AMBIENT NOISE AND THE COMMUNICATION OF PREDATION RISK BETWEEN PARENT AND NESTLING TREE SWALLOWS (*TACHYCINETA BICOLOR)*

by

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ABSTRACT

Ambient noise masks important acoustic signals used in a variety of communication systems. Nestling birds communicate with their parents using loud begging calls that convey their need for food, but these calls can also attract predators to the nest. Parents can counteract this vulnerability by using alarm calls to silence begging nestlings, if predators are nearby. Noise could, however, mask alarm calls and increase predation risk for begging nestlings.

In the first chapter of my study, I played back parental alarm calls to broods of 5, 10, and 15 day old tree swallow (*Tachycineta bicolor*) nestlings to determine if nestlings respond to parental alarm calls. I then played back parental alarm calls to 15 day old nestlings in the presence of white noise to determine if noise affects this response. I found that younger nestlings did not respond to alarm calls, but that 15 day old nestlings responded to alarm calls by falling silent and crouching in the nest. I also found that the magnitude of this response decreased in the presence of noise. Noise interferes with the ability of nestlings to respond appropriately to parental alarm calls, which may, in turn, increase their risk of predation.

In the second chapter of my study, I compared features of parental alarm calls to ambient noise levels at nest sites to determine if adult tree swallows adjust their alarm calls to improve signal transmission in noise. I found that tree swallows do not modify their alarm calls in response to ambient noise, suggesting these calls are not altered to improve transmission.

Overall, my results suggest that communication of predation risk between parents and nestlings is negatively affected by noise. My results may be the first to suggest that this communication system is negatively affected by noise. The relationship between noise and predation risk is complex, and further work is required to determine if impaired communication could have implications for reproductive success.

LIST OF ABBREVIATIONS USED

cm	Centimetres
dB	Decibel
F	F-test statistic
h	Hours
Hz	Hertz
kHz	Kilohertz
m	Metres
n	Sample size
p	Statistical probability
s	Seconds
SE	Standard error
SPL	Sound pressure level
μPa	Micropascal
X^2	Chi-squared test statistic

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CHAPTER 1: INTRODUCTION

Auditory signals are a versatile and important component of the communication systems of many animal species, capable of transmitting information over long distances and to a broad network of receivers (Naguib & Wiley 2001; McGregor 2005). The effective transmission of auditory signals, however, is dependent on the environment through which the signal must travel. A number of factors, such as signaling distance, humidity, or environmental noise, may all alter the structure of a signal as it is transmitted from signaler to receiver (Hauser 1996). For example, signal strength decreases as distance to a receiver increases, signals are attenuated as they pass through media such as water or humid air, and signals are masked as increasing levels of environmental noise reduce the signal-to-noise ratio (Hauser 1996). These changes may then affect how recipients perceive the original signal.

Noise interference with auditory signals

In recent years, anthropogenic noise has become a major contributor to overall levels of environmental noise in both marine and terrestrial environments (Nowacek et al. 2007; Slabbekoorn & Ripmeester 2008). Elevated levels of environmental noise have become increasingly problematic for animals that use auditory signals to communicate, as high levels of noise often completely mask these signals (Barber et al. 2009).

The masking effects of noise affect a multitude of species and extend to a wide array of auditory communication systems, often with negative consequences (Laiolo 2010). For example, noise decreases the ability of predators to detect prey, thus decreasing foraging efficiency (Siemers & Schaub 2011). Noise also prevents predator detection by prey species, leading to increased predation or increased vigilance behaviour at a cost of reduced feeding time (Quinn et al. 2006; Rabin et al. 2006; Chan et al. 2010). Noise can also affect breeding success by influencing the production and transmission of songs and calls used to attract mates (Miller et al. 2000; Foote et al. 2004; Penna et al. 2004; Sun & Narins 2005), and by affecting the perception of mate quality by receivers (Habib et al. 2007). Some signalers, though, may be able to prevent masking of their signals by adjusting signal features, such as frequency or amplitude, to improve transmission in noise (Hu & Cardoso 2010; Brumm & Zollinger 2011).

The negative effects of noise, however, are particularly salient for breeding birds, as birds breeding in noisy areas have lower reproductive success than birds breeding in quiet areas (Barton & Holmes 2007; Halfwerk et al. 2011). One proposed explanation for this reduction in reproductive success is that noise impairs communication between parents and offspring, specifically with regard to feeding signals (Schroeder et al. 2012).

Parent-offspring communication: Begging

Much of the previous work describing parent-offspring communication in birds has focused on signals associated with the delivery of food to nestlings.

Nestling birds use begging calls to advertise hunger to their parents and to compete for parental provisioning during feeding visits (Budden & Wright 2001). As nestling hunger increases, the intensity of the begging calls increases (Budden & Wright 2001). Specifically, begging call duration, rate, and amplitude (in older nestlings) all increase as hunger increases (Saino et al. 2000; Leonard & Horn 2001). Parents then use the information encoded in nestling begging calls to gauge feeding rates to broods as a whole (Kilner et al. 1999; Glassey & Forbes 2002), and to discriminate among individual nestlings (Leonard & Horn 2001).

Though begging calls confer an obvious benefit on the nestlings, in terms of allocation of food resources, the production of these calls may also come at a cost. Predators may use nestling begging calls to locate nests, thus increasing nestling vulnerability to predation. In playback experiments, for example, artificial nests broadcasting nestling begging calls experienced higher predation rates than silent nests (Leech & Leonard 1997; Dearborn 1999; Haff & Magrath 2011). Furthermore, nests broadcasting high rates of begging calls experienced more predation than those broadcasting low rates of begging calls (Haskell 1994; Dearborn 1999), and those broadcasting calls with higher amplitudes experienced increased predation by avian predators (McDonald et al. 2009).

If begging calls betray nest locations and increase predation risk, parents may counteract this vulnerability by modulating the production of nestling begging calls with "switch-on" or "switch-off" signals, communicating to nestlings to either start or stop calling, respectively. Parents that use contact calls to stimulate otherwise silent nestlings to beg may be able to "switch-on" nestling begging only when there is no immediate risk of predation (Leonard et al. 1997; Madden et al. 2004; Magrath et al. 2007). But nestlings sometimes vocalize in the absence of parents, in response to parental departure, movement, vibration, or other non-call stimuli (Madden et al. 2004; Leonard & Horn 2011). Parents may then use alarm calls to silence begging nestlings, effectively “switching-off” begging elicited by non-parental cues if there is a threat of predation (Madden et al. 2004; Platzen & Magrath 2004).

Alarm calls

Alarm calls are important acoustic signals used by both birds and mammals to communicate about predators. Initially studied in mammals, distinct alarm calls were produced in association with predator type or the urgency of a predation threat (Seyfarth & Cheney 1980; Manser 2001). Birds also show variability in alarm call use based on context, often using two types of structurally different alarm calls: mobbing calls and aerial flee calls (Marler 1955). Mobbing calls are produced in response to terrestrial or perched predators, which nearby birds will approach and harass, and are designed to identify and localize the predator (Marler 1955; Hauser 1996). Aerial calls are produced in response to predatory birds, from which nearby birds will flee, and are designed to be minimally detectable by the predator (Marler 1955; Hauser 1996). Both mobbing and aerial calls tend to contain information about predator type and distance from the signaler, which provides context about the predation threat (Ficken & Witkin 1977; Arroyo & Mougeot, 2001; Baker & Becker 2002; Fassanella & Fernandez 2009). For example, when threats are highest, the rate of alarm calls or the number of elements in calls often increases (Baker & Becker

2002; Leavesley & Magrath 2004; Vanderhoff & Eason 2008; Fallow & Magrath 2010). Based on the information encoded in these alarm calls, the receiver is able to assess risk and make defensive decisions based on context (Kleindorfer et al. 2004).

Intended receivers of alarm calls are thought to include conspecifics (e.g. Baker & Becker 2002), predators (e.g. Winkler 1992), and nestlings (e.g. Davies et al. 2004), but recent work suggests that the intended receiver may vary based on context (Yorzinski & Patricelli 2010). For example, signalers may direct alarm calls to conspecifics during threats of aerial predation, when it is beneficial to communicate without simultaneously alerting predators, while signalers may direct alarm calls to perched or terrestrial predators to alert them of detection (Hauser 1996; Yorzinski & Patricelli 2010). Additionally, adult birds of several species eavesdrop on and respond to the alarm calls of other local species (Magrath et al. 2007; Fallow & Magrath 2010; Hetrick & Sieving 2011), suggesting that a broad network of receivers may receive alarm calls, as opposed to a specified individual receiver.

Young birds, then, may be part of a network of signal receivers that respond to the alarm calls of adults for their own defensive benefit (Peake 2005). Responding to alarm calls may indeed be an innate behaviour for all young birds, as evidence suggests both precocial hatchlings (e.g. Goth 2001) and altricial nestlings (e.g. Davies et al. 2004) respond innately to alarm calls.

