Alarm Calling in the Context of Flying Predator Stimuli: A Field Study of Carolina Chickadees (*Poecile carolinensis*)

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Christopher Erik Zachau

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Abstract

This study describes chick-a-dee calling behavior of Carolina chickadees (*Poecile carolinensis*) in the presence of "flying" predator models. Previous experimental research with black-capped chickadees *(Poecile atricapilla)* as well as Mexican chickadees (*Poecile sclateri*) suggested a relationship between the presence of predator stimuli and the note composition of chick-a-dee calls.

Carolina chickadees were presented with two types of stimuli in field settings. These models were painted to resemble either a predatory sharp-shinned hawk (*Accipiter striatus*) or a blue jay (*Cyanocitta cristata*). Models consisted of pairs of five varying shapes, making ten models in all. A randomly chosen model was covered with a cloth and attached to a zip-line fastened to a tree about five meters high. During the procedure the cloth was removed and the model was released, causing it to "fly" to the opposite end of the zip line, which was attached at ground level. These trials were audio recorded at 20 field sites in eastern Tennessee from January - March 2010 and January - February 2011.

Chickadees produced more C notes in response to hawk models than to blue jay models. Additionally, chickadees produced more A and C notes as well as more total notes during the post-exposure period than during the pre-exposure period for both the hawk and the blue jay conditions.

The chickadees' increased production of C notes in response to the hawk stimuli is consistent with previous research conducted on Mexican chickadees, potentially suggesting that the call structure of Carolina chickadees in threatening predator contexts is more similar to that of Mexican, rather than black-capped chickadees. Finally, chickadees increased production of A

notes and C notes to the presence of both model types, providing support for the “Better Safe Than Sorry” strategy.

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CHAPTER I

INTRODUCTION

Birds from the Paridae family such as chickadees and titmice often form overwintering social flocks, using their calls as a means of communication (S.M. Smith, 1991). The chick-a-dee call produced by black-capped chickadees *(Poecile atricapillus)*, for example, can be used to alert the flock to a food source (Ficken, 1981), and has also been shown to signify variation in predators' body size through changes in the specific patterning and composition of note types in calls (Templeton & Greene, 2007).

In the current study, members of mixed flocks comprising Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*) and white-breasted nuthatches (*Sitta carolinensis*) were presented with moving avian models while at feeding stands. The purpose of this study was to describe the variation within chick-a-dee calling behavior due to the presence of moving avian models.

Several techniques have been employed to study alarm-calling behavior in social species. Captive experiments performed with laboratory-housed animals (e.g. Baker & Becker, 2002; Evans, Evans, & Marler, 1993) allow for a large amount of control, ensuring that potential extraneous confounding variables are minimized. Conversely, captive animals have the potential of behaving differently from their wild counterparts, thereby producing results that can potentially not be generalized to wild populations. At no fault to the researcher, it may be very difficult to provide a suitable habitat with the correct environmental cues necessary to allow the animals to behave as they would in the wild, rather than to simply respond to the stress of their

artificial habitat. Such issues can make it extremely difficult to determine the natural variables causing a specific behavior.

Studies involving unmanipulated field studies are associated with their own list of benefits and problems. In such experiments, direct interactions between the observers and the subjects are minimized as much as possible (Ficken & Witkin, 1977; Martin & Bateson, 2007). By allowing the subject to presumably behave as it would naturally, the observers are therefore able to record data without the fear of any manipulations tainting their results. This amount of freedom on the part of subject however, can create issues in terms of how difficult the animal might be to observe, or even with how frequently the behaviors in question are expressed. Furthermore, there is an inability to infer causality (Martin & Bateson, 2007). While these problems pose several unavoidable difficulties, the present study took a combination of both approaches, in that wild, unenclosed birds were experimentally presented with potentially threatening stimuli.

The alarm calls produced by social species may encode more information than has been previously assumed. For example, specific situations have been found to elicit distinctly different alarm calls, implying the existence of situation-specific information within the calls (Ackers & Slobodchikoff, 1999; Evans, Evans & Marler, 1993; Gottfried, Andrews & Haug, 1985; Marler, 1956). Evans and Marler (1995) suggest that specific variables such as the shape and proximity of the predatory threat may cause the alarm caller to vary its signal. Additionally, the researchers went on to suggest that one of the primary influences on the specifics of a caller's signal might be the presence or absence of conspecifics in the area.

Seyfarth, Cheney, and Marler (1980) discovered that vervet monkeys (*Cercopithecus*

aethiops) produce distinct alarm calls for leopards (*Panthera pardus*), martial eagles (*Polemaetus bellicosus*), and pythons (*Python sebae*). While each predatory stimulus was associated with its own set of threats (leopards and pythons being terrestrial and eagles being avian), they also discovered that each call's elicited response among conspecifics was distinct. For example, calls produced in response to leopards caused conspecifics to climb into the branches of the nearest tree, calls in the eagle context caused conspecifics to take cover in dense vegetation, and finally calls in the python context caused the monkeys to inspect the ground around them. The monkeys' context-specific reactions therefore implied that each alarm call encoded not only information about a general threat, but about the specific nature of the approaching predator.

