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The Impact of Ambient Noise on Eastern Bluebird (Sialia sialis) Nestling Begging

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The Impact of Ambient Noise on Eastern Bluebird (*Sialia sialis*) Nestling Begging

A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelors of Science in **Biology** from
The College of William and Mary

by

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ABSTRACT

A growing body of evidence suggests that environmental ambient noises, particularly anthropogenic noises from urbanization, impact animal acoustic systems. In this study, I tested whether eastern bluebird (*Sialia sialis*) nestlings adjust their begging calls to decrease the interference of ambient noise by recording chick begging along a disturbance gradient. Mean call feature measurements differed with age, with older birds calling more loudly but less frequently and for shorter durations. Call SNR, amplitude, rate, length, and frequency range measured 15 meters away from the nest were lower than measurements inside the nest box, indicating that the environment impacted the propagation of nestling vocalizations. Contrary to my prediction, eastern bluebird nestlings did not increase the amplitude of their begging calls nor did they vary other structural characteristics of vocalizations, even though signal to noise ratio (SNR) of nestling vocalizations decreased as ambient noise amplitude increased along the disturbance gradient. Interestingly, I found that prevalent weather conditions of temperature and humidity attenuated nestling begging calls. Specifically, in warmer more humid weather, while nestling call amplitude and rate as recorded inside the nest box increased, the begging calls attenuated outside the nest box. These results indicate that loud ambient noises likely mask chick begging calls, which suggests that chicks and parents may experience fitness consequences in noisy environments because of inaccurate or inefficient parent-offspring communication.

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INTRODUCTION

Acoustic Communication and Ambient Noise

Acoustic communication is a fundamental means through which animals interact and build social relationships. Among other functions, acoustic communication facilitates such interactions as mate attraction, territorial defense, and parent-offspring interactions, which are crucial to the life histories of animals (Brumm and Slabbekoorn, 2005).

The basic model of acoustic communication involves three elements (FIG. 1). First, a sender creates an acoustic signal, such as a bird vocalization, designed to convey a message to a receiver. This signal, once transmitted, travels through an environment to reach a receiver. Upon receiving the acoustic signal, the receiver interprets the signal and alters its behavior accordingly.

Acoustic signals are subject to degradation during their transmission from a sender to a receiver due to physical phenomena (Slabbekoorn, 2007). Attenuation, irregular amplitude fluctuations, and reverberations may occur as a result of microclimate factors, atmospheric spread, air turbulence, reflections from the ground and buildings, and scatter due to vegetation, among other factors (Slabbekoorn, 2007; Brumm, 2004). Attenuation refers to the decrease of the signal strength, or the intensity of the sound wave in physical terms, as it travels across the environment. In general, higher frequencies attenuate faster than lower frequencies (Wiley and Richards, 1982). Irregular amplitude fluctuations are fluctuations of the amplitude of the signal that reaches the receiver, which is mainly caused by scattering due to air turbulence (Richards and Wiley, 1980). The degree of amplitude fluctuations varies with the frequency of the wave, prevailing weather conditions, as well as the time of day (Richards and Wiley, 1980).

Reverberations, or echoes of the original sound reflecting off surfaces (Slabbekoorn, 2007), are another cause of signal distortion, especially in forested areas with vegetation (Richards and Wiley, 1980). Reverberations disrupt signal temporal structure because the reverberated signal reaches the receiver after the original signal reaches the receiver and may interact with, and possibly even mask, the original signal (Slabbekoorn 2007).

(1)SENDER   **(2)ENVIRONMENTAL OBSTACLES**   **(3)RECEIVER**

RESPONSE
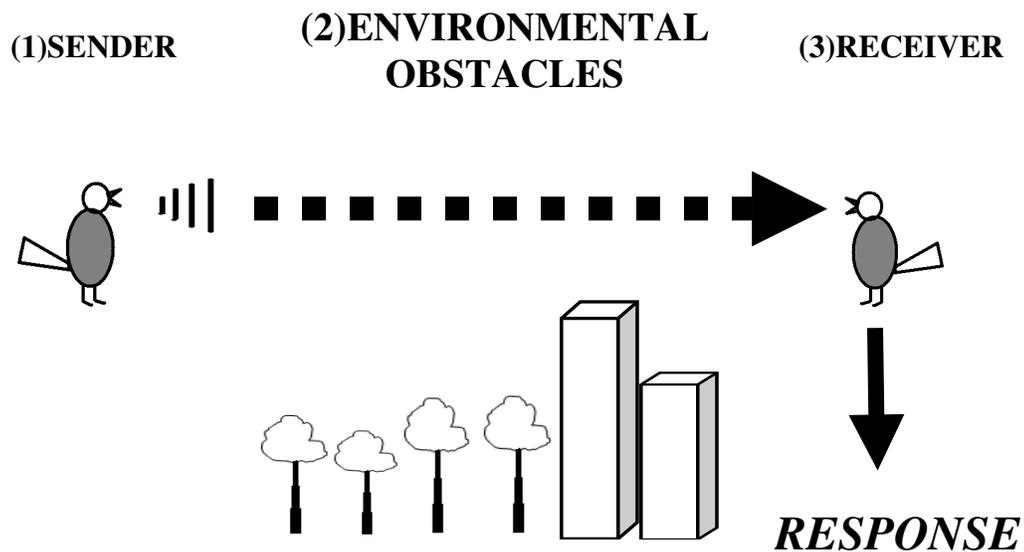
Fig 1. Schematic diagram of a basic acoustic communication model in which a sender (1) emits a coded message, which travels through an environment (2) to reach a receiver (3). The receiver then decodes the signal through sensory pathways in the brain and reacts accordingly. In its transmission, the acoustic signal travels through obstacles including microclimate factors, reflective surfaces, vegetation, water, and ambient noise, which may alter the original message of the sender by changing the structure of the signal or by masking part of the signal. Attenuation, irregular amplitude fluctuations , and reverberations are common ways in which acoustic signals may degrade.

Acoustic communication is further constrained by ambient noise, the subject of primary concern to this study. Noise can generally be defined as "any factor that reduces the ability of a receiver to detect a signal or to discriminate one signal from another (Brumm and Slabbekoorn, 2005)." While noise is classified into internal noise, which

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originates in the receiver's sensory pathway, or external noise, which originates in the environment of the receiver, it is the latter type of noise that is frequently studied in acoustic communication research and which is commonly referred to as ambient noise. Specifically, ambient noise consists of the sounds that occur in the "background" of an environment (Brumm and Slabbekoorn, 2005), which affects the transmission and fidelity of acoustic signals as they travel through an environment from a sender to a receiver (Patricelli and Blickley, 2006).

Ambient noise can be classified according to its sources. Background noises produced by biotic sources, such as vocalizations from other animals, and abiotic noises, such as moving vegetation, wind, flowing water, and rain, are common ambient noises that pose natural constraints to the propagation of acoustic signals (Brumm and Slabbekoorn, 2005). Additionally, anthropogenic noises, such as noise from traffic or machinery, present major selection pressures for animal acoustic signals.

To date, scientists have studied ambient noise in a myriad of environments, such as forests, grasslands, streams, oceans, and urban areas (Slabbekoorn and Peet, 2003) and have discovered that the nature of ambient noise varies considerably from habitat to habitat (Brumm, 2004). For instance, while some background noises, like the ebb of tides, are continuous, others are unpredictable, isolated events, such as a falling tree in a forest. Furthermore, some ambient noises mask a narrow range of frequencies whereas others cover a broad range of vocal signal frequencies. For example, wind constitutes a major source of low-frequency ambient noise in terrestrial habitats while waves, wind and rain in marine environments produce ambient noise over a broad range of frequencies (Brumm and Slabbekoorn, 2005). The species composition within a habitat further

influences the biotic ambient noise within that habitat (Slabbekoorn, 2004). For instance, arthropods might produce a significant component of the background noise in one environment, but bird songs might constitute a major source of ambient noise in another environment, such as a forest (Brumm and Slabbekoorn, 2005).