Young altricial nestlings are particularly vulnerable to predation, as they are often limited in mobility and constrained by a nest (Hauser 1996; Caro 2005). If, however, nestlings become alerted to a predation threat via parental alarm calls before a predator has reached the nest, they may effectively defend themselves by silencing calls to prevent detection and by crouching in the nest or abandoning the nest altogether (e.g. Schaller & Emlen 1961; Kleindorfer et al. 1996; Lima 2009).

Purpose of study

If altricial nestlings attract predators to the nest with their begging calls, but also innately respond to alarm calls, parents may use alarm calls to signal predation risk to their nestlings and prompt them to stop calling and behave defensively. The effectiveness of a parental warning signal relies on the ability of parents to effectively communicate with nestlings. Factors that may interfere with this communication, such as noise, could decrease any anti-predator benefits provided to nestlings by parental modulation of begging behaviour.

The purpose of my study, then, was to determine if parent tree swallows (*Tachycineta bicolor*) communicate predation risk to nestlings and if this communication system is negatively affected by noise. In chapter two, I examine the responses of 5, 10, and 15 day old tree swallow nestlings to parental alarm calls, and then determine if 15 day old nestlings (the only age group to respond to alarm calls) maintain a response to alarm calls in noise. In chapter three, I examine whether adult tree swallows adjust features of their alarm calls in relation to ambient noise levels at their nests in ways that might improve signal transmission in noise. These chapters are followed by a general discussion of the implications of noise on the communication of predation risk and the consequences for reproductive success.

Study site and study species

Study site

This study was conducted at three field sites in King's County, Nova Scotia, Canada (45°5'0"N 64°22'0"W). Two sites were apple orchards, and the third site was an open field near a river. Nest boxes, measuring 30 x 15 x 15 cm and mounted on poles, were present at each nest site. In 2011, tree swallows occupied 26 of 31 nest boxes at the first field site, 6 of 16 at the second field site, and 28 of 38 at the third. In 2012, tree swallows occupied 25 of 30, 8 of 15, and 29 of 37 nest boxes at respective field sites. Of these nests, 3 (5%) were depredated in 2011, and 29 (36%) were depredated in 2012.

Study species

Breeding biology

Tree swallows are secondary cavity-nesting passerines that breed in Nova Scotia from mid-April to late August (Tufts 1961). While they typically nest in natural cavities in trees (Rendell & Robertson 1989), they will also nest in nest boxes (Chapman 1966), making them an ideal subject for field studies. Tree swallows normally rear one brood per year, with egg laying beginning in mid May (Tufts 1961). In 2011 and 2012, the average clutch size of the population of swallows nesting at the study site was 5.6 (± 0.09, n = 121), and the average brood size was 4.8 (± 0.14, n = 90). After a 14-day incubation period, nestlings begin to hatch. The nestling period typically lasts from 18-22 days, during which time nestlings are dependent on parents for warmth and food (Winkler et al. 2011). Both males and females share duties such as nest building, feeding, and nest defense, though this may vary between populations (Winkler et al. 2011).

Nestling begging

When parents arrive at the nest with food, they produce contact calls, which stimulate a begging display by nestlings (Leonard et al. 1997). The display comprises both postural begging (i.e. gaping, stretching toward parent) and begging calls, both of which are used to communicate with parents and to compete with siblings for food (Leonard et al. 2003). Nestlings that gape first, stretch higher, and call at higher rates are the first to be fed by parents during a feeding visit (Leonard & Horn 1996; 2001b). As nestlings age, begging calls become louder and have a wider frequency range, and nestlings beg to stimuli other than parental calls, such as the sound of a parent or predator landing on the nest box (Leonard & Horn 2001a; Leonard et al. 2004). Furthermore, loud begging calls, whether elicited by parents or other stimuli, can attract predators to the nest (Leech & Leonard 1997; Leonard & Horn 2006).

Parental defense

Parent tree swallows are territorial and will defend a radius of six to eight meters around their nest (Robertson & Gibbs 1982). Parents also defend their nests from potential predators by alarm calling and diving rapidly and repeatedly at predators in their territory (Winkler 1992; 1994). The intensity of these defensive behaviours varies with several factors, including predator type (Winkler 1992), weather (Harris 1979), parental personality (Betini & Norris 2012), and brood value (Hainstock et al. 2009). Typically, however, defending birds give alarm calls (average frequency range ~3500 – 6000 Hz) from 5-20 m above the nest before diving within 0.5-2 m of the predator, then pulling sharply out of the dive, ascending above the nest and repeating this sequence of behaviours (Winkler 1992; Sharman et al. 1994). Neighbouring birds will occasionally join parents defending their nests, responding to alarm calls made by defending parents (Winkler 1994). The role neighbouring birds play in nest defense is limited to passive defense, i.e. mobbing, where birds circle above the nest and alarm call with parents but do not dive at the predator (Winkler 1994).

Parent-offspring communication in noise

Noise has been shown to negatively affect communication between parent and nestling tree swallows. In noise, nestlings miss the arrival of their parents more often than in quiet (Leonard & Horn 2012), and parents fail to discriminate between nestlings signaling elevated levels of hunger (Leonard & Horn 2005).

To compensate for the masking effects of noise, nestlings adjust their begging calls in ways that should improve signal transmission. Nestlings exposed to chronic noise use begging calls that have higher minimum frequencies and smaller frequency ranges, compared to nestlings that are not exposed to chronic noise (Leonard & Horn 2008). Also, as noise levels at nests increase, nestlings increase the length, amplitude, and frequency range of their begging calls (Leonard & Horn 2005). These adjustments - specifically call amplitude - help to restore communication with parents and, thus, preferential feeding by parents (Leonard & Horn 2005).

CHAPTER 2: NESTLING RESPONSE TO ALARM CALLS IN NOISE

2.1 INTRODUCTION

Ambient noise is a significant impediment to the transmission and reception of acoustic signals (Brumm & Slabbekoorn 2005). Although much ambient noise arises from natural sources such as wind and rain, it is increasingly generated from anthropogenic sources (Barber et al. 2009). Increasing levels of anthropogenic noise can mask important acoustic signals used in a variety of communication systems and thus may pose a conservation concern for some species (Schroeder et al. 2012).

Nestling passerine birds produce loud begging calls when soliciting care from their parents (Wright & Leonard 2002). Begging calls contain information on nestling need and condition (Leonard & Horn 2001; Sacchi et al. 2002) and parents use the information encoded in the calls to decide which nestling to feed (Leonard & Horn 2001). Although begging calls confer an obvious benefit, they also carry costs such as increased predation risk. Indeed, artificial and natural nests broadcasting conspicuous begging calls have higher predation rates than their quieter counterparts (Leech & Leonard 2001; Haff & Magrath 2011; Ibanez-Alamo & Arco 2012).

If begging calls betray nest location and increase predation risk, parents may counteract this vulnerability by modulating the production of nestling begging calls. Specifically, in the presence of predators parents may use alarm calls to silence calling nestlings (Madden et al. 2004; Platzen & Magrath 2004) thereby reducing the chances that the predator will find the nest. The ability of parents to control nestling begging and, thus, vulnerability to predation, relies on effective communication with the nestlings.

To date, there have been no studies on the effects of ambient noise on the communication of predation risk between parents and young. If ambient noise interferes with the transmission of parental alarm calls, then it could reduce the reproductive success of birds breeding in noisy areas (Barton & Holmes 2007; Halfwerk et al. 2011; Kociolek et al. 2011; Schroeder et al. 2012). The main goal of this study, therefore, was to determine if ambient noise affected the response of nestling tree swallows (*Tachycineta bicolor*) to parental alarm calls. The study was divided into two parts, first to establish that nestling tree swallows alter their begging behaviour in response to parental alarm calls, and then test whether the response of nestlings to parental alarm calls is inhibited in the presence of ambient noise.

2.2. MATERIAL AND METHODS

I conducted this study in the Gaspereau Valley of Nova Scotia, Canada (45.0712, -64.3379), from May – July 2011 and 2012, using a population of box-nesting tree swallows (see General Introduction for site details).

2.2a Nestling response to parental alarm calls

To test whether tree swallow nestlings alter begging behaviour in response to parental alarm calls and whether the response varies with age, I presented nestlings from each of 26 broods with playback of parental alarm calls (alarm treatment) and background noise (control treatment) when nestlings were 5, 10, and 15 days old. Brood size remained constant within a brood, but varied between broods, for the duration of the experiment, with an average brood size of 4.8 (± 0.25, range 2 – 7, n = 22). Playbacks consisted of two contact calls, used to stimulate begging (Leonard et al. 1997), each followed by 1 s of silence and then a sequence of either alarm calls (mean duration: 4.7 s ± 0.02 s, range: 4.4 – 4.9 s; Figure 2.1a) as recorded in the field, or background noise of the same duration (Figure 2.1b) and from the same recording session as the alarm calls.

