THE EFFECT OF NEST ACOUSTICS ON THE BEGGING CALLS OF NESTLING TREE SWALLOWS

by

Elizabeth Fairhurst

Submitted in partial fulfillment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
December 2010

DALHOUSIE UNIVERSITY

DEPARTMENT OF BIOLOGY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "THE EFFECT OF NEST ACOUSTICS ON THE BEGGING CALLS OF NESTLING TREE SWALLOWS" by Elizabeth Fairhurst in partial fulfillment of the requirements for the degree of Master of Science.

Dated: December 6, 2010

Supervisor: __________________________________

Readers: __________________________________

____

DALHOUSIE UNIVERSITY

DATE: December 6, 2010

AUTHOR: Elizabeth Fairhurst

TITLE: THE EFFECT OF NEST ACOUSTICS ON THE BEGGING CALLS OF NESTLING TREE SWALLOWS

DEPARTMENT OR SCHOOL: Department of Biology

DEGREE: M.Sc. CONVOCATION: May YEAR: 2011

Permission is herewith granted to Dalhousie University to circulate and to have copied for non-commercial purposes, at its discretion, the above title upon the request of individuals or institutions. I understand that my thesis will be electronically available to the public.

The author attests that permission has been obtained for the use of any copyrighted material appearing in the thesis (other than the brief excerpts requiring only proper acknowledgement in scholarly writing), and that all such use is clearly acknowledged.

Signature of Author

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Animals' long-distance acoustic signal structure minimizes habitat-specific attenuation and distortion, but it is unknown how environmental acoustics shape the signals of dependent young, or short-range signals generally. I investigated the influence of the nest environment on nestling tree swallows' begging calls by relating nest reverberation and resonance to nest structure; relating call features to nest reverberation, resonance and structure; and testing whether call structure reduced distortion in the home nest. Reverberation was stronger in wider cavities with intact ceilings. Nestlings used shorter calls in more reverberant cavities, and longer calls with higher middle frequency and lower minimum frequency in wider cavities with smoother walls, but did not adjust call frequency in relation to resonance. Calls originally produced in a given nest did not transmit with less distortion than calls originally produced in other nests. These findings suggest that the nest environment may shape the structure of begging calls.

ACKNOWLEDGEMENTS

I thank my supervisor, Marty Leonard, for her intellectual, emotional and financial support during my time at Dalhousie, and for making me a much better writer. I thank Andy Horn for his guidance on technical matters, and for providing helpful feedback and insight throughout the journey. I thank Leslie Phillmore for her feedback on both my research proposal and my thesis and other assistance in between. I thank Colleen Barber for her feedback on my research proposal, and Peter McGregor for his feedback on my thesis. I thank my wonderful field assistants Greg Britten, Maureen Murray and Jessica Roy for remaining chipper despite long days doing improbable things in a canoe. I thank my labmates – Gabrielle Beaulieu, Greg Breed, Catherine Dale, Bob Farmer, Krista Patriquin, Hendrik Reers, and Rob Ronconi – for their ideas, companionship, and welcome sense of perspective. I thank Devon Johnstone, Steph Mogensen and many other friends for their emotional support. I especially thank my parents and sister for continuing to support me despite my long absence from Vancouver.

This research was made possible financially by an NSERC Discovery Grant to Marty Leonard, an NSERC Canada Graduate Scholarship to myself, and monies from the Dr. Patrick Lett fund. I thank Ian Folkins for lending me his canoe, Dennis Phillips for allowing me to use his sound-attenuating room, and Chris Wright for designing and assembling my nest camera. Finally, I thank the Life Sciences Centre for maintaining its basic structural integrity for the duration of my stay.

CHAPTER 1 INTRODUCTION

Animal communication is a strikingly diverse component of animal behaviour. Signals convey a diversity of information, ranging from advertisements of reproductive status to warnings about approaching predators. Signal form varies as much as signal function; information is conveyed using a diversity of sensory modalities (including visual, acoustic, chemical, tactile, or electric signals), and both form and function vary across species, populations, and individuals. In order to understand this diversity in animal signals, much research effort has been devoted to exploring the forces shaping signal design (Kroodsma et al. 1982; Endler 1992; Krebs and Davies 1993; Kroodsma and Miller 1996; Johnstone 1997; Bradbury and Vehrencamp 1998; Catchpole and Slater 2008).

An important selective factor thought to influence the design of many animal signals is the environment in which the signal is transmitted. Animals live in environments that are often noisy, dark or densely vegetated, and thus suboptimal for signal transmission (Bradbury and Vehrencamp 1998). Habitats vary in the combination of obstacles they impose, as well as the severity of those obstacles. For example, a habitat that is dark and quiet poses challenges to visual, but not acoustic signals. Meanwhile, brightly lit and windy habitats have the opposite effect, and habitats that are dimly lit and prone to echoes pose challenges to both. Using one signaling modality over another to sidestep a habitat’s most obvious transmission obstacles can often improve a signal’s chances of being detected, but in the natural world signals will face one or more transmission constraints no matter what sensory modality they exploit (Krebs and Davies 1993; Bradbury and Vehrencamp 1998).

My thesis will focus on the environmental constraints faced by acoustic signals, as well as the contribution of the environment to the structure of these signals. Although acoustic signals have the advantage of being able to transmit better than visual signals at low light levels, and to carry over longer distances than visual, chemical, tactile or electric signals (Bradbury and Vehrencamp 1998; Catchpole and Slater 2008), their transmission is not without challenges. In fact, as I will outline below, the constraints imposed on long-distance acoustic signals by the environment are hypothesized to have played a significant role in shaping the structure of these signals (Morton 1975; Hansen 1979; Rothstein and Fleischer 1987). Under this 'acoustic adaptation hypothesis,' the amplitude, frequency and temporal patterning of signals are thought to be structured in ways that reduce attenuation and degradation under a habitat's particular transmission constraints. This hypothesis is used to explain the divergent signal types used by animals inhabiting acoustically different environments (Morton 1975; Hansen 1979; Wiley and Richards 1978; Rothstein and Fleischer 1987; reviewed in Ey and Fischer 2009).

The environmental factors that shape acoustic communication can be divided into two categories: those that affect the audibility of signals, i.e. change their amplitude relative to background noise, and those that affect the distortion of signals, i.e. change their information-containing amplitude, frequency and temporal patterns (Wiley and Richards 1982). These environmental factors are diverse in origin, but signalers respond to them by altering their signals in predictable ways. Below, I will review the major obstacles to acoustic communication in air, and describe the ways animals adapt their calls and songs in response to these obstacles. I will then apply these general principles to a novel and specific communication system, namely parent-offspring communication, and present my current research in the context of acoustic constraints and adaptations.

1.1 CONSTRAINTS ON ACOUSTIC SIGNAL TRANSMISSION

1.1.1 Audibility of Signals

Factors that affect the audibility of signals act by reducing the signal-to-noise ratio (the decibel difference in amplitude between the signal and background noise). Audibility-based constraints include those that attenuate the signal (reduce its amplitude) as it passes through the environment, and those that mask it (drown it out) with background noise. Both attenuation and masking reduce the likelihood that a receiver will detect the signal (Wiley and Richards 1982). Below I discuss each in turn.

Attenuation

Attenuation was the first audibility constraint to be recognized as a major selective force shaping acoustic signals, under the acoustic adaptation hypothesis (Wiley and Richards 1982). Signal attenuation comes from four sources, three of which have the potential to influence signal design by determining optimal frequencies for signal transmission. The first source of attenuation, spherical spreading, is simply the reduction in signal energy by 6 decibels per doubling of distance from the source if the source approximates a point source, omni-directional emitter. It affects all frequencies equally, and acts in the same way regardless of atmospheric conditions or habitat, and thus cannot explain differences in design between signals (Wiley and Richards 1982; Catchpole and Slater 2008).

The second source of attenuation, atmospheric absorption, refers to the absorption of sound energy by the air medium, which disproportionately attenuates high frequency sound waves (Wiley and Richards 1978). In a simplified situation in which only the effect of atmospheric absorption is considered, signals in the low to intermediate frequency range (1-4 kHz) will be favoured because they will transmit farther than higher frequency signals (Wiley and Richards 1978; Wiley and Richards 1982).

The third source of attenuation is scatter, or the reflection, refraction and diffraction of sound waves by vegetation and atmospheric turbulence, ultimately resulting in fewer sound waves traveling directly from the sound source to the receiver (Richards and Wiley 1980; Wiley and Richards 1982). Scatter by vegetation, which occurs when sound waves hit leaves, trunks and branches, occurs more in closed (forest) habitats than in open habitats (such as grasslands; e.g. Morton 1975).

Scatter can also occur as a result of atmospheric turbulence, which consists of pockets, layers and vortices of air with different temperature or velocity than their surroundings. Discontinuities in air temperature occur when pockets and layers of hot, low-density air rise from the sun-warmed ground (Bradbury and Vehrencamp 1998) or form temperature gradients above forest canopies (Wiley and Richards 1982). Discontinuities in air velocity occur when wind blows over irregular surfaces, forming small eddies or whirlwinds that differ in density from the surroundings (Wiley and Richards 1982; Bradbury and Vehrencamp 1998). Both forms of atmospheric discontinuities create heterogeneity in the acoustic impedance of the medium, i.e. the property responsible for determining the speed of sound. When sound waves pass through these impedance heterogeneities, they change velocity and direction (i.e. are refracted), much as light waves behave upon entering a medium with a different index of refraction (e.g. Cromer 1994).

Both vegetation and atmospheric turbulence attenuate high frequency sounds more than lower frequency sounds, largely because their wavelengths, which are shorter relative to the size of the obstacles in their path, are more likely to scatter (Wiley and Richards 1982). Thus, any scattering conditions will favour the use of low to intermediate frequencies for acoustic signaling (Richards and Wiley 1980; Wiley and Richards 1982). However, unlike previously mentioned types of attenuation, the effect of scatter differs between habitats; high frequency attenuation is greater in forests than in open habitats due to the higher prevalence of scattering surfaces, and as a result forest-based signalers generally call at lower frequencies than open habitat signalers. This difference in call frequency has been observed between forest and open habitat species in both mammals (rodents, Le Roux et al. 2002; but not cats, Peters et al. 2009; Peters and Peters 2010) and birds (Morton 1975; Blumstein and Turner 2005; Boncoraglio and Saino 2007; Cardoso and Price 2010), as well as within species across habitats (Hunter and Krebs 1979; Nicholls and Goldizen 2006; Derryberry 2009). Overall, frequency-dependent attenuation from scatter has a strong role in determining acoustic signal frequency.

The fourth source of attenuation, namely boundary interference, is interference between direct sound waves (those traveling straight from the sender to the receiver) and waves that have taken an indirect path due to reflection by the ground, as well as extra waves propagated in and along the surface of the ground. Boundary interference strongly attenuates very low frequency sounds made within 1-2 metres of the ground (Wiley and Richards 1982). Between boundary interference and high-frequency attenuation by atmospheric absorption and scatter, animals signaling from near the ground are left with relatively narrow frequency ranges, or ‘sound windows,’ at which their calls will transmit unimpeded. The call frequencies used by ground-based signalers therefore fall within these sound windows (Morton 1975; Richards and Wiley 1980).

Masking by Ambient Noise

The second audibility-related constraint on acoustic transmission is ambient or background noise (reviewed in Brumm and Slabbekoorn 2005). Ambient noise falling in the same frequency range as the signal will reduce the signal-to-noise ratio, making it less easily detected and discriminated by potential receivers (e.g. Klump 1996; Brumm and Todt 2002; Lohr et al. 2003).

Responses by the signaler to the masking effects of ambient noise primarily restore the signal-to-noise ratio to detectable levels. Some animals do this by increasing the ‘signal’ component of the ratio, simply by calling or singing at higher amplitudes (the Lombard effect; reviewed in Brumm and Slabbekoorn 2005). This response has been observed across taxa, from birds (Brumm and Todt 2002; Pytte et al. 2003; Brumm 2004) to anurans (Lopez et al. 1988) to primates (Brumm et al. 2004). Other animals decrease the ‘noise’ component of the ratio by shifting their signals to frequencies containing less noise energy (Brumm and Slabbekoorn 2005). This response has been observed in birds (Slabbekoorn and Peet 2003; Patricelli and Blickley 2006; Slabbekoorn and den Boer-Visser 2006; Halfwerk and Slabbekoorn 2009; Kirschel et al. 2009; Parris and Schneider 2009; Hu and Cardoso 2010), primates (de la Torre and Snowdon 2002; Schneider et al. 2008), anurans (Cunnington and Fahrig 2010), and fish (Lugli 2010). When ambient noise is intermittent, signalers either build redundancy into the signal to ensure that the obliteration of one syllable does not mean outright signaling failure (Lengagne et al. 1999; reviewed in Brumm and Slabbekoorn 2005), or adjust signal timing so as not to overlap with predictable bursts of noise (e.g. other animals' vocalizations; Ficken et al. 1974).

1.1.2 Distortion of Signals

In addition to attenuation, signals can also become distorted in their amplitude, frequency and time domains. The two acoustic phenomena responsible for signal distortion are reverberation and irregular amplitude fluctuations (Wiley and Richards 1982), described below.

Reverberation

Reverberation can be defined as the elongation and decay of sound waves as a result of reflection and scattering by objects in the environment (Wiley and Richards 1978; Richards and Wiley 1980; Forrest 1994). For a short time after a direct sound wave reaches a receiver, waves (from the same original sound) which have been reflected and scattered by these objects and therefore have taken a longer path to the receiver, will continue to arrive, forming an 'echo tail' after the end of the direct sound wave (Wiley and Richards 1978; Wiley and Richards 1982).

Reverberation makes it difficult for receivers to distinguish between closely spaced signal elements (rapidly amplitude-modulated signals), as the echo tail from one element overlaps with the start of the next element (Catchpole and Slater 2008). As such, repetitive and rapidly amplitude-modulated signals such as trills do not transmit well in highly reverberant environments such as forests, where leaves reflect and scatter sound waves. Consistent with this constraint, a smaller proportion of forest bird species use trills in their songs than bird species of open habitats (Wiley and Richards 1982).

In addition to limiting rates of amplitude modulation in habitats with many reflecting surfaces, reverberation also limits rates of frequency modulation, i.e. repetition rate of short signal units containing a range of frequencies. Reverberation causes temporal overlap between the echo tail at one frequency and the onset of the next frequency; in highly reverberant habitats such as forests, this blending of frequencies may hinder receivers' ability to make out frequency patterns in rapidly frequency-modulated signals (Catchpole and Slater 2008). This may explain the tendency of forest-dwelling bird species to use long, whistle-like notes, which sweep only slowly through their frequency range (Richards and Wiley 1980), and fewer trills (Nicholls and Goldizen 2006). It may also be the reason that both within and between species, signalers in more densely vegetated habitats trill more slowly (e.g. Nottebohm 1975; Derryberry 2009), with fewer notes (Hunter and Krebs 1979), and with narrower frequency ranges (Tubaro and Segura 1994; Tubaro and Lijtmaer 2006), or simply use fewer trills as a proportion of their overall signal (Nicholls and Goldizen 2006).