The "active space" of a signaler refers to the broadcast area in which the signal can be detected by a receiver, which is determined by the signal amplitude as well as the characteristics of ambient noise (Brumm et al., 2004). To detect an acoustic signal, the signal-to-noise ratio (SNR) of a vocalization, which is the ratio of the amplitude of the vocalization to the amplitude of ambient noise, must be above the auditory detection threshold of the receiver (Patricelli and Blickley, 2006). For animal vocalization within the same frequency range as the background noise, signal masking may occur if the SNR of a vocalization lies below the receiver's detection threshold. In other words, high background noise decreases the SNR of a vocalization, which reduces the auditory detection of the receiver (Klump, 1996). It is important to keep in mind, however, that the auditory detection threshold is not a fixed amplitude point above which receivers can detect sound (Stebbins, 1983). A more precise definition of the concept of threshold is that it is the sound level, within a range of middle intensity sound levels, which the receiver detects 50% of the time, on average (Stebbins, 1983).

As follows from the previous discussion of SNR, the degree to which the frequency of an animal vocalization overlaps the frequency of background noise is of major importance to animals, as signal interference may occur for acoustic signals that overlap with ambient noise (Brumm and Slabbekoorn, 2005). The resulting degradation of the signal may change the structure of the acoustic signal significantly enough to

impact the fidelity, or accuracy, of the original message. As successful acoustic communication is crucial in many animal interactions, vocal signal degradation could result in fitness consequences for both the sender and the receiver (Patricelli and Blickley, 2006).

Sender's Response to Environmental Noise

The amplitude, frequency structure, temporal structure, and vocal delivery timing are prominent features of animal vocalizations (Patricelli and Blickley, 2006). By adjusting one or all four features, animals may reduce the masking effects of ambient noise, thus increasing the chance that their vocalizations reach the receiver.

In physical terms, the amplitude of a sound wave is the change in pressure of air molecules as a sound wave passes by, whereby higher amplitude sound waves carry higher amounts of energy (Bradbury and Vehrencamp, 1998). The intensity of a vocalization is the average amount of energy per unit area per unit time of the sound wave traveling in a specific direction, usually given in terms of decibel (dB) units. What is perceived as loudness, therefore, is the intensity of a sound. Various bird species possess varying discriminatory ability to detect sound intensity level differences (Stebbins, 1983). For example, cowbirds (*Molothrus ater)* and canaries (*Serinus canaria*) can detect tones that differ by only 1.5 dB within their sensitive frequency range while other species such as the red-winged blackbird (*Agelaius phoeniceus*) can only detect differences of 3.0 dB (Stebbins, 1983).

Birds also demonstrate the ability to detect differences in frequency, or pitch, of sounds. The frequency of a sound wave is the number of cycles of the wave per second

(Bradbury and Vehrencamp, 1998). Laboratory studies of a number of species revealed birds are sensitive to frequency differences as small as 10 Hz for vocalizations within their sensitive range of 1 to 2 kHz (Stebbins, 1983). However, field studies indicate that birds' responses often do not significantly change to frequency alterations that are 2-3 standard deviations (SD) from the mean frequency in the population (Patricelli and Blickley, 2006).

Temporal structure and vocal delivery timing are other signal features that can be easily manipulated. Temporal structure of vocalizations describe how they are composed, such as the spacing of notes and syllables, as well as serial redundancy, or how often notes and syllables are repeated in a series of calls (Brumm, 2004). Vocal delivery timing involves how many times a particular song is repeated before a bird switches to another song type, as well as how vocalizations are timed in relation to other ambient noises and interspecies vocalizations (Patricelli and Blickley, 2006).

To date, evidence suggests that animals can adjust the above-mentioned features of vocalizations to reduce signal degradation in the short-term. For instance, nightingales (*Luscinia megarhynchos*) demonstrated vocal amplitude adjustment according to the noise level in their natural environment, increasing vocal amplitude in relation to environmental ambient noise (Brumm, 2004). This tendency to increase the amplitude of a vocalization is termed the "Lombard effect". Laboratory experiments demonstrated that nightingale song intensity levels could be adjusted 10 dB, on average, which indicates the potential for amplitude adjustment within the natural constraints of signal production (Brumm and Todt, 2003). The common marmoset (*Callithrix jacchus*) also

increased their call amplitude in response to increased ambient white noise (Brumm et al. 2004).

Several studies also document intraspecies variation in signal frequency between environments with different levels of ambient noise. For example, in a field study of little greenbuls (*Andropadus virens*), males in rainforests with low amplitude ambient noise sang low-frequency notes, while birds in louder ecotone forests did not use these low frequency notes, as they would have be masked by background noise (Slabberkoorn, 2002). Black-faced warblers (*Abroscopus schisticeps*) have been found to use ultrasonic harmonics, possibly to avoid the masking effects of ambient noise from streams (Narins et al, 2004). Signal frequency adjustment in this manner is proposed to be adaptive because common sources of ambient noise such as traffic and torrents produce sounds with low frequency energy; shifting a signal to higher frequencies, therefore, reduces masking by those ambient noises (Brumm and Slater, 2006). Further, it is possible that birds in louder environments simply do not learn the song components in lower frequencies due to masking (Brumm and Slater, 2006).

Adjustment of signal temporal structure and vocal delivery timing has also been documented. For instance, common marmosets increased call syllable duration in the presence of white noise (Brumm et al., 2004). King penguins (*Aptenodytes patagonicus*) and Japanese quail (*Coturnix coturnix japonica*) increased the serial redundancy of vocalizations with increased environmental noise (as reviewed by Brumm, 2004). Chaffinch (*Fringilla coelebes*) males in louder woodland areas, such as those near waterfalls and torrents, sang longer bouts of repeating song types when compared to males in quieter environments, suggesting that males adjusted song redundancy to

overcome the signal interference in high ambient environments (Brumm and Slater, 2006). Adjusting the timing of vocal signal delivery is another mechanism to avoid signal masking, especially masking due to heterospecific vocalizations (Brumm, 2006). Studies revealed that two species of neotropical tree frogs (*Eleutherodactylus coqui* and *E. portoricensis*) avoided signal overlap by preferentially singing during the silent intervals that existed in the playback of heterospecific calls and bursts of noise (Zelick and Narins, 1983). More recently, nightingales adjust their song timing to avoid masking by heterospecific songs in a lab setting, preferentially singing during the silent windows between heterospecific songs (Brumm, 2006).

Long-term changes of the structure of vocalizations are another solution to environmental masking. Currently, there are three hypotheses that seek to explain such changes. The developmental modification hypothesis proposes that the ability to change the vocal structure to reduce masking is dependent on vocal plasticity and the ability to detect masking through auditory feedback, a process where birds compare the vocalizations they produce to a template produced during development (Patricelli and Blickley, 2006). The selection attrition hypothesis (Wood and Yezerinac 2006) suggests that birds may use only the unmasked songs from the many templates that they produce during development. This proposal in only relevant to some bird species, as not all bird species experience selective attrition during development (Patricelli and Blickley, 2006). Finally, the passive acquisition hypothesis suggests that birds only acquire unmasked segments of songs (Rabin and Green 2002) during the sensitive period during which they learn songs (Hultsch and Todt 2004). This hypothesis is only relevant to birds that experience song learning in noisy environments.