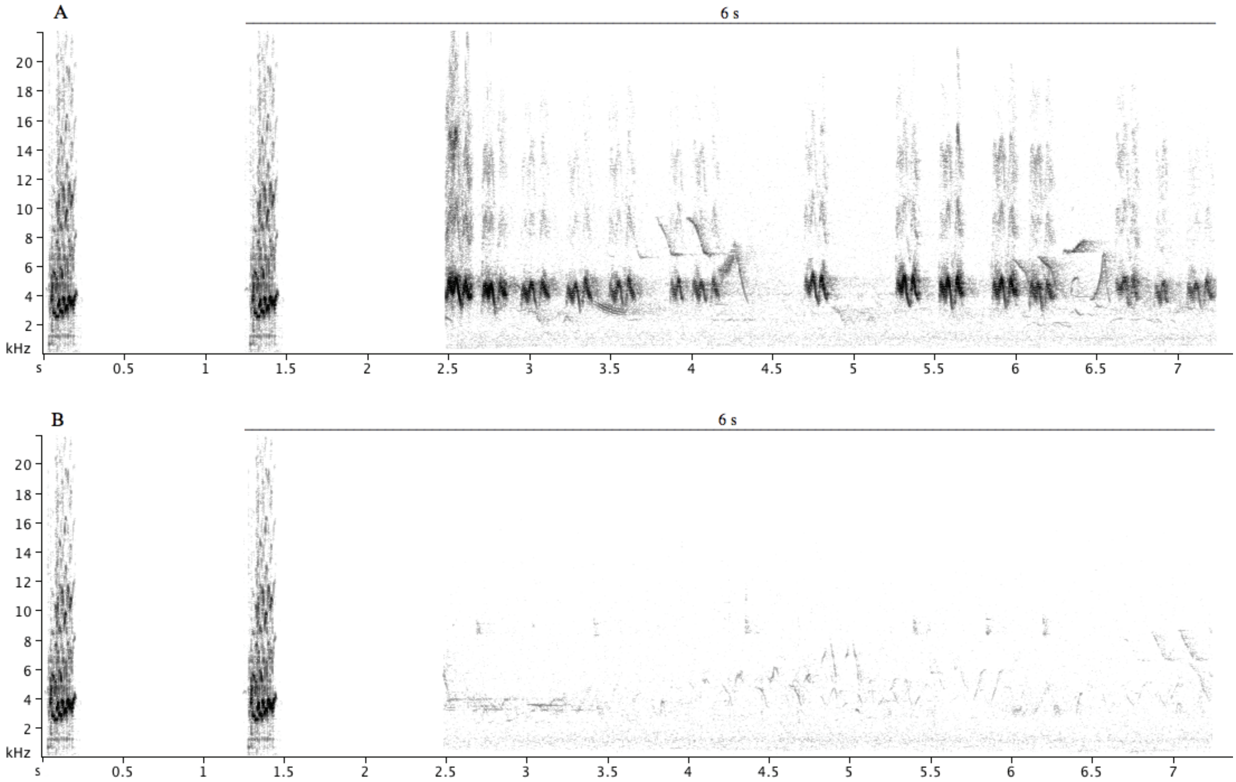

Figure 2.1. Alarm (a) and control (b) playback sequences; the spectrogram was produced in Raven with a Hanning window function at a sample rate of 1040, 3-dB filter bandwidth at 61 Hz and overlap set to 95%.

I recorded contact calls and alarm calls when nestlings were 1 to 3 days old, between 0600 h and 1000 h. When parents were away from the nest, I suspended a Sennheiser wireless lapel microphone, attached to a Marantz PMD471 sound recorder, inside the nest box approximately 5 cm above the centre of the nest cup. I recorded contact calls during the next five parental visits.

To elicit alarm calls, I placed a decoy of a common crow (*Corvus brachyrhynchos*) (Avery Greenhead Gear FFD Elite-series crow decoy, 18" long by 6" tall) on a tripod, 1 m to the left of the nest box, with the crow facing the box entrance and the base of the crow level with the base of the box. I taped a Sennheiser wireless lapel microphone, attached to a Marantz PMD471 sound recorder, underneath the box, oriented toward the crow decoy. I set up all equipment while parents were away from the nest box. Beginning with the return of a parent to the nest box, I recorded alarm calls for 5 minutes or until neighboring birds exhibited mobbing behaviour. I considered the first bird to approach the nest while alarm calling or diving at the model to be a parent, as parents actively defend their nests by alarm calling and repeatedly diving at predators (Winkler 1992). Neighboring birds passively defend nests by mobbing (circling above the nest) and calling with parents, but do not dive toward predators (Winkler 1994). If more than one bird arrived at a nest during a recording session, I recorded when each bird arrived and used differences in defensive behaviour (i.e. diving or not diving) to differentiate between parents and neighboring birds. If neighbouring birds arrived at the nest, I concluded the recording session upon their arrival. The order in which contact and alarm calls were recorded was alternated from nest to nest and recordings at the same nest were separated by at least five minutes.

Recordings were uploaded to a MacBook Pro computer, high-pass filtered at 2 kHz, and edited for playback using Audacity version 1.3.13-beta (Audacity Team 2011).

To determine if alarm calls stop or reduce begging, we needed to stimulate nestlings to beg and then present the alarm calls before the begging stopped naturally. The experiment was therefore designed so that if nestlings begged to the contact calls, they would still be begging when they received the treatment sound. Thus, the time from the beginning of the second contact call to the end of the treatment sound was 6s, which is approximately the duration of a begging event following a contact call at day 5 post-hatch (Leonard & Horn, unpublished data). I selected the first two contact calls of the recording session for the playback tape. I selected an unmanipulated section of recorded alarm calls, beginning with the first parental alarm call on the recording, that produced the requisite 6 s interval (i.e. length of alarm call sequence = 6 s – [length of 2nd contact call + 1 s silence]).

Approximately 24 h before each playback experiment, I opened the hinged side door of a nest box and inserted a piece of Plexiglas into the opening. I then wrapped this side of the box with a black plastic bag, which would cover the recording equipment the next day. On the day of the playback, I suspended a lapel microphone inside the nest box (as in contact call recordings) and set up a tripod with a Canon Optura 300 digital video camcorder about 30 cm from the Plexiglas wall of the nest box. The camera was adjusted such that the nest was centered in its field of view. I wrapped a black plastic bag around the camera and the open side of the nest box, so the box interior remained dark during filming. I placed a KOSS speaker on a tripod, 1 m to the left and level with the base of the nest box, with the speaker facing the nest box opening.

Alarm and control sequences were played when parents were away from the nest and at the levels at which they were recorded. Both the contact and alarm calls played to nestlings were of their own parents. Alarm and control playbacks at each nest were separated by 5 minutes of silence and the order in which they were presented was alternated between nests, but constant within nests across ages.

To determine if alarm calls affected nestling calling, I imported audio recordings into Audacity version 1.3.13-beta (Audacity Team 2011). Using the time display in Audacity as a guide, I calculated calling duration by noting whether nestlings were calling every 0.5 s, beginning with the treatment sound and continuing for two minutes or until the nestlings were silent for 10 s.

I also examined whether alarm calls affected a visual component of the begging display: postural begging intensity. Although this component is not likely to attract predators to the nest, stretching toward the nest opening could increase the chances of a nestling being taken once a predator was at the nest. I imported the video recordings into iMovie HD 6.0.4. Beginning 10 s before the treatment sound started and continuing for two minutes, each time a nestling begged I recorded its begging intensity, as well as every change in its intensity, on the following scale: 0 = head down, beak closed, sitting on tarsi; 1 = head down, gaping, sitting; 2 = head up, gaping, sitting; 3 = 2 + neck stretched upward; 4 = 3 + body lifted off tarsi; 5 = 4 + wings waving. To test if treatment sounds affected begging intensity, for each nestling I calculated the difference in begging intensity immediately before, and 1 s after, the treatment sound began. Nestlings that switched from begging to non-begging behaviours (see below) after the treatment (i.e. nestlings in all broods at 15 days and 2 broods at 10 days) were excluded from the analysis of begging intensity. I also determined the length of time individual nestlings continued postural begging after the treatment sounds were played (hereafter referred to as "begging duration"), measured from the start of the treatment sound until the nestling stopped postural begging (intensity score of 0) or switched to a non-begging behaviour.

I recorded all non-begging behaviours that occurred after the treatment sound began. In previous studies, passerine nestlings have responded to alarm calls by crouching (e.g. Knight & Temple 1988; Kleindorfer et al. 1996), which has been defined as lowering the body into the nest cup, such that the level of the nestling's beak shifts in position from nest rim to nest middle, with the head withdrawn (Schaller & Emlen 1961; Kleindorfer et al. 1996). I recorded the presence (1) or absence (0) of crouching for each nestling following the initiation of the treatment sound. If a nestling crouched, I also recorded the length of time between the beginning of the treatment sound and the onset of crouching (i.e. time to crouch).

The final sample size for each age was reduced because of technical difficulties, poor weather, or nestlings failing to respond to the contact calls (audio data: day 5: alarm treatment (AT) n = 3 broods, control treatment (CT) n = 4 broods; day 10: AT n = 12, CT n = 14; day 15: AT n = 13, CT n = 16; video data: day 5: AT n = 7, CT n = 5; day 10: AT n = 11, CT n = 11; day 15: AT n = 11, CT n = 9).

