male song parameters, since species have presumably experienced selection to optimize signal transmission in particular environments (Brumm & Naguib 2009; Kirschel et al. 2009; Morton 1975). We investigated the relationship between habitat structure and eastern bluebird song parameters in an attempt to understand the relative impacts of habitat structure and environmental noise on bluebird song. None of the song PCs were influenced by habitat structure: Both temporal and spectral parameters were consistent regardless of whether the habitat was open or closed, acoustically hard or soft (Brown & Handford 2000; Forrest 1994). Given that eastern bluebirds are adapted to fairly variable environments (Gowaty & Plissner 1998), this should, perhaps, come as no surprise; they may have evolved a fair amount of vocal plasticity in response to generations of nesting in unpredictable habitats.

The lack of relationship between habitat and bluebird song parameters lends further support to our suggestion that changes in song amplitude and peak frequency are related to ambient noise conditions, rather than being influenced by a correlate of noise. At the same time, we did find that SNR strongly decreased in habitats with more anthropogenic features. This relationship persisted even when we controlled for ambient noise, suggesting that something about the habitat itself was responsible for reduced SNR. Future work is needed to determine whether particular habitat structures, materials, or layouts were responsible for suppressing signal transmission, amplifying noise, or both.

Finally, we explored the relationship between acoustic parameters and breeding success. The overall lack of strong relationships between male song and fitness parameters—even when environmental noise and habitat structure have been controlled for—is surprising. Like most songbirds, eastern bluebirds use song to attract mates and defend territories (Gowaty & Plissner 1998; Huntsman & Ritchison 2002), as well as to coordinate chick care efforts (Huntsman & Ritchison 2002) with their mates. Male song is generally thought to indicate some aspect of male quality (Buchanan et al. 2003; Forstmeier et al. 2002; Gil et al. 2006; MacDonald et al. 2006; Nowicki et al. 2000; Spencer et al. 2003, 2004; Stewart & MacDougall-Shackleton 2008), thus allowing females to select good mates, and/or enabling males to avoid particularly dangerous rivals.

If this is true for eastern bluebirds, then "quality" may not translate directly to breeding success, but rather may indicate another characteristic, such as physical condition (Stewart & MacDougall-Shackleton 2008), familiarity with the local habitat (Stewart & MacDougall-Shackleton 2008), or ability to provide for the female during incubation (Gill 2007; Siefferman & Hill 2005). Alternatively, despite the fact that we included 8 different male song characteristics in our analysis, it is possible that we failed to measure the song traits most indicative of male quality—for instance, the total number of songs per bout, or the total number of bouts per day. These characteristics might also be influenced by ambient noise, if males choose to sing less during particular acoustic disturbances, or if they are forced to sacrifice total amount sung in order to achieve the frequency and/or amplitude levels required to escape masking. Unfortunately, our sample size for this analysis (n = 15) was relatively small, and we admit that it should therefore be interpreted cautiously. However, the intriguing trends we observed highlight the importance of including this type of analysis in future anthropogenic noise research in order to explore not only whether ambient noise reduces fitness, but also the potential mechanisms by which this process might occur.

Altogether, the current study, like our previous work on eastern bluebirds, provides evidence that some species are capable of coexisting with humans across a variety of anthropogenic habitats (Kight 2005; Kight & Swaddle 2007). Despite the anthropogenic changes in their acoustic space, bluebirds appear to have the behavioral flexibility to continue communicating and breeding successfully, indicating that there are neither short-term nor long-term drawbacks to their proximity to humans. However, as with most previous anthropogenic noise research (Bermudez-Cuamatzin et al. 2009; Fernández-Juricic et al. 2005; Leader et al. 2008; Leader et al. 2005; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Slabbekoorn et al. 2007; Wood & Yezerinac 2006), our work focuses on a species that chooses to live in disturbed territories even when there are vacancies in nearby remote areas (Kight, unpub. data). Additionally, bluebirds have been living near humans for hundreds of years (Gowaty & Plissner 1998; Zimmerman 2007). Their behavioral flexibility likely stems from a pre-adaptation to disturbed habitats, an evolved response to unpredictable human disturbances, substantial phenotypic plasticity, or a combination of all three. Species with different life history traits and requirements are likely to have a more constrained reaction norm—particularly when they have evolved to prefer less variable habitats and have had little historical experience with human disturbances.

Another possibility that has not yet been examined in any anthropogenic noise research is a potential threshold response to noise pollution. It makes intuitive sense that there may be a value of ambient noise beyond which birds are simply not capable of compensating. Thus far, this may have gone undetected because chosen study areas did not include extremely loud sites, or because chosen study species did not inhabit the loudest anthropogenic sites (*e.g.* industrial areas). Experimental work is needed to evaluate whether there is an acoustic boundary beyond which no amount of vocal flexibility will enable species to communicate effectively in noisy habitats. As human expansion continues, such knowledge will be increasingly important so that attempts can be made to prevent noise from exceeding any critical limits.

Anthropogenic study systems may also provide an excellent opportunity to conduct "natural experiments" to investigate the relative strengths of environmental pressures at different life history stages. For instance, the song a male produces is a product of many factors, including his condition (past and present), his morphology, his original song tutor, his audience, and his current environmental setting (Beecher & Burt 2004; Boncoraglio & Saino 2007; Buchanan et al. 2004; Derryberry 2009; Gil & Gahr 2002; Gil et al. 2006; Griebmann & Naguib 2002; Hultsch & Todt 2004; Kroodmsa 2004; Luther 2009; MacDougall-Shackleton et al. 2009; Marler & Peters 1987; Morton 1975; Nowicki et al. 1998; Nowicki et al. 2002; Podos 2001). Longitudinal studies documenting all of these variables (and more) in ever-changing anthropogenic environments can be used to understand which parameters are most sensitive to change, and therefore are most likely to cause permanent alterations to vocal performance if they are manipulated. It is also possible to document fluctuations in male song parameters and "vocabulary," both within individual males and across successive generations (Baker & Boylan 1995; Baker & Gammons 2008; Derryberry 2007, 2009). This will allow us to understand how environmental constraints (caused by habitat structure and ambient noise, and mediated by behaviors such as mate choice and immigration) can underlie the evolution of communication within a species. These data offer important insights into the potential long-term influences of anthropogenic pressures on animal communication in the future.

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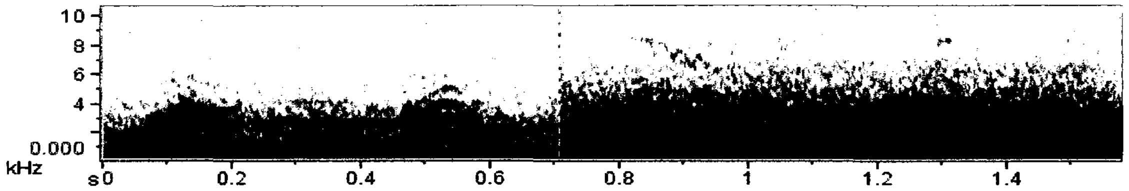


Figure 3.1. Examples of eastern bluebird song. Both samples were collected from a single male singing from the same perch during a single song bout. These represent the quietest (left) and loudest (right) levels of background noise recorded from this site. These samples indicate the amount of variation in environmental noise that can be present within a single site. Additionally, as the high-noise sample on the right demonstrates, ambient noise (in this case, caused predominantly by vehicular traffic from a nearby road) poses a considerable masking threat, particularly to the lower-frequency portions of bluebird vocalizations.