Areas of urban development present excellent opportunities to study how animal vocalizations change in a rapidly altering environment. It is expected that two billion people will find homes in newly developed urban areas within the next two decades (Slabbekoorn and Ripmeester, 2008). Urban areas pose unique challenges due to warmer temperatures, higher amounts of chemical pollution, artificial lighting, low vegetation and different predators and food availability relative to species' natural habitats, as well as the presence of impervious surfaces, such as streets and buildings (Slabbekoorn and Ripmeester, 2008). As demonstrated by higher baseline cortecosterone levels of male birds living in cities, such characteristics of urban environments may be relatively more stressful for some animal species (Bonier et al. 2007). Studies demonstrate that increased environmental noise from road traffic are associated with a decrease in the number of individuals of species, as well as a decline in species number (as reviewed in Brumm, 2004). A growing body of literature also documents the impact of urban noise, traffic noise in particular, on animal acoustic communication in a variety of species. For example, great tits (*Paris major*) in urban areas with high traffic noise sang with higher minimum frequencies than birds in quieter environments, suggesting great tits manipulate their songs to avoid interference from urban noise (Slabbekoorn and Peet, 2003). In addition to singing with higher-frequency low notes in urban areas, song sparrows (*Melospiza melodia*) sang the low frequency portions of their songs with relatively lower amplitude when compared to higher frequency song portions (Wood and Yezernick 2006). Birds have been ideal subjects to study the effects of environmental noise on the propagation and transmission of acoustic signals because of their extensive vocal repertoire and their use of vocal signals in many facets of their lives (Klump, 1996).

Bird Communication

While birds use sight in their daily interactions, acoustic communication also plays an important role in avian communication, especially when communicating over long distances, such as through vegetation, when vision might be obstructed (Stebbins, 1983). Birds utilize the syrinx, an organ located near the broncho-tracheal junction, to produce the various sounds used to communicate within species, as well as in interspecific communication (Stebbins, 1983). Like mammals, birds possess an external ear and an ear canal that leads to an eardrum, which allows the amplification of sound energy of certain frequencies (Stebbins, 1983). Experiments have revealed that birds are sensitive to sound frequencies as low as 0.5Hz, while the upper end of hearing of some birds lie near 8kHz. Further, bird species produce some of the most complex vocalizations in the animal kingdom (Lewis, 1983). Importantly, the ability of some birds to alter their vocal repertoire due to learning is an important reason why birds have been used extensively to study acoustic communication in changing environments (Lewis, 1983).

Fitness Costs of Environmental Noise

Signal degradation due to environmental noise poses potential fitness consequences in terms of reproductive success in many birds (Patricelli and Blickley, 2006). In addition, birds' adjustment of vocal signal structure to overcome signal degradation has the potential for associated fitness costs (Patricelli, 2006). Importantly, it is necessary to consider whether there is a net fitness benefit of vocal adjustment (Patricelli and Blickley, 2006). The improved transmission and/or detectability of signals gained by signal adjustments might not necessarily confer a selective advantage as those adjustments to

vocal signals are associated with costs, such as higher energetic expenditure to produce them (Patricelli and Blickley, 2006). For example, increasing the amplitude or rate of repetitions of a signal could pose energy costs to the vocalizing animal. Chaffinch males sang shorter bouts of song types that contained faster trills, which suggests that high rates of repetition are more difficult to produce due to motor fatigue (Brumm and Slater, 2006). High frequency notes and syllables might be more energetically costly to produce, as well. In addition, while higher frequencies are better at overcoming the masking effects of low frequency ambient noise, they are less efficient at transmission than lower frequencies, which could results in signal attenuation over long distances, an additional problem to consider (as reviewed in Patricelli and Blickley, 2006).

Changes in the structure of a vocalization could also impact the receiver's recognition of the signal, impeding the intended response from the receiver (refer to FIG. 1). Scientists have studied the impact of ambient noise and vocal adjustment in female choice. Vocalizations play a crucial role in females' recognition and assessment of potential males, as well as in maintaining pair bonds (Patricelli and Blickley, 2006). If males change the frequency of their vocalizations, conspecific females that prefer low-frequency notes, might no longer recognize them as potential males or find them attractive (Wood and Yezerinac, 2006, Patricelli and Blickely, 2006). For example, female grey partridges (*Perdix perdix*) preferred males that called using lower frequencies as well as longer call durations, suggesting that females used call features to assess male condition (Beani and Dessi-Fulgheri, 1995). Similarly, dropping low frequency notes from a song repertoire could potentially diminish the attractiveness of a

male to females preferring males with a wide song repertoire (Patricelli and Blickley, 2006).

A recent laboratory study aptly demonstrates the impact of ambient noise on female preference of zebra finches (*Taeniopygia guttata*) (Swaddle and Page, 2007). Zebra finches were an interesting study species because females normally prefer their pair-bonded male to novel males, resulting in low rates of extra-pair paternity. Pair-bonds in zebra finches are maintained through a combination of visual, tactile, an auditory cues, with auditory cues playing important roles in mate identification, among other functions. Tests of female zebra finch preference for their pair-bonded males relative to extra-pair males under three levels of ambient white noise (low amplitude white noise at 45dB, intermediate-amplitude white noise at 75 dB, and high-amplitude white noise at 90dB) revealed that as the amplitude of ambient white noise increased, the female's preference for her pair-bonded male decreased. This decrease in preference reached a point where at the high white noise treatment, females did not show preference for their pair-bonded male over novel extra-pair males. This study reveals the possibility that high environmental noise could erode pair-bond preferences to allow for extra-pair copulation, which is potentially a significant fitness cost for male zebra finches.

Vocal adjustment resulting from ambient noise can present tradeoffs for male-male competition, similarly to those presented for female choice. For example, as threat displays are often low frequency vocalizations, an increase in frequency of a threat display to avoid masking may result in the vocalizing male being perceived as less threatening (Patricelli and Blickley, 2006). Bird species, such as Song Sparrows, employ song matching to establish and defend territories (Beecher et al., 2000). Song matching

is a technique used in territorial defense whereby males defending a territory replies to an intruding male's song with the song type that is most similar to the intruder's song within its own repertoire. This method is used to convey the threat of attack to the intruder. Males who drop low frequency notes from a song might, therefore, be less effective at song matching and consequently less successful at defending its territory (Patricelli and Blickley, 2006).

There are still other types of communication that can be affected by environmental noise and have fitness consequences. For example, 'adjusted' vocalizations may influence the risk of predation for the signaler, as the adjusted songs may be more conspicuous or easier to locate. There is also little current knowledge of how alarm calls, flight calls, food calls, and begging calls are adjusted in the presence of ambient noise, yet all of these vocalizations impact avian fitness.

Chick Begging

The evolution of extravagant begging behavior in young birds has been explained most commonly in terms of parent-offspring conflict and the handicap theory. As evolutionary success is measured in terms of allele propagation, the parent-offspring conflict theory suggests that best strategy for a parent to adopt is the one that yields the maximum lifetime reproductive success, or the largest number of offspring that survive to reproduce and pass on one's alleles (Trivers, 1974). Offspring, on the other hand, will benefit most by recruiting more than their fair share of parental care, resulting in a conflict of interest between generations (Trivers, 1974). The handicap theory alternatively proposes that because of associated physical or physiological constraints and costs, chick begging is an

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"honest" indication of chick need, and therefore accurately conveys this need to parents to solicit the appropriate parental care (as reviewed by Villasenōr and Drummond, 2007). "Need" is defined by the fitness benefit a chick gains from receiving a unit of food, which is typically determined by chick body condition (measured by size and/or mass) and for how long the chick has been food deprived (Villasenōr and Drummond, 2007). A recent study of blue-footed booby (*Sula nebouxii*) chick begging indicates that chick begging is an honest indication of need as chicks in poor condition and chicks that were food deprivation begged more intensely than chicks in normal condition and chicks that were fed (Villasenōr and Drummond, 2007). Barn swallow (*Hirundo rustica*) nestlings that were food deprived also begged at a higher rate than control nestlings (Sacchi et al., 2002). Further, research has documented that begging is energetically costly to chicks. For example, the metabolic rate of tree swallow (*Tachycineta bicolor*) chicks while begging was 1.27 times that of their resting metabolic rate (RMR) (as reviewed by Kilner, 2001). In addition, canary (*Serinus canaria*) chicks that were in the higher begging treatment group, where chicks had to beg for longer durations before receiving food, gained less weight than their siblings who had to beg for a shorter duration (Kilner, 2001).