Amplitude Fluctuations

In open habitats, where reverberation is less prevalent, acoustic signals may become distorted as they are scattered by atmospheric turbulence or reflected by non-stationary objects such as leaves moving in the breeze (Wiley and Richards 1978; Wiley and Richards 1982). Constructive and destructive interference between scattered and direct sound waves generates unpredictable, frequent bursts of high and low amplitude in the signal, i.e. irregular amplitude fluctuations (Wiley and Richards 1982; Brown and

Handford 2000). As the information content of a signal is coded partially by its internal amplitude patterning, any signal long enough to pick up irregular amplitude fluctuations can easily have its information content masked (Wiley and Richards 1982).

Signalers in open, turbulent habitats must, therefore, condense the information into syllables shorter than the interval between irregular amplitude fluctuations and repeat these packets rapidly (Wiley and Richards 1982). As previously mentioned, this trill-like structure is in fact the song structure found most often in the birds of open habitats (Wiley and Richards 1982).

1.2 TESTS OF THE ACOUSTIC ADAPTATION HYPOTHESIS

Frequency-dependent attenuation, masking by ambient noise, reverberation, and irregular amplitude fluctuations all exert a strong influence over the acoustic structure of long-distance signals (Forrest 1994; Ey and Fischer 2009). Differences in these transmission constraints between habitats lead to differences in the structure of the signals used therein, consistent with the predictions of the acoustic adaptation hypothesis.

The adaptive value of habitat-specific call structure, i.e. the ability of calls to transmit with less distortion in the habitat where the signaler lives, has been tested using field transmission experiments, wherein long-distance mating and territorial calls have been broadcast and re-recorded in multiple habitats (e.g. Brown et al. 1995; Daniel and Blumstein 1998; Brown and Handford 2000; Couldridge and van Staaden 2004; Kroon and Westcott 2006; Proppe et al. 2010; Trefry and Hik 2010). These studies compare within each broadcast habitat the amount of attenuation and degradation incurred by native signals (calls broadcast in their own habitat) and foreign signals (calls broadcast outside their native habitat). If call features are adaptive, native signals should be less attenuated and degraded than foreign signals (reviewed in Boncoraglio and Saino 2007).

These transmission experiments show that certain signals transmit with less degradation of frequency and amplitude patterns in their native habitat, suggesting that they are adapted to the acoustics of the native habitat. Tonal whistles and rapidly amplitude-modulated trills, typically found in forest and open habitat birds respectively, consistently transmit with less degradation in their native habitats than the inverse (Brown and Handford 1996, 2000), and the songs of some bird species (Proppe et al. 2010) likewise transmit optimally in the signaler's native habitat relative to other habitats (though this pattern is not found in small mammals; Trefry and Hik 2010). In other tests, native calls outperform non-native calls in certain habitats (insects, Couldridge and van Staaden 2004; but see Kroon and Westcott 2006 for some birds, and Daniel and Blumstein 1998 for some mammals). The superior transmission performance of native calls, at least in some taxa and signaling systems, lends further support to the acoustic adaptation hypothesis, suggesting that habitat-specific call features can be adaptations for improved transmission of long-distance calls, especially when comparing broad-scale differences between forests and open habitats.

1.3 TRANSMISSION CONSTRAINTS IN PARENT-OFFSPRING COMMUNICATION

While habitat acoustics are clearly important to the long-distance mate attraction and territorial defense signals of adult animals (reviewed in Ey and Fischer 2009), it is not clear how they influence signal design in other acoustic communication systems. One such system is parent-offspring communication, which typically includes short-distance signals used between dependent young and their parents. A key component of parent-offspring communication found in many taxonomic groups is the begging display, where young animals convey information to their parents on nutritional and thermal state, age, sex, health, and rank within brood using a complex suite of signals (reviewed in Kilner and Johnstone 1997; Wright and Leonard 2002; Kilner and Hinde 2008). In nestling birds, which I will focus on here, begging consists of vocalizations, gaping and posturing, and in altricial species takes place in a nest, which may be either an enclosed (e.g. burrow or tree cavity) or an open (e.g. open cup) space. As begging signals encode a diversity of information that parents use to make care-related decisions, such as feeding rate and which nestling to feed (Wright and Leonard 2002), it is important that they are transmitted accurately to the receiving parent.

Despite the short-distance nature of parent-offspring communication, recent evidence suggests that transmission constraints shape signal design in both the visual (Kilner and Davies 1998; Avilés et al. 2008; Wiebe and Slagsvold 2009) and acoustic (Leonard and Horn 2005; Leonard and Horn 2008; Fairhurst et al. in prep) components of nestling begging. Firstly, the efficacy of visual components of the signal is constrained by light levels within the nest. Nestlings open their brightly coloured mouths as part of the overall begging display, and parents use this display in conjunction with nestling posturing and calling to make feeding decisions (Kilner 2002; Heeb et al. 2003). As dim lighting makes it more difficult for parents to see nestlings' waiting mouths, selection has favoured mouth coloration that improves detectability, in the form of flanges that contrast starkly with gape and body colour (e.g. Kilner and Davies 1998; Heeb et al. 2003; Wiebe and Slagsvold 2009). Species with darker nest environments have stronger compensatory responses in coloration; the nestlings of cavity-nesting species have sharper visual contrasts between flanges and body coloration than nestlings of open cup nesters (Avilés et al. 2008).

Transmission of the acoustic component of begging signals can also be constrained by the environment. Because the likelihood of a nestling receiving food depends on the parent's ability to reliably distinguish call features (Leonard and Horn 2005), it is important that the begging signal transmit with adequate audibility and minimal degradation. Ambient noise has been shown to inhibit parental discrimination between nestlings calling at different rates (Leonard and Horn 2005). In response to this constraint, nestling tree swallows (*Tachycineta bicolor*) increase the length, amplitude and frequency range of their calls with the amplitude of ambient noise at the nest (Leonard and Horn 2005). Similarly, nestling tree swallows exposed to white noise increase their call amplitude (Leonard and Horn 2005) and minimum frequency, and reduce their call frequency range (Leonard and Horn 2008), relative to control nestlings. A similar effect is found in nestling American dippers (*Cinclus mexicanus*), which increase call amplitude and frequency in response to louder ambient noise (Fairhurst et al. in prep). These types of call adjustments should enable parents to distinguish between nestlings signaling different levels of hunger and to make the appropriate feeding decisions (Leonard and Horn 2005). Thus, even for these short-distance signals, environmental constraints can induce changes in the acoustic structure of calls.

A second, yet-unexplored constraint to the effective transmission of begging calls is the nest itself. Reflection and absorption of sound waves by nest walls could alter begging calls via reverberation, resonance and attenuation (described below). These constraints may be particularly important for cavity- and burrow-nesting species, whose begging calls are made within small, enclosed spaces (Horn and Leonard 2002). There has been no attention to this possibility in the literature, perhaps because begging calls are short-distance signals and one might therefore not expect them to be as strongly affected by the acoustic environment as long-distance signals (Horn and Leonard 2002).

Research in other systems, however, suggests that the acoustics of small, enclosed spaces can alter the transmission of sound. Many burrow- and cavity-dwelling animals shape their long- and short-distance signals according to the acoustic properties of their enclosed calling locations. Bornean tree-hole frogs (*Metaphrynella sundana*), for instance, search for and call at the resonant frequency of the tree hole. This frequency, which is the wavelength at which sound waves are most amplified by constructive interference of reflected waves, changes on short temporal scales due to rising and falling water levels in the cavity. Once frogs have found this frequency, they focus their calling effort on it, and increase call duration when calling at the resonant frequency (Lardner and bin Lakim 2002). Subterranean rodents (*Ctenomys talarum, Fukomys* spp.) also adjust their calls to their acoustic space, calling at low frequencies to avoid high-frequency attenuation in their burrows (Schleich and Busch 2002; Lange et al. 2007). Other species actively create acoustic spaces that amplify their calls, including mole crickets (*Scapteriscus acletus*), which dig horn-shaped resonant burrows to amplify their outgoing calls (Bennet-Clark 1987), and other crickets (*Rufocephalus* sp.), which build similarly resonant burrows (Bailey et al. 2001). Still others create acoustic spaces that amplify incoming rather than outgoing calls, as has been observed in *Eupsophus* frogs, whose burrows amplify the incoming calls of other individuals (Penna and Solís 1996; Penna 2004; Penna and Marquez 2007). The amplification induced by enclosed spaces is not unsubstantial; in crickets, for example, sounds made in burrows are amplified 24 dB relative to sounds made in free air (Bennet-Clark 1987). This research suggests that the acoustics of the immediate environment may be a key force shaping the vocal signals of animals living in small spaces. In light of this, the begging calls of nestling birds inside cavity nests may very well be affected by the acoustics of the nest.

Currently nothing is known about the internal acoustics of nests, or what effect the acoustic properties of the nest might have on call structure. In this thesis, I describe the nest acoustics of the tree swallow (a secondary cavity-nesting species), and test the relationship between begging call structure and nest acoustics. Below, I describe predictions about the constraints the nest cavity might impose on begging call transmission and the ways in which nestlings of this species might vary their calls in response to variation in nest acoustics.

I expect two acoustic properties to affect the transmission of sounds produced within cavity nests. The first acoustic property is reverberation (Horn and Leonard 2002), or the elongation and decay of sounds caused by scattered sound waves. I expect reverberation to be stronger (producing longer echo tails on sounds) in nests with more irregular internal surfaces, which present more reflecting surfaces in a greater variety of orientations to redirect sound waves and increase the path length of scattered waves. I also expect reverberation to be stronger in larger nests, as the time taken for echo tails to decay in an enclosed space increases in proportion to the ratio of volume to surface area (e.g. Raichel 2006). I further expect reverberation to be stronger in completely enclosed nests where neither end of the nest is open to the external environment, thereby allowing reflection of sound waves off both ends of the cavity.

Reverberation should affect begging calls by causing overlap between scattered waves from early parts of the calls and the direct waves of remaining parts (Wiley and Richards 1982). If a call sweeps upward or downward in frequency over its duration, as begging calls often do (e.g. Leonard and Horn 2008), scattered and direct waves will differ in frequency; overlap of these frequencies may interfere with parents' ability to resolve the call's frequency structure and pick out the information contained therein. However, if the signal's frequency changes less from start to finish, i.e. its frequency range is smaller, the severity of contrast between overlapping frequencies, and hence the amount of distortion, will be lessened (Slabbekoorn et al. 2002). Therefore, if nestlings adjust calls to overcome the effects of reverberation, I predict that calls made in highly reverberant nests should have smaller frequency ranges than those from less reverberant nests. As a secondary prediction, I predict that nestling calls in more reverberant nests will be longer, not due to active adjustment by nestlings, but rather due to the addition of echo tails.

The second acoustic property of nests that could affect begging calls is resonance, or amplification caused by constructive interference between direct and reflected sound waves within the nest. Sounds traveling through an enclosed space will inevitably reflect off the internal walls and interfere with other waves on their return path. When this interference is constructive (waves arrive in phase and their amplitudes combine), amplification results. Constructive interference within an enclosed space, termed resonance, occurs only for frequencies whose wavelengths allow them to traverse the given space and return in the correct phase to add constructively; the wavelength of these resonant frequencies thus depends on the dimensions and shape of the space (e.g. Cromer 1994). If nestlings adjust calls in response to these frequency-dependent patterns of amplification, in order to make their calls more audible to parents, I expect them to shift their call frequencies to overlap with amplified (resonant) frequencies.

1.4 CURRENT STUDY: NEST ACOUSTICS AND BEGGING CALL DESIGN

Given the importance of communication to so many aspects of animals' lives (e.g. Krebs and Davies 1993; Bradbury and Vehrencamp 1998; Wright and Leonard 2002), it is critical that we understand the forces shaping signal design. Much is known about the factors influencing the design of adult animal signals (e.g. Kroodsma et al. 1982; Kroodsma and Miller 1996; Bradbury and Vehrencamp 1998; Catchpole and Slater 2008), but less is known about the signals used by young animals. Because failure of offspring-to-parent communication directly impacts survival, signaling during the dependent juvenile period is among the most critical to an individual's fitness (Wright and Leonard 2002; Kilner and Hinde 2008). If we wish to understand how this signaling system operates, we must investigate all the forces capable of shaping both the evolved and individually controlled components of offspring signals. This will help us understand not only the design of signals used in parent-offspring communication, but also more generally the factors influencing the form of short-distance signals.

The overall goal of my study was to determine how nest acoustics affected the structure of begging calls, using the tree swallow as a model species. Nestling tree swallows must communicate to their parents from the confines of a tree cavity or nest box (Robertson et al. 1992), so they are an ideal species in which to study both nest acoustics and their effect on begging call design.

In Part I of my study, I investigated the relationship between nest acoustics and begging call structure in tree swallows nesting in natural tree cavities. I had three specific objectives. First, I related the amount of reverberation induced by nest cavities to their physical structure by testing my predictions that reverberation would be stronger in nests that were larger, closed on both ends, and more irregular in wall surface texture. I did this by broadcasting pure tones inside cavities and measuring the extent to which they acquired echo tails. I then compared the reverberation strength of each cavity to its structural properties (height, diameter, openness, and wall texture).

Second, to relate call structure to reverberation in the nest and test my predictions that nestlings would reduce call frequency range and that calls would be elongated in more reverberant nest cavities, I measured the frequency range and length of begging calls and related those features to the reverberation strength of the nest cavity.

Third, as nothing is yet known about the effect of the nest environment on nestling calls, and as this was an exploratory study, I tested whether nestling calls varied directly with the nest cavity’s structural properties. I had no explicit predictions for how call properties might depend on cavity structure.

Fourth, to test whether nestling calls were less acoustically distorted by their own nest environment than other calls (cf. transmission tests of the acoustic adaptation hypothesis, above), I broadcast and recorded begging calls from all nests inside each nest cavity and compared the amount of distortion they experienced. If calls are shaped by the acoustic properties of the nest, I predicted that calls re-recorded in the nest cavity in which they were produced would experience less distortion than calls originally produced in other nests.

In Part II of my study, I conducted an experiment to test the prediction (above) that nestlings would adjust their call frequencies to overlap with and thus be amplified by the resonant frequencies of their nest environment. I modified the resonant frequencies of nest boxes used by tree swallows by inserting an artificial ceiling at one of two heights, creating two treatments of nest box that differed in volume. I compared the minimum, maximum and peak call frequency of nestlings raised in the high ceiling treatment to those in the low treatment, with the expectation that these features would differ between treatments if nestlings adjusted their call frequencies in relation to resonance. I also tested whether calls' overall frequency spectra were more similar to the resonance spectra of their own treatment than they were to the other treatment.

CHAPTER 2 METHODS

Study Species

The tree swallow is a medium-sized swallow that breeds across central and northern North America, and winters mainly in Florida and along the Gulf of Mexico. It nests readily in nest boxes, but its natural nest sites are tree cavities excavated by other species, such as woodpeckers (Robertson et al. 1992). The cavities used by this species vary in a variety of ways, including cavity volume and stage of decay (Rendell and Robertson 1989). If the acoustics of enclosed spaces are affected by size, shape, and wall properties, then natural variation in tree cavities should translate into acoustically variable calling sites, thus making tree swallows an ideal study species for the effect of enclosed-space acoustics on short-range communication.