I conducted all analyses using R version 2.14.0 (R Development Core Team 2011). To analyze calling duration, change in begging intensity, and begging duration, I used a generalized mixed model with restricted maximum likelihood estimation, with treatment (alarm or control) and age (5, 10, or 15 days) as fixed factors, and nest as a random factor. To assess significance, I used a sub-model routine, in which the fixed effect of interest was removed from the model, and the new model was then compared to the original model using Wald's Chi-square statistic. Time to crouch was compared with time to stop begging using a one-way ANOVA.

2.2b Nestling response to alarm calls in noise

To test whether nestling response to alarm calls is affected by ambient noise, I played the alarm treatment described above to each of 23 broods at 15 days post-hatch, in the presence (noise treatment) and absence (control treatment) of white noise. I restricted this experiment to day 15 because nestlings only responded significantly to alarm calls at this age (see results).

During the noise treatment, I played white noise set at 65 dB SPL (reference level 20 μPa), which is close to the upper limit of natural noise recorded in nest boxes in the field (41-67 dB SPL [Leonard & Horn 2005]), from inside the nest, beginning 30 minutes before the alarm treatment began and continuing until it ended. During the control treatment, no noise was played. Noise was played from a pair of earbud speakers placed in the nest material, on opposite sides of the nest, centered and oriented to face the nestlings. Speakers were attached to a HipStreet HS-T29 Mp3 player, placed inside a plastic bag and taped to the back of the nest box. This equipment was in place for both noise and control treatments. The order of noise and control treatments was alternated between nests, and treatments were separated by 30 minutes. I measured calling duration, presence of crouching, and time to crouch (the responses affected by alarm calls), as in the first experiment.

The final sample size was reduced (audio data: noise treatment $n = 18$, control treatment $n = 18$; video data: noise treatment $n = 15$, control treatment $n = 18$) for the reasons described above. I analyzed calling duration using a generalized mixed model with restricted maximum likelihood estimation, with treatment (noise or control) as a fixed factor, and nest as a random factor.

2.3. RESULTS

2.3a. Nestling response to parental alarm calls

Calling duration did not vary significantly with treatment ($X^2 = 0.91$, df = 1 $p = 0.34$), or age ($X^2 = 0.19$, df = 2; $p = 0.91$), but did show a significant interaction between treatment and age ($X^2 = 11.76$, df = 2, $p = 0.0028$; Figure 2.2), with calling duration decreasing in response to the alarm treatment and increasing in response to the control treatment with age.

The average change in begging intensity did not vary significantly with treatment ($X^2 = 0.85$, df = 1, $p = 0.36$), age ($X^2 = 1.53$, df = 1, $p = 0.22$), or their interaction ($X^2 = 0.02$, df = 1, $p = 0.88$). Average begging duration did not vary with treatment ($X^2 = 1.33$, df = 1, $p = 0.25$) but did vary significantly with age ($X^2 = 15.64$, df = 2, $p = 0.0004$; Figure 2.3), with nestlings begging for shorter durations as they aged. The interaction between treatment and age was not significant ($X^2 = 1.70$, df = 2, $p = 0.43$).

Crouching was only observed following alarm treatments, and if crouching occurred, all begging nestlings in the brood crouched, with the exception of a single nestling in one brood that did not crouch with its brood mates. By day 15, 100% (11/11) of broods crouched in response to alarm calls, as opposed to 18% (2/11) at day 10 and 0% (0/7) at day 5. The time taken by nestlings to crouch in the nest following the alarm treatment (mean ± s.e.: 1.10 ± 0.21 s) was significantly faster than the time taken by nestlings to lower their bodies back into the nest (i.e. having returned to a begging score of 0) after begging in the control treatment (mean ± s.e.: 8.88 ± 1.82 s; one-way ANOVA F(1, 9.24) = 18.08, $p = 0.002$).

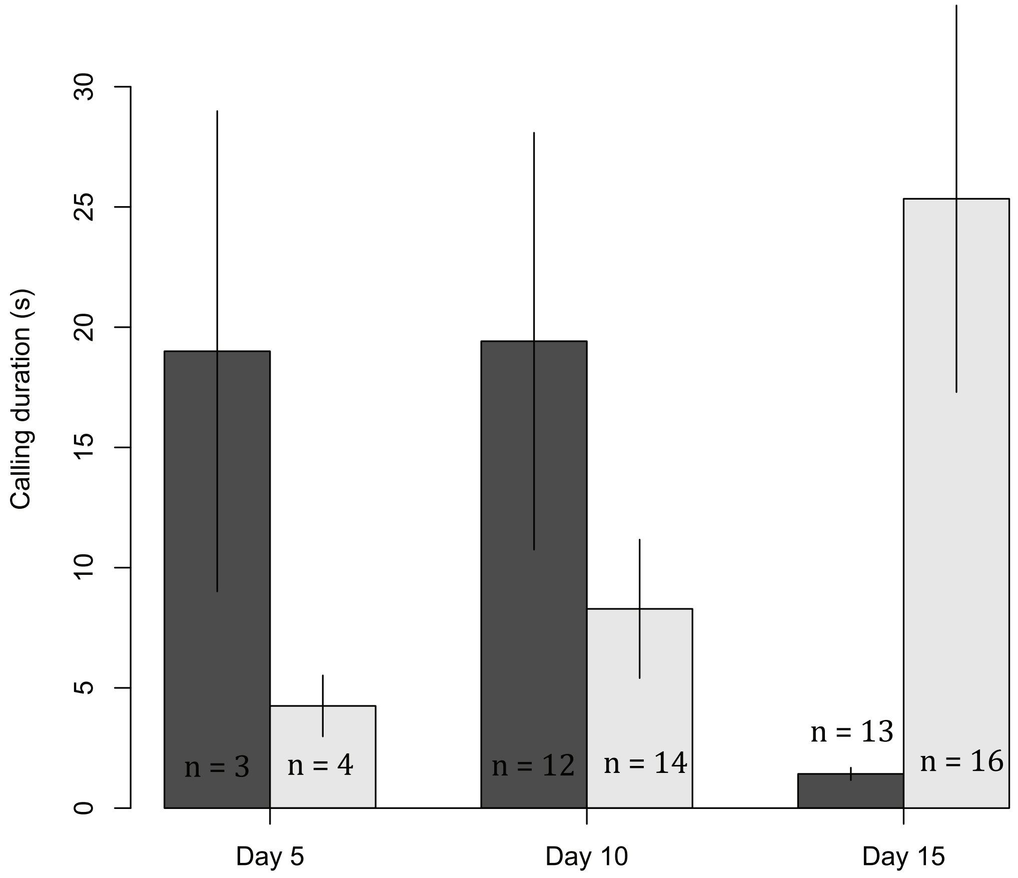

Figure 2.2. Mean (± s.e.) calling duration (s) for tree swallow nestlings after alarm (dark bars) or control (light bars) playbacks at days 5, 10, and 15 post-hatch. Bars represent means of the observed data.

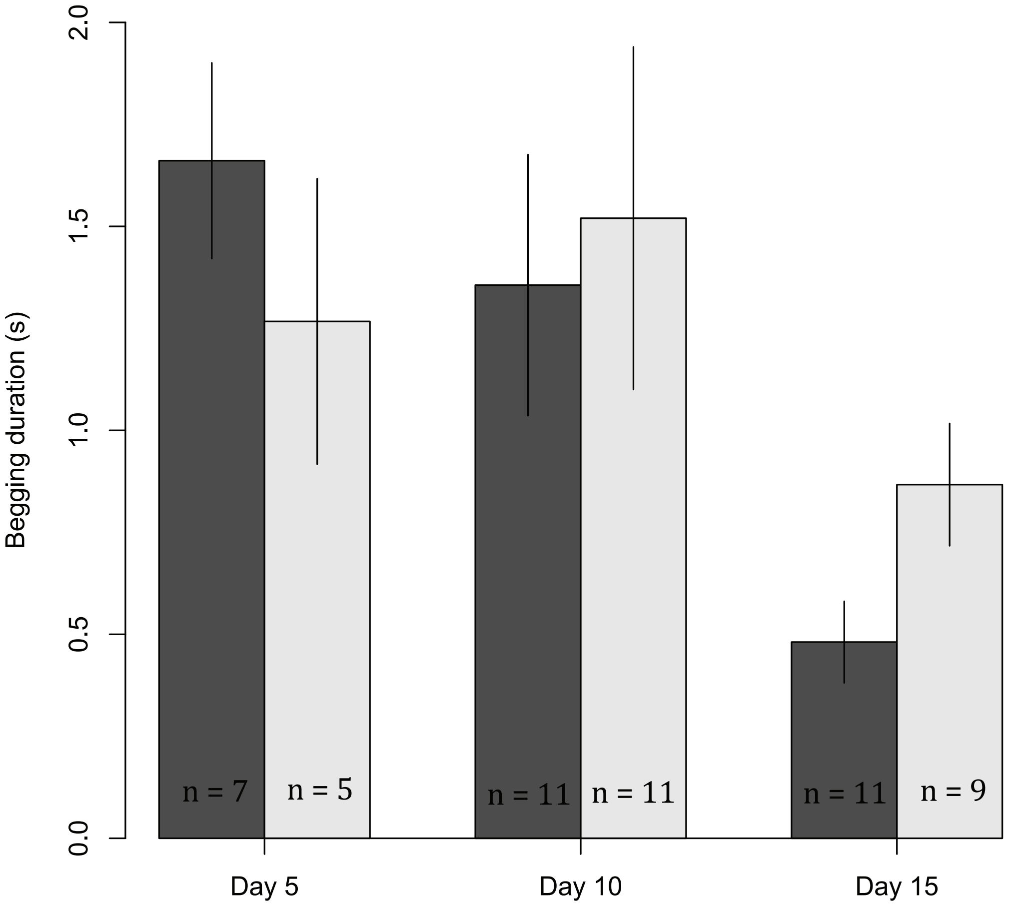

Figure 2.3. Mean (± s.e.) begging duration (s) for tree swallow nestlings after alarm (dark bars) or control (light bars) playbacks at days 5, 10, and 15 post-hatch. Bars represent means of the observed data.