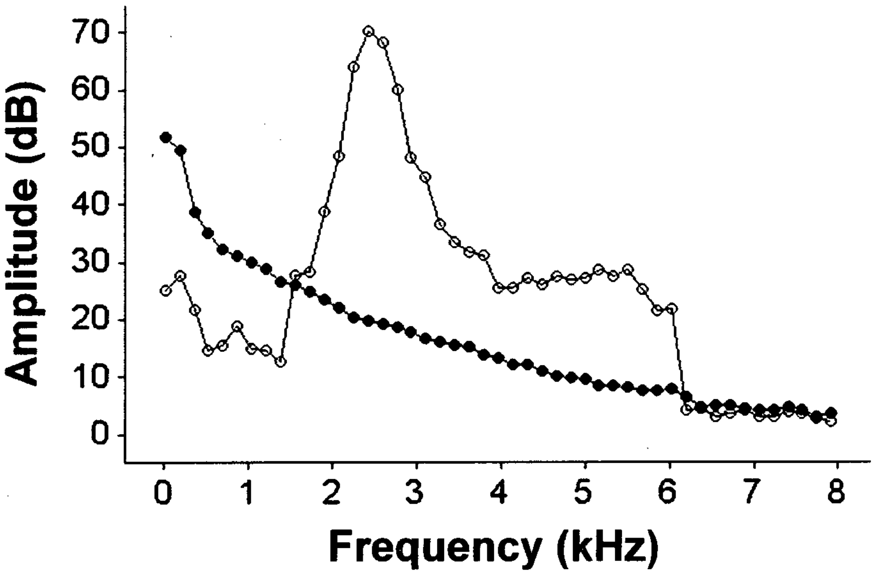
Variable	**PC1 (32.3%)**	**PC2 (18.2%)**	**PC3 (15.2%)**	**PC4 (12.5%)**
Song length	0.560	-0.707	0.063	0.017
# song elements	0.531	-0.700	-0.057	0.057
Internote distance	0.181	-0.221	0.733	-0.141
Minimum kHz	-0.598	-0.313	-0.306	0.031
Maximum kHz	0.833	0.353	-0.151	-0.082
Peak kHz	0.164	-0.197	-0.714	-0.400
kHz range	0.906	0.393	-0.034	-0.072
Average song dB	-0.227	-0.010	0.207	-0.897

Table 3.1. Loading factors for PCA of eastern bluebird male song parameters. Percentages indicate the amount of variance explained by each PC.

Variable	**PC1 (51.2% of variance)**
dB of noise	-0.715
kHz of noise	0.715

Table 3.2. Loading factors for PCA of environmental noise conditions at eastern bluebird breeding territories.

(a)


Amplitude (dB)
70
60
50
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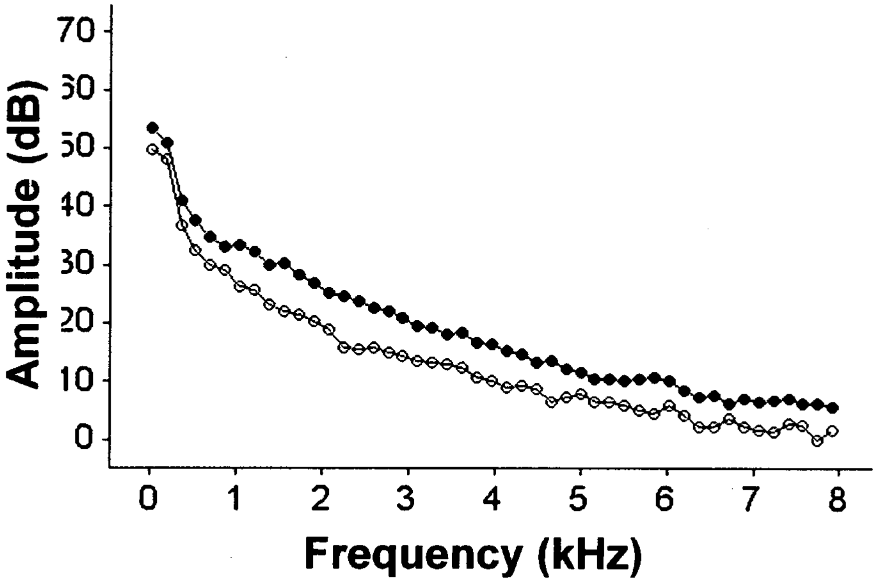
4
5
6
7
8
Frequency (kHz)

(b)


Amplitude (dB)
70
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Frequency (kHz)

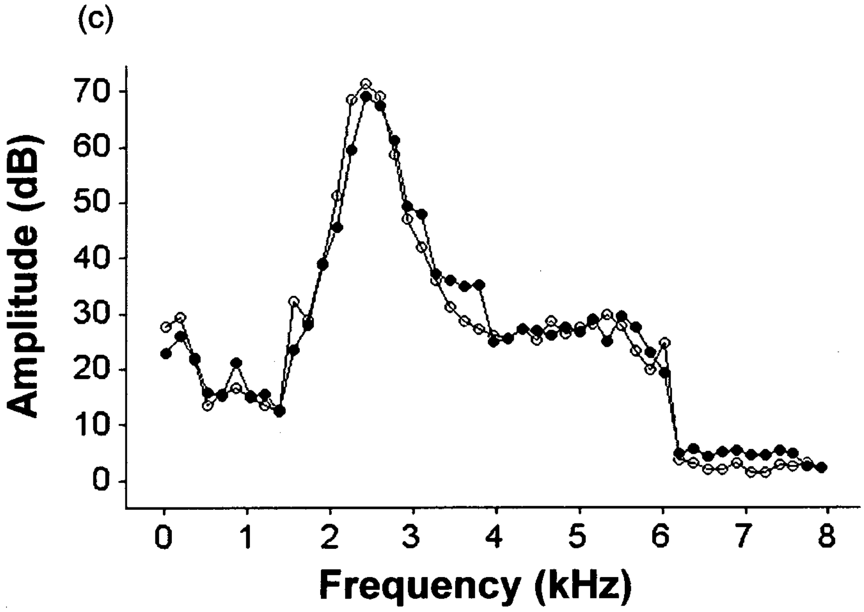

Figure 3.2. Power spectra of environmental noise and eastern bluebird song. (a) Power spectra of environmental noise in eastern bluebird territories (closed circles) and corresponding male song (open circles). These spectra were created by averaging across all environmental noise and male song measurements, respectively. (b) Comparison of environmental noise spectra during the lowest and highest levels of noise experienced while recording at active territories. These spectra were created by averaging spectral values across the highest and lowest recordings taken at all sites.

(c) Comparison of male song spectra in response to high levels of ambient noise (closed circles) and low levels of ambient noise (open circles). These spectra were created by averaging spectral values for all songs collected from males under each site's highest and lowest ambient noise conditions, respectively.

Variable	**PC1 (48.2%)**	**PC2 (35.2%)**
Short impervious surface (< 3m)	0.491	-0.727
Short vegetation (grass, shrubs)	-0.943	-0.223
Tall impervious surface (< 3m)	0.567	-0.588
Trees (forest and ornamental)	0.691	0.695

Table 3.3. Loading factors for PCA of all habitat within a 90 m radius of active eastern bluebird nest boxes. Percentages indicate the amount of variance explained by each PC.

Variable	**PC1 (43.4%)**	**PC2 (33.8%)**
Brood condition	-0.816	0.034
Brood growth	0.726	0.452
Productivity	0.333	-0.899

Table 3.4. Loading factors of PCA of three measures of eastern bluebird breeding success. Percentages indicate amount of variance explained by each PC.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
(a)					
1	Year, habitat PC1	70.67	0	0.381	1
2	Year, habitat PC2	71.06	0.387	0.314	0.824
3	Year, habitat PC1, habitat PC2	72.30	1.63	0.169	0.442
4	Year, habitat PC1, habitat PC2, habitat PC1*PC2	72.72	2.05	0.137	0.359
(b)					
1	Year, habitat PC2	67.80	0	0.398	1
2	Year, habitat PC1	68.16	0.363	0.332	0.834
3	Year, habitat PC1, habitat PC2	69.93	1.838	0.159	0.399
4	Year, habitat PC1, habitat PC2, habitat PC1*PC2	70.34	2.549	0.111	0.280

Table 3.5. Values used in generalized linear regression models to explore effects of habitat (PC1 and PC2) on average noise levels (5a) and variation in noise levels (5b) in eastern bluebird breeding territories.