Study Sites

Fieldwork was conducted on tree swallows nesting in natural tree cavities and nest boxes near Wolfville, Nova Scotia, Canada (45° 05' N, 64° 32' W) between 9 May and 16 July 2008 and 2 May and 13 July 2009. Natural cavities were found in standing trees in and around three reservoir lakes (Black River Lake, Little River Lake, and Methals Lake) on the Gaspereau River tributary system. I discovered 20 active nests (egg stage or later) in natural cavities, 19 of which were inside dead trees (pine snags) and one of which was in a live tree. Most cavities were located inside the main tree trunk where they had been either excavated by primary cavity nesters or formed by decay (n =18), but others were located inside other parts of the tree, including a hollow branch (n = 1) and an upended hollow root (n = 1). I also worked with a population of tree swallows that use a subset of 105 nest boxes, located at four sites (three apple orchards and one old field) in the Gaspereau Valley (see Leonard and Horn 1996 for a description of the sites). Nest boxes were constructed of wood, and were of standard shape and size (see Part II); nest boxes built in different years were evenly distributed between treatments.

2.1 PART I. NATURAL NEST ACOUSTICS

2.1.1 Fieldwork and Acoustic Measurements

Monitoring of Natural Nests

To locate natural nests, I surveyed each lake every 2-3 days in May and looked for signs of nesting activity, including the presence of tree swallows near snags and visible nest-building activity. Once an active nest was located, I observed it for up to one hour, from a distance of 20-30 m, every two days to determine its nesting stage. I considered the nest to be at the nest-building stage, if I observed birds carrying nest materials to the entrance (Robertson et al. 1992). Once nest-building activity stopped, I used an infrared camera mounted on a pole (modified from Boland and Phillips 2005) to observe the nest contents every two days until the end of the egg-laying stage, which I defined as the point where no new eggs appeared and the female was often on the nest. I then observed nests every 2-3 days from a distance of 20-30 m until the expected hatch date, to determine whether the nest was still active (indicated by an adult bird entering or leaving the nest within one hour of my arrival), at which point I checked the nest for hatching every two days by camera. All broods contained 4-6 nestlings, but accurate determination of brood size beyond this estimate was impossible due to image clarity limitations. I measured nestling age as the number of days following the first hatched egg (hatch day = day 1), and watched for continued nestling survival and fledging by observing nests for signs of parental visits every 3-4 days after day 10. I considered fledging to have occurred when I saw parents feeding nestlings in the nest on one observation day, and saw multiple tree swallows (including the greyer juveniles) flying in the vicinity of the nest tree on the following observation day.

Physical Structure of Natural Nests

Nest cavities were cylindrical in shape, but varied in internal height and diameter, openness (open nests = cavities with one end of the cavity open to the external environment; closed nests = top of cavity closed) and wall texture. I measured the internal height and diameter of each nest cavity to the nearest cm using a small ruler inserted by hand into the cavity. I considered cavity height as the distance between the centre of the nest cup and the ceiling above the nest for a closed nest and the point at which the cavity wall above the nest ended for an open nest. I measured diameter as the distance between the interior wall at the cavity entrance and the wall directly opposite; while cavities were not always constant in diameter along their entire lengths, this standardized measuring location represented the nearest set of walls with which begging call sound waves might interact, and thus it was the most relevant diameter to measure. In four of twenty nests, I was unable to take these measurements because the nest snag was too tall or too unstable to access; thus the sample size for both internal cavity dimensions was 16 nests. Finally, I classified nest wall texture as smooth (only fine-scale relief < 1-2 cm) or lumpy (larger ridges, crevices and lumps > 2 cm above or below the main wall surface). Sample size for both wall texture and cavity openness was 20 nests.

Effect of Nest Structure on Reverberation

To measure reverberation in each nest, I broadcast and re-recorded 130 pure tones (16-bit, WAVE format, created in Audacity 1.2.5) within each nest following fledging. These tones comprised one single-frequency tone every 50 Hz from 2-8.5 kHz, spaced at 500 ms intervals, corresponding to the average length (50 ms), frequency range and amplitude (65 dB at 10 cm as measured using a Radio Shack 33-2005 sound level meter; Leonard and Horn 2005) of tree swallow begging calls as measured in this study. Re-measuring these tones after broadcast, allowed me to determine how much of an echo tail was added to sounds by reverberation, which in turn might predict changes in begging call features (e.g. Slabbekoorn et al. 2002; Nicholls and Goldizen 2006; Darden et al. 2008; Dingle et al. 2008). I broadcast these tones using equipment that collectively had a flat frequency response in the frequency range of nestling calls, namely from an Apple iPod through a Sennheiser MX40 earbud headphone that I placed via an extension pole in the centre of each nest cup. I oriented the headphone toward the cavity entrance, in the same way as a nestling gape, as the best way to approximate the directionality of calling nestlings. I recorded the broadcast tones on a Marantz PMD 671 solid state digital recorder at 16 bits and a sampling rate of 44.1 kHz, using a Sennheiser EW 312 G2 wireless lapel microphone angled slightly into the nest cavity from a standardized location atop the nest entrance to approximate the location of a listening parent, using a second extension pole.

I measured the amount of reverberation experienced by each pure tone by measuring the root mean squared (RMS) amplitude (dimensionless sample units) of the 50 ms tone, and then of the 200 ms period immediately following it, within a 500 Hz frequency range surrounding the tone's central frequency (Raven Pro 1.4; Charif et al. 2010). The 200 ms post-tone period represents the maximum length of echo tail, or smear of sound diminishing in amplitude after the tone, visibly detectable on the spectrogram of any tone I broadcast and re-recorded in any nest (Richards and Wiley 1980). As all recorded echo tails are encompassed within this time range, a higher RMS amplitude during the post-tone period indicates the presence of more scattered waves during that period, and thus more reverberation (e.g. Richards and Wiley 1980; Slabbekoorn et al. 2002; Dingle et al. 2008). I calculated a reverberation index for each tone by subtracting the tone amplitude from the post-tone amplitude. A larger (less negative) reverberation index would indicate stronger reverberation in the cavity, due to more scattered waves forming an echo tail during the post-tone period, reducing the difference in amplitude between this period and the original tone itself (cf. Wiley and Richards 1980; Dingle et al. 2008). I averaged this index across the full set of tones to obtain a single reverberation index for each nest cavity, which was a measure of reverberation strength that could be compared between cavities (Dingle et al. 2008).

Effect of Reverberation on Begging Call Features

To determine if nestling begging calls varied with reverberation in the nest cavity, I recorded the begging calls of 10-day-old nestlings during parental feeding visits. At 10 days tree swallow nestlings can manipulate various elements of their begging calls (including call rate, length, amplitude and frequency) in response to hunger (Leonard and

Horn 2006), and could thus plausibly manipulate call features in response to other factors such as nest acoustics.

I recorded begging calls *in situ* because it was impossible to remove nestlings given the height and advanced stage of decay of most nest snags. I placed a lapel microphone at the top of the nest entrance as previously described, angling it into the nest (10-15 cm from nestlings on average) without blocking access to parents. To ensure that hunger levels were relatively constant across nests, thereby reducing the possibility that call features would differ between nests based on differences in hunger, I retreated 20-30 m, and waited until parents had resumed feeding for one hour before I began recording. I then recorded calls, as described above, during the first five visits that followed the one-hour period.

To relate begging call features to the nest's reverberation index, I measured the first ten non-overlapping calls that were also free of parental or external noises, in each of the five visits, for a total of 50 calls per nest (Fig. 1). For each call, I measured call length (ms) in Raven's waveform view, and frequency range (kHz; maximum - minimum frequency) in the spectrogram view (Hamming window, 289 Hz filter bandwidth, displaying 2 s of recording in the sound window). I excluded call harmonics from my measurements. I averaged the ten measurements for each call feature within each visit, and used the five resulting visit means in the analyses described below.

Effect of Nest Structure on Begging Call Features

Although I was primarily interested in the effect of reverberation (above) and resonance (see nest box experiment, below) on begging call features, I also tested whether nests' structural properties (described above) directly predicted call features, as nothing is currently known of what effect the nest environment has on begging calls. To do this, I measured call length and frequency range on the 50 calls per nest described above, as well as minimum, maximum, and middle frequency (kHz; measured in the spectrogram view as above; Fig. 1). I measured middle frequency, or the midpoint between minimum and maximum frequencies, rather than the more traditionally measured peak frequency because if one is interested in comparing frequency features as emitted by nestlings, peak frequency cannot be compared between calls recorded in acoustically different recording environments. Recorded peak frequency for a given call differs between recording environments (Appendix A), presumably because frequencies within the call will be amplified if they correspond to recording environment resonant frequencies. As I was unable to record nestlings in a standardized recording environment, I decided to use middle frequency as an alternative measure of calls' overall frequency position.

Call Transmission Experiment

To determine whether begging calls re-recorded in the nest cavity in which they were produced transmitted with less distortion than calls originally produced in other nests, as would be expected if nestlings adjusted their calls to reduce distortion, I broadcast and recorded 275 of the begging calls measured above (the first five measured calls in each of the five parental visits in each of 11 nests) within each nest cavity following fledging, using the same protocol used for broadcasting and recording pure tones. To prepare calls for broadcast, I bandstop filtered them to remove low-frequency background noise from the original recordings (0-1500 Hz; Charif et al. 2010), grouped the five calls from each parental visit together, and arranged these groups (i.e. 55 groups of five calls) in random order.

I then quantified how much each call had been distorted during transmission by comparing the in-nest recording with a recording of the same call broadcast in a free field. I reasoned that differences in call features between the two recordings could be attributed to differences in the recording environments, specifically the acoustic properties of the nest environment. To obtain a free field recording of each call, I broadcast and re-recorded the calls in a 241 cm wide x 211 cm deep x 203 cm high, single-walled Eckel sound-attenuating room (described in Ishigami and Phillips 2008). The walls of this room were lined with 5 cm Auralex foam wedges, the ceiling was covered with eggshell foam, and the floor was carpeted. I controlled for equipment and setup effects by using the same headphone and microphone described above, mounted on 1 m vertical poles spaced 10 cm apart to approximate the distance between headphone and microphone during nest broadcast.

To quantify nest-induced call distortion, I used Raven's spectrogram correlator (bandstop filtered 0-1500 Hz, normalized, linear power; Charif et al. 2010) to compare each call's free field spectrogram with its spectrogram when broadcast and recorded in the nest. The correlator compared the amplitude and frequency structure of the two calls, and produced a spectrogram correlation value (range 0 to 1) indicating how similar the two calls' structures were. A high correlation value indicated that a call broadcast in the nest was more similar to its free field recording (e.g. Holland et al. 1996; Leonard and Horn 2001c; Leonard et al. 2009), and was therefore less distorted by the nest environment, than a call with a lower correlation value. I then compared the correlation values of calls re-recorded in the nest cavity in which they were produced to those of calls originally produced in other nests, for each broadcast nest. I expected calls of the former category would have higher spectrogram correlation values (lower distortion) than calls of the latter category.

2.1.2 Statistical Analyses

Effect of Nest Structure on Reverberation

To determine which natural nest features influence reverberation index within the cavity, I used multiple linear regression (R Development Core Team 2009) to relate the reverberation index to the cavity's internal height and diameter, openness (open or closed), and wall texture (smooth or lumpy). In this and all subsequent parametric tests, I fit the full linear model (here, Reverberation Index ~ Height + Diameter + Openness + Wall Texture), removed non-significant terms ($P > 0.05$) in a stepwise fashion until only significant terms remained, and then checked that order of removal did not change the final model. Significance for each term was determined by comparing the fit of the significant model to that of the significant model plus the term of interest. I visually checked residuals for homoscedasticity and normality, as well as formally tested them for normality using the Shapiro-Wilk test. Residuals for the reverberation index model just described were not significantly non-normal (Shapiro-Wilk: $W = 0.89$, $P = 0.058$), so variables were left untransformed.

Effect of Reverberation on Begging Call Features

To test whether nestlings reduced the frequency range of their calls in response to greater reverberation in their nest cavity, as well as whether calls were elongated by more reverberant cavities, I used linear mixed effects models (restricted maximum likelihood; Pinheiro et al. 2009) with frequency range or call length as the dependent variable, reverberation index as the fixed effect, and nest as the random effect (model: Call Feature ~ Reverberation Index, random = ~1|Nest). In this and all subsequent analyses where call features were measured on multiple calls per nest, including nest as the random effect ensured that different values from the same nest were not treated as independent data points. Residuals in the current models were normally distributed (Shapiro-Wilk: frequency range W = 0.98, P = 0.38; call length W = 0.99, P = 0.85), so variables were left untransformed.

Effect of Nest Structure on Begging Call Features

I tested whether begging call features varied in relation to the structural properties of the nest, using linear mixed effects models with call feature (call length; minimum, maximum or middle frequency; or frequency range) as the dependent variable, nest structural properties (cavity height, diameter, openness, and wall texture) as fixed effects, and nest as a random effect (model: Call Feature ~ Height + Diameter + Openness + Wall Texture, random = ~1|Nest). I log-transformed the minimum frequency data to remedy non-normality in its model residuals (Shapiro-Wilk: before transformation W = 0.95, P = 0.033; after transformation W = 0.86, P = 0.13), and Box-Cox transformed the middle frequency data (before W = 0.94, P = 0.018; after W = 0.967, P = 0.22; Fox 2009). I did not transform the call length, maximum frequency or frequency range data as the residuals for all three models were normally distributed (call length W = 0.98, P = 0.67; maximum frequency W = 0.98, P = 0.48; frequency range W = 0.98, P = 0.45).

Call Transmission Experiment

To determine whether calls re-recorded in the nest cavity in which they were produced transmitted with less distortion than calls originally produced in other nests, I used a two-sample paired Wilcoxon signed rank test (R Development Core Team 2009) to compare the mean spectrogram correlation coefficients for calls from each category in each nest, with the alternative hypothesis that the spectrogram correlation coefficients for the former would be higher than those for the latter. I used this non-parametric test rather than the parametric alternative (i.e. a paired t test) because correlation values, which were limited to between 0 and 1, were negatively skewed (clustered in the 0.8-0.9 range).