2.3b. Nestling response to alarm calls in noise

Calling duration varied significantly with treatment (X^2 = 8.15, df = 1, *p* = 0.004; Figure 2.4), with bouts being significantly longer in the noise treatment than in the control treatment.

Crouching was observed after the playback of alarm calls in both treatments, although significantly fewer broods crouched in the noise treatment than in the control treatment (noise: 4/15 broods, control: 18/18; X^2 = 16.64, df = 1, *p* < 0.0001). The time to crouch for nestlings in the noise treatment did not, however, differ significantly from the control treatment (mean ± s.e. noise: 1.42 ± 0.49 s; control: 1.21 ± 0.15 s; one-way ANOVA F(1, 3.12) = 0.58, *p* = 0.50).

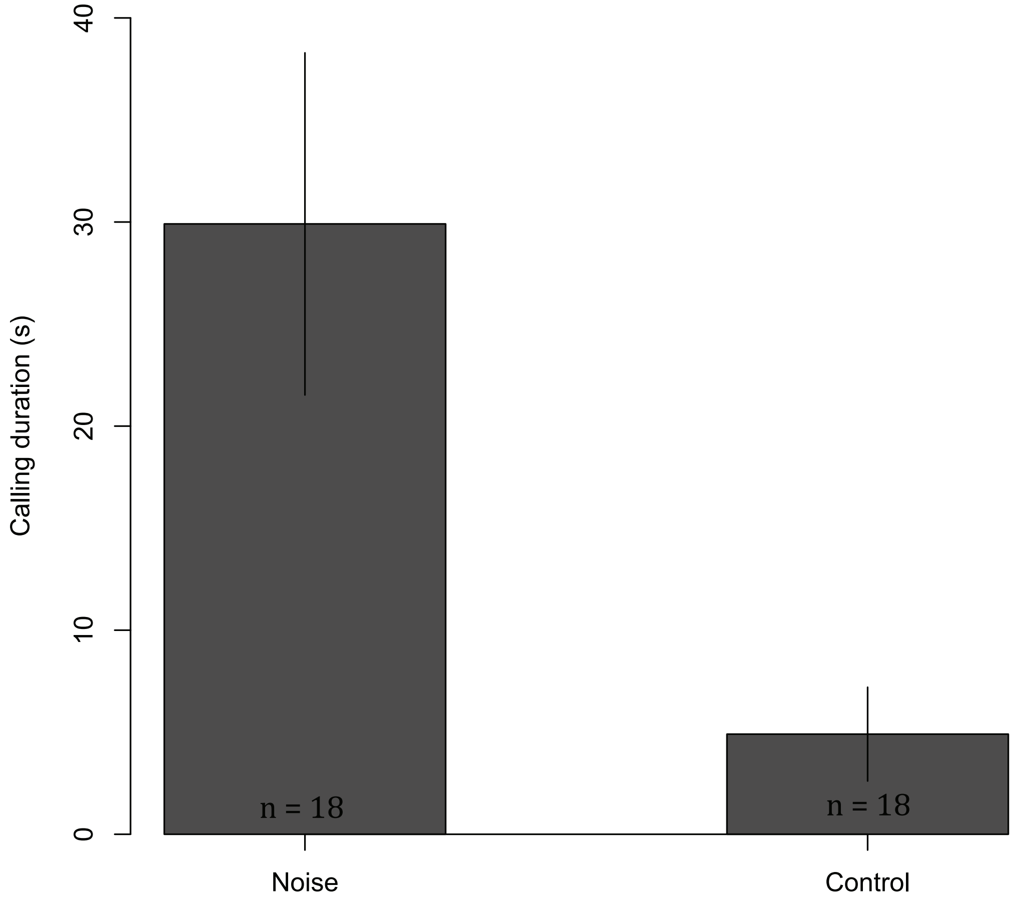

Figure 2.4. Mean (± s.e.) calling duration (s) for 15 day old tree swallow nestlings after playback of parental alarm calls in noise and control treatments. Bars represent means of the observed data.

2.4. DISCUSSION

Older tree swallow nestlings responded to parental alarm calls and did so by reducing the duration of begging call bouts and crouching in the nest. This response was, however, affected by the presence of noise. Nestlings called longer following alarm calls presented in noise than in a quiet control and fewer nestlings crouched in response to alarm calls in noise than in the control treatment. These results suggest that noise can reduce nestling response to parental alarm calls.

2.4a Nestling response to parental alarm calls

Older tree swallow nestlings responded to parental alarm calls by reducing calling duration and crouching in the nest. This result is consistent with the results of previous studies that also found that nestlings reduce calling and/or crouch in response to alarm calls (Knight & Temple 1986; Madden et al. 2004; Platzen & Magrath 2004; Serra & Fernandez 2011). I did not present the nestlings with a neutral control sound such as a local bird song, so the possibility that this response was simply a general response to an adult call cannot be ruled out. This is unlikely, however, because the response to the alarm calls was consistent with previous studies, and nestlings across a variety of ages showed no anti-predator behaviour in response to neutral calls of other species in studies where such controls were used (Davies et al. 2004; Madden et al. 2004; Anderson et al. 2009).

Begging calls attract predators to the nest (Leech & Leonard 1997), so stopping or reducing calling in the presence of predators may reduce predation risk (Haff & Magrath 2011). In addition, crouching, which included nestlings lowering their bodies in the nest, moving away from the nest box opening, and raising expendable tail feathers above the head, may reduce nestling conspicuousness and accessibility to predators at the nest (Knight & Temple 1988; Moller et al. 2006).

Only the oldest nestlings responded to parental alarm calls. One explanation for the change in response with age is that younger nestlings have not yet developed the ability to perceive alarm calls (Britan-Powell & Dooling 2004; Lock & Hauber 2012). Younger nestlings, however, called longer after playback of alarm calls compared to control sounds, suggesting they may indeed hear the call. The ability to discriminate call meaning may develop with age, so young nestlings may interpret an alarm call as an indicator of parental presence rather than as a warning signal (Caro 2005). Additionally, a change in response with age may be due to a change in vulnerability to predation (Platzen & Magrath 2005). Young tree swallow nestlings generally beg only in response to parental contact calls, but older nestlings also beg to additional stimuli in the absence of parents (Leonard & Horn 2001; Leonard et al. 2004). Increased begging leads to increased calling, which may then increase the chance of a predator detecting the nest (Haff & Magrath 2011). Furthermore, the amplitude of begging calls increases with age (Leonard & Horn 2006), which may make nests more obvious to predators (Dearborn 1999, McDonald et al. 2009). Nestlings may become vulnerable to aerial predation at fledging, and fledglings of some species concordantly respond to alarm calls signaling the presence of aerial predators, which they do not do as nestlings (Magrath et al. 2006). A response to parental alarm calls may, therefore, develop with age in response to increased predation risk.

2.4b. Nestling response to alarm calls in noise

These results suggest that noise dampens the response of nestlings to parental alarm calls. Specifically, nestlings called for longer following parental alarm calls and were less likely to crouch in noisy conditions than quieter conditions. Both responses may increase the risk of predation in noise.

Previous studies of communication between parents and young have shown that noise negatively affects signaling in this system. Nestlings are more likely to miss the arrival of a parent with food in the presence of noise (Leonard & Horn 2012), and cues that parents use when making feeding decisions may be obscured by noise (Leonard & Horn 2005). The current study extends our understanding of the impacts of noise by showing that nestling responses to alarm calls are reduced in noise. If communication of predation risk between parents and offspring breaks down in the presence of noise, nestlings may miss threats and be left vulnerable to predation (Barber et al. 2009). Together, these studies support the idea that the masking of important acoustic signals could result in decreased reproductive success for birds breeding in noisy areas (Barber et al. 2009; Halfwerk et al. 2011; Schroeder et al. 2012).

The results of this study suggest that nestling responses are reduced in noise because noise masks alarm call signals. However, another possible explanation for behavioural differences in noise is that nestlings respond strategically to the presence of noise rather than the perceived absence of alarm calls. If noise masks begging calls, nestlings may be protected from detection by predators, and predation costs associated with calling may be reduced. Under these circumstances, nestlings may continue to call despite hearing a parental alarm, particularly if the benefit of continued calling (i.e. receiving food) outweighs a reduced predation cost.