Parameter	B	SE	95% Confidence Intervals	
			Lower	Upper
(a)				
Year (2007)	0.627	0.466	-0.287	1.54
Year (2008)	0	0	0	0
Habitat PC1	0.076	0.119	0.421	-0.269
Habitat PC2	0.018	0.176	-0.188	0.225
Habitat PC1*PC2	0.018	0.105	-0.215	0.251
(b)				
Year (2007)	-0.547	0.427	-0.138	0.289
Year (2008)	0	0	0	0
Habitat PC1	0.002	0.087	-0.168	0.172
Habitat PC2	-0.061	0.143	-0.341	0.220
Habitat PC1*PC2	-0.004	0.095	-0.189	0.182

Table 3.6. Parameters included in final model explaining the relationship between environment and both average (6a) and variation in (6b) ambient noise levels.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
(a)					
1	Year, male size, habitat PC2	69.73	0	0.34	1
2	Year, male size, habitat PC1	69.83	0.098	0.326	0.952
3	Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2	71.03	1.30	0.178	0.521
4	Year, male size, habitat PC1, habitat PC2	71.33	1.60	0.154	0.450
(b)					
1	Year, male size, habitat PC1	66.56	0	0.361	1
2	Year, male size, habitat PC2	66.58	0.023	0.357	0.989
3	Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2	68.40	0.184	0.144	0.398
4	Year, male size, habitat PC1, habitat PC2	68.46	0.190	0.139	0.387
(c)					
1	Year, male size, habitat PC1	54.37	0	0.416	1
2	Year, male size, habitat PC2	55.62	1.25	0.223	0.536
3	Year, male size, habitat PC1, habitat PC2	55.9	1.48	0.198	0.477
4	Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2	56.24	1.87	0.164	0.394
(d)					
1	Year, male size, habitat PC1	63.00	0	0.454	1
2	Year, male size, habitat PC2	64.04	1.04	0.270	0.594
3	Year, male size, habitat PC1, habitat PC2	65.05	2.05	0.163	0.358
4	Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2	65.77	2.77	0.114	0.250
(e)					
1	**Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2**	**302.72**	**0**	**0.997**	**1**
2	Year, male size, habitat PC1, habitat PC2	314.52	11.8	0.003	0.003
3	Year, male size, habitat PC1	325.16	22.44	1E-05	1E-05
4	Year, male size, habitat PC2	328.91	26.18	2E-06	2E-06

Table 3.7. Values used in generalized linear regression models to explore effects of habitat on male song PCs 1 – 4 (7a – 7d) and SNR (7e).

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
(a)				
Year (2007)	-0.553	0.465	-1.46	0.358
Year (2008)	0	0	0	0
Male size	-0.071	0.102	-0.298	0.102
Habitat PC1	0.077	0.104	-0.242	0.164
Habitat PC2	-0.05	0.187	-0.290	0.444
Habitat PC1*PC2	-0.099	0.166	-0.376	0.276
(b)				
Year (2007)	-0.556	0.451	-0.144	0.327
Year (2008)	0	0	0	0
Male size	-0.139	0.113	-0.361	0.083
Habitat PC1	0.013	0.155	-0.290	0.317
Habitat PC2	-0.002	0.096	-0.191	0.186
Habitat PC1*PC2	0.035	0.138	-0.234	0.305
(c)				
Year (2007)	-0.377	0.300	-0.966	0.211
Year (2008)	0	0	0	0
Male size	0.058	0.071	-0.08	0.196
Habitat PC1	0.132	0.162	-0.185	0.449
Habitat PC2	-0.032	0.088	-0.204	0.140
Habitat PC1*PC2	-0.054	0.143	-0.335	0.227
(d)				
Year (2007)	0.204	0.328	-0.440	0.846
Year (2008)	0	0	0	0
Male size	-0.139	0.184	-0.503	0.217
Habitat PC1	0.106	0.108	-0.132	0.289
Habitat PC2	-0.013	0.129	-0.269	0.236
Habitat PC1*PC2	0.011	0.094	-0.174	0.195
(e)				
Year (2007)	0.670	148.8	-291	292.3
Year (2008)	0	0	0	0
Male size	-79.6	44.0	-6.91	165.7
Habitat PC1	-144.7	60.8	-233.5	4.71
Habitat PC2	-19.7	70.5	-157.9	118.4
Habitat PC1*PC2	-83.0	110.5	-299.5	133.5

Table 3.8. Parameters included in final models explaining the relationship between habitat and male song PCs 1 – 4 (8a – 8e) and SNR (8f).

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	Year, male size, CID, noise PC1, song PC1, song PC4	56.27	0.000	0.088	-1.000
2	Year, male size, CID, noise PC1, song PC1	56.30	0.023	0.087	-0.989
3	Year, male size, CID, noise PC1, song PC1, song PC3, song PC4	56.30	0.023	0.087	-0.989
4	Year, male size, CID, habitat PC1, noise PC1, song PC1, song PC3, song PC4	56.57	0.297	0.076	-0.862
5	Year, male size, CID, noise PC1, song PC1, song PC3	56.80	0.523	0.068	-0.770
6	Year, male size, CID, habitat PC1, noise PC1, song CP1, song PC2, song PC4	57.43	1.152	0.049	-0.562
7	Year, male size, CID, noise PC1, song PC1, song PC2, song PC4	57.45	1.172	0.049	-0.557
8	Year, male size, CID, nosie PC1, song PC1, song PC2, song PC4	57.46	1.185	0.049	-0.553
9	Year, male size, CID, habitat PC1, habitat PC2, noise PC1, song PC1, song PC3, song PC4	57.51	1.240	0.047	-0.538
10	Year, male size, CID, habitat PC1, noise PC1, song PC1, song PC2, song PC3	57.60	1.330	0.045	-0.514
11	Year, male size, CID, habitat PC1, noise PC1, song PC1, song PC2, song PC3, song PC4	57.74	1.467	0.042	-0.480
12	Year, male size, CID, noise PC1, song PC1, song PC2, song PC3	57.90	1.630	0.039	-0.443
13	Year, male size, CID, song PC1, song PC4	58.16	1.883	0.034	-0.390
14	Year, male size, CID, song PC1, song PC3, song PC4	58.40	2.124	0.030	-0.346
15	Year, male size, CID, habitat PC1, noise PC1, song PC1, song PC2, song PC3, song PC4	58.43	2.155	0.030	-0.340
16	Year, male size, CID, habitat PC1, habitat PC2, noise PC1, song PC1, song PC2, song PC3, song PC4	58.60	2.328	0.027	-0.312
17	Year, male size, CID, habitat PC1, habitat PC2, noise PC1, song PC1, song PC2, song PC4	58.73	2.451	0.026	-0.294
18	Year, male size, CID, habitat PC1, habitat PC2, noise PC1, song PC1, song PC2, song PC3	58.78	2.507	0.025	-0.286
19	Year, male size, CID, song PC1, song PC2, song PC3, song PC4	59.33	3.058	0.019	-0.217
20	Year, male size, CID, song PC1	59.56	3.283	0.017	-0.194
21	Year, male size, CID, habitat PC1, song PC1, song PC2, song PC3, song PC4	60.17	3.900	0.013	-0.142

Table 3.9. Summary of the models included in the final, averaged model explaining the relationship between breeding PC1 *faster growth/poorer condition* and male song characteristics (while controlling for habitat features and environmental noise).

Parameter	B	SE	95% Confidence Intervals Lower	 Upper
Year (2007)	-0.667	0.542	-1.19	-0.110
Year (2008)	0	0	0	0
Male size	-0.137	0.134	-0.265	0.003
CID	-0.004	0.018	-0.002	0.015
Habitat PC1	-0.079	0.157	-0.239	0.075
Habitat PC2	-0.02	0.229	-0.266	0.192
Noise PC1	-0.379	0.269	-0.660	-0.121
Song PC1	-0.532	0.327	-0.854	-0.200
Song PC2	-0.007	0.200	-0.195	0.205
Song PC3	-0.114	0.241	-0.365	0.117
Song PC4	-0.186	0.256	-0.441	0.070

Table 3.10. Values for final, averaged model exploring the relationships between breeding PC1 *faster growth/poorer condition* and male song (while controlling for habitat features and environmental noise).