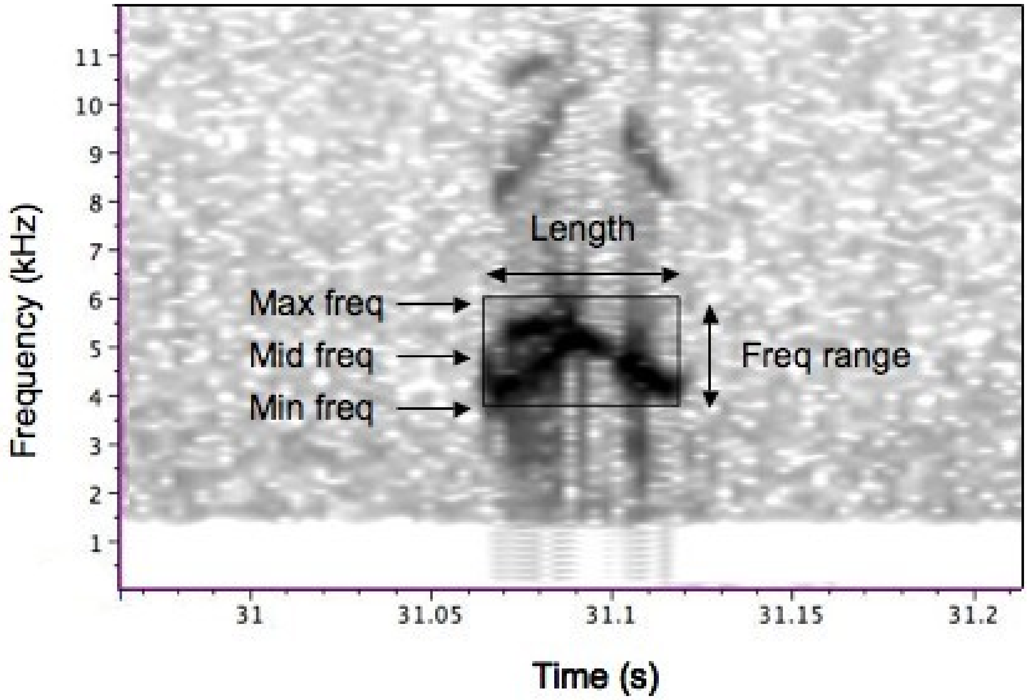

Figure 1 Spectrogram illustrating begging call features measured in nestling tree swallows in natural nest cavities. Middle frequency is the midpoint between maximum and minimum frequency, and frequency range is the difference between maximum and minimum frequencies. Frequency features were measured in the spectrogram view, and call length was measured in the waveform view (Charif et al. 2010).

2.2 PART II. MODIFIED NEST BOX EXPERIMENT

2.2.1 Fieldwork and Acoustic Measurements

Assignment of Nest Box Treatments

To experimentally test whether nestlings adjust the frequency structure of their begging calls in response to the resonance environment, I modified the ceiling height of tree swallow nest boxes to create two acoustic environment treatments that differed in their resonant frequencies, and then compared the structure of calls given by nestlings raised in the two environments. I expected that if nestlings benefited from amplification of their calls by resonance, they would shift their call frequencies to overlap with the resonant frequencies of their own treatment, in which case call frequency features should differ between treatments and their call spectra should be more similar to the resonance spectrum of their treatment than to the other treatment. I manipulated ceiling height because I wanted to test how nestlings responded to differences in resonance, and ceiling height was the most easily manipulable dimension of nest boxes, as it could be easily altered post-hatching without removing or altering the size of the nest.

I checked nest boxes every two days for signs of nest-building and egg-laying activity, and then began checking daily for hatching on the earliest expected hatch date. I assigned nests to treatments at hatch, alternating between treatments to balance for hatch date, and balancing for brood size and study site.

To create the two nest box treatments, I modified the ceiling height of standard slope-roofed wooden nest boxes (Fig. 2) by inserting a 14.0 x 14.0 cm x 0.6 cm plywood false ceiling at one of two heights: high (mean ± SE: 25.8 ± 0.3 cm above the centre of the nest, n = 17) or low (21.8 ± 0.1 cm above the nest, n = 18). I chose these heights because they were within the natural range of cavity heights encountered by tree swallows using natural tree cavities, and the difference between treatment heights was possible to achieve without replacing existing nest boxes (e.g. by removing and raising the existing roof). By using identical nest boxes for the two treatments before adding the false ceilings, I controlled for any other acoustic differences between treatments, ensuring that the only difference was in ceiling height. When nestlings were 1-2 days old, I transferred each brood temporarily to a fabric-lined box warmed with a hot water bottle, while I affixed the ceiling insert at the appropriate height in their nest box. There was no mortality or abandonment associated with the addition of the ceiling inserts.

Resonance Characteristics of Nest Box Treatments

To describe the differences in resonance between nest box treatments, I broadcast and re-recorded in each nest box 30 s of white noise (16-bit, WAVE format, created in Audacity 1.2.5) with energy evenly distributed across frequencies within the nestling call frequency range of 2-8.5 kHz, following the broadcast and recording protocol described above for pure tones in natural nest cavities. Once this noise had passed through the nest box interior, it no longer had an even distribution of energy: due to resonance, certain frequencies were amplified. I used Raven's selection spectrum function (Hamming window, 289 Hz filter bandwidth; Charif et al. 2010) to generate an average power value (dB) for each 21.5 Hz frequency bin (the minimum frequency resolution available) in the white noise between 2 and 8.5 kHz. This set of values, hereafter referred to as a resonance spectrum, indicates the amount of amplification experienced by sound in each frequency bin in the broadcast white noise. Noise frequencies coinciding with the box's resonant frequencies are amplified relative to other frequencies, and thus appear as local maxima in the resonance spectrum (Fig. 3; Penna 2004). Using this method, I obtained a resonance spectrum for each treatment nest box, as well as for the recording box described in the next section.

Effect of Nest Box Treatment on Begging Call Features

When nestlings were 10 days old, I removed broods from their nest box and replaced the treatment box with a standardized recording box (19.0 cm x 18.0 cm x 27.0 cm on the short side/30.5 cm on the long side) that was used for recording all nestlings. This recording box allowed me to record nestlings from both treatments in a different resonance environment than their treatment box, which was important because resonance in the recording environment, irrespective of call adjustments by nestlings, can change the measured peak frequency; Appendix A). The recording box contained a cotton towel nest cup of approximately the same size as a tree swallow nest (2-5 cm deep in the bottom of the nest box), and had the lapel microphone attached to the inner wall above the entrance. Once parents resumed feeding following the change in boxes, I recorded the nestlings' begging calls, using the equipment described previously, for 30 minutes or until at least five parental feeding visits had occurred. To test whether call frequency differed between treatments, I measured call frequency features (minimum and maximum frequency as in Part I, kHz; and peak frequency, or frequency with the highest amplitude, kHz). I expected that if nestlings shifted the frequency location of their calls to overlap with the resonant frequencies of their box treatment, then these call features would differ between treatments.

To determine whether nestlings adjusted the overall frequency structure of their calls (as opposed to the specific frequency measures mentioned above) to coincide with the resonant frequencies of their nest box treatment or the recording box (which might happen if nestlings rapidly adjust their calls to the environment in which they find themselves), I calculated a frequency spectrum for each call (i.e. a set of average power values (dB) for each 21.5 Hz frequency bin between 2 and 8.5 kHz across the length of the call) following the protocol used to generate resonance spectra above. I calculated the mean resonance spectra for all high treatment boxes, low treatment boxes, and recording boxes. I then calculated how similar the frequency structure of each call was to the resonance spectrum of each nest box type (high ceiling treatment, low ceiling treatment, or recording box) by correlating each call spectrum's set of average power values with those from the mean resonance spectrum of each nest box type. I then calculated the mean correlation coefficient for each resonance spectrum type for all calls within each nest. I expected that if nestlings aligned their call frequencies with their treatment's resonant frequencies, then low treatment calls would be more highly correlated to the resonance spectrum of the low treatment than they would be to the high treatment and vice versa for high treatment calls. I also expected that if such call feature changes persisted longer than the time scale of the recording, they would be more highly correlated to the resonance spectrum of their treatment than they would be to the resonance spectrum of the recording box. If nestlings altered call frequency rapidly in response to the new acoustic environment of the recording box, I expected them to have higher correlation coefficients with the recording box resonance spectrum than with their treatment resonance spectrum. I only report results from this section that are immediately relevant to the questions asked, i.e. the effect of the resonance spectrum that call spectra were compared to, and the effect of the interaction between call treatment and resonance spectrum.

2.2.2 Statistical Analyses

Resonance Characteristics of Nest Box Treatments

To determine whether box treatments produced characteristic resonance patterns, I correlated the resonance spectrum (set of frequency bin amplitude values) for each treatment nest box with that of each other nest box (not including itself). If ceiling treatments differed in resonance patterns, I expected that the resonance spectra within treatments would be more similar than those across treatments. I tested whether spectrum correlation coefficients were higher for within treatment pairs than between treatment pairs, using a one-tailed Mann-Whitney U test. I chose to use this non-parametric test because the data were not normally distributed (Shapiro-Wilk: same treatment $W = 0.96$, $P < 0.001$; different treatment $W = 0.95$, $P < 0.001$) and transformations could not correct this.

Effect of Nest Box Treatment on Begging Call Features

To test whether call frequency varied with nest box ceiling treatment, I compared call frequency features (minimum, maximum, and peak frequency) between treatments using linear mixed effects models, with call feature as the dependent variable, ceiling treatment as a fixed effect, and nest as a random effect (model: Call Feature ~ Treatment, random = ~1|Nest). I used Tukey's HSD tests to compare group means for resonance spectra (Hothorn et al. 2008). Residuals were normally distributed (Shapiro-Wilk:

minimum frequency W = 0.99, P = 0.32; maximum frequency W = 0.99, P = 0.42; peak frequency W = 0.99, P = 0.36), so variables were left untransformed.

To test whether call spectra were more similar to their own treatment's resonance spectrum than to the other treatment's spectrum, I used a linear mixed effects model with call/resonance spectrum correlation coefficient as the dependent variable; call treatment (ceiling treatment of the nest the calls came from), resonance treatment (ceiling treatment to whose resonance spectrum calls were compared) and their interaction as fixed effects; and calls' source nest box as the random effect (model: Spectrum Correlation Coefficient ~ Call Treatment + Resonance Treatment + Call Treatment:Resonance Treatment, random = ~1|Nest). This grouping structure modified the model's error term to appropriately account for the reuse of the same call spectra in correlations with each resonance spectrum. If calls of either treatment were more similar than calls of the other treatment to the resonance spectrum of any of the box types, this would show up as a significant call treatment-resonance treatment interaction in the model. Residuals did not deviate from normality (Shapiro-Wilk: W = 0.98, P = 0.10), so variables were left untransformed.

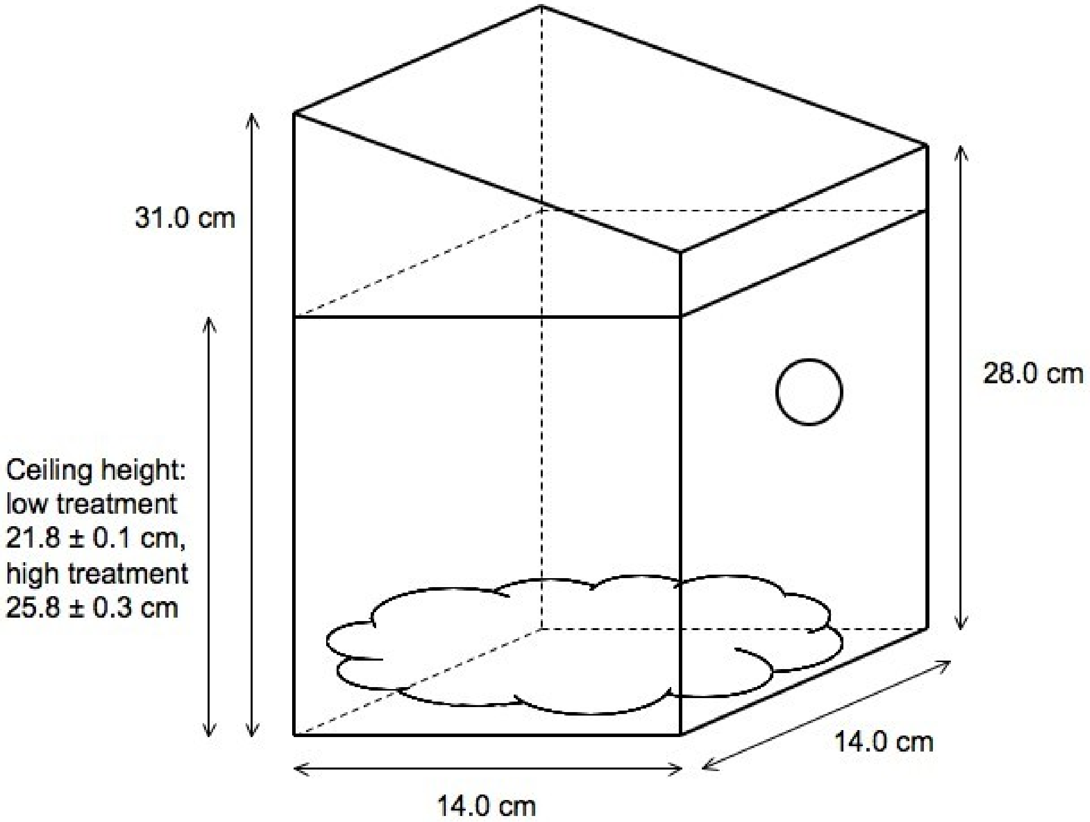

Figure 2 Ceiling height treatments used to modify tree swallow nest boxes. A flat wooden insert was used to set the ceiling height of each box at one of two levels: high or low. Treatment ceiling heights indicated in diagram are mean ± SE distance between the centre of the nest cup and the ceiling itself.