A third explanation for extravagant begging behavior suggests that chick begging has evolved to overcome obstacles in transmission, in order to preserve signal fidelity (Leonard and Horn, 2005). To date, there has been just one study of begging calls under noisy environmental conditions that addresses this theory. Leonard and Horn (2005) investigated the design of begging signals of tree swallows in a comprehensive study that included experimental approaches both in the field and in the lab. To evaluate the

association between chick call features and ambient noise levels, the experimenters recorded the begging of chicks in the field after food depriving all but one chick from each nest for 30 minutes, during which time parents fed the single nestling in the box. After 30 minutes, the rest of the chicks were returned to the nest and chick begging calls recorded. Next, in order to determine whether white noise impacts nestling calls, the researchers used play back of white noise simultaneously with the playback of parental calls to a control chick and an experimental chick from each nest in the laboratory. Finally, the investigators presented parents with two treatments of chick call amplitudes, a *Soft* treatment in which chick calls were masked by white noise and a *Loud* treatment with a high SNR of chick calls, to evaluate how the chick call adjustment to noise impacted parental behavior. The researchers found that in the field, tree swallow chick begging call amplitude, length and frequency range increased with elevated environmental noise, while only chick call amplitude increased in response to the playback of noise in the lab. This study further demonstrated that loud environmental noise eroded parents' discriminatory ability to detect higher rates of calls, which tree swallow parents had preferred in an earlier study, importantly indicating changes in parental behavior in response to ambient noise.

Eastern Bluebirds and Chick Begging Calls

In my study, I intended to evaluate the impact of ambient noise on the structure of eastern bluebird (*Sialia sialis*) chick begging calls.   Eastern bluebirds are small thrushes found from Ontario to Mexico (Gowaty, 1998). This brightly colored bird nests in secondary cavities, whether naturally occurring, built by other animals, or by humans (i.e. nest

boxes). Eastern bluebird breeding pairs form in early spring and nest building typically occurs during late February and early March. Pairs commonly lay multiple clutches within a single breeding season, with the first eggs hatching as early as late February and the last broods hatching as late as September. Young eastern bluebirds are altricial at hatching and solicit parental care with stereotypical opened beaked calls and up-stretched necks. Parents typically feed nestlings adult and larval invertebrates (mostly insects and spiders), while also maintaining nest sanitation by carrying away fecal sacs excreted by the chicks. In our study population, parents visited nests as regularly as every 10-15 minutes or as sparsely as 30-45 minutes. Prior to opening their eyes, nestlings use short, high pitched *peep* calls in response to the noise of parents arriving at the nest (Gowaty and Plissner, 1998). Based on previous studies indicating chick begging confers chick need (Villasenōr and Drummond, 2007, Sacchi et al., 2002), I assumed that the fidelity of these calls are crucial to the growth, development and ultimately, to chick fitness. Considering this fundamental role of chick vocalization in determining nestling fitness, I sought to generalize findings on chick begging in ambient noise. In this study, I investigated the impact of ambient noise on eastern bluebird nestling begging calls across a noise-disturbance gradient in the rapidly suburbanizing city of Williamsburg, VA.

Study Goals

I hypothesized that eastern bluebird chick begging calls will vary along the disturbance gradient in a manner that decreases the interference of ambient noise. The major goals of this study were to determine whether:

i)   The structure (amplitude, lowest frequency, highest frequency, frequency range, duration, and rate) of eastern bluebird chick begging calls varies across broods along a disturbance gradient, in a manner that increases the SNR as ambient noise increases. Based on previous research (refer to *Senders Response to Environmental Noise* section), I predicted that as the amplitude of ambient noise increases, chick call amplitude, highest frequency note, call duration, and call rate will increase while call frequency range will decrease with increased ambient noise.

ii) The perceived begging call structure, as it is recorded by microphones, changes with increasing distance away from nest box. Specifically, I predicted that the perceived chick call amplitude, highest frequency note, frequency range, call duration, and call rate will decrease directly outside the nest box (as measured at 1.5cm above nest box), when compared to inside the nest, based on what I know about the degradation of signals during transmission (refer to FIG. 1).

iii) The begging call structure changes with brood age. As Eastern bluebirds are oscines (Gowaty and Plissner, 1998) with the ability to learn, I predicted that bluebirds adjust their begging calls to decrease the interference of ambient noise. I can partially evaluate this prediction by comparing chick call structure between day 7 and day 10. Predictions for this goal are similar to those proposed for goal (i).

iv) The perceived structure of chick begging calls differ inside nests than outside. My predictions for this goal were similar to those in goal (ii) (chick begging signals will degrade as they transmit from inside the box to outside the box).

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METHODS

A 400-box eastern bluebird population has been previously established around Williamsburg, Va by our lab. From these boxes, I sampled 19 nests between May and July 2007. Of the 19 nests, 3 sites were on campus, 3 sites were in golf courses, 2 sites were next to roads, 1 site was next to a park parking lot, 6 sites were located near the fields, wooded areas, and roads within the property of a hospital, 1 site was in a clump of trees next to a recreational field, 2 sites were on fields, and 1 site was in a state park. These sites provided a variety of environments and different levels of human disturbance to establish a disturbance gradient for my study.

a) Calibrating Mic

Before using mics in the field, I calibrated the microphones in a sound-proof booth using the calibration instructions provided on the Raven software website, with the assistance of a graduate student. This calibration was necessary in order to allow comparison of the recordings taken from the two types of microphones we used to record chick begging. We first measured the amplitude of computer generated pure tones of known amplitude. We then recorded the same pure tones in Raven Pro 1.2 using the mic we wanted to calibrate. Using the RMS (root mean square) amplitude feature in Raven, we measured the recorded amplitude of the pure tones, taking the average of 5 measurements. The ratio of the reference measurement of the pure tones to the measurements made in Raven gave the calibration constant. The "true amplitude" of recordings made in the field could be obtained by multiplying the RMS amplitude measurement given in Raven by the calibration constant. If needed, we could convert the dimensionless kU amplitude

measurements in Raven to decibels using the following formula: dB = 20 log (calibrated RMS pressure/ reference pressure), where the reference pressure is 2×10^{-5} Pa.

b) Measuring Begging Calls

I recorded the begging calls of eastern bluebird chicks using a Sennheiser ME67 shotgun microphone (when recording outside the nest) and a Sennheiser e608 microphone (when recording on the nest box, as the shotgun microphone would not fit in the box), recording on a Marantz PMD660 solid-state recorder. Recordings were taken from 1.5cm directly above the nest box, and at distances of 15m and 40m in all four cardinal compass directions (using Sennheiser ME67), and inside the nest box (using Sennheiser e608). Recordings taken from outside the nest used the nest as the central reference point and recordings were taken at a height of approximately 1.6m above the ground from the North, East, South, and West of nest, in respective order at each distance. After setting up the recording equipment at each recording point (microphone facing the nest attached to recorder mounted on a tripod), I observed the nest from a distance of 20-40m so as not to disturb the parents. I observed the site and recorded until a parent fed the chicks or until 40 minutes elapsed. Each nest was visited twice, once when the nestlings were 7 days of age and again at day 10.