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	Year, male size, CID, song PC2	64.70	0.000	0.066	-1.000
2	Year, male size, CID, song PC2, song PC3	64.86	0.164	0.060	-0.921
3	Year, male size, CID, song PC3	65.20	0.500	0.051	-0.779
4	Year, male size, CID, song PC2, song PC4	65.22	0.523	0.050	-0.770
5	Year, male size, CID, song PC2, song PC3, song PC4	65.25	0.554	0.050	-0.758
6	Year, male size, CID, song PC1, song PC2, song PC3	65.27	0.571	0.049	-0.752
7	Year, male size, CID, song PC3, song PC4	65.59	0.888	0.042	-0.641
8	Year, male size, CID, song PC1, song PC2, song PC3, song PC4	65.59	0.893	0.042	-0.640
9	Year, male size, CID, song PC1, song PC2, song PC4	65.60	0.896	0.042	-0.639
10	Year, male size, CID, noise PC, song PC2, song PC3, song PC4	65.72	1.016	0.039	-0.602
11	Year, male size, CID, song PC1, song PC3, song PC4	65.80	1.100	0.038	-0.577
12	Year male size, CID, noise PC, song PC1, song PC2, song PC3	65.80	1.105	0.038	-0.576
13	Year, male size, CID, noise PC, song PC1, song PC2, song PC3, song PC4	65.97	1.272	0.035	-0.529
14	Year, male size, CID, habitat PC1, noise PC, song PC2, song PC3, song PC4	66.03	1.329	0.034	-0.515
15	Year, male size, CID, habitat PC1, song PC1, song PC2, song PC3, song PC4	66.04	1.339	0.034	-0.512
16	Year, male size, CID, noise PC, song PC1, song PC2, song PC4	66.07	1.370	0.033	-0.504
17	Year, male size, CID, noise PC, song PC1, song PC3, song PC4	66.28	1.578	0.030	-0.454

18	Year, male size, CID, habitat PC1, noise PC, song PC1, song PC2, song PC3, song PC4	66.30	1.597	0.029	-0.450
19	Year, male size, CID, habitat PC1, noise PC, song PC1, song PC2, song PC3	66.30	1.604	0.029	-0.448
20	Year, male size, CID, habitat PC1, noise PC, song PC1, song PC2, song PC4	66.42	1.719	0.028	-0.423
21	Year, male size, CID, habitat PC2, noise PC, song PC1, song PC2, song PC3, song PC4	66.61	1.914	0.025	-0.384
22	Year, male size, CID, habitat PC1, habitat PC2, noise PC, song PC2, song PC3, song PC4	66.63	1.935	0.025	-0.380
23	Year, male size, CID, habitat PC1, habitat PC2, noise PC, song PC1, song PC2, song PC3, song PC4	66.63	1.935	0.025	-0.380
24	Year, male size, CID, habitat PC1, noise PC, song PC1, song PC3, song PC4	66.66	1.965	0.025	-0.374
25	Year, male size, CID, habitat PC1, habitat PC2, song PC1, song PC2, song PC3, song PC4	66.74	2.042	0.024	-0.360
26	Year, male size, CID, habitat PC1, habitat PC2, noise PC, song PC1, song PC2, song PC3	66.92	0.022	0.022	-0.330
27	Year, male size, CID, habitat PC1, habitat PC2, noise PC, song PC1, song PC2, song PC4	67.19	0.019	0.019	-0.288
28	Year, male size, CID, habitat PC1, habitat PC2, noise PC, song PC1, song PC3, song PC4	67.37	0.017	0.017	-0.264

Table 3.11. Summary of the models included in the final, averaged model explaining the relationship between breeding PC2 *fewer chicks/faster growth* and male song characteristics (while controlling for habitat features and environmental noise).

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
Year (2007)	-1.32	0.731	-2.05	-0.592
Year (2008)	0	0	0	0
Male size	0.040	0.166	-0.131	0.200
CID	0.006	0.010	-0.005	0.016
Habitat PC1	0.058	0.174	-0.115	0.232
Habitat PC2	0.019	0.115	-0.096	0.134
Noise PC1	0.040	0.228	-0.189	0.268
Song PC1	-0.072	0.271	-0.342	0.199
Song PC2	-0.221	0.319	-0.548	0.091
Song PC3	0.072	0.347	-0.273	0.420
Song PC4	-0.029	0.306	-0.335	0.277

Table 3.12. Values for final, averaged model exploring the relationships between breeding PC2 *fewer chicks/faster growth* and male song (while controlling for habitat features and environmental noise).

CHAPTER 4

DO EASTERN BLUEBIRD FITNESS INDICATORS RELATE TO ANTHROPOGENIC NOISE?

4.1 INTRODUCTION

Anthropogenic activities can affect the sound space of wildlife in a number of ways. Habitat modifications alter the acoustic environments through which signals propagate (Warren et al. 2006), both by changing spatial structure (*e.g.* open vs. closed) and by altering the materials they comprise (Katti & Warren 2004; Leader et al. 2005; Slabbekoorn et al. 2007; Warren et al. 2006). Changes to the habitat, as well as the presence of human activities, may affect species assemblages (Bayne et al. 2008; Parris & Scneider 2008; Rheindt 2003), disrupting the processes that allow multiple species to communicate effectively while sharing acoustic space (Luther 2009; Penteriani 2003; Planqué & Slabbekoorn 2008). Additionally, anthropogenic activities can introduce significant noise into the environment: The loudest sounds, which may exceed 100 dB (Habib et al. 2007; Hanson 2008), can be detected a fair distance from the source (Bayne et al. 2008; Habib et al. 2007; Rheindt 2003) and threaten to mask vocal communication (Bee & Micheyl 2008; Bee & Swanson 2007; Katti & Warren 2004; Patricelli & Blickley 2006; Slabbekoorn & Peet 2003).

Animals of several taxa (*e.g.*, marine mammals (Foote et al. 2004; Miksis-Olds & Tyack 2009; Morisaka et al. 2005), frogs (Kaiser & Hammers 2009; Lengagne 2008; Parris et al. 2009; Sun & Narins 2005), squirrels (Rabin et al.

2003), and birds (Fernández-Juricic et al. 2005; Katti & Warren 2004; Leader et al. 2005; Leonard & Horn 2005, 2008; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006) appear capable of altering their vocalizations in order to escape or mitigate masking. Of these species, birds are particularly noteworthy, as they seem to employ the widest range of vocal adjustments, including shifts in frequency (Fernández-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006) and amplitude (Brumm 2004b; Brumm 2006; Wood & Yezerinac 2006), as well as changes to singing rate (Fernández-Juricic et al. 2005) and song composition (Leonard & Horn 2008). Some species may even change the time of day during which they sing (Fuller et al. 2007).

Despite this behavioral flexibility, birds communicating in noisy environments may still experience additional costs. Although the short-term energetic costs associated with vocal modifications remain unclear (Gil & Gahr 2002; Oberweger & Goller 2001; Ward et al. 2003), two recent studies suggest possible longer-term, fitness risks. In a Canadian population of ovenbirds (*Seiurus aurocapillus*), males occupying noisy territories were significantly less able to procure mates; furthermore, noisy sites contained a disproportionate number of young male breeders (Habib et al. 2007). Taken together, these results imply that male ovenbirds may view noisy territories as sub-par and therefore avoid them when possible. Males' inability to attract mates suggests that females also dislike noisy sites, or that they are unable to hear, and therefore locate, advertising males—or both. Regardless of the exact mechanism, it is clear that the presence of noise pollution could have serious implications for breeding success in this system.