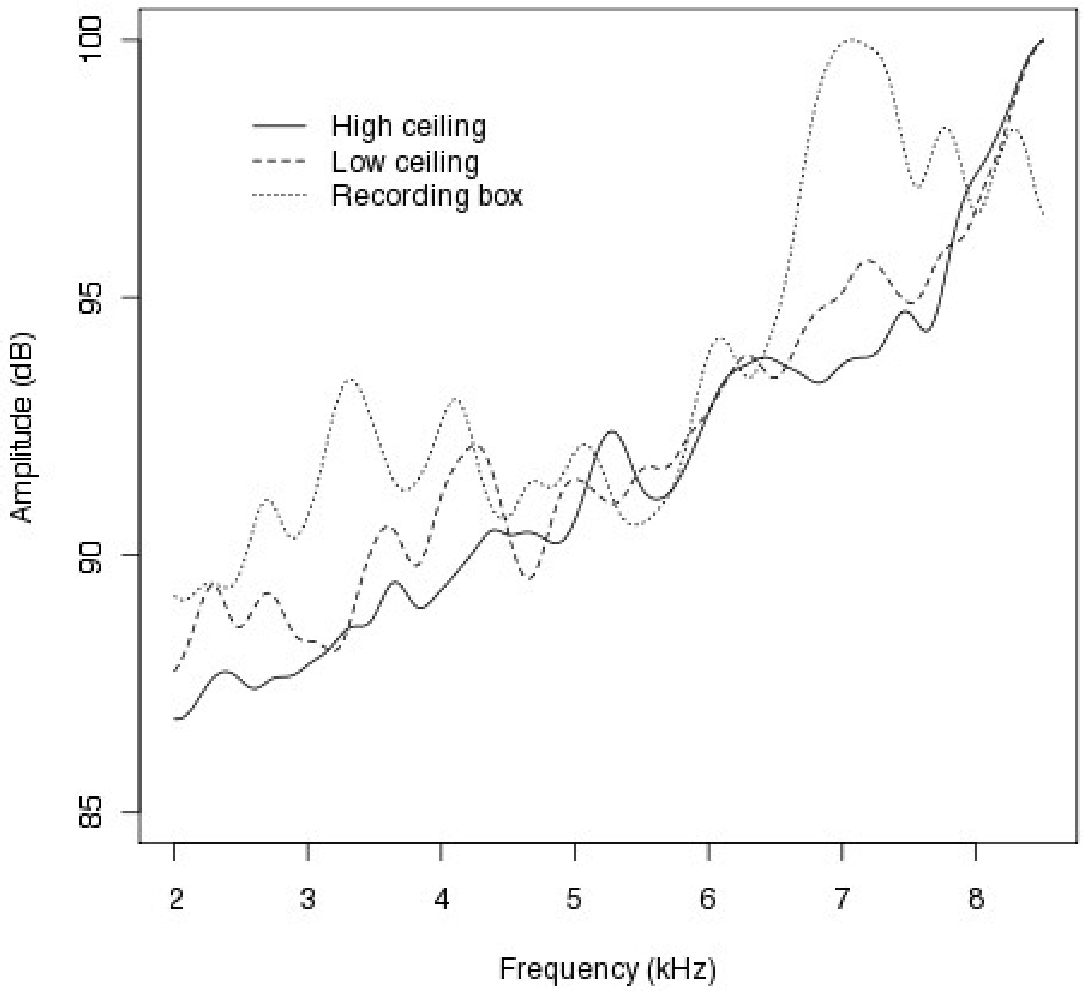

Figure 3 Mean resonance spectra for high and low ceiling nest box treatments, and recording box. Resonant frequencies are local maxima (peaks) in the spectra.

CHAPTER 3 RESULTS

3.1 PART I. NATURAL NEST ACOUSTICS

Physical Structure of Natural Nests

Natural nest cavities varied in internal dimensions; cavity height (mean ± SE) averaged 29.9 ± 5.0 cm (range 10.0-87.0 cm, n = 16), and cavity diameter averaged 12.6 ± 0.9 cm (range 8.0-22.0 cm, n = 16). Thirteen of 20 nest cavities had smooth walls, while seven had lumpy walls. Eleven of 20 nest cavities were closed, while nine were open.

Effect of Nest Structure on Reverberation

The reverberation index increased significantly with cavity diameter ($F_{1,13} = 5.06$, $P = 0.043$; Fig. 4) and closed cavities showed a tendency towards larger reverberation indices than open cavities ($F_{1,13} = 3.84$, $P = 0.072$; Fig. 5). The reverberation index did not vary with cavity height ($F_{1,12} = 0.52$, $P = 0.49$) or wall texture ($F_{1,12} = 0.09$, $P = 0.78$).

Effect of Reverberation on Begging Call Features

Call length showed a near significant decrease with reverberation index ($F_{1,9} = 4.35$, $P = 0.067$), while frequency range did not vary with the reverberation index of the cavity ($F_{1,9} = 1.51$, $P = 0.25$).

Effect of Nest Structure on Begging Call Features

Call length, middle frequency and minimum frequency all varied with nest diameter and wall texture (Table 1). Specifically, call length and middle frequency increased, and minimum frequency decreased, with increasing cavity diameter (Figs. 6-8). Calls were also longer and middle frequencies higher in smooth-walled nests than in lumpy-walled nests, while minimum frequencies were lower in smooth-walled nests. Nest diameter was not included in the final call length model despite near significance (Table 1); its inclusion or exclusion did not change the significance of the effect of nest texture on call length. Neither maximum frequency nor frequency range varied with nest physical properties (Table 1).

Call Transmission Experiment

Calls re-recorded in the nest cavity in which they were produced showed higher spectrogram correlation coefficients than calls originally produced in other nests in 8 out of 11 nests, but overall correlation coefficients of the former were not significantly greater than those of the latter ($V = 42$, $P = 0.23$).

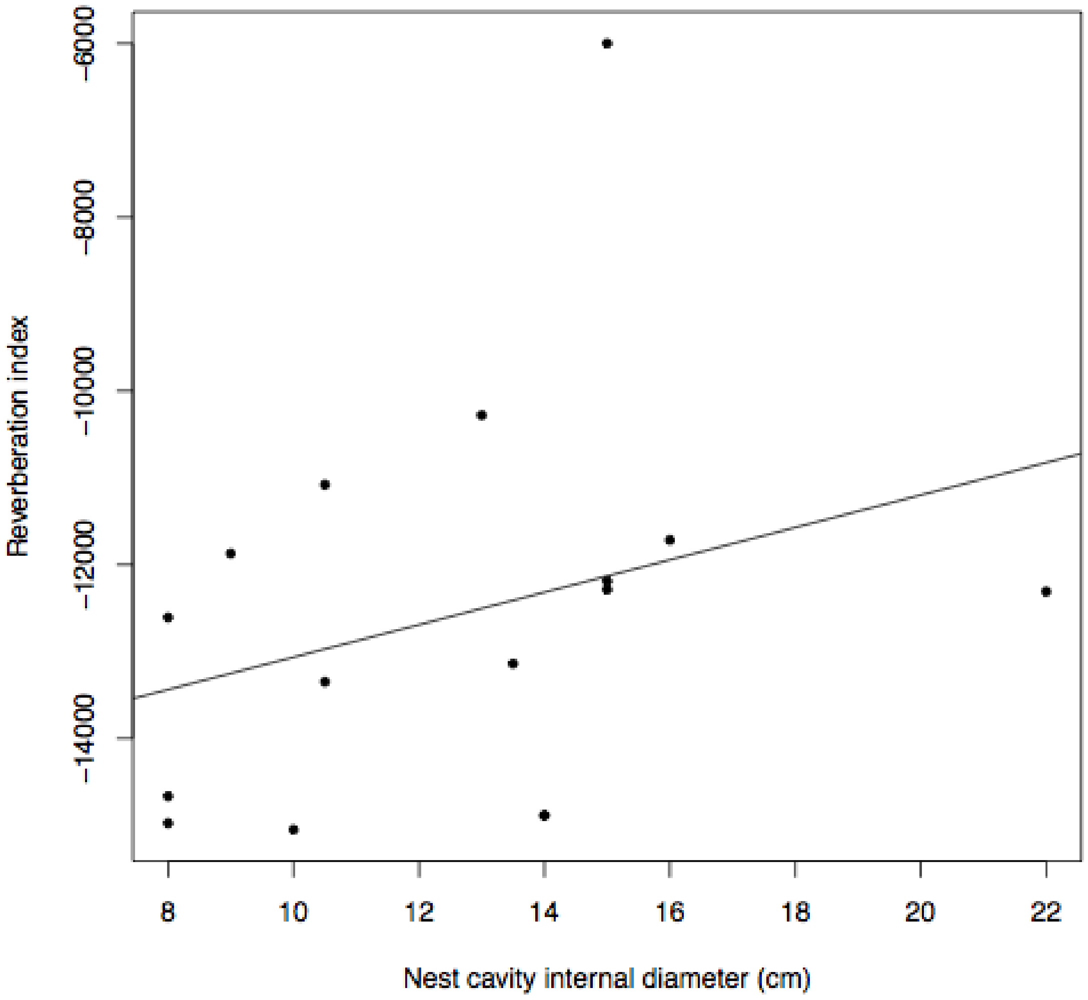

Figure 4 Reverberation index (dimensionless sample units; see text for description) of tree swallow natural nest cavities in relation to cavity diameter (cm). A larger reverberation index indicates that the echo tail is longer on sounds made in that nest, and thus reverberation is stronger. Significant trend in data remains when apparent outliers are removed.

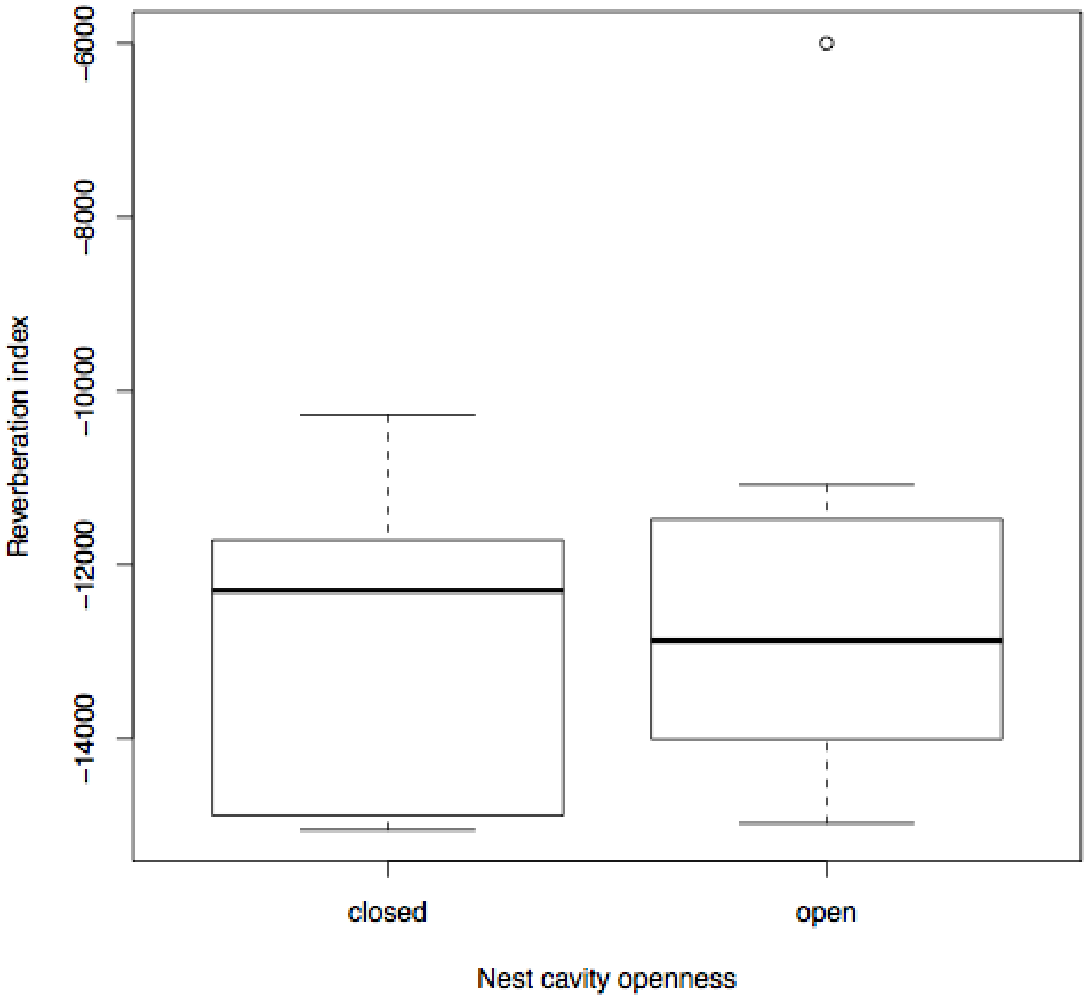

Figure 5 Boxplot showing median and quartile boundaries of reverberation index (dimensionless sample units; see text for description) of closed and open tree swallow natural nest cavities. A larger reverberation index indicates that the echo tail is longer on sounds made in that nest, and thus reverberation is stronger.

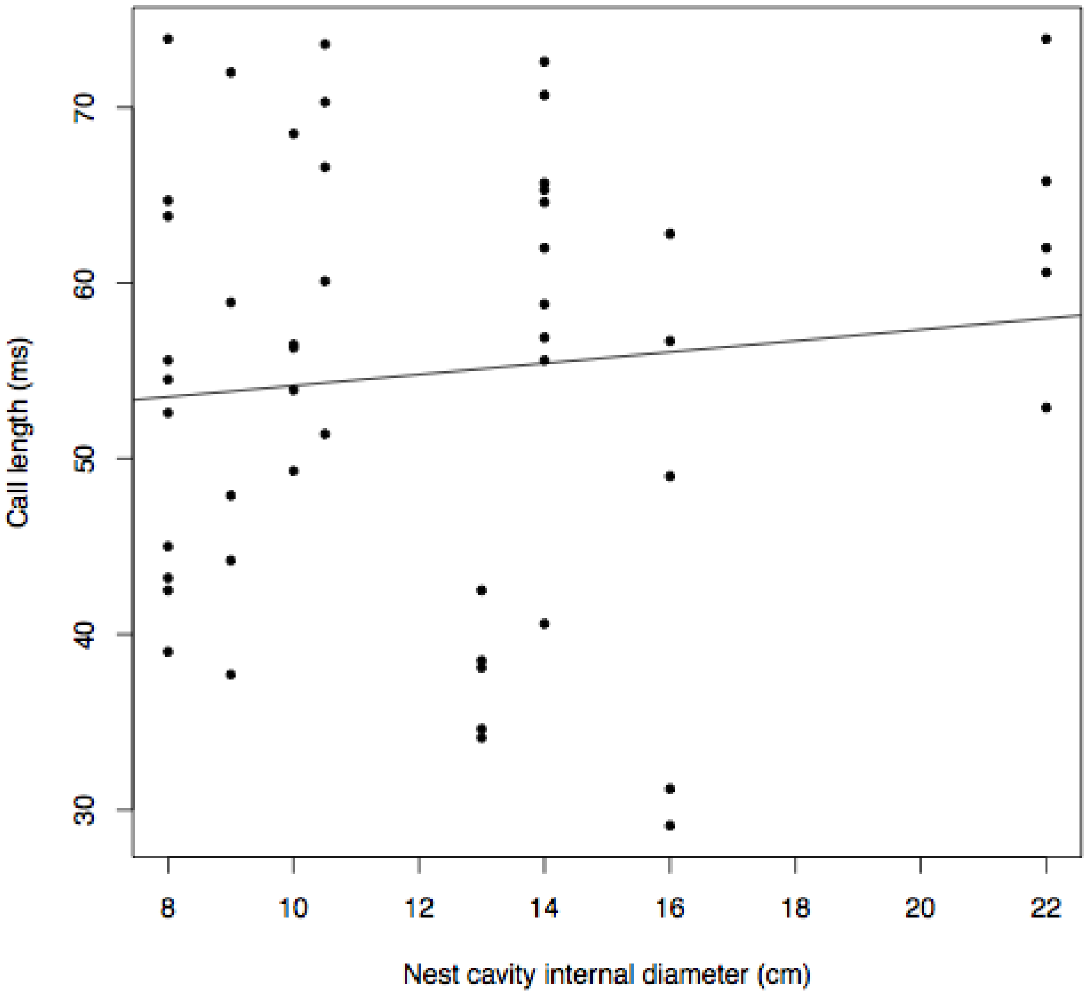

Figure 6 Call length (ms) of nestling tree swallows' begging calls in relation to natural nest cavity diameter (cm). Each point on the figure represents the mean value for calls made during one parental visit, and vertically stacked data points (five points per nest) are visits from a single nest. Analyses handle non-independence of these points by incorporating nest as a random effect.