In addition to chick begging recordings, I took a number of other measurements to reduce confounding variables that may influence nestling vocalizations and/or ambient noise using a Kestrel 4000 weather meter: air temperature (measured to 0.1 degree farenhite) and humidity (to 0.1%) inside and outside the box, and wind speed (to 0.1 meters/sec). The Kestrel weather meter was unavailable during several days of data

collection. In those instances, I was unable to obtain environmental measurements inside the nest box while I obtained ambient temperature, humidity, and wind measurements from a weather station located on campus at the Keck Environmental Field Laboratory. After recording the chick begging, I also measured chick mass (with an electronic balance to 0.1g precision) and measured chick wing length (unflattened wing chord with dial calipers to 0.1mm precision). Chick mass and wing length were averaged across each nest boxes on each day to give one measurement per box per day

At most nest sites I did not obtain recordings from precisely all four cardinal directions at each distance, most commonly due to physical barriers of buildings, roads, dense vegetation, or the presence of water bodies. In such instances, I moved to a new location within 5 meters of the intended point of recording, when possible.

c) *Measuring Call Features, Ambient Noise and Analysis*

I digitized recordings and measured call structural features using Raven 1.2 software and measured the following features: RMS amplitude, which is the average of the square of each point of a selection of the chick call waveform in Raven (in dimensionless kU), lowest frequency (Hz), highest frequency (Hz), frequency range (difference between highest frequency and lowest frequency in Hz) and duration of calls (sec). I measured each feature every 5 seconds from the beginning to the end of 1 bout of calls, which was located visually by the presence of chick calls on the spectrograph and auditorily when I heard the characteristic chick calls, and averaged these measurements to get a value for each measurement. To measure ambient amplitude, I measured 5 seconds of ambient noise immediately preceding and following a bout of calls and averaged these 2 values to

obtain the ambient amplitude measurement for each recording. Both ambient amplitude and call amplitude were calibrated using the calibration constant obtained earlier. I then calculated the SNR (call amplitude/ambient amplitude) and call rate (# calls/duration of call bout (sec)). Finally, I averaged measurements at each location to obtain one value per distance for each day of recording.

For my analysis, I used SPSS 14.0 software to run Generalized Linear Mixed Models using the following explanatory variables in each model: Site as an among-subjects factor, Age and Distance as within-subjects factors, Inbox temperature, Inbox humidity, Outside temperature, Outside humidity, Calibrated ambient noise amplitude. Dependent variables included RMS amplitude, lowest frequency, highest frequency, frequency range, duration, rate, and SNR. My final model only used data from inside the nest box and at 15m as nestling vocalizations did not appear on a majority of the spectrographs for the recordings taken at 40m.

RESULTS

Sources of Ambient Noise at Study Sites

The most common source of biotic ambient noise near nest boxes was vocalizations from other bird species, while wind provided a minor abiotic source of ambient noise. Anthropogenic sources of ambient noise included vehicles, operation of machinery including drills, lawnmowers, and an air conditioning unit.

Begging Calls

Table one provides estimated marginal means for call features measured on day 7 and day 10. I found that while call amplitude and SNR increased with age, nestling call rate and duration decreased with age (Refer to Fig 3 and 4). Mean call features of SNR, amplitude, call rate, and duration all significantly decreased at 15m when compared to inside the nest box (Refer to Table 2, Figure 3 and 4).

The SNR of calls decreased significantly as the ambient noise level increased at the nest site (β = -7.44, df = 1 p = 0.001). I found no significant associations between any other call feature and ambient noise.

Interestingly, I found significant associations between chick call features and the environmental variables of temperature and humidity. Chick call amplitude (β = -1.14, df = 1, p < 0.00) frequency range (β = -92.54, df = 1, p = 0.035), SNR (β = -5.32, df = 1, p < 0.001), and call rate (β = -0.184, df = 1, p < 0.001) all decreased significantly as the ambient temperature outside of the nest site increased.

I found an opposite correlation when looking at chick call features and environmental measurements inside the nest box. Specifically, chick call amplitude (β = 0.985, df = 1, p = 0.000) and SNR (β = 0.631, df = 1, p = 0.035) increased significantly as the ambient temperature increased while call rate increased (β = 0.209, df = 1, p < 0.001) with warmer temperatures outside the nest box.

Fig 2. Comparison of various spectrographs of recordings taken inside the nest box (a,b) and at 15m (c,d), demonstrating the variation in ambient noise level, frequency, intensity, rate and physical structure of chick begging calls.
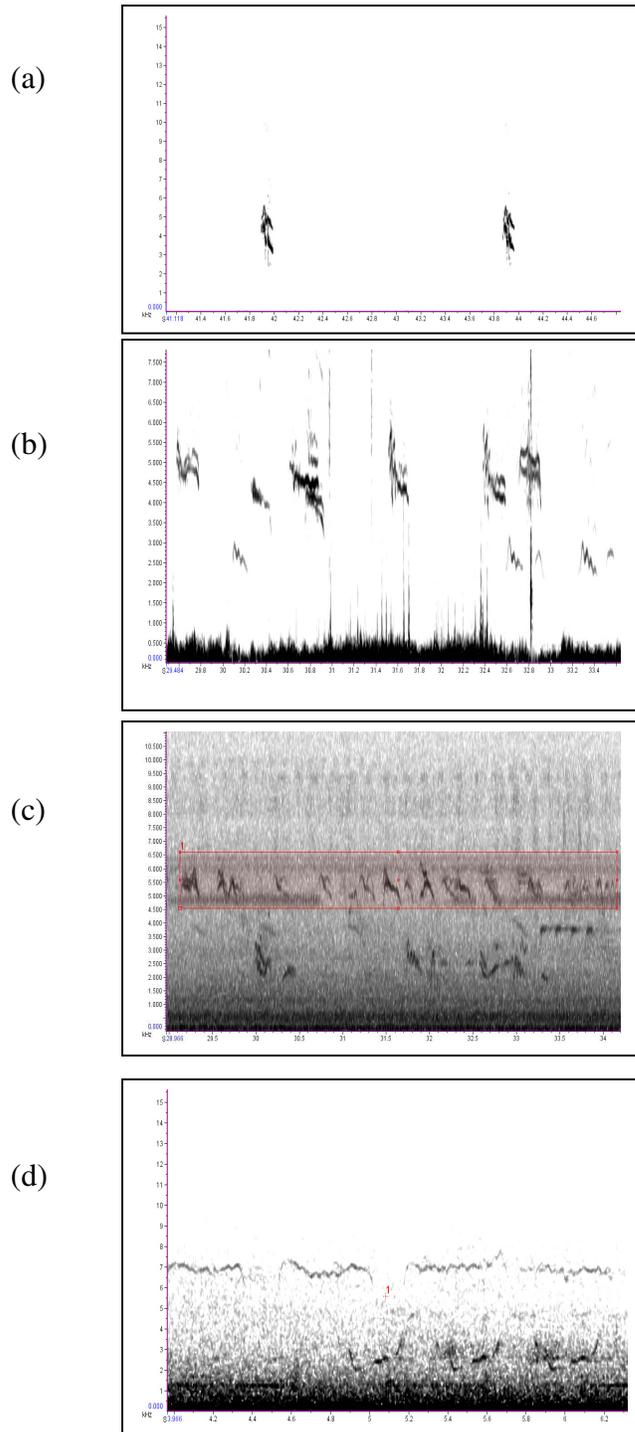
Table 1. Summary of estimated marginal means of chick call features and 95% Wald confidence intervals for 7 and 10 days of age. * indicates significance at p < 0.05.