Likewise, an aviary study on zebra finches (*Taeniopygia guttata*) demonstrated a waning female preference for their pair-bonded mates in response to increasing levels of ambient noise (Swaddle & Page 2007). The authors suggest that this may have been due to masking of pair-bond vocalizations between mates. In the wild, this could lead to higher levels of divorce between breeding attempts, as well as higher levels of cuckoldry within breeding attempts—two more ways that ambient noise might reduce individual fitness.

Birds may suffer fitness costs even when they are able to use vocal adjustments to escape masking. Males' songs are used for a variety of purposes, including attracting potential mates and warning off rival males (Marler & Slabbekoorn 2004). Altering song parameters may alter the meaning contained within these vocal signals (Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008). Males who sing at higher frequencies—the most commonly-observed vocal alteration in response to anthropogenic noise (Fernández-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Slabbekoorn & Peet 2003; Wood & Yezerinac 2006)—or who sing slower songs (Fernández-Juricic et al. 2005) may sound smaller and/or less powerful (Ryan & Brenowitz 1985). This could lead to their attracting poorer-quality females, and/or not acquiring a mate until later in the season—both of which could reduce the quality and/or number of young produced. Additionally, these males might suffer an increased number of territorial intrusions by rivals, perhaps increasing the possibility of extra-pair copulations and, thus, cuckoldry rates.

Thus, it is clear that anthropogenic noise might potentially affect nesting success in a number of ways. However, no research to date has explicitly investigated potential fitness costs of breeding in noisy territories. To bridge that gap, we have studied a population of eastern bluebirds (*Sialia sialis*) nesting across an anthropogenic disturbance gradient. We have previously demonstrated that these birds show a degree of behavioral flexibility in the presence of anthropogenic disturbance: They generally tend to react only to the disturbance events that are most likely to cause them harm (e.g. naturalistic disturbances such as pedestrians walking dogs; unpublished data), and although adults alter their time budgets in response to nearby anthropogenic activities, they appear to do so in such a way as to buffer their young from any corresponding negative impacts (Kight 2005; Kight & Swaddle 2007). In other words, they are reasonably tolerant to anthropogenic disturbance; hence, any relation between noise and fitness is unlikely to be mediated solely by a correlation between noise and disturbance in this species.

Although we have measured the impacts of specific disturbance events in bluebird territories, we have not previously investigated the potential effects of larger-scale, environment-wide anthropogenic disturbances, such as noise pollution. For the current study, we quantified acoustic conditions in active bluebird territories, concentrating on the amplitude and peak frequency of anthropogenic noise within the frequency bandwidth used for bluebird song. We predicted that, in noisier environments, cuckoldry rates would be higher, while brood condition, brood growth rate, and total number of chicks fledged per nest would be lower.

4.2 METHODS

4.2.1 Study site and species description

We studied wild populations of cavity-nesting eastern bluebirds during the breeding seasons of 2007 and 2008. We have collected data from these populations since 2002, taking advantage of the birds' willingness to occupy a network of wooden nest boxes distributed across a disturbance gradient in Williamsburg, VA, USA. Previous work indicates that the physical condition of nesting adults, availability of resources, offspring provisioning rates, and depredation rates do not differ among boxes (Burdge 2009; Hubbard 2008; Kight 2005) such that the primary difference between breeding territories is the level and type of anthropogenic disturbance to which they are exposed (Kight, unpub. data). However, as noted above, eastern bluebirds appear to be fairly disturbance tolerant across this gradient, and direct anthropogenic disturbance (*e.g.* motor vehicles, pedestrians) does not reliably explain fitness variation in this population (Kight 2005; Kight & Swaddle 2007). Therefore, we feel this is a good system for studying the additional contribution of noise in explaining possible fitness differences among nests and individual males. Other information about the nest boxes and their placement have been described in detail elsewhere (Le Clerc et al. 2005).

4.2.2 Evaluating environmental noise

We recorded environmental noise at 43 nest boxes between 0700 and 1700 hours during the breeding seasons of 2007-2009. Pilot data indicated that environmental noise conditions were not greatly affected by time of day ($R = -0.163$, $p = 0.390$), time of season ($R = -0.245$, $p = 0.200$), or year ($R = -0.04$, $p = 0.764$). Therefore, we did not always collect recordings while a focal pair was in residence, as this allowed us to minimize potentially negative effects of our intrusion on the territories during breeding efforts.

All recordings were taken using a Sennheiser ME-67 shotgun microphone and Marantz PMD 660 solid state recorder. In each territory, the microphone was positioned approximately 20 m from the nest box, positioned parallel with the ground at a height of approximately 1 m. Modeling our methods after Brumm (2006), we then collected recordings in each of the cardinal compass directions in order to obtain a noise sampling representative of the entire territory. We collected 45 seconds of ambient noise recording in each direction, for a total of 3 minutes from each site. Using Raven 1.3 acoustic analysis software (Cornell Lab of Ornithology, Ithaca, NY), we extracted three 0.05 s clips from each direction, sampling approximately every 15 seconds of the recording.

We chose to focus our analysis on the 1000-5000 kHz frequency range only, since all eastern bluebird vocalizations occur within this bandwidth, with an emphasis on the 2000-4000 kHz range (Huntsman & Ritchison 2002) (Chapter 3). This frequency bandwidth also includes the bulk of anthropogenic ambient noise (Fernández-Juricic et al. 2005; Slabbekoorn & Peet 2003; Wood &

Yezerinac 2006). Prior to analysis, all clips were bandpass filtered between 1000 and 5000 kHz. We then measured three aspects of ambient noise: peak frequency (the frequency with the maximum power), average RMS amplitude, and peak RMS amplitude (the loudest amplitude recorded over the duration of the clip). For each site, we averaged all 12 values (4 directions x 3 clips per direction) obtained for both of the acoustic traits, in order to yield one average measure for each trait per territory. These values were then entered into a principal components analysis (PCA), which yielded a single principal component (PC) with $\lambda>1$ (Table 1a). This PC (hereafter called *Sound PC*) explained 65.4% of the variance and loaded negatively for peak frequency and positively for both amplitude measurements. Therefore, as *Sound PC* increased, ambient noises became louder and lower-pitched.

4.2.3 Collecting blood and demographic data

All active nests were monitored throughout the March-August breeding seasons of 2007 and 2008. Methods for monitoring are described in greater detail elsewhere (Kight 2005; Kight & Swaddle 2007; Le Clerc et al. 2005). Briefly, we visited boxes weekly throughout the egg-laying period and then bi-weekly during the chick growth period. This allowed us to determine when the clutch was initiated, how many eggs were laid, a growth index (residual of wing length against age, averaged for a brood) and a body condition index (residual of mass against wing length, averaged for a brood), and the total number of fledglings produced (referred to henceforth as *productivity*). It is important to note that both the growth and condition indices were derived from residual values which results in negative values for approximately half of the broods.

Each nestling received a U.S. Fish and Wildlife Service aluminum band, as well as a unique combination of color bands. Parents who were not already marked from previous years of research were captured and similarly banded during blood collection (see below).

When chicks were 10-14 days old, we collected blood samples using brachial venipuncture. We were unable to obtain blood or tissue samples from unhatched eggs or from nestlings that died. This is because eastern bluebirds often remove both from their nests, and we could not consistently arrive at the nest in time to collect these unpredictable data samples.

We captured parents using trap doors placed in the box, or mist nets into which the birds were lured using playback and/or a decoy model bluebird. When possible, we also collected blood samples from neighboring adults who were potential extra-pair parents. Blood was collected into heparinized capillary tubes and then immediately transferred to QIAcard FTA spots (Qiagen). These were allowed to dry completely and then were sealed into small multibarrier pouches for storage at room temperature.