2.4c. Conclusion

My results indicate that older tree swallow nestlings may be more vulnerable to predation in noise if communication about predation risk is masked. However, how parents communicate predation risk to nestlings in the presence of noise has not been studied. If tree swallow nestlings are unable to detect alarm calls in noise, parents may adjust features of their alarm calls to maintain the communication of predation risk with nestlings (Chapter 3).

CHAPTER 3: MODIFICATION OF PARENTAL ALARM CALLS IN NOISE

3.1. INTRODUCTION

Elevated levels of ambient noise have become increasingly problematic for animals that use auditory signals to communicate. Noise from anthropogenic sources is contributing to natural ambient noise spectrums, interfering with both the transmission and reception of important acoustic signals used in many communication systems (Brumm & Slabbekoorn 2005; Barber et al. 2009).

Breeding birds experience reduced reproductive success in noisy areas, suspected to be a consequence of the negative effects of noise (Froman et al. 2002; Habib et al. 2007). Fledgling mass and number are both lower in broods in noisy areas than in broods in quiet areas, independent of clutch size (Halfwerk et al. 2011; Schroeder et al. 2012). One explanation for reduced reproductive success is that noise impairs parent-offspring communication (Halfwerk et al. 2011). Indeed noise appears to interfere with the reception of calls associated with feeding and hunger (Leonard & Horn 2005, 2012) and female parents provision their broods less frequently in noisy areas than in quiet areas, possibly because noise masks begging calls used by parents to gauge provisioning rate (Schroeder et al. 2012). These latter results may explain the reduced reproductive success of breeding birds in noise.

Noise may also interfere with communication of predation risk between parents and offspring, which may also negatively affect reproductive success (Chapter 2). Nestling begging calls can attract predators to the nest (Ibanez-Alamo & Arco 2012), but parents may mitigate predation risk to nestlings by using alarm calls to warn them of nearby predators (Madden et al. 2004). Nestlings respond to alarm calls defensively by falling silent and crouching in the nest (Platzen & Magrath 2004; Chapter 2). In noise, however, nestlings fail to respond to parental alarm calls and continue calling despite the threat of predation (Chapter 2).

Parents may compensate for the masking effects of noise, however, by adjusting their alarm calls to improve signal transmission (Lowry et al. 2012). In noise, adult birds of many species adjust call amplitude (Pytte et al. 2002; Brumm 2004), frequency (Slabbekoorn & Peet 2003; Hu & Cardoso 2009; Francis et al. 2011), duration (Francis et al. 2011), tonality (Hanna et al. 2011), and/or rate (Slabbekoorn & den Boer-Visser 2006; Potvin et al. 2011) to maintain effective communication with receivers. If adults adjust their alarm calls in noise, they may improve communication of predation risk to nestlings and restore the defensive benefits of alarm calls that are lost in noise.

The main goal of my study, then, was to determine if adult tree swallows (*Tachycineta bicolor*) adjust features of their alarm calls in relation to ambient noise levels at their nests, in ways consistent with improving signal transmission in noise.

3.2. MATERIAL AND METHODS

I conducted this study in the Gaspereau Valley of Nova Scotia, Canada, from May – July 2012, using a population of box-nesting tree swallows (see General Introduction for site details)

To test whether adult tree swallows alter their alarm calls in relation to noise, I recorded parental alarm calls, as described in Chapter 2, and ambient noise levels at each of 33 nests. Calls were recorded between 0600 h and 1000 h, when nestlings were 1 to 3 days old. Immediately following the conclusion of an alarm call recording session, I removed the crow decoy placed at the nest to elicit alarm calls and recorded ambient noise at each nest for 10 minutes.

Recordings were uploaded to a MacBook Pro computer and analyzed using Raven Pro version 1.4 (Bioacoustics Research Program, 2011). I analyzed calls from recordings where I was certain only one bird was calling at the beginning of the recording period. In the event that additional birds were recruited to the nest after the recording period began, I analyzed calls recorded in the interval prior to their arrival. Parents were present but did not call at six nests, and these recordings were excluded from analysis. An additional eight recordings were excluded from analysis because both parents were present at the nest for the entire length of the recording, and it was unclear whether one or both birds were calling at the beginning of the recording. Final sample size, then, was reduced from n = 33 to n = 19.

To measure call features, I created a spectrogram with a Hann window function at a sample rate of 1040, 3-dB filter bandwidth at 61 Hz and overlap set to 95%. I calculated call rate (calls/min) by counting the number of alarm calls made in a 1-minute interval, beginning with the first recorded alarm call. For recordings where additional birds were recruited within this 1-minute interval, I counted calls and calculated call rate within the period of time before the additional bird(s) arrived and converted to calls/min. I also measured call length (s), minimum frequency (Hz), maximum frequency (Hz), peak frequency

(Hz), and frequency range (Hz) of the first five alarm calls recorded at each nest, and then calculated the mean value for each feature per nest. These call features were chosen for analysis because avian signalers have been shown to adjust these features in noise (Brumm & Slabbekoorn 2005). Call amplitude was not analyzed because the position of the microphone during recording sessions was static, while the distance of the calling parent was dynamic. Inconsistent distance between the microphone and a calling parent during the recording period could have caused inconsistencies in recorded call amplitude, leading to an inaccurate measure of this call feature.

To determine the ambient noise level at each nest, I measured the average power (dB) in 2-second samples taken every minute for 10 minutes across three frequency bands (0-3000 Hz, 3000-6000 Hz, 6000-9000 Hz) (n = 30 measurements per nest). Sampling within these frequency bands allowed for the calculation of noise levels across the entire frequency range of noise at my nest sites, as well as specifically within the frequency range that overlaps with - and therefore may interfere with - alarm calls (3000-6000 Hz, Sharman et al. 1994). I averaged power levels across all three frequency bands to determine the noise level across the entire frequency range (0-9000 Hz) of the noise at each nest site, and I also averaged power levels within the 3000-6000 Hz band to determine the noise level within this frequency range.

Using R version 2.14.0 (R Development Core Team 2011), I used linear regressions to analyze the effects of ambient noise levels on individual call features. Measures of call rate and call length were not normally distributed, and were log-transformed before analysis. Two outliers, identified with a box plot and confirmed as outlying data points by Grubb's test ($p < 0.0001$), were also removed from the call rate analysis.

3.3. RESULTS

The ambient noise levels at nest sites ranged from 57.15 to 75.79 dB (mean ± SE 63.97 ± 0.70) across the entire frequency range of the noise (0-9000 Hz), and from 56.47 to 75.38 dB (mean ± SE 62.94 ± 0.75) in the 3000-6000 Hz frequency range. Birds, traffic (including farm machinery), a river, and wind contributed energy to the noise spectrum at these nests.

Alarm call rate, length, minimum frequency, maximum frequency, peak frequency, and frequency range did not vary significantly with either ambient noise levels across the entire frequency range of the noise or the ambient noise levels in the 3000-6000 Hz frequency range (Table 3.1; Figures 3.1, 3.2).

Table 3.1. Results of linear regressions comparing tree swallow alarm call features with ambient noise levels at nest sites in a 0-9000 Hz frequency range and a 3000-6000 Hz frequency range

Noise	**Alarm call feature**	$F_{1,17}$	***p***
0-9000 Hz	Rate (calls/min)	2.02 ($F_{1,15}$)	0.18
	Length (s)	0.085	0.77
	Min. freq. (Hz)	0.40	0.53
	Max. freq. (Hz)	3.00	0.10
	Peak freq. (Hz)	1.54	0.23
	Freq. range (Hz)	0.21	0.65
3000-6000 Hz	Rate (calls/min)	0.20 ($F_{1,15}$)	0.66
	Length (s)	0.095	0.76
	Min. freq. (Hz)	0.00018	0.99
	Max. freq. (Hz)	0.017	0.90
	Peak freq. (Hz)	1.06	0.32
	Freq. range (Hz)	0.0041	0.95