Call Feature	Age	Mean	95% Wald CI	
			Lower	Upper
SNR*	7	3.62	-1.47	8.71
	10	19.84	15.25	24.44
Call amplitude (kU)*	7	2.29	1.39	3.19
	10	4.60	3.42	5.79
Call rate (calls/sec)*	7	2.61	2.43	2.79
	10	1.81	1.66	1.96
Call bought Length (sec)*	7	44.23	35.89	52.57
	10	2.22	-7.70	12.14
Frequency Range (Hz)	7	1455.97	1279.86	1632.08
	10	1354.76	1162.19	1547.34
Lowest Frequency (Hz)	7	4860.90	4251.25	5470.55
	10	5138.75	4188.59	6088.91
Highest Frequency (Hz)	7	6316.87	5739.35	6894.38
	10	6493.52	5541.84	7445.20

Table 2. Summary of estimated marginal means of chick call features and 95% Wald confidence intervals for inside the nest box and at 15m. * indicates significance at $p < 0.05$.

Call Feature	Distance(m)	Mean	95% Wald CI	
			Lower	Upper
SNR*	0	19.03	15.49	22.58
	15	4.43	1.25	7.60
Call amplitude (kU)*	0	6.36	5.54	7.17
	15	0.53	-0.34	1.41
Call rate (calls/sec)*	0	2.38	2.27	2.49
	15	2.03	1.82	2.25
Call bought length(sec)*	0	31.12	27.37	34.88
	15	15.33	10.62	20.03
Frequency range (Hz)*	0	1887.67	1731.27	2044.07
	15	923.07	832.37	1013.77
Lowest frequency (Hz)	0	4633.60	4320.59	4946.62
	15	5366.05	4811.62	5920.47
Highest frequency (Hz)	0	6521.27	6161.48	6881.07
	15	6289.11	5806.42	6771.81

Table 3. Summary of the direction of associations between chick begging call features and increases in ambient noise amplitude, air temperature inside and outside the box, and relative humidity inside and outside the box. + signifies a significant positive relationship; - signifies a significant negative relationship; NS signifies a non-significant relationship (at $p < 0.05$). N= 24

Call feature	Ambient noise amplitude	Air temperature		Relative humidity	
		Inside	Outside	Inside	Outside
SNR	-	+	-	NS	NS
Call amplitude	NS	+	-	NS	NS
Call rate	NS	+	-	+	-
Call bout length	NS	NS	NS	+	-
Frequency range	NS	NS	-	NS	NS
Lowest frequency	NS	NS	NS	NS	NS
Highest frequency	NS	NS	NS	NS	NS

I observed a similar pattern of opposite relationships inside the nest box when compared to outside the nest box when looking at the correlations between chick call features and humidity. As the humidity outside the nest box increased, the call bout length (β = -1.623, df = 1, p = 0.015) and rate of calling of chicks (β = -0.048, df = 1, p < 0.001) decreased while the length (β = 2.587, df = 1, p = 0.003) and rate of calls (β = 0.071, df = 0.88, p < 0.001) increased with increasing humidity inside the nest box.

Finally, linear regressions between chick fitness, as measured by chick mass and wing length, and ambient noise yielded no significant results.

Fig 3. Estimated marginal means of SNR, call amplitude, call rate, and call bout length for age 7 and age 10. Standard error included.
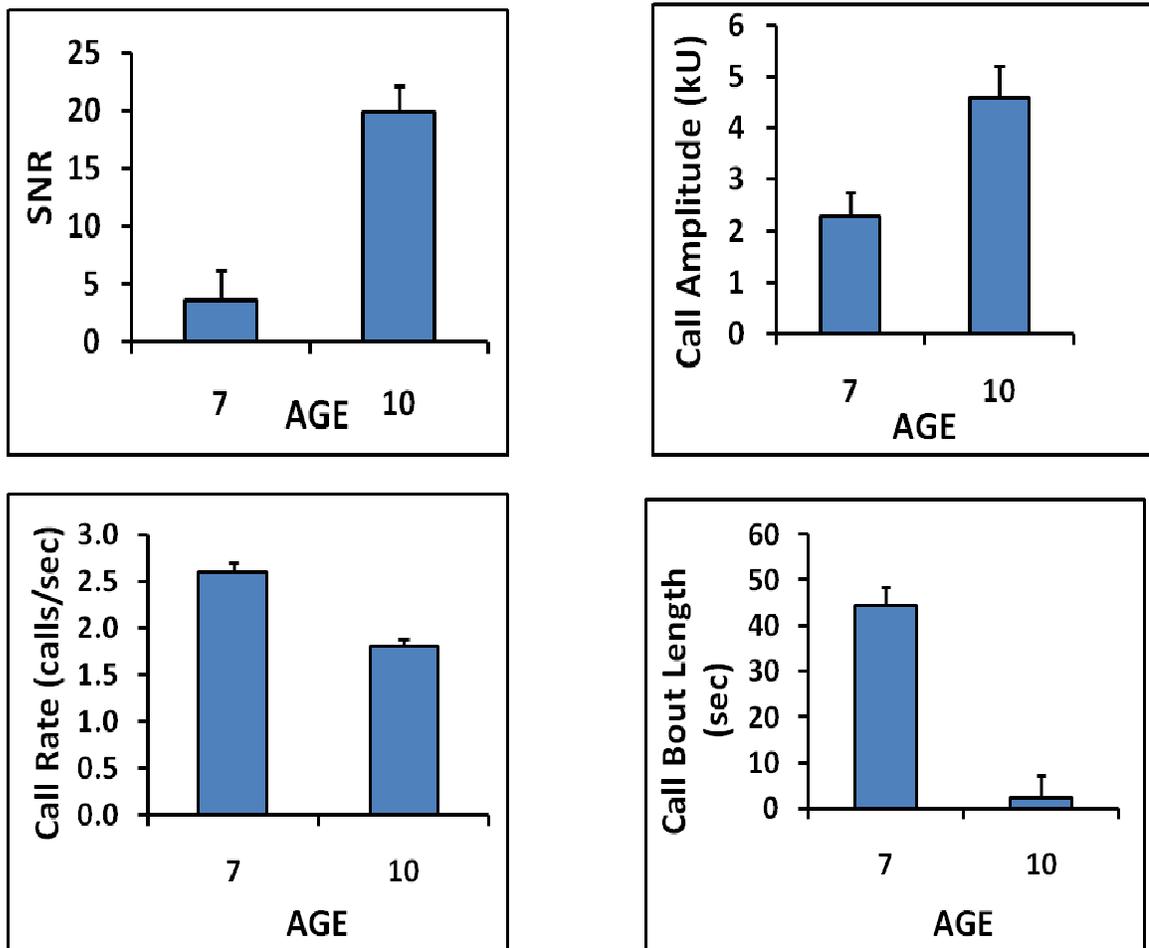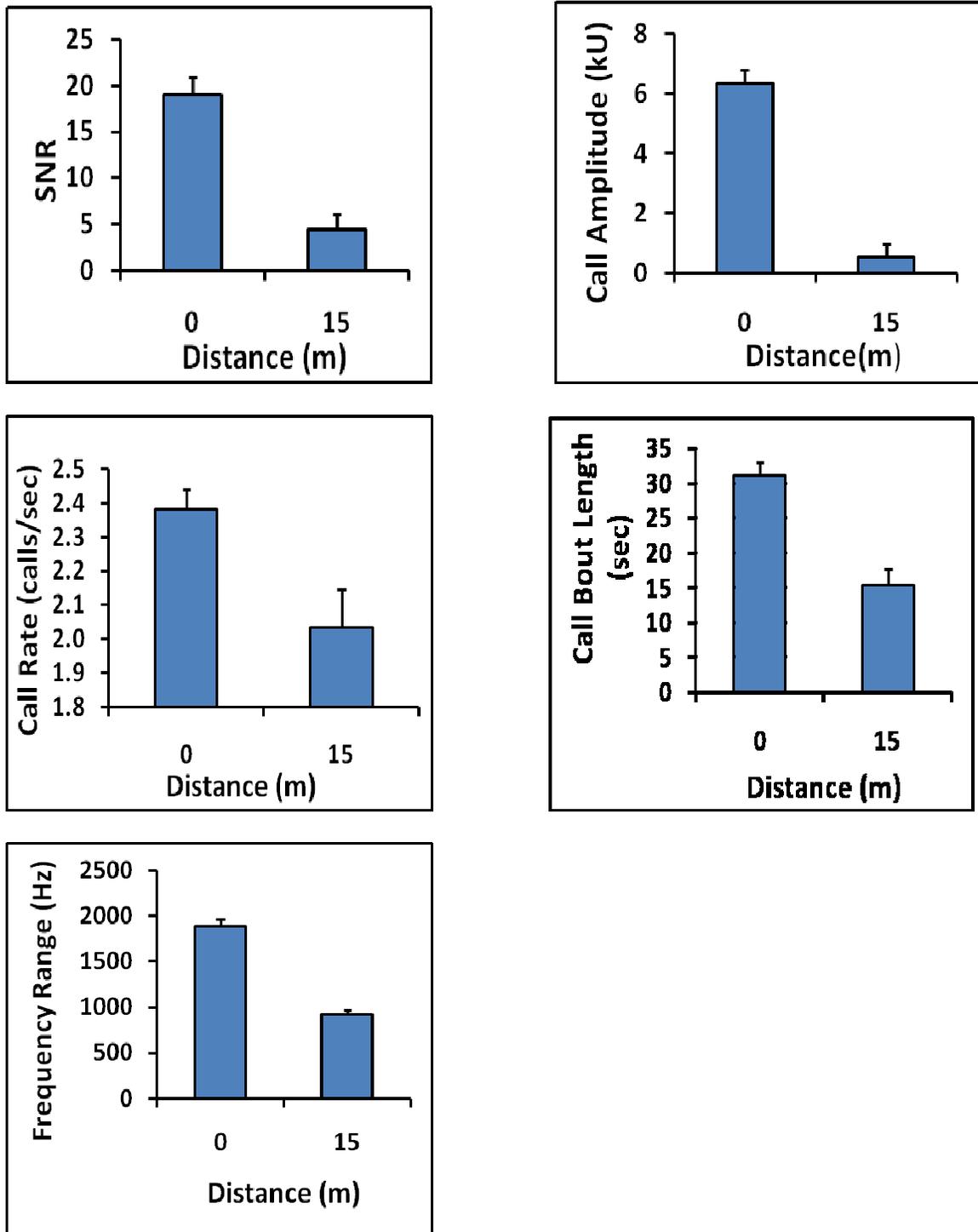
Fig 4. Estimated marginal means of SNR, call amplitude, call rate, call bout length, and frequency range inside the nest and at 15m. Standard error included.