4.2.4 Genotyping individuals

Blood samples were purified using one of two methods: QIAamp DNA Micro Kit (Qiagen, Hilden, Germany) or Whatman FTA Purification Reagent (Whatman Ltd., Maidstone, UK). Products from both methods were then amplified according to previously established methods (Faircloth et al. 2006). We focused our genotyping efforts on six tetranucleotide microsatellite loci that had previously been shown to have high allelic variability in eastern bluebirds (Faircloth et al. 2006): Sialia8, Sialia11, Sialia24, Sialia27, Sialia36, and Sialia37. We confirmed the validity of all primer sets for our population by generating 5 polymerase chain reaction (PCR) products for each micrsosatellite locus. We combined 0.25-0.5 µl of each PCR product with Rox 500 size standard and electrophoresed on an ABI 3130 Genetic Analyzer (Applied Biosystems Inc., Foster City, CA). Alleles were binned by hand following visual inspection in GeneMapper 3.5 (Applied Biosystems Inc., Foster City, CA).

Preliminary analyses with CERVUS v.3.0.3(Marshall et al. 1998) and GENEPOP 4.0 (Raymond & Rousset 1995a, b) both indicated the presence of subpopulation structure across our samples. This was not surprising, given that our sites were spatially clustered in four distinct areas, each separated by a minimum of two miles. Additionally, there is fairly high site fidelity amongst our population of eastern bluebirds (unpublished data). Therefore, for allele frequency calculations and all further paternity analyses, we examined each subpopulation separately.

Allele frequencies were established by CERVUS. For some loci in some of the subpopulations, insufficient genotyping had been performed to provide an adequate sample size for Hardy-Weinberg equilibrium calculations (see below); in all other cases, however, the loci were in Hardy-Weinberg equilibrium. We then used CERVUS to assign paternity across 43 nests. Because a preliminary analysis indicated possible egg-dumping, we conducted a parent-pair analysis rather than a straightforward paternity test. Candidate parents were all adults sampled within each subpopulation. Parameters were as follows: number of candidate mothers = 2, of which half were sampled; number of candidate fathers = 3, of which two thirds were sampled; error rate was 0.036 (calculated from mother-offspring mismatches in our dataset); confidence levels were 95 and 99%. The average exclusion probability across all nests was 98.5%.

Although we had originally attempted to genotype birds at all 6 focal loci, this was not always possible due to some technical difficulties. Ultimately, we conducted paternity tests using all individuals that had been genotyped at 3 or more loci (total n = 146 chicks and 67 adults; mean number loci = 5.20). This caused us to examine incomplete broods for 9 nests (20.9%). We have attempted to correct for this imbalance in our statistical analyses (see below). Cuckoldry rate was calculated as: (number of extrapair young)/(total number of nestlings).

4.2.5 Statistical Analyses

We utilized an information theoretic model selection approach (Burnham & Anderson 2002) to evaluate the effects of habitat on sound propagation. For each dependent variable, a candidate set of models was determined *a priori.*

Because eastern bluebirds nest multiple times throughout the season, boxes are often reused, by both the original occupants or by replacements. This was the case in 6 of 43 boxes sampled here. We created a factor variable, "repeat," with values of 1, 2, or 3, corresponding to breeding attempt in each box. The inclusion of this factor in all analyses allowed us to use all the data collected while correcting for potential effects of pseudoreplication. It is important to note that "repeat" is distinct from "clutch initiation date" (CID), which was also included in models for all breeding parameters. Many reproductive parameters exhibit seasonal variation (Dijkstra et al. 1990; Godfray & Shaw 1987; Verhulst et al. 1995), so we wished to explore whether differences in lay date altered any relationships we found between environment and breeding success. In our population of bluebirds, the appearance of first clutches at different breeding sites is staggered; additionally, many birds suffer failed first clutches, and many others relocate to new boxes between separate breeding attempts. For a combination of all these reasons, it was often the case that, for instance, a box's first sampled "repeat" was later in the season (high CID) rather than early in the season (low CID), as one might predict. Thus, each of these two variables represents a different influence on the breeding parameters, and is therefore included in the models for distinct reasons.

Because breeding density is known to affect reproductive parameters in a number of species (Ahola et al. 2009; Broyer 2009), we also included this variable in all models. Density was represented by a PC (*Density PC*) derived from a PCA on three factors: the number of boxes within a 400 m radius of the nest box, the number of boxes within an 800 m radius of the nest box, and the distance to nearest box (Table 1b). The 800 m-radius measurement was included in addition to the 400 m-radius measurement in order to more fully account for relative position of the box within the breeding area (*e.g.* at the edge of a group of territories, or in the middle), which could influence density-dependent effects such as competition for resources. The PCA yielded a single PC that accounted for 61.4% of the variance. The PC loaded highly for the number of boxes within both 400 m and 800 m of the focal box, but negatively for distance to nearest box.

When examining the effects of environmental noise on cuckoldry rates, we included another control variable, "proportion sampled." As mentioned previously, some broods were incompletely sampled. In a small number of cases, blood samples were insufficient for paternity analyses. Additionally, as mentioned above, we were unable to sample deceased young. Cumulatively, this left us with several incomplete broods. Rather than exclude these nests entirely, or analyze potentially artificially inflated cuckoldry rates, we included "proportion sampled" in order to adjust for brood size effects.

Finally, all models also contained the sound PC described above. Because CID and density were likely to interact with each other and with sound, we also included all two-way interactions involving these three covariates, as well as the main effect.

We used SPSS v. 15 (LEAD Technologies, Inc., Chicago, Illinois) to run generalized linear mixed models (GLMM) in order to determine Akaike's Information Criterion (AIC) for each model. These values were used to calculate AIC_c (which corrects AIC for small sample sizes), Δ- AIC_c (the difference between the model with the lowest AIC_c and each subsequent model), Akaike weight (an indicator of support for each model), and model likelihood. We then used model averaging(Mitchell 2008) to incorporate weighted parameter estimates from all models with Δ-AIC <4.0(Burnham & Anderson 2002). Prior to running all statistical analyses, we checked distributions of all variables were checked for normality and transformed them where necessary.

4.3 RESULTS

4.3.1 Cuckoldry rates and environmental noise

Three models were within 4 AIC_c units of each other and best explained the effects of environmental noise on cuckoldry rates (Table 2). *Density PC* and *Sound PC* each appeared in two of the top three models. The standard errors (SE) of all terms in the final, averaged model overlap with zero (Table 3), indicating little support for an effect of environmental noise or breeding density on cuckoldry among eastern bluebirds. In general, these results did not support our prediction, that increased ambient noise levels would be associated with higher cuckoldry rates.

4.3.2 Brood condition and environmental noise

Four models were within 4 AIC_c units of each other and best explained the effects of environmental noise on brood condition (Table 4). *Density PC* and *Sound PC* each appeared in three of the top four models. Again, the SE of all terms in the final, averaged model overlap with zero (Table 5), indicating little support for strong effects of environmental noise or breeding density on brood condition among eastern bluebirds. However, while the SE ranges of both *Sound PC* and the interaction term were more or less symmetrical around zero, that of *Density PC* was skewed to one side. This indicates a weakly (positive) relationship between the condition of eastern bluebird broods and the number of neighbors breeding nearby. Again, these results fail to support our prediction that increased ambient noise levels would be associated with poorer brood condition.

4.3.3 Brood growth and environmental noise

Two models were within 4 AIC_c units of each other and best explained the effects of environmental noise on our brood growth index (Table 6). *Density PC* and *Sound PC* appeared in both models. However, the range of standard errors of *Density PC* overlaps with zero (Table 7), indicating little effect of this parameter on brood growth. The range of standard errors for *Sound PC*, however, suggests a positive relationship between environmental noise and brood growth rate: In louder sites, broods grew at a faster rate. Further, there was a strong relationship between brood growth rate and the interaction term between the density and sound PCs.

At lower breeding densities, brood growth declines as ambient noise levels increase (Figure 1a), while the opposite relationship is found between growth and ambient noise at sites with higher breeding densities (Figure 1b). We did not anticipate the strong effect of breeding density on brood growth. Thus, although we predicted the relationship between ambient noise levels and brood growth seen at lower-density sites, we did not expect that strong positive relationship observed at sites with higher breeding densities.