Manser, Seyfarth, and Cheney (2002) suggested that southern African mongeese (*Surakarta suricatta*) also encode predator-specific information in their calls. The alarm calls were polarized into those associated with terrestrial predators, and those associated with avian predators. The researchers also pointed out that the mongeese seemed to attach a level of threat or "urgency" to each call, such that a call was categorized as a response to a terrestrial or avian predator with a high, medium, or low level of urgency.

While such mammalian species show evidence of specialized alarm calling behavior, certain avian species seem to possess such complex behavior as well. For example, Marler (1955) suggested that chaffinches (*Fringilla coelebs*) emit a different alarm response for flying as opposed to perched avian predators. Marler found that that flying raptors were met with a pure alarm call of a very high frequency, presumably making it very difficult for the predator to detect the location of the caller (Jones and Hill, 2001). Interestingly, in the case of a perched raptor, the

corresponding alarm call featured a wide range of low frequency notes, potentially implying an aggressive response (like one associated with mobbing behavior) rather than an evasive one as in the flying context (Marler, 1955).

Additionally, Evans, Evans, and Marler (1993) found that domesticated roosters (*Gallus gallus*) alarm call differently as they are presented with either a video of a flying hawk, or a video of a raccoon (*Procyon lotor*). Even at times when a rooster's alarm call was played on the monitor, each condition (avian or terrestrial) was accompanied by the corresponding reaction by conspecifics, again suggesting not only that specific information is being transmitted by the caller, but that such information is also being received and processed by conspecifics.

The current study focused on the Carolina chickadee (*Poecile carolinensis*) as it exists in mixed flocks consisting of tufted titmice (*Baeolophus bicolor*) and white-breasted nuthatches (*Sitta carolinensis*). Chickadees live year-round in the southeastern United States and feed on small insects and seeds (Mostrom, Curry, and Lohr, 2002). Despite remaining in the same area year round, social structure is season-dependent, with spring and summer constituting pairing and producing offspring. The mixed flocks that are the focal point of this study are then formed in the autumn and continuing through winter, during which male/female pairs join titmice and nuthatch pairs. These other species can then benefit from the alarm calling behavior of the chickadee (Sullivan, 1985; Dolby & Grubb, 1998; Forsman & Mönkkönen, 2001).

The chickadee alarm call can potentially be used to warn conspecifics or other members of the mixed flock of a predatory threat. Individual components of the call, known as notes, can be potentially varied in diverse contexts to convey an enormous amount of information (Hailman, 1989). For example, S.T. Smith (1972) suggests that chickadees vary their note

patterns to convey information about social interactions, flight, and even predatory information. Whereas alarm calls are generally though to be difficult to localize, thus allowing the caller to evade detection, mobbing calls are thought to actually draw attention to the location of the caller (Marler, 1955; Morton, 1977). Mobbing calls involve low, loud calls designed to gather conspecifics around a predator in an effort to drive it from the area (Curio, 1978).

The Carolina chickadee's call system closely resembles that of its relative, the black-capped chickadee. This system has been divided into notes known as A, B, C, and D notes, which can be varied due to context (Hailman, Ficken, & Ficken, 1985; Ficken, Ficken, & Witkin, 1978). For example, captive black-capped chickadees' calls contained more D notes in the presence of a small rather than a large predatory stimulus (Templeton, Greene & Davis, 2005). In the wild, smaller predatory birds are more likely to prey on small passerines like chickadees than are larger raptors, and it would therefore be advantageous to signal more strongly in the former case than the latter. Black-capped chickadees have also shown the ability to signal proximity to a threat, by signaling more quickly, and with more A notes and fewer B notes when a prairie falcon (*Falco mexicanus*) was shown at 1 meter as opposed to 6 meters away (Baker & Becker, 2002).

The present study consisted of analyzing the alarm calls produced by Carolina chickadees (Figure 1) and classifying the notes as either A, C, or D notes, or other (such as B, D hybrid, and H; Lucas & Freeberg, 2007; Freeberg, 2008). A notes are whistled, relatively pure-tone notes with a high peak frequency and typically little frequency modulation. Conversely, C notes are more complex, resulting in a harsh sound as compared to A notes, and with much greater frequency modulation. Finally, D notes are relatively uniform in frequency and have a broadband acoustic pattern (Hailman et al., 1985; Bloomfield, Phillmore, Weisman, & Sturdy, 2005; Lucas

& Freeberg, 2007). Because of this uniformity of structure, variation of D notes is thought to arise in the quantity of notes in a call, rather than specific differences in duration, pitch, or frequency within each specific note. Furthermore, Morton (1977) points out that birds show evidence of using "Motivation-Structural Rules" within their alarm signals. These rules explain how, based on birds' use of either low-frequency sounds when in an aggressive state, and high-pitched sounds when frightened, such signals can predict the specific motivations behind their production (Morton, 1977). In the case of Carolina chickadees, this low-frequency response can be thought of as D notes (mobbing calls), while a high-frequency response could be thought of as A notes (alarm calls) (Marler, 1956). C notes would represent a more intermediate and possibly mixed-motivational state on the part of the caller.