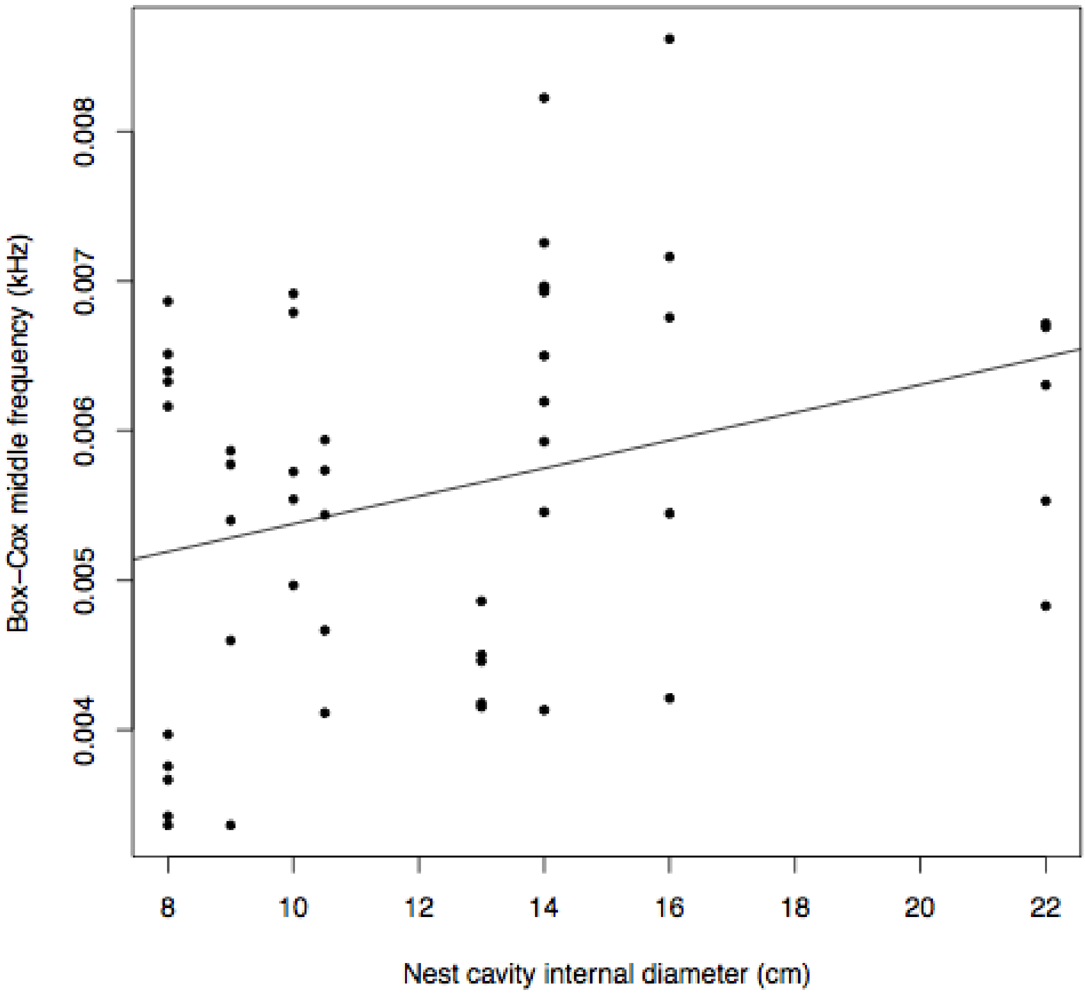

Figure 7 Box-Cox transformed middle frequency (kHz) of nestling tree swallows' begging calls in relation to natural nest cavity diameter (cm). Each point on the figure represents the mean value for calls made during one parental visit, and vertically stacked data points (five points per nest) are visits from a single nest. Analyses handle non-independence of these points by incorporating nest as a random effect.

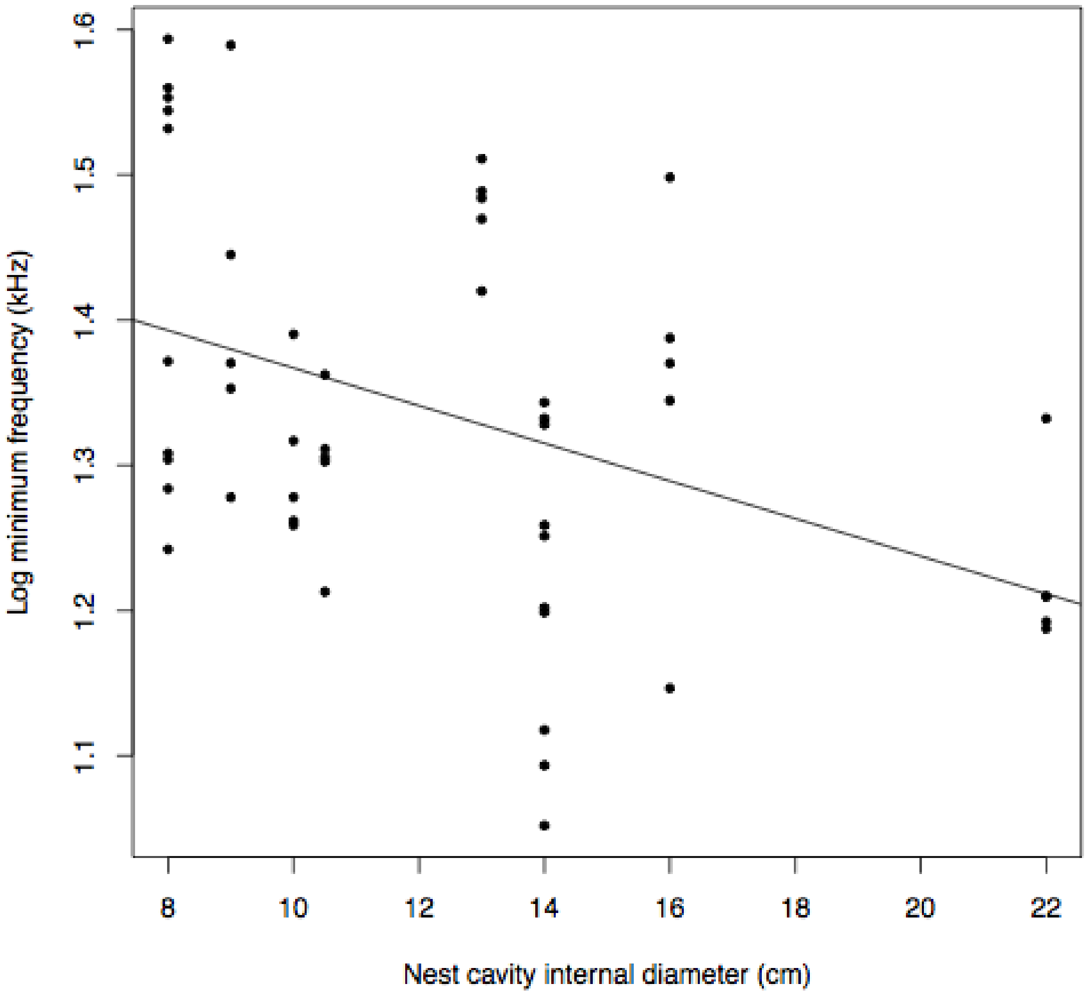

Figure 8 Log-transformed minimum frequency (kHz) of nestling tree swallows' begging calls in relation to natural nest cavity diameter (cm). Each point on the figure represents the mean value for calls made during one parental visit, and vertically stacked data points (five points per nest) are visits from a single nest. Analyses handle non-independence of these points by incorporating nest as a random effect.

Table 1 Influence of natural nest cavity properties on features of the begging calls of nestling tree swallows. Cavity features include internal height (cm), internal diameter (cm), cavity openness (open or closed), and wall texture (smooth or lumpy). Results obtained using linear mixed effects models (REML) for each call feature. Terms remaining in the final models indicated in bold text. Significance indicated by asterisks: *** (P < 0.001), ** (P < 0.01), * (P < 0.05), † (P ~ 0.05).

Call feature	Internal height			Internal diameter			Openness			Wall texture		
	F	df	P	F	df	P	F	df	P	F	df	P
call length (ms)	0.01	1,7	0.93	5.35	1,7	0.054 (†)	0.12	1,8	0.74	**6.90**	**1,9**	**0.028 (*)**
minimum frequency (kHz)	0.15	1,6	0.71	**32.10**	**1,7**	**0.001 (**)**	0.00	1,6	0.95	**32.48**	**1,7**	**0.001 (**)**
maximum frequency (kHz)	0.31	1,8	0.59	0.06	1,8	0.81	1.13	1,19	0.32	0.01	1,9	0.91
middle frequency (kHz)	0.43	1,6	0.54	**7.04**	**1,7**	**0.033 (*)**	4.05	1,6	0.09	**14.12**	**1,7**	**0.007 (**)**
frequency range (kHz)	0.05	1,8	0.83	1.21	1,8	0.30	0.07	1,9	0.80	2.22	1,9	0.17

3.2 PART II. MODIFIED NEST BOX EXPERIMENT

Resonance Characteristics of Nest Box Treatments

The resonance spectrum correlation coefficients within ceiling treatments were significantly larger than between ceiling treatments (mean ± SE, within: 0.789 ± 0.006; between: 0.775 ± 0.005; W = 48765, P = 0.015), indicating that the two ceiling treatments produced characteristic acoustic environments in terms of which frequencies they amplified.

Effect of Nest Box Treatment on Begging Call Features

None of the call frequency features differed significantly between ceiling treatments (Table 2). This is not because the calls from each treatment converged on the resonance spectrum of the recording box, because call spectra overall were more similar to (had higher correlation coefficients with) the resonance spectra of treatment boxes than they were to the resonance spectrum of the recording box ($F_{2,65}$ = 80.49, P < 0.001; low > recording box: t = 7.84, df = 65, P < 0.001; high > recording box: t = 12.56, df = 65, P < 0.001). Call spectra from both treatments were more similar to the high ceiling resonance spectrum than they were to the low ceiling resonance spectrum (t = 4.72, df = 65, P < 0.001). There was also a significant call home treatment/resonance spectrum interaction ($F_{3,65}$ = 2.87, P = 0.043); low treatment call spectra were more similar than high treatment call spectra to the recording box spectrum (t = 2.05, df = 65, P = 0.044). This suggests that nestlings did not adjust the overall spectral patterning of their calls in response to resonance in the nest, but also did not rapidly shift their call spectra to match that of the recording box.

Table 2 Effect of nest box ceiling treatment (mean call feature per treatment ± SE) on nestling tree swallow begging call frequency features (n = 35 nests; 17 high treatment, 18 low treatment).

Call feature	High treatment	Low treatment	F	df	P
minimum frequency (kHz)	3.66 ± 0.05	3.71 ± 0.06	0.11	1,33	0.75
maximum frequency (kHz)	6.19 ± 0.06	6.35 ± 0.08	0.71	1,33	0.41
peak frequency (kHz)	5.13 ± 0.05	5.21 ± 0.07	0.34	1,33	0.57

CHAPTER 4 DISCUSSION

This study shows for the first time that the begging calls of nestling birds vary with structural features of the cavity nest.

I found that tree swallows' natural nest cavities varied in their acoustic properties. As predicted, nest cavities that were larger in diameter and closed off on both ends were more reverberant environments than cavities that were smaller in diameter or open to the external environment. Contrary to my predictions, begging calls were shorter in more reverberant cavities, rather than longer as I expected if calls were elongated by reflected sound waves. Also contrary to my predictions, begging call frequency range did not vary in relation to the amount of reverberation in the nest cavity; calls in more reverberant cavities were not narrower in frequency range, as expected if nestlings were adjusting their calls to reduce distortion induced by frequency overlap. Call features did, however, vary with some structural features of the nest. Calls were longer and had higher middle frequencies and lower minimum frequencies in nests with larger diameters and smoother textured walls. Finally, calls re-recorded in the nest cavity in which they were produced were not less distorted than calls originally produced in other nests as would be expected if nestlings adjusted call features to minimize distortion in the home nest.

Calls' frequency features did not vary in relation to nest box resonance treatment, as would be expected if nestlings adjusted their call frequencies to overlap with nest resonant frequencies. This result did not appear to be a function of nestlings from both treatments rapidly adjusting their calls to the resonance spectrum of the recording box, because call spectra were more similar to the resonance spectra of both the high and low treatment boxes than they were to the resonance spectrum of the recording box.

In the sections that follow, I will discuss my results in relation to my original predictions, and present alternative hypotheses that could explain the patterns observed. Because there has been no previous work describing either the acoustics of birds' nests or how they might relate to call structure, my discussion of these points is largely speculative.

4.1 NEST ACOUSTICS AND THEIR EFFECT ON CALL FEATURES

These results suggest that despite variation among nest cavities in reverberation and resonance, call length was the only call feature that varied in relation to either of these acoustic properties, with calls being shorter in more reverberant cavities. The response of animals to reverberation in enclosed spaces has not previously been studied, so it is unknown whether alteration of call length is a typical response to this acoustic property. However, if this call adjustment functions to reduce call degradation by reverberation, it may explain why in the majority of natural nest cavities, calls originally produced in a given nest transmitted with less degradation than calls originally produced in other nests. The lack of response to nest resonance, meanwhile, puts nestlings in contrast with other animals living in enclosed spaces, which adjust their call frequency to either take advantage of resonance-induced call amplification (by overlapping call frequency with calling site resonant frequency; Lardner and bin Lakim 2002), or avoid high-frequency attenuation (Schleich and Busch 2002; Lange et al. 2007).

There are several non-mutually exclusive explanations for why nestling tree swallows might not have adjusted call frequency features in relation to reverberation and resonance in their nests. First, nestlings may not adjust their call frequency range in response to reverberation because the reverberation strength of nest cavities is insufficient to cause substantial distortion of signals. I predicted that reverberation would degrade begging signals and that nestlings would adjust calls in response, as occurs with long-range signals in reverberant environments (Wiley and Richards 1978; Richards and Wiley 1980; Forrest 1994). However, nest cavities contain many fewer (and much less complex) reflecting surfaces than are encountered by long-distance signals traveling through forests (Wiley and Richards 1978; Richards and Wiley 1980; Forrest 1994), so it is plausible that the number of sound waves reflecting off the cavity walls, and hence the amplitude of echo tails, was insufficient to degrade this short-range signal and prompt a compensatory call feature adjustment in nestlings.

The possibly weak effect of reverberation on call distortion may be even further reduced by the directionality of begging calls. If begging calls are aimed toward the parent, most of the sound energy of the call may be concentrated in the space directly between the calling nestling and the parent (e.g. Witkin 1977; Hunter et al. 1986; Yorzinski and Patricelli 2010), thus reducing the likelihood of sound waves reflecting off the nest walls. The pure tones used to test for reverberation in this study developed measurable echo tails despite being broadcast in the same direction as nestling calls, suggesting that nestling calls would also be subject to the effects of reverberation, but again, it is possible that these reflected sound waves were simply too few to distort nestling calls enough to prompt a nestling response.