4.3.4 Productivity and environmental noise

Three models were within 4 AIC_c units of each other and best explained the relationship between environmental noise and eastern bluebird productivity (Table 8). *Sound PC* appeared in all three models, while *Density PC* appeared in two of the final three models. The standard errors for both *Density PC* and the interaction term between density and sound both overlapped with zero (Table 9). However, the range of SE values for *Density PC* is skewed, suggesting that breeding density may have an important, if weak, positive relationship with productivity. The SE values for *Sound PC* are also skewed, suggesting that this variable may have an important negative impact on the number of fledglings produced at eastern bluebird nests. This supports our prediction that ambient noise levels would be associated with reduced productivity.

4.4 DISCUSSION

Here we show that two habitat variables, ambient noise and breeding density, are associated with changes in bluebird breeding parameters. Although many studies have suggested that anthropogenic noise might have implications for avian populations, none have reported associations with breeding parameters in order to explore whether ambient noise conditions might influence reproductive output. Thus, our research offers the first evidence (albeit correlative) that sound levels may be moderately related to at least two breeding parameters: a brood growth index (which was positively affected by ambient noise levels) and nest productivity (which was negatively affected by ambient noise). Density, which may also be influenced by anthropogenic activities (Baudains & Lloyd 2007; Chace & Walsh 2006; Markovchick-Nicholls et al. 2007; Opdam & Wiens 2002; Trombulak & Frissell 2000), also played an important role in influencing three of four breeding success measures examined here.

Our results suggest a complex interplay of density, sound, and breeding success. Density was associated with increases in brood condition and overall productivity, while sound was associated with decreases in productivity. We also found interesting interactions between sound and density. In this case, we have reported increased brood growth rates in areas with both high breeding densities and high ambient noise levels, suggesting a positive synergistic effect of these factors. Cumulatively, these results indicate that anthropogenic habitats, which often have both high breeding densities and loud ambient noise levels, may have both positive (higher condition and productivity due to density) and negative (lower productivity due to sound) impacts on resident breeders. The exact outcome will be dependent on the relative amounts of each of these environmental variables (and, likely, other variables that have not been considered here).

When attempting to interpret our results, it is important to consider that both density and ambient noise are associated with, and may here be proxies for, other environmental factors. For instance, our lower-density sites were, overwhelmingly, more “natural” areas, further from anthropogenic influences. These sites tended to have more complex, dense habitats, with higher numbers of shrubs and trees (Chapter 2). Thus, *Density PC* may be interpreted not only as the number of neighboring birds (and, thus, potential competitors or extra-pair mates), but also as habitat suitability, accessibility of resources, or even number of predators. Similarly, as has been noted before by other researchers, ambient noise is often associated with other anthropogenic influences, including recreational activities, landscaped habitat, and edge effects (Bayne et al. 2008; Habib et al. 2007). However, since many of these direct disturbance factors do not seem to explain variations in productivity and brood growth in our system, noise may explain some additional factor present in our focal territories.

We have used four measures of breeding success—cuckoldry rates, brood growth and condition, and productivity—as a proxy for fitness, with the general result that while fitness is positively impacted by breeding density, it is negatively impacted by ambient noise. There are many potential mechanisms responsible for these relationships. For instance, both growth rate and overall productivity may be reduced as a result of physiological and/or morphological deficiencies caused by the presence of the noise stress itself (at any point during the embryo-chick growth process). In fact, as certain ambient noise conditions have been shown to cause premature birth, it is also possible that some chicks hatched early and never caught up to their less-disturbed counterparts. Unfortunately, we did not able to collect the data required to test this hypothesis. Noise stress might also decrease parents’ condition, preventing them from adequately caring for their young. Alternatively, the presence of noise might force behavioral tradeoffs that have negative consequences for growing chicks. For instance, if adults in noisy territories are more vigilant and more cautious, they may spend less time foraging for food or attending to young. Increased noise levels might also obscure the begging calls of chicks, leading to lagging condition and growth rates that could, ultimately, decrease productivity. Clearly, more work is needed to isolate and identify which of these potential processes (or others) are responsible for influencing the relationships between density, sound, and fitness.

Overall, our results suggest that bluebird boxes should be placed in quieter areas in order to maximize their reproductive output. For now, it is unclear whether the birds would also benefit from closely-positioned boxes (creating a higher density), or whether the density effects reported here derive from other environmental factors related to high densities. More generally, our work clearly indicates that several measures of breeding success can be altered by habitat factors (noise and density) associated with anthropogenic activities. This is an important step forward in understanding not only how humans affect the health and persistence of wild populations, but also what can be done to mitigate these impacts. More experimental research is needed to disentangle the effects of "density" and "sound," *per se*, and the many other habitat factors associated with them. Although there are some excellent "natural" study sites that may facilitate this effort (Bayne et al. 2008; Habib et al. 2007), their numbers are few. Noise research, specifically, and anthropogenic disturbance research, in general, will be greatly improved by experimental manipulations in the future. For instance, manipulations of habitat structure, food availability, number of interactions with nearby neighbors, and both source and location of noise will all help to indicate whether density and sound impact breeding directly, or whether they are proxies for other environmental variables.

Additionally, our documentation of individual breeding attempts is only a first step. More work should be done to characterize the impacts of noise and density on fledgling success, recruitment, and dispersal. While our short-term data indicate that anthropogenic activities can have a negative effect on avian breeding efforts, the longer-term data are necessary for understanding whether entire populations are threatened.

Just as species and life stages may vary in their responses to anthropogenic activities, so too may habitats. We found that increased noise levels at our sites were associated with lower-pitched sounds and that areas with anthropogenic acoustic alterations also had structural alterations: Louder sites tended to have higher traffic levels, more impervious surface, and more open lawn, while quieter areas had more trees and shrubs and less physical disturbance (Chapter 2). However, these patterns are likely to be affected by factors such as region, climate, and local economy, and may differ greatly even over a single species' range. For this reason, a number of similar studies are needed in other types of habitat so that broader patterns linking land use, noise levels, and breeding parameters can be uncovered.

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(a) Noise Variable	PC1 (65.4% of variance)
Peak kHz	-0.294
Average dB	0.969
Maximum dB	0.969
(b) Density Variable	**PC1 (61.4% variance)**
Boxes w/in 400 m	0.952
Boxes w/in 800 m	0.859
Distance to nearest box	-0.444

Table 4.1. Loading factors for PCAs of ambient noise (a) and breeding density (b) variables for eastern bluebird territories.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Repeat, sound, proportion sampled**	**59.79**	**0**	**0.471**	**1**
2	**Repeat, density, proportion sampled**	**60.11**	**0.323**	**0.401**	**0.851**
3	**Repeat, sound, density, proportion sampled**	**62.97**	**3.18**	**0.096**	**0.204**
4	Repeat, sound, density, proportion sampled,	65.38	5.60	0.029	0.061
5	Repeat, sound, density, proportion sampled, CID,	70.10	10.32	0.003	0.006
6	Repeat, sound, density, proportion sampled, CID,	80.11	20.32	1.8E-05	3.86E-05
7	Repeat, sound, density, proportion sampled, CID,	88.97	30.19	1.3E-07	2.78E-07
8	Repeat, sound, density, proportion sampled, CID,	99.36	39.57	1.2E-09	2.56E-09

Table 4.2. Values used in linear regression models to explore effects of ambient noise environment on cuckoldry rates of breeding eastern bluebirds.