In the present study, mixed flocks containing Carolina chickadees were presented with one of two avian models: a sharp-shinned hawk (*Accipiter striatus*) or a blue jay (*Cyanocitta cristata*). The sharp-shinned hawk is a small (24-34 cm in length) predator that relies on surprise and quick speed to capture prey such as small songbirds, including Carolina chickadees, from feeders (Bildstein & Meyer, 2000). The blue jay is a small (25-20 cm in length) brightly colored song bird known only rarely to be aggressive in rare instances toward conspecifics, and to feed on fruits, seeds, and at times small animals (Tarvin & Woolfenden, 1999). Blue jays are not thought of as a threat to adult songbirds like those making up the mixed flock.

Interactions with predators normally cause prey to attend to the threat, and to focus all behavior on defense and evasion (Cockrem & Silverin, 2002). These altered behaviors due to attending to a threat often include alarm calling (Baker & Becker, 2002; Bartmess-LeVasseur, et al., 2010). Previous research on alarm calls in the context of predator stimuli has typically been

done using stationary or “perched” predatory models stationed at various distances from the subject animal (Baker & Becker, 2002; Templeton, Greene, & Davis 2005). Both in the case of using stationary models as well as in Templeton et al.’s (2005) study involving the presentation of live predators, subjects modified their alarm calls in relationship to the specific predatory threat.

While such research using perched predatory stimuli has produced a variety of interesting results, it is noteworthy that such perching behavior near prey is extremely uncommon behavior for predatory species (Ekman, 1989; Hegner, 1985). Schleidt, Shalter, & Moura-Neto (2011) reference the ethological experiments done by both Lorenz and Tinbergen, suggesting that variation in the shape and size of moving predator stimuli can cause varying levels of threat or “selective habituation”. These results imply that the specific characteristics of flying predator stimuli can affect the response produced by songbirds (Schleidt et al., 2011). Therefore, stimuli in the present study were attached to a 23 meter zip-line cable with one end attached to a tree roughly 5 meters above the ground. These models were covered with a cloth before presentation, and I predicted that the moving hawk models would cause members of the mixed flock to produce more alarm calls as compared to the moving blue jay models. Ficken, Hailman & Hailman (1994) suggested that in Mexican chickadees (*Poecile sclateri*), more C notes were produced in the context of experimental presentations of a perched hawk model, leading me to expect that the same might occur in the case of Carolina chickadees. Conversely, Freeberg (2008) found in a naturalistic observational study that the presence of a hawk flying through the area caused Carolina chickadees to call with an increase of A notes, leading me to expect the same results in the present study. Finally, I expected that the hawk models would elicit more D

notes from chickadees than would the blue jay models given the greater threat posed by hawk stimuli (Templeton et al., 2005).

The blue jay models were used to test these predictions in that they could be perceived as less threatening and therefore not elicit the same reaction as the hawk models. Because the blue jay model's natural behavior does not include predation of the species that make up the mixed flock, I expected that the conditions in which such models were used would not elicit any, or at least many fewer, alarm calls than would the hawk models. Alternately, if chickadees respond strongly to both the hawk and the blue jay models, this would suggest support for the "Better Safe Than Sorry" strategy. This theory states that when few costs or negative repercussions exist as a result of a false alarm call, it would be advantageous for individuals to alarm call in situations with an ambiguous level of threat (Haftorn, 2000).

CHAPTER II

METHODOLOGY

Prior to the study taking place, several pilot trials were attempted during the fall and winter of 2009 and 2010. These trials involved using various lengths of cable, as well as the use of a variety of predator stimulus presentation techniques. The purpose of the pilot study was to get reliable calling behavior from birds prior to and after release of predator models.

Study Sites

The study was conducted at 20 field sites in three locations: The University of Tennessee Forest Resources, Research, and Education Center (UTFRREC), in Oak Ridge, TN; Ijams Nature Center, Knoxville, TN; and Norris Dam State Park in Lake City, TN. Predator models were presented at 14 sites at UTFRREC, 2 sites at Ijams Nature Center, and 4 sites at Norris Dam State Park. Each site was separated from the nearest adjacent site by at least 400 meters, ensuring that each site constituted an individual flock (Freeberg & Lucas, 2002; Bartmess-LeVasseur et al. 2010).