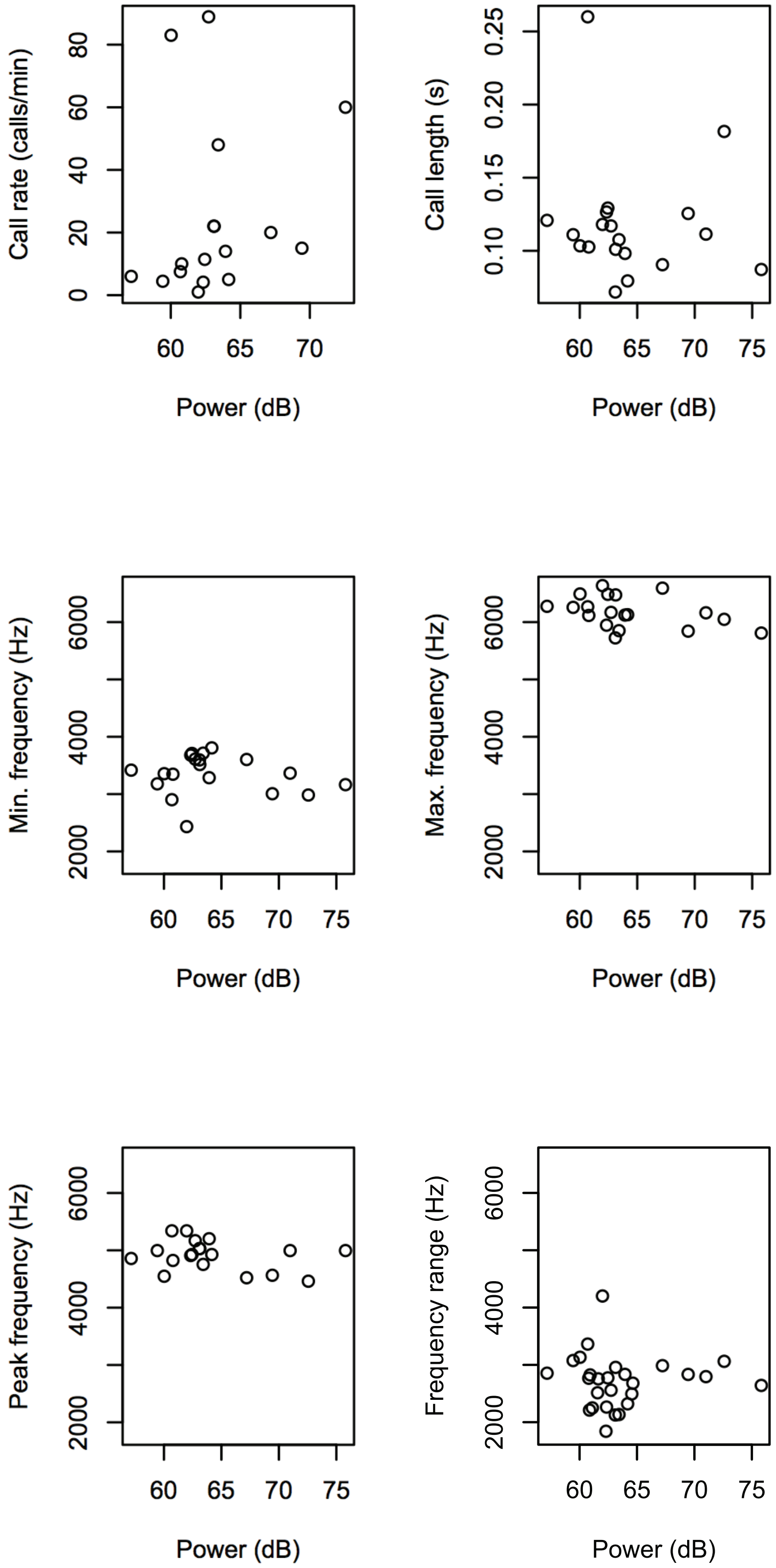

Figure 3.1. Alarm call features of adult tree swallows in relation to mean power (dB) of ambient noise across a 0 - 9000 Hz frequency range over 19 broods

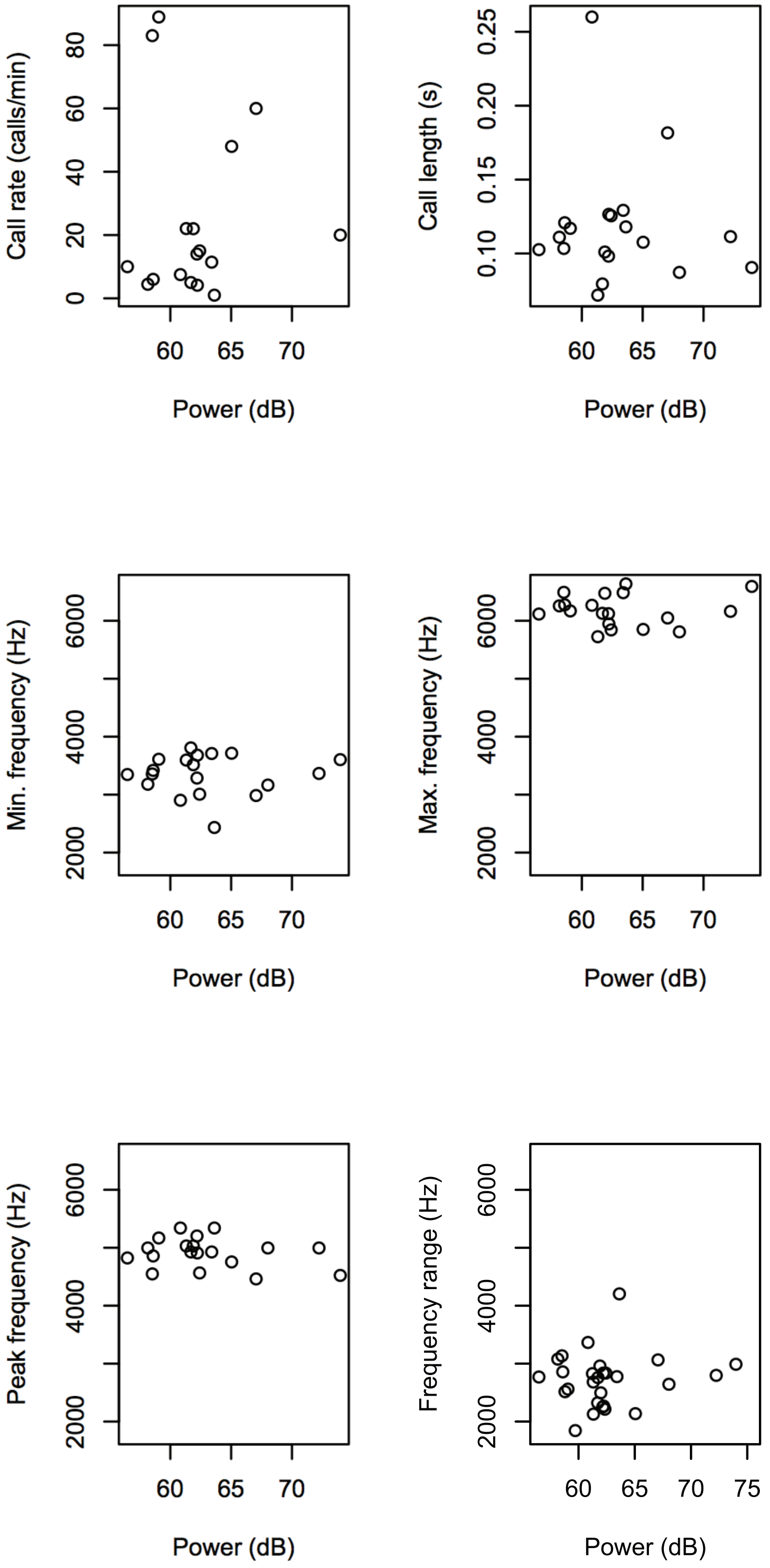

Figure 3.2. Alarm call features of adult tree swallows in relation to mean power (dB) of ambient noise across a 3000 - 6000 Hz frequency range over 19 broods

2.4. DISCUSSION

I found that tree swallow alarm call rate, length, minimum frequency, maximum frequency, peak frequency, and frequency range did not vary in relation to ambient noise levels at nest sites. These results suggest that adult tree swallows do not modify their alarm calls in response to increased levels of ambient noise.

These results are contrary to those of previous work showing that adult birds are capable of adjusting a variety of call features in noise. Adult birds of many species adjust one or more of call rate (Slabbekoorn & den Boer-Visser 2006; Potvin et al. 2011), length (Francis et al. 2011), frequency (Slabbekoorn & Peet 2003; Hu & Cardoso 2009; Francis et al. 2011), or amplitude (Pytte et al. 2002; Brumm 2004) in noise. Much of this work focuses on songs, which are sung faster, louder, and with higher minimum frequencies in noisy areas than quiet areas (Slabbekoorn & Peet 2003; Brumm 2004; Slabberkoorn & den Boer-Visser 2006; Potvin et al. 2011). Songs are long, complex, learned vocalizations modified by auditory feedback, and therefore may be more plastic in their production than the shorter, simpler, innate calls that were the focus of my study (Catchpole & Slater 1995; Marler 2004; Tumer & Brainard 2007). Plasticity may lend to more flexibility for songs, but not calls, in noise, which may explain why features of tree swallow alarm calls did not change in noise as would be expected of songs.

Another possible explanation for the discrepancies between my results and previous work is that I was unable to measure call amplitude, which may indeed be adjusted in noise. Regulation of vocal amplitude to improve signal transmission in noise is a common adaptation for birds, and has been noted in several species, including nestling tree swallows (Leonard & Horn 2005; Brumm & Zollinger 2011). Furthermore, recent work specifically focused on the transmission of alarm calls in noise suggests that alarm call amplitude may be increased in noise (Lowry et al. 2012). It is plausible, then, that adult tree swallows may also increase the amplitude of their alarm calls in noise, and as I was unable to measure alarm call amplitude in my study, I may not have detected this adjustment. However, as nestlings did not typically respond to parental alarm calls in noise (Chapter 2), it is not likely that parents were adjusting the amplitude of their calls to reduce masking of the signal.