Parameter	**B**	**SE**	**95% Confidence Intervals**	
			Lower	**Upper**
Repeat (1)	-0.093	0.402	-0.495	0.309
Repeat (2)	0.213	0.314	-0.101	0.527
Repeat (3)	0	0	0	0
Proportion sampled	-1.10	0.814	-1.92	-0.289
Density PC	0.006	0.030	-0.024	0.036
Sound PC	0.065	0.772	-0.253	0.384

Table 4.3. Parameters included in final, averaged model explaining the relationship between environmental noise and cuckoldry rates.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Repeat, sound, density, sound*density**	**177.44**	**0**	**0.3492**	**1**
2	**Repeat, density**	**178.07**	**0.635**	**0.2542**	**0.7280**
3	**Repeat, sound, density**	**178.24**	**0.807**	**0.2332**	**0.6680**
4	**Repeat, sound**	**179.17**	**1.734**	**0.1467**	**0.4202**
5	Repeat, sound, density, CID, sound*density	183.76	6.322	0.0148	0.0424
6	Repeat, sound, density, CID, sound*density, CID*density	188.03	10.59	0.00175	0.0050
7	Repeat, sound, density, CID, sound*density, CID*density, CID*sound	194.24	16.81	7.83E-05	0.0002
8	Repeat, sound, density, CID, sound*density, CID*density, CID*sound,	198.83	21.39	7.91E-06	2.26E-05

Table 4.4. Values used in linear regression models to explore effects of ambient noise environment on brood condition of breeding eastern bluebirds.

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
Repeat (1)	1.38	1.55	-0.174	2.93
Repeat (2)	1.41	1.59	-0.187	3.00
Repeat (3)	0	0	0	0
Density	0.341	0.362	-0.021	0.702
Sound	0.065	-0.252	-0.253	0.384
Density*sound	-0.126	0.289	-0.415	0.162

Table 4.5. Parameters included in final, averaged model explaining the relationship between environmental noise and brood condition.

Model	Parameters	AICc	Δ-AICc	Weight	Likelihood
1	**Repeat, sound, density**	**226.96**	**0**	**0.7965**	**1**
2	**Repeat, sound, density, sound*density**	**230.77**	**3.804**	**0.1189**	**0.1492**
3	Repeat, sound, density, CID, sound*density	231.58	4.614	0.0793	0.0996
4	Repeat, sound, density, CID, sound*density, CID*sound	237.15	10.18	0.0049	0.0061
5	Repeat, sound, density, CID, sound*density, CID*sound, CID*density	242.56	15.60	0.0003	0.0004
6	Repeat, sound, density, CID, sound*density, CID*sound, CID*density, CID*sound*density	244.78	17.82	0.0001	0.0001

Table 4.6. Values used in linear regression models to explore effects of ambient noise environment on brood growth rates of breeding eastern bluebirds.

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
Repeat (1)	-4.61	3.17	-7.78	-1.44
Repeat (2)	-4.45	3.50	-7.95	-0.952
Repeat (3)	0	0	0	0
Density	0.099	0.714	-0.615	0.814
Sound	0.332	0.688	-0.356	1.02
Density*sound	0.954	0.025	0.155	1.75

Table 4.7. Parameters included in final, averaged model explaining the relationship between environmental noise and brood growth rates.

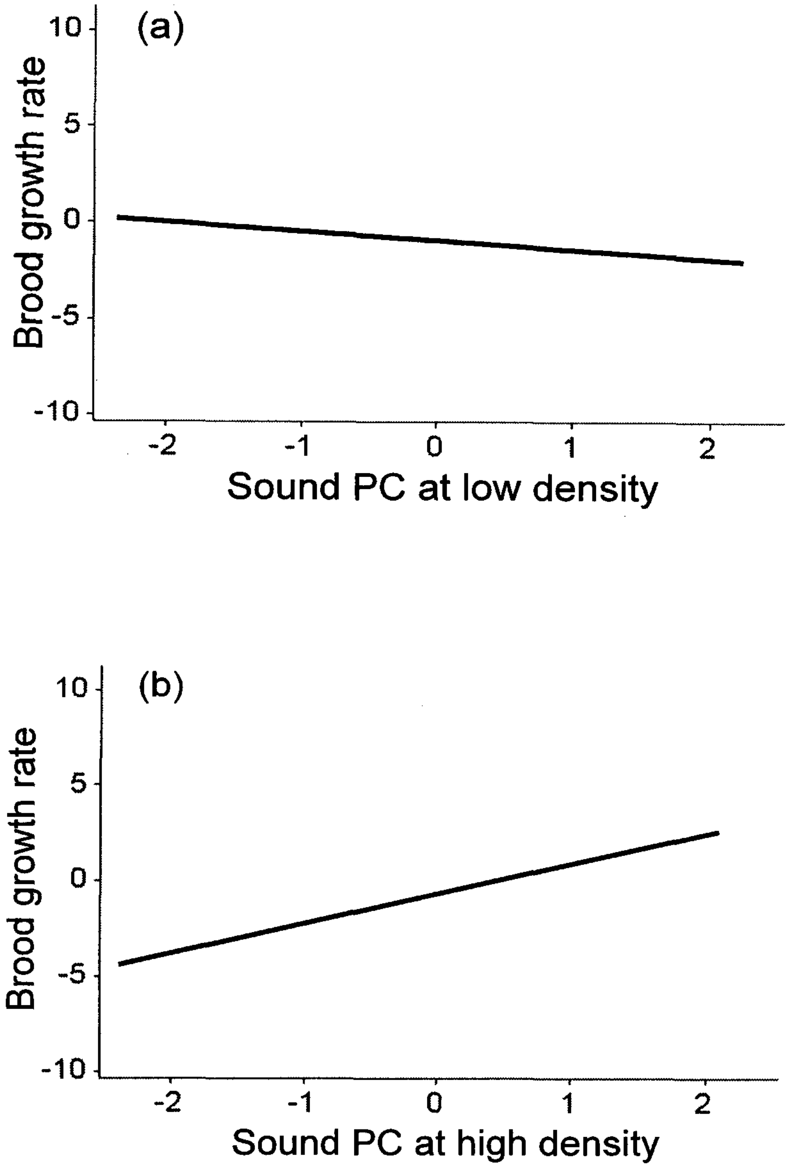

Figure 4.1. Visualization of the different interactions between brood growth rate and environmental noise at low (a) and high (b) breeding densities. Density values were classified as "high" and "low" if they fell above or below the median value, respectively. These categories were not used in the analysis, but are useful for visualizing the relationship, as demonstrated by the regression line, between brood growth rate and the interaction term, sound PC*density. At lower breeding densities, brood growth rate declines with increasing environmental noise; however, the opposite relationship is true at higher breeding densities.

MODEL	PARAMETERS	AICc	Δ-AICc	WEIGHT	LIKELIHOOD
1	**Repeat, sound, density**	**142.47**	**0**	**0.5263**	**1**
2	**Repeat, sound, density, sound*density**	**143.48**	**1.008**	**0.3179**	**0.6041**
3	**Repeat, sound**	**145.01**	**2.545**	**0.1474**	**0.2801**
4	Repeat, sound, density, CID, sound*density	150.89	8.424	0.0078	0.0148
5	Repeat, sound, density, CID, sound*density, CID*density	156.17	13.70	0.0006	0.0011
6	Repeat, sound, density, CID, sound*density, CID*density, CID*sound	163.05	20.58	1.79E-05	3.4E-05
7	Repeat, sound, density, CID, sound*density, CID*density, CID*sound, CID*sound*density	167.65	25.18	1.79E-06	3.4E-06

Table 4.8. Values used in linear regression models to explore effects of ambient noise environment on productivity of breeding eastern bluebirds.

			95% Confidence Intervals	
Parameter	**B**	**SE**	**Lower**	**Upper**
Repeat (1)	-0.039	1.02	-1.055	0.979
Repeat (2)	-0.439	0.900	-1.34	0.462
Repeat (3)	0	0	0	0
Sound	-0.549	0.366	-0.915	-0.183
Density	0.372	0.596	-0.224	0.968
Density*sound	0.011	0.025	-0.014	0.036

Table 4.9. Parameters included in final, averaged model explaining the relationship between environmental noise and eastern bluebird productivity.

VITA

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