DISCUSSION

This study demonstrated that the signal to noise ratio of eastern bluebird nestling vocalizations significantly decreases as the amount of ambient noise near the nest increases. Further, chick call features attenuated with increasing temperature and humidity outside the nest. Contrary to my prediction, nestling call amplitude did not increase in response to the ambient noise level near the nest box. However, chick call features varied with both the age of the nestling and the distance from the nest; chicks called louder but at a slower rate for a shorter time when they were older while call features all attenuated with distance from the nest.

Study Limitations

While I collected data from 19 separate sites, I was unable to obtain full sets of data for a majority of the sites due to technical challenges, parents not visiting nest while we were recording (especially when mics were attached to the inside of nest), and commonly, due to the inability to discern chick begging calls on Raven, particularly at 40m. As a result, I combined my data from day 7 and day 10 for 15m and inside the nest box to run my final analysis, for a final sample size of 24. This prevented me from addressing intricacies I had hoped to tease apart in goal (ii). Further, my results that nestling call features, particularly call amplitude, did not vary with ambient noise could be partially an outcome of the reduction of sampling sites to 11 nests with full data, which my lab will have to explore in the future with a larger study.

Discussion of Results

My finding that bluebird chick calls have a significantly reduced amplitude, SNR, frequency range, and call rate at 15m when compared to measurements taken inside the nest box clearly demonstrates that bluebird chick calls attenuate as they travel outward from their source in the nest box, contributing to the existing literature that the environment degrades acoustic signals during their transmission (Brumm, 2005). Relevant to my sites, physical phenomena including vegetation, wind turbulence, as well as ambient noise, both from heterospecific vocalizations, as well as from anthropogenic sources, would have played a role in signal degradation. Signal attenuation in the environment due to these factors can, therefore, result in inefficient communication between bluebird nestlings and parents. Further, other aspects of urban environments associated with increased traffic and noise, including increased disturbance events, increased impervious surface, and decreased vegetation (Slabbekoorn and Ripmeester, 2008) might play an important role in the availability of food and parental behavior and should be explored in future studies.

If bluebird parents hear only parts of nestling vocalizations, they are more likely to underestimate chick need, given that chick begging is an honest indication of chick hunger and condition (Villasenōr and Drummond, 2007). While no direct evidence exists which indicates that eastern bluebird chick calls are an honest signal, nestlings of other species of birds including the blue-footed booby (Villasenōr and Drummond, 2007) and tree swallows (Sacchi et al., 2002) beg to demonstrate need. Another consequence of impaired communication for nestlings can occur during predatory events. If such an event occurs while the parents are away from the nest, bluebird chicks might not be able

to communicate their state of vulnerability as effectively, if vocalizations attenuate in the environment. It would be interesting to address these predictions by conducting a laboratory study to investigate the response time of parents to chick alarm calls in white noise. If proven successful, a field study using playbacks of chick alarm calls should be conducted to evaluate parental responses to chicks under ambient noise constrains in their natural habitats. More immediately, an appropriate next step for our lab will be to investigate the impact of the physical environment on eastern bluebird nestling vocalizations. Specifically, the immediate territory of the nest box can be mapped using Geographic Information System (GIS) software to evaluate the impact of the type of vegetation, such as grasses, shrubs, and trees, as well as the ratio of vegetative surface to other obstructions, such as buildings.

Implicit in this study, was the assumption that eastern bluebird nestling vocalizations are used by parents to determine chick need when they are away from the nest. However, studies have not explicitly investigated whether chick vocalizations are important to parental care when parents are not in direct contact with their young. It is possible that parents only use chick vocalizations within a specific broadcast area from the nest. Investigating how parents use nestling vocalizations when they are away from the nest box is another crucial step to understanding how ambient noise may impact parental perception of begging and their subsequent care-taking behavior.

I found that signal-to-noise-ratio (SNR) of chick calls decreased as the amplitude of ambient noise increased, further supporting the idea that background noise constrains the propagation of acoustic signals (Slabbekoorn, 2007). The result that eastern bluebird nestlings did not adjust their begging calls as ambient noise increased demonstrates that,

unlike tree swallow nestlings (Leonard and Horn, 2005), eastern bluebird nestlings do not adjust their begging calls to overcome the constraints of ambient noise. Previous studies in my lab demonstrated that eastern bluebird males have the ability to increase their vocalization in response to ambient noise level. One conclusion I can draw from these results is that eastern bluebird nestlings might not have the physiological capability to adjust vocalizations at age 7 and 10. Further, no studies, to my knowledge, have investigated eastern bluebirds' sensitive period in which they learn songs. Observations indicate that the basic *Peep, Zeee, and Tu-a-wee* of bluebird nestlings require little learning (Gowaty and Plissner, 1998), so it is possible that bluebird chicks are unable to learn to adjust their vocalizations according to ambient noise during their early days of development. A third possibility is that nestlings do not perceive differences in ambient noise to begin with. Regardless of the reason, however, I can surmise that bluebird chicks are more vulnerable to constraints posed by ambient noise than either adult bluebirds or nestlings of other species because they do not (or cannot) adjust their vocalizations. Natural selection is likely to shape the evolution of acoustic communication in a manner that reduces signal masking and increases signal fidelity (Brumm and Slabbekoorn, 2005). Nestling begging calls that do not reach the parents are likely to result in negative consequences for both the chicks and parents. Chicks that cannot adjust begging signals to overcome environmental constraints are likely to be fed less, and therefore less fit, than those that produce signals that overcome the masking effects of ambient noise. From the parent's perspective, overcoming ambient noise constraints that may preclude chick begging detection will improve their overall fitness by being able to better take care of nestlings until they fledge from the nest.