An additional possibility is that nestlings actually encounter less reverberation than I measured, because I broadcast tones in nest cavities in the absence of nestlings. Nestlings may absorb some of the sound waves that might otherwise reflect off the cavity floor, thereby reducing the amount of reverberation occurring. However, the nest cup itself, which is often densely packed with grass or pine needles and lined with feathers (Robertson et al. 1992), must also absorb a substantial number of sound waves, so the difference in acoustics of nests with and without nestlings may not be particularly strong. It would be relatively simple in future, however, to test the effect of nestling presence on reverberation by broadcasting pure tones in nest boxes in both the presence and absence of nestlings, and comparing reverberation indices between the two. Using this method, one could also test whether different nest materials (e.g. grass or pine needles, and the number of feathers used) also affect reverberation in the nest cavity.

Nestlings may also not adjust call frequency range to reduce distortion in the nest because their parents either do not use the internal structure of the begging signal to ascertain nestling need, or cannot distinguish between calls that differ in these features (including distorted or non-distorted calls). Although nestlings adjust their call frequency range in relation to background noise (Leonard and Horn 2005), and although call frequency features vary with nestling hunger (Leonard and Horn 2006) and thermal need (Leonard and Horn 2001a), call rate is the only call feature known to be used by parent tree swallows in making feeding decisions (Leonard and Horn 2001b; Leonard and Horn 2005). Thus, if parents' hearing is not attuned to differences in the frequency patterning of calls, there may be no benefit to adjusting call frequency to reduce distortion.

Concerning resonance, nestlings may not align their calls with the resonant frequencies of their nest cavities because there is no benefit to amplifying their begging calls. Signalers that do exploit the resonance of their calling space (e.g. Bennet-Clark 1987; Bailey et al. 2001; Lardner and bin Lakim 2002) benefit from amplification because it maximizes the active space of their long-distance signals and enables those signals to reach as many potential receivers as possible (Marten and Marler 1977). In the case of nestlings, one might not imagine there to be a benefit to amplifying the begging call because audibility might not be a major constraint over the short distances between nestlings and parents. However, previous work with tree swallows shows that natural levels of background noise interfere with parents' ability to distinguish differences in call features signaling hunger (Leonard and Horn 2005), and that nestling tree swallows increase vocal amplitude in response to louder natural background noise at the nest (Leonard and Horn 2005). As there appears to be a benefit to call amplification under the background noise conditions found at the nest boxes used in this study (as they were the same sites used in Leonard and Horn 2005), it is not clear why nestlings would not adjust the frequencies of their calls to take advantage of the resonant frequencies of the nest box, particularly if the alternative strategy, of actively emitting louder calls, is more energetically costly (e.g. Warren et al. 2006).

A second reason why nestling calls might not vary in relation to nest resonance is that even if exploiting resonance provides an energetic benefit when communicating to parents over noise, it may also carry a cost by making calls more conspicuous to predators. More conspicuous begging calls, including those with higher amplitudes, are more likely to attract predators (reviewed in Magrath et al. 2010). Although species that nest in cavities, such as tree swallows, are less susceptible to predation than open-cup nesters and can thus have more conspicuous calls (Haskell 1994, 1999; see also Briskie et al. 1999), begging calls have been shown to attract predators to tree swallow nests (Leech and Leonard 1997), so presumably amplifying begging calls would make nestlings more vulnerable.

Two additional general explanations may explain why nestlings do not adjust call frequency features in relation to nest reverberation and resonance. Begging calls may not vary with nest acoustics because nestlings at this age are physiologically or neurologically unable to make such adjustments to call features. However, this is unlikely, because other studies have shown that nestling tree swallows as young as five days old are able to vary their calls' frequency features in response to noise at the nest (Leonard and Horn 2008). As the predicted response of nestlings to both reverberation and resonance in the nest cavity involves adjustments of call frequency, it is unlikely that nestlings did not respond to these nest acoustic features because they were physiologically unable to do so.

Finally, nestlings may not adjust their calls' frequency features in relation to nest acoustics because the effect of acoustics may be drowned out by other, more influential factors that I was unable to account for here. Chief among these could be brood size, which I could not measure accurately in natural nests. If, for example, nestlings adjust their call frequency to minimize overlap with other nestlings' calls in the same way adult long-distance signalers partition the acoustic space (e.g. Miller 1982), nestlings from larger broods could use a greater diversity of frequencies, thereby preventing their call frequencies from matching resonant frequencies (although nestling tree swallows do not appear to adjust call frequency in response to the presence of nestmates; Leonard and Horn 2001c). Other unmeasured factors affecting call features could include nestling sex (e.g. Saino et al. 2003; Boncoraglio et al. 2008; Liu et al. 2009), size (e.g. Leonard and

Horn 2001a), or condition (e.g. Sacchi et al. 2002; Quillfeldt et al. 2004, Quillfeldt et al. 2006), the latter mediated by factors such as availability of insects (Ardia 2006), thermal conditions during incubation (Ardia et al. 2010), or parental experience (Lombardo and Thorpe 2010). Any of these factors could have masked the effect of nest acoustics.

4.2 NEST PHYSICAL FEATURES AND THEIR EFFECT ON CALL FEATURES

Although call structure did not vary in relation to reverberation and resonance, I did find that some call features varied with the structure of the nest. Again, there are several non-mutually exclusive explanations for why I might have observed these patterns.

First, call features may have varied with the physical properties of nests for acoustic reasons. I directly examined whether call features varied in relation to the two most likely acoustic properties of a small enclosed cavity, i.e. reverberation and resonance. However, acoustic properties that I did not measure, such as sound absorption, may also have varied across nests and might explain some of the patterns I observed between calls in nests with different structural properties. In particular, wall texture may correlate with wall hardness and thus whether surfaces reflect or absorb sound (as well as whether certain frequencies would be more absorbed than others). In particular, if lumpy nest walls are more absorptive of low-frequency sounds, nestlings may have shifted their calls' minimum frequencies upwards to avoid this attenuation.

Another possibility is that the distance to the nest entrance, and thus to parents, varies with nest diameter and nestlings adjust their calls based on how far they are from the parents. Because nest materials generally fill the entire cavity floor, nestlings at the back of the nest in wider cavities may be farther from the entrance than the same nestlings in narrower cavities, and the increase in call length with cavity diameter may reflect these nestlings' attempts to increase conspicuousness to parents despite the increased distance. This explanation is consistent with previous studies on nestling tree swallows that showed that call features normally used to signal hunger (Leonard and Horn 2001a) increased when nestlings were experimentally constrained at a distance from the nest box opening (prompting an increase in call rate; Leonard et al. 2003), as well as when the parent's ability to distinguish between hunger-coding call features was inhibited by noise (prompting an increase in call length; Leonard and Horn 2005), suggesting that nestlings might alter both call features to increase conspicuousness to parents.

An alternative explanation for why nestlings use longer calls with lower minimum frequencies in wider cavities, is that if (as hypothesized above) the individual nestlings within a brood are on average farther from the nest entrance in wider cavities, they may be less vulnerable to predation (e.g. Czeszczewik and Walankiewicz 2003), and therefore may not need to minimize call locatability. The increased length and lower minimum frequency of calls in wider cavities are consistent with the types of call features one might expect to find in nestlings facing lower predation pressure; longer calls may be more conspicuous, and lower frequency calls are more easily located by predators (e.g. Briskie et al. 1999), so it is plausible that predation risk may cause the observed relationship between these call features and cavity diameter. Both this and the previous explanation, however, assume that the average nestling is farther from the nest entrance in wider cavities, so this assumption would have to be tested.

A third hypothesis for the observed relationship between call features and nest structure is that different widths of cavities may also differ in levels of background noise. Sounds coming from outside the nest cavity are greatly attenuated once they enter that space (e.g. Lampe et al. 2004), and if wider cavities are located inside wider trees with thicker walls that block more sound, external background noise may be more attenuated in wider cavities than narrower cavities. This is plausible, as the widest cavities in my study were located within larger tree trunks than the narrowest cavities. If noise levels in the nest are influenced by wall thickness, nestlings in narrower, potentially noisier nests might benefit from using higher minimum call frequencies, as has been found in nestling tree swallows exposed to long-term white noise (Leonard and Horn 2008). One could test this hypothesis by recording standardized background noise from within nest boxes of different sizes and wall thicknesses, and testing whether attenuation depends on cavity size, wall thickness, or both.

Finally, call minimum frequency may be lower in wider cavities if these cavities are cooler during the daytime than narrower cavities, due to greater temperature buffering by the thicker walls of larger trees (Coombs et al. 2010) and dissipation of nestling-generated heat (e.g. Chaplin et al. 2002) over a larger air volume. Nestling tree swallows exposed to cooler temperatures have previously been shown to call with a lower peak frequency than warmer nestlings (Leonard and Horn 2001a), and so if cavity temperature drives calls to lower minimum frequencies in wider cavities, it would be consistent with previous findings. One could test the possibility that cavity temperature contributes to the observed effect of cavity diameter on begging call features by measuring the internal temperature of nest cavities during the daytime feeding hours, and testing whether wider cavities are indeed cooler.

4.3 CONCLUSION

The results of my study show that nestling begging calls vary in relation to nest structure, and that they also adjust call length according to the reverberation strength of the nest cavity. This suggests a role of the nest environment in shaping begging calls, via both reverberation and either an acoustic factor I was unable to measure or the relationship between nest physical structure and another environmental parameter that directly causes nestlings to adjust calls (e.g. distance from parents or predators, background noise, or nest cavity temperature). If variation in the physical environment of the nest affects call structure in nestlings generally, it could explain differences in calls between species with different nest structures. For example, differences in call features between cavity-nesting and open cup-nesting species have thus far been attributed to differences in predation risk (Haskell 1994, 1999). However, if nest cavities or burrows alter the frequency or amplitude structure of calls, or cause substantially more attenuation than open cup nests, or if the cavities or burrows of different species differ acoustically, this could also drive call variation between species. In conclusion, the nest environment may be important to signal design, and the mechanisms behind this relationship bear further investigation.

REFERENCES

Ardia, D.R. 2006. Geographic variation in the trade-off between nestling growth rate and body condition in the tree swallow. *Condor* 108: 601-611.

Ardia, D.R., J.H. Pérez, and E.D. Clotfelter. 2010. Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proc. R. Soc. B* 277: 1881-1888.

Avilés, J.M., T. Pérez-Contreras, C. Navarro, and J.J. Soler. 2008. Dark nests and conspicuousness in color patterns of nestlings of altricial birds. *Am. Nat.* 171: 327-338.

Bailey, W.J., H.C. Bennet-Clark, and N.H. Fletcher. 2001. Acoustics of a small Australian burrowing cricket: the control of low-frequency pure-tone songs. *J. Exp. Biol.* 204: 2827-2841.

Bennet-Clark, H.C. 1987. The tuned singing burrow of mole crickets. *J. Exp. Biol.* 128: 383-409.

Blumstein, D.T., and A.C. Turner. 2005. Can the acoustic adaptation hypothesis predict the structure of Australian birdsong? *Acta Ethol.* 15: 35-44.

Boland, C.R.J., and R.M. Phillips. 2005. A small, lightweight, and inexpensive "burrowscope" for viewing nest contents of tunnel-nesting birds. *J. Field Ornithol.* 76: 21-26.

Boncoraglio, G., and N. Saino. 2007. Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustic adaptation hypothesis. *Funct. Ecol.* 21: 134-142.

Boncoraglio, G., R. Martinelli, and N. Saino. 2008. Sex-related asymmetry in competitive ability of sexually monomorphic barn swallow nestlings. *Behav. Ecol. Sociobiol.* 62: 729-738.

Bradbury, J.W., and S.L. Vehnrencamp. 1998. Principles of animal communication. Sunderland: Sinauer.

Briskie, J.V., P.R. Martin, and T.E. Martin. 1999. Nest predation and the evolution of nestling begging calls. *Proc. R. Soc. Lond. B* 266: 2153-2159.

Brown, C.H., R. Gomez, and P.M. Waser. 1995. Old World monkey vocalizations: adaptation to the local habitat? *Anim. Behav.* 50: 945-961.

Brown, T.J., and P. Handford. 1996. Acoustic signal amplitude patterns: A computer simulation investigation of the acoustic adaptation hypothesis. *Condor* 98: 608-623.

Brown, T.J., and P. Handford. 2000. Sound design for vocalizations: Quality in the woods, consistency in the fields. *Condor* 102: 81-92.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 73: 434-440.

Brumm, H., and H. Slabbekoorn. 2005. Acoustic communication in noise. *Adv. Stud. Behav.* 35: 151-209.

Brumm, H., and D. Todt. 2002. Noise-dependent song amplitude regulation in a territorial songbird. *Anim. Behav.*. 63: 891-897.

Brumm, H., K. Voss, I. Köllmer, and D. Todt. 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. *J. Exp. Biol.* 207: 443-448.

Cardoso, G., and T.D. Price. 2010. Community convergence in bird song. *Evol. Ecol.* 24: 447-461.

Catchpole, C.K., and P.J.B. Slater. 2008. Bird song: biological themes and variations, 2nd ed. New York: Cambridge University Press.

Chaplin, S.B., M.L. Cervenka, and A.C. Mickelson. 2002. Thermal environment of the nest during development of tree swallow (*Tachycineta bicolor*) chicks. *Auk* 119: 845-851.

Charif, R.A., A.M. Waack, and L.M. Strickman. 2010. Raven Pro 1.4 User's Manual. Cornell Laboratory of Ornithology, Ithaca, NY.

Coombs, A.B., J. Bowman, and C.J. Garroway. 2010. Thermal properties of tree cavities during winter in a northern hardwood forest. *J. Wildlife Manage.* 74: 1875-1881.

Couldridge, V.C.K., and M.J. van Staaden. 2004. Habitat-dependent transmission of male advertisement calls in bladder grasshoppers (Orthoptera; Pneumoridae). *J. Exp. Biol.* 207: 2777-2786.

Cromer, A.H. 1994. Physics for the life sciences, 2nd ed. New York: The McGraw-Hill Companies, Inc.

Cunnington, G.M., and L. Fahrig. 2010. Plasticity in the vocalizations of anurans in response to traffic noise. *Acta Oecol*. 36: 463-470.

Czeszczewik, D., and W. Walankiewicz. 2003. Natural nest sites of the Pied Flycatcher *Ficedula hypoleuca* in a primeval forest. *Ardea* 91: 221-230.

Daniel, J.C., and D.T. Blumstein. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. *Anim. Behav.* 56: 1517-1528.

Darden, S.K., S.B. Pedersen, O.N. Larsen, and T. Dabelsteen. 2008. Sound transmission at ground level in a short-grass prairie habitat and its implications for long-range communication in the swift fox *Vulpes velox*. *J. Acoust. Soc. Am.* 124: 758-766.

Derryberry, E.P. 2009. Morphology and habitat explains variation in white-crowned sparrow song. *Am. Nat.* 174: 24-33.