My study also did not take place in an urban environment, which may explain why my results are not consistent with those of previous studies. Previous work describing the adjustment of call features in noisy environments has focused on birds located in urban areas, with average ambient noise levels ranging from 58.5 – 65.8 dB (e.g. Wood & Yezerinac 2006; Hu & Cardoso 2010; Seger-Fullam et al. 2011; Lowry et al. 2012). The average ambient noise level at nest sites used in this study is comparable, however, which suggests that noise at these sites may be enough of a disturbance to warrant call adjustments. Urban noise, however, is often generated constantly (Barber et al. 2009), while the noise at our study sites was generated intermittently by farm machinery, highway traffic, and redwing blackbird (*Agelaius phoeniceus*) calls. Birds may not adjust the features of their calls to improve signal transmission if noise is not a consistent barrier to communication, but rather preferentially produce calls during periods of quiet or silence (Bergen & Abs 1997).

Additionally, adults may not adjust their alarm calls with respect to noise levels at their nest sites if the primary purpose of alarm calls is not to communicate with nestlings, but to instead communicate with predators, with whom signal transmission may not be compromised by noise. Alarm call use often increases after nestlings hatch, suggesting they may be used to communicate with nestlings, but this may also be a measure of increased nest defense meant to discourage predators from preying on an increasingly valuable brood (Fasanella & Fernandez 2009; Colombelli-Negrel & Robertson 2010). Tree swallow nest defense is purportedly directed toward predators, to either distract them or encourage them to leave the nest, with adults often approaching the predator within 0.5-2 m while defending their nests (Winkler 1992). As acoustic signals degrade over long distances, alarm calling within close range of the predator may help to prevent signal degradation in noise and, thus, may preserve effective communication in noisy areas (Hauser 1996). Furthermore, when communicating specifically with predators, some passerines (e.g. dark-eyed juncos [*Junco hyemalis*], yellow-rumped warblers [*Dendroica coronata*]) increase the directionality of their alarm calls to facilitate signal transmission to intended recipients (Yorzinski & Patricelli 2010). If short signaling distances and high directionality help catalyze signal transmission to predators, adult tree swallows may not adjust features of their alarm calls in noise if the call can be effectively transmitted to predators without call modification.

2.4a Conclusion

My results suggest that adult tree swallows do not adjust features of their alarm calls in relation to noise levels at their nest sites. If parents do not adjust their alarm calls in noise, however, nestlings may not receive the signal of a predation threat, as suggested in chapter 2. In the general discussion following this chapter, I will discuss the relationship between noise and predation, and consider whether impaired communication about risk may affect predation rates in noise.

CHAPTER 4: GENERAL DISCUSSION

The results of my study suggest that noise significantly affects the communication of predation risk between parent and nestling tree swallows. Older nestlings respond to parental alarm calls by falling silent and crouching in the nest; both responses are reduced in noise. Parents, meanwhile, do not adjust their alarm calls with respect to noise levels at their nests. If nestlings do not receive alarm signals in noise, communication of predation risk ultimately breaks down, thus, making nestlings vulnerable to predation. My study adds to the growing body of evidence suggesting that acoustic communication is impaired by noise, and, specifically, that reproductive success may decrease in noise due to impaired communication between parents and offspring.

Parent-offspring communication as a factor in reproductive success

The results of my study provide a new perspective from which to consider recent work examining the effects of impaired parent-offspring communication on reproductive success (Halfwerk et al. 2011; Schroeder et al. 2012). Studies of reproductive success in noise have proposed several mechanisms to explain findings that reproductive success decreases in noise, including inability to assess mate quality, parental inexperience, and physiological stress of parents or nestlings, but have found less support for these mechanisms than for impaired parent-offspring communication. These studies proposed that masked signals of hunger could explain the effects noise on reproductive success, but they did not consider the role of other parent-offspring communication systems that may be affected by noise.

Both studies found that nestling survival decreased in noise, but it was not clear whether fewer nestlings survived to fledging due to higher instances of starvation, higher instances of predation, or other factors (Halfwerk et al. 2011; Schroeder et al. 2012). Evidence suggests that noise affects communication and also that reproductive success is lower in noise, but the link between the two is not clear in every case. For instance, female house sparrows (*Passer domesticus*) reduce feeding rates in noise, which may have led to reduced reproductive success in this species (Schroeder et al. 2012). Similarly, both nestling begging and parental feeding decisions in tree swallows were affected by noise (Leonard & Horn 2005, 2012), but nestlings raised in noise did not differ in mass from those raised in quiet nests (Leonard & Horn 2008). This suggests, at least for this species, that noise would be unlikely to result in increased levels of starvation.

Higher instances of predation in noise could also explain reduced nestling survival. To date, though, studies examining reproductive success in noise have not reported whether predation rates differed between quiet and noisy nesting areas (Halfwerk et al. 2011; Schroeder et al. 2012). If predation rates are higher in noise, my results could help explain decreased nestling survival, as nestlings may be more vulnerable to predation in noise. Future studies of reproductive success should examine nest predation rates in noise, and should consider masked signals of risk as a factor that may affect both predation rates and reproductive success.

Nest predation in noise

My results suggest that nestlings may be more vulnerable to predation in noise, and thus it might be expected that predation rates increase in noise. However, the relationship between noise and predation rates may be more complex than suggested here. For example, if noise masks begging calls or causes differential dispersal of predators or prey species, noise may prevent predators from locating nests, and may decrease instances of nest predation.

Nestling predation rates in noise have not yet been explicitly studied, but noise may indirectly increase nestling survival by masking begging calls that predators use to detect nests. Parents have difficulty discerning the begging calls of nestlings in noise, suggesting that noise does mask these calls (Leonard & Horn 2005), and it is possible that acoustically orienting predators may similarly be unable to detect these cues (Seimers & Schaub 2011). If noise prevents predators from detecting begging nestlings, then the inability of parents to communicate predation risk to nestlings in noise may not negatively influence nestling survival. On the other hand, nestlings increase the amplitude, length, and minimum frequency of their begging calls in noise, presumably to improve communication with parents (Leonard & Horn 2005, 2008). These adjustments decrease the masking effects of noise, which may improve signal reception by eavesdropping predators. Nestlings that adjust their begging calls in noise, particularly by increasing call amplitude, may indeed be more easily located by predators and, thus, more vulnerable to predation (Haskell 1994; Dearborn 1999). Parental failure to silence nestlings in these circumstances, then, could negatively influence nestling survival and reproductive success.

Another way in which noise could reduce nest predation is if the distribution of predators and prey is affected by noise. The distribution of animals within a community is often altered in noisy areas (Barton & Holmes 2007; Francis et al. 2009). Animals that are negatively affected by noise tend to relocate to areas that are less noisy (Bayne et al. 2008), while those that are unaffected by noise or can somehow compensate for its negative effects will remain in the noisy area (Francis et al. 2011). Some species, then, may find themselves separated from their natural predators, leading to decreased predation rates. For example, shrub-nestling songbirds nesting in noisy areas experienced increased reproductive success compared to those nesting in quiet areas, possibly because western scrub-jays (*Aphelocoma californica*), a predatory species, were less abundant in noisy areas than quiet areas (Barton & Holmes 2007; Francis et al. 2009). Some tree swallow nest predators are negatively affected by noise (e.g. chipmunks [*Tamias spp.*]; Pietrucha 2010), while others are successful in noisy areas (e.g. raccoons [*Procyon lotor*], crows [*Corvus brachyrhynchos*], and feral cats; Winkler et al. 2011), suggesting that some, but not necessarily all, tree swallow predators may be deterred from noisy nesting areas. Again, if parents cannot silence begging nestlings and noise does not mask begging calls, nestlings may be vulnerable to an array of predators.

Future work

This study adds support to the body of work suggesting that parent-offspring communication is impaired by noise, but approaches this topic from the viewpoint of predation risk. Parent birds have previously been found to communicate predation risk to their nestlings, but this study may be the first to suggest that noise negatively interferes with this communication system. The relationship between predation risk and noise is not straightforward, however, and additional work is needed to determine consequent impacts on reproductive success.

Though communication of predation risk is affected by noise, parent and nestling birds may be able to compensate for increased nestling vulnerability in other ways. For example, animals that have a reduced ability to detect auditory cues of approaching predators in noise will increase vigilance behaviour (Quinn et al. 2006; Rabin et al. 2006). Though adult tree swallows are likely to detect nest predators visually (Winkler 1992), they may increase vigilance behaviour to compensate for their reduced ability to transmit auditory cues to nestlings, detecting predators earlier and preventing them from reaching defenseless nestlings. Also, nestlings may be able to independently assess predation risk by eavesdropping on predator calls or footsteps, and may be able to defend themselves without parental signals of a predation threat (Haff & Magrath 2010). As a cavity nesting species, however, tree swallow nestlings would likely rely on auditory cues to detect predators, and may lose any ability to independently detect predators if these cues are masked by noise.

Further study from the perspective of predators could also be useful in understanding how noise affects predation rates and consequent reproductive success for breeding birds. Specifically, investigations of the ability of predators to detect begging calls in noise or the distribution of predatory species in noise could contribute to our understanding of predator-prey relationships and how they are affected by noise.

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