As mentioned above, this study did not find call features of amplitude, frequency, or timing to relate to ambient noise, nor did I find any associations between chick fitness and ambient noise. While mean chick call amplitude and corresponding SNR was higher on day 10 as compared to day 7, for example, I cannot infer whether this results from learned changes in nestling calls, or whether this is a result from an associated increase in mass and, therefore, ability to create louder vocalizations. No study to date has explicitly studied the physiology of nestling begging to determine whether larger nestlings have the ability to produce louder sounds, which is another area that needs future attention.

Another possibility for the result that chicks did not adjust call features to ambient noise levels is that a tradeoff may exist between the energetic demands of begging call adjustment to overcome ambient noise and greater transmission of begging. The returns in parental care may be insufficient to maintain the high energy expenditure required for longer call duration, or other adjustments of begging calls (Kilner, 2001). In other words, there may be net costs to adjusting begging calls in noisy environments

In addition, unlike adult birds that have periods of high vocal activity early in the day, which often coincides with periods of high road traffic in the mornings (Slabbekoorn and Ripmeester, 2008), bluebird chicks beg throughout the day. It is possible that bluebird chicks living in noisier environments allocated more energy or adjusted their begging calls, to coincide with predictable lulls in traffic and other environmental noise, in order to maximize on parental care during those times to make up for decreased parental care during times of high environmental noise. We know that some species including neotropical tree frogs (Zelick and Narins, 1983) and nightingales (Brumm, 2006) have the ability to adjust vocal delivery timing to escape masking from

heterospecific vocalizations. It would be interesting to investigate whether young animals can learn to do the same in response to ambient noise by studying chicks' allocation of energy for sound production throughout the day. Further, previous research suggests that some species of birds increase the serial redundancy of syllables of calls to improve signal transmission (for example, Brumm and Slater 2006). While this study revealed perceived chick call rate is lower further away from the nest, I did not specifically investigate whether the redundancy of specific syllables varied throughout the disturbance gradient, which would be another interesting addition to future studies.

The opposing relationships between chick call features and environmental measurements (temperature and humidity) inside versus outside the nest box may suggest differential environment influences on the biotic processes of chick begging production as compared to the physical processes of sound propagation. For example, as the temperature increased within the nest, chicks called louder and at a higher rate, increasing the SNR. However, the begging calls that reached the microphone outside the nest box at higher temperatures were softer, with a lower SNR, and also a slower rate of calling. The diminishing properties of chick call features as they travel through the environment during warmer days may be a result of the corresponding higher humidity during warmer days. Higher temperatures allow the atmosphere to hold more moisture, which generally absorbs sound waves, resulting in loss of sound pressure (Bradbury and Vehrencamp, 1998). Another possibility for these results is that chicks may be responding to parental behavior. During warmer temperatures, bluebird parents may feed at a lower rate in order to reduce body heat generated to stay cool. Chicks may call at a higher rate and increased amplitude, therefore, because they are fed less and are hungrier during warmer

days. This, combined with decreased signal transmission during warmer days, could explain the higher intensity of calls during higher temperatures. Another important possibility is that chicks have a greater need for parental care in warmer and more humid days but this need, in the form of calls of higher rate and amplitude, is not conveyed to the parents due to greater signal attenuation in warmer and more humid temperatures. This is a novel finding that should be explored further in future studies. However, this hypothesis rests on the determination of whether bluebird chick calls are an honest indication of need.

In future studies, the direction that nest boxes face should be recorded as one might expect begging calls to be louder when perceived from the front of the nest rather than the back, indicating that the direction of how nest boxes are placed relative to perching and foraging sites might be important in parent-offspring communication. It is further possible that the position of the nest box influences how nestlings perceive noise. For example, if loud traffic noises are emitted directly in front of the nest box entrance, nestlings might perceive that noise to be louder than if the traffic noise was emitted from behind the nest box, which could results in variable nestling response, even though the noise itself may be the same.

I also did not explicitly record adult vocalizations, which we know in other species vary with ambient noise, in terms of amplitude, frequency, serial redundancy, and vocal delivery timing (as reviewed by Patricelli and Blickley, 2006). No studies, to the best of my knowledge, have investigated whether there is a correlation between variation in adult vocalizations and offspring vocalizations throughout a noise gradient.

Investigating such interactions between parents and offspring is an important next step, as vocal signal adjustment in one is unlikely to occur in isolation of the other.

Future research should also take into consideration ambient noise's impact on parental behavior as it has been demonstrated that parental feeding preferences can be eroded by ambient noise (Leonard and Horn, 2005). As mentioned in the introduction, I observed variation in the parental feeding rates at different nests. It would, therefore, be interesting to determine whether parental feeding rates are correlated with ambient noise levels. If increased intensity and rate of chick begging calls are associated with increased parental feeding rate, there may be fitness consequences for parents. For example, parents may experience a tradeoff between increased chick fitness due to increased parental care and decreased energy allocation to self-maintenance. In this study, however, bluebird nestlings decreased begging rate and duration with age. One possibility for this result is that parents fed older chicks with larger pieces of food, which might take nestlings a longer period of time to digest, resulting in a lower rate of calling.

Importantly, research should consider parental response to chick's vocal adjustments, as well as the impact of ambient noise on parental discrimination of chick begging and resulting parental behavior. These goals can be accomplished with playback experiments in the lab, as well as in the field, similar to the ones conducted by Leonard and Horn (2005). For example, a laboratory study could play back white noise simultaneously with the playback of parental calls to a control chick and an experimental chick taken from nests in the field to investigate whether chicks adjust their calls in response to ambient noise. Next, to test whether chick calls influence parental behavior, a field study could play two treatments of chick call amplitudes to parents after removing

chicks from the nest. Two fed nestlings could be placed on opposite sides of a nest box with an associated speaker playing either a soft or loud treatment of begging calls. The soft treatment would playback chick calls that are masked by white noise while the loud treatment would playback chick calls with a high SNR. Quantifying the number of times the parent fed the soft treatment chick relative to the loud treatment chick would help determine parental response to ambient noise.

CONCLUSION

Increasing evidence suggests that anthropogenic noises from urbanization impacts animal acoustic systems. In this study, I investigated whether eastern bluebird nestling begging calls vary along a disturbance gradient of ambient noise. Contrary to my prediction and a previous study of tree swallow nestlings, this study found that eastern bluebird nestlings do not increase the amplitude of their begging calls nor do they vary the structural characteristics, including frequency of vocalizations, rate of calls, and duration of calls, with ambient noise. However, I found that prevalent weather conditions of temperature and humidity attenuate begging calls. Specifically, in warmer more humid weather, eastern bluebird nestling vocalizations attenuate outside the nest box, which is consistent with research conducted on the propagation of sound in various mediums and temperatures. Further, I found that mean call feature measurements differed with age, with older birds calling more loudly but less frequently and for shorter durations. These observations may relate to nestlings' physical increase in size and the reduced feeding rate of parents as nestlings process larger but fewer food items as nestlings age. Finally,

this research indicates that increased ambient noise is associated with a decrease in signal to noise ratio of nestling vocalizations. In other words, loud ambient noises likely mask chick begging calls, which suggests that chicks and parents may experience fitness consequences in noisy environments because of inaccurate or inefficient communication between parents and their offspring. I suggest that future studies explore the impact of ambient noise on parental behavior and aspects of parent-offspring communication and conflict related to raising a brood of nestlings.

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