Dingle, C., W. Halfwerk, and H. Slabbekoorn. 2008. Habitat-dependent song divergence at subspecies level in the grey-breasted wood-wren. *J. Evol. Biol.* 21: 1079-1089.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* 139: S125-S153.

Ey, E., and J. Fischer. 2009. The "acoustic adaptation hypothesis" – a review of the evidence from birds, anurans and mammals. *Bioacoustics* 19: 21-48.

Fairhurst, E.N., E.A. Krebs, E.A. Gillis, and D.J. Green. In prep. Begging to be heard: Signaling in an acoustically variable environment.

Ficken, R.W., M.S. Ficken, and J.P. Hailman. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* 183: 762-763.

Forrest, T.G. 1994. From sender to receiver: Propagation and environmental effects on acoustic signals. *Am. Zool.* 34: 644-654.

Fox, J. 2009. car: Companion to applied regression. R package version 1.2-16. URL: http://CRAN.R-project.org/package=car.

Halfwerk, W., and H. Slabbekoorn. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Anim. Behav.* 78: 1301-1307.

Hansen, P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Anim. Behav.* 27: 1270-1271.

Haskell, D. 1994. Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proc. Biol. Sci.* 257: 161-164.

Haskell, D.G. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Anim. Behav.* 57: 893-901.

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

Holland, J., P.K. McGregor, and C.L. Rowe. 1996. Changes in microgeographic song variation of the Corn Bunting *Miliaria calandra*. *J. Avian Biol.* 27: 47-55.

Horn, A.G., and M.L. Leonard. 2002. Efficacy and the design of begging signals. In *The evolution of begging: competition, cooperation and communication* (ed. J. Wright and M.L. Leonard), pp.127-141. Dordrecht: Kluwer Academic Publishers.

Hothorn, T., F. Bretz and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical J.* 50: 346-363.

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

Hunter, M.L., A. Kacelnik, J. Roberts, and M. Vuillermoz. 1986. Directionality of avian vocalizations: a laboratory study. *Condor* 88: 371-375.

Hunter, M.L., and J.R. Krebs. 1979. Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. *J. Anim. Ecol.* 48: 759-785.

Ishigami, Y. and D.P. Phillips. 2008. Effect of stimulus hemifield on free-field auditory saltation. *Hearing Res.* 241: 97-102.

Johnstone, R.A. 1997. The evolution of animal signals. In *Behavioural ecology: an evolutionary approach, 4th ed* (ed. J.R. Krebs and N.B. Davies), pp. 155-178. Osney Mead: Blackwell Science Ltd.

Kilner, R.M. 2002. The evolution of complex begging displays. In *The evolution of begging: competition, cooperation and communication* (ed. J. Wright and M.L. Leonard), pp. 87-106. Dordrecht: Kluwer Academic Publishers.

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

Kilner, R., and C.A. Hinde. 2008. Information warfare and parent-offspring conflict. *Adv. Stud. Behav.* 38: 283-336.

Kilner, R., and R.A. Johnstone. 1997. Begging the question: are offspring solicitation behaviours signals of need? *TREE* 12: 11-15.

Kirschel, A.N.G., D.T. Blumstein, R.E. Cohen, W. Buermann, T.B. Smith, and H. Slabbekoorn. 2009. Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. *Behav. Ecol.* 20: 1089-1095.

Klump, G.M. 1996. Bird communication in a noisy world. In *Ecology and evolution of acoustic communication in birds* (ed. D.E. Kroodsma and E.H. Miller), pp. 321-338. Ithaca: Cornell University Press.

Krebs, J.R., and N.B. Davies. 1993. An introduction to behavioural ecology, 3rd ed. Oxford: Blackwell Science Ltd.

Kroodsma, D.E., and E.H. Miller (eds.). 1996. Ecology and evolution of acoustic communication in birds. Ithaca: Cornell University Press.

Kroodsma, D.E., E.H. Miller, and H. Ouellet (eds.). 1982. Acoustic communication in birds, volume 1: production, perception, and design features of sounds. New York: Academic Press, Inc.

Kroon, F.J., and D.A. Westcott. 2006. Song variation and habitat structure in the Golden Bowerbird. *Emu* 106: 263-272.

Lampe, H.M., T. Dabelsteen, O.N. Larsen, and S.B. Pedersen. 2004. Degradation of song in a species using nesting holes: the Pied Flycatcher *Ficedula hypoleuca*. *An. Acad. Bras. Cienc.* 76: 264-266.

Lange, S., H. Burda, R.E. Wegner, P. Dammann, S. Begall and M. Kawalika. 2007. Living in a "stethoscope": burrow-acoustics promote auditory specializations in subterranean rodents. *Naturwissenschaften* 94: 134-138.

Lardner, B., and M. bin Lakim. 2002. Tree-hole frogs exploit resonance effects. *Nature* 420: 475.

Le Roux, A., T.P. Jackson and M.I. Cherry. 2002. Differences in alarm vocalizations of sympatric populations of the whistling rats, *Parotomys brantsii* and *P. littledalei* (Rodentia: Muridae). *J. Zool. Lond.* 257: 189-194.

Leech, S.M., and M.L. Leonard. 1997. Begging and the risk of predation in nestling birds. *Behav. Ecol.* 8: 644-646.

Lengagne, T., T. Aubin, J. Lauga, and P. Jouventin. 1999. How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proc. R. Soc. Lond. B* 266: 1623-1628.

Leonard, M.L., and A.G. Horn. 1996. Provisioning rules in tree swallows. *Behav. Ecol. Sociobiol.* 38: 341-347.

Leonard, M.L., and A.G. Horn. 2001a. Acoustic signalling of hunger and thermal state by nestling tree swallows. *Anim. Behav.* 61: 87-93.

Leonard, M.L, and A.G. Horn. 2001b. Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behav. Ecol. Sociobiol.* 49: 170-175.

Leonard, M.L., and A.G. Horn. 2001c. Dynamics of calling by tree swallow (*Tachycineta bicolor*) nestmates. *Behav. Ecol. Sociobiol.* 50: 430-435.

Leonard, M.L., and A.G. Horn. 2005. Ambient noise and the design of begging signals. *Proc. R. Soc. B* 272: 651-656.

Leonard, M.L., and A.G. Horn. 2006. Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). *Ethology* 112: 1020-1026.

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

Leonard, M.L., A.G. Horn, and A. Dorland. 2009. Does begging call convergence increase feeding rates to nestling tree swallows *Tachycineta bicolor*? *J. Avian Biol.* 40: 243-247.

Leonard, M.L., A.G. Horn, and E. Parks. 2003. The role of posturing and calling in the begging display of nestling birds. *Behav. Ecol. Sociobiol.* 54: 188-193.

Liu, W.-c., K. Wada, and F. Nottebohm. 2009. Variable food begging calls are harbingers of vocal learning. *PLoS ONE* 4: e5929.

Lohr, B., T.F. Wright, and R.J. Dooling. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Anim. Behav.* 65: 763-777.

Lombardo, M.P., and P.A. Thorpe. 2010. Local breeding experience and the reproductive performance of tree swallows. *J. Field Ornithol.* 81: 294-301.

Lopez, P.T., P.M. Narins, E.R. Lewis and S.W. Moore. 1988. Acoustically induced call modification in the white-lipped frog, *Leptodactylus albilabris*. *Anim. Behav.* 36: 1295-1308.

Lugli, M. 2010. Sounds of shallow water fishes pitch within the quiet window of the habitat ambient noise. *J. Comp. Physiol. A* 196: 439-451.

Magrath, R.D., T.M. Haff, A.G. Horn, and M.L. Leonard. 2010. Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. *Adv. Study Behav.* 41: 187-253.

Marten, K., and P. Marler. 1977. Sound transmission and its significance for animal vocalization: I. Temperate habitats. *Behav. Ecol. Sociobiol.* 2: 271-290.

Miller, E.H. 1982. Character and variance shift in acoustic signals of birds. In *Acoustic communication in birds, volume 1: production, perception, and design features of sounds* (ed. D.E. Kroodsma, E.H. Miller, and H. Ouellet), pp. 253-295. New York: Academic Press.

Morton, E.S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* 109: 17-34.

Nicholls, J.A., and A.W. Goldizen. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. *J. Anim. Ecol.* 75: 549-558.

Nottebohm, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *Am. Nat.* 109: 605-624.

Parris, K.M., and A. Schneider. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecol. Soc.* 14: 29.

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

Penna, M. 2004. Amplification and spectral shifts of vocalizations inside burrows of the frog *Eupsophus calcaratus* (Leptodactylidae). *J. Acoust. Soc. Am.* 116: 1254-1260.

Penna, M., and R. Marquez. 2007. Amplification and spectral modification of incoming vocalizations inside burrows of the frog *Eupsophus roseus* (Leptodactylidae). *Bioacoustics* 16: 245-259.

Penna, M., and R. Solís. 1996. Influence of burrow acoustics on sound reception by frogs *Eupsophus* (Leptodactylidae). *Anim. Behav.* 51: 255-263.

Peters, G., L. Baum, M.K. Peters, and B. Tonkin-Leyhausen. 2009. Spectral characteristics of intense mew calls in cat species of the genus *Felis* (Mammalia: Carnivora: Felidae). *J. Ethol.* 27: 221-237.

Peters, G., and M. K. Peters. 2010. Long-distance call evolution in the Felidae: effects of body weight, habitat, and phylogeny. *Biol. J. Linn. Soc.* 101: 487-500.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and the R Core Team. 2009. nlme: Linear and nonlinear mixed effects models. R package version 3.1-96.

Proppe, D.S., L.L. Bloomfield, and C.B. Sturdy. 2010. Acoustic transmission of the chick-a-dee call of the Black-capped Chickadee (*Poecile atricapillus*): forest structure and note function. *Can. J. Zool.* 88: 788-794.

Pytte, C.L., K.M. Rusch, and M.S. Ficken. 2003. Regulation of vocal amplitude by the blue-throated hummingbird, *Lampornis clemenciae*. *Anim. Behav.* 66: 703-710.

Quillfeldt, P., J.F. Masello, I.J. Strange, and K.L. Buchanan. 2006. Begging and provisioning of thin-billed prions, *Pachyptila belcheri*, are related to testosterone and corticosterone. *Anim. Behav.* 71: 1359-1369.

Quillfeldt, P., J.F. Masello, and K.C. Hamer. 2004. Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. *Anim. Behav.* 68: 613-620.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.

Raichel, D.R. 2006. The science and applications of acoustics, 2nd ed. New York: Springer Science+Business Media, Inc.

Rendell, W.B., and R.J. Robertson. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. *Condor* 91: 875-885.

Richards, D.G., and R.H. Wiley. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Nat.* 115: 381-399.

Robertson, R.J., B.J. Stutchbury and R.R. Cohen. 1992. Tree swallow. In *The Birds of North America Online* (ed. A. Poole). Ithaca: Cornell Lab of Ornithology. URL: http://bna.birds.cornell.edu/bna/species/011.

Rothstein, S.I., and R.C. Fleischer. 1987. Vocal dialects and their possible relation to honest status signalling in the brown-headed cowbird. *Condor* 89: 1-23.

Sacchi, R., N. Saino, and P. Galeotti. 2002. Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behav. Ecol.* 13: 268-273.

Saino, N., P. Galeotti, R. Sacchi, G. Boncoraglio, R. Martinelli, and A.P. Møller. 2003. Sex differences in begging vocalizations of nestling barn swallows, *Hirundo rustica*. *Anim. Behav.* 66: 1003-1010.

Schleich, C.E. and C. Busch. 2002. Acoustic signals of a solitary subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae): physical characteristics and behavioural correlates. *J. Ethol.* 20: 123-131.

Schneider, C., K. Hodges, J. Fischer, and K. Hammerschmidt. 2008. Acoustic niches of Siberut primates. *Int. J. Primatol.* 29: 601-613.

Slabbekoorn, H., and A. den Boer-Visser. 2006. Cities change the songs of birds. *Curr. Biol.* 16: 2326-2331.

Slabbekoorn, H., J. Ellers and T.B. Smith. 2002. Birdsong and sound transmission: the benefits of reverberations. *Condor* 104: 564-573.

Slabbekoorn, H., and M. Peet. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424: 267.

de la Torre, S., and C.T. Snowdon. 2002. Environmental correlates of vocal communication of wild pygmy marmosets, *Cebuella pygmaea*. *Anim. Behav.* 63: 847-856.

Trefry, S.A., and D.S. Hik. 2010. Variation in pika (*Ochotona collaris*, *O. princeps*) vocalizations within and between populations. *Ecography* 33: 784-795.

Tubaro, P.L., and D.A. Lijtmaer. 2006. Environmental correlates of song structure in forest grosbeaks and saltators. *Condor* 108: 120-129.

Tubaro, P.L., and E.T. Segura. 1994. Dialect differences in the song of *Zonotrichia capensis* in the southern pampas: a test of the acoustic adaptation hypothesis. *Condor* 96: 1084-1088.

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

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

Wiley, R.H., and D.G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3: 69-94.

Wiley, R.H., and D.G. Richards. 1982. Adaptations for acoustic communication in birds: Sound transmission and signal detection. In *Acoustic communication in birds, volume 1: production, perception, and design features of sounds* (ed. D.E. Kroodsma, E.H. Miller, and H. Ouellet), pp. 131-181. New York: Academic Press.

Witkin, S.R. 1977. The importance of directional sound radiation in avian vocalization. *Condor* 79: 490-493.

Wright, J., and M.L. Leonard (eds.). 2002. The evolution of nestling begging: competition, cooperation and communication. Dordrecht: Kluwer Academic Publishers.

Yorzinski, J.L., and G. Patricelli. 2010. Birds adjust acoustic directionality to beam their antipredator calls to predators and conspecifics. *Proc. R. Soc. B* 277: 923-932.

APPENDIX A Dependence of Call Peak Frequency Measurement on Recording Environment Acoustics

If one is interested in comparing begging calls' peak frequency or overall frequency structure as emitted by nestlings across nests, one cannot do so if calls are recorded in nests with different resonant frequencies. Amplification of different sound frequencies by the nest environment has the potential to introduce an artifact into the recording; rather than recording the call's frequency structure as emitted by the nestling, one may end up recording something resembling the original frequency structure, but with certain frequencies (those coinciding with the nest cavity's resonant frequencies) amplified relative to others.

I tested whether recorded peak frequency differs depending on the nest cavity in which calls are recorded by broadcasting and recording the same set of nestling calls in different nest cavities (see transmission experiment in Part I of this study). I measured the peak frequency (kHz) of each call following broadcast in each nest, and then tested whether broadcast in different nest cavities produced characteristic peak frequencies using a linear mixed effects model with peak frequency following broadcast as the dependent variable, broadcast nest as the fixed effect, and the calls' home nest as the random effect.

I found that change in peak frequency differed significantly between broadcast nests ($F_{10,100} = 12.23$, $P < 0.001$). This supported my prediction that different nest cavities would differentially alter the measured peak frequency of calls made within them, and provided justification for my decision to use a standardized recording environment to test the effects of resonance on nestling begging calls (see Part II).