Each site had a feeding station, consisting of a wooden board (~25 cm x 40 cm x 2 cm) attached to the top of a steel pole (~1.8 m tall) driven into the ground, with each standing about 1.5 m high. Prior to each trial period, the stand was stocked with ~50 g of a 1:1 mix of black oil sunflower seed and safflower seed. Additionally, the sites were stocked every 10-14 days over the fall and winter as a means to establish the sites as irregular food sources for the mixed flocks.

Set-Up

Trials were conducted at the test sites from January to March 2010 and January 2010 to February 2011 between 0900 and 1430 EST. After stocking the stand as stated above, equipment was assembled. A deer stand ladder was attached to a tree ~10 m from the feeding stand. This ladder was then used to chain one end of a 23 m cable to the tree ~5 m high, with the other end either being chained to a tree at ground level, or to the ground using a standard tent stake. The cable was positioned such that it passed to roughly 1 m from the feeding station at its closest point. A Sennheiser ME-66 microphone was then mounted on a microphone stand ~1 m from the stand such that it was aiming at both the feeding station and the tree with the ladder attached to it (Figure 2 & 3). A randomly selected model was then attached to the highest point of the cable, and covered entirely with a cloth.

Models

Ten models of wooden construction were used as stimuli (Figures 4, 5 & 6). Using Bird Vision UV Reflective Decoy Paint from Reel Wings Decoy Co. Inc.©, five of these models were painted to resemble the color pattern of a predatory sharp-shinned hawk (*Accipiter striatus*; Bildstein & Meyer, 2000), while the other five served as the control and were painted to resemble the color pattern of a blue jay (*Cyanocitta cristata*; Tarvin & Woolfenden, 1999). I used ultra-violet paint because small passerines, including blue tits (*Cyanistes caeruleus*), show heightened sensitivity to ultra-violet cues (Church, Bennett, Cuthill, & Partridge, 1998; Derim-Oglu, & Maximov, 1993). These findings indicate that using such cues on predator models may

better emulate the natural stimulus than non-UV-based paint. These model types were selected because they represented naturally occurring species at all of the test sites, and their varying threat levels would therefore be familiar to the birds being studied. Sharp-shinned hawks are predators of small songbirds while blue jays are not, and both species have been observed in the vicinity of the sites in the past. There were five pairs of size-matched hawk and blue jay models. This variety within the size and shape of stimuli was created in an effort to minimize the study's potential for pseudo-replication (Hurlbert, 1984).

Because each pair of models was a different shape and size (Figure 6), efforts were made to standardize the weights of each, thus ensuring a similar "flight" time and speed for each model. Each model was weighed using a Salter Suspended Weigher Model 235. The A models weighed 830 grams, the B models weighed 720 grams, the C models weighed 460 grams, the D models weighed 450 grams, and the E models weighed 550 grams. In order to standardize these weights, Eagle Claw® Egg Sinker fishing weights, weighing 50 grams each, were used. Therefore, using this method, the E models were given 6 weights, the C and D models were given 8 weights, the B models were given 2 weights, and the A models were used without any weights. By standardizing the weight of each model, the typical flight time of each model was slightly less than 4 seconds for the 23 m cable, suggesting a model flight velocity of 5.72 m/s.

Recording Procedure

At the onset of each recording session the date, location, site, temperature, model being used, and weather conditions were noted before the trial took place. Thereafter it was noted each

time a bird took seed from the stand, as well as other notable behaviors such as group reactions to the trial, the presence of other stimuli, etc.

For each site, the model in use was randomly determined (Table 1). During each trial, birds were recorded as they took seed from the stand for ~2 min, at which point the cloth was removed from the model and the model was released and allowed to “fly” to the opposite end of the cable. Following this presentation, the birds were recorded as they returned to the stand, with their actual return to the stand constituting the end of the recording session. Carolina chickadees, tufted titmice, and nuthatches were present during each recording session unless otherwise noted (Table 1), and a Carolina chickadee had to be present at the feeding stand in order for the model to be released.

Call Analysis and Data Processing

The calls of the three species as well as observer commentary were recorded before, during, and after the model presentation, using a Sennheiser ME-66 microphone connected to a Marantz PMD660 Solid State Recorder. These recordings were then analyzed using Cool Edit Pro version 2.0 (Syntrillium Software) with a sample rate of 44.1 kHz. In Cool Edit Pro 2.0 we visualized each sound file with 256 bands of resolution in spectrogram form using the Blackmann-Harris windowing function (Figure 1).

Calls were separated into those produced 30 seconds prior to model release and 30 seconds after model release and were analyzed for note type (A, C, and D). In order to be included in the analysis of the study, calls were required to contain at least two notes, and appear clearly enough on the spectrogram so as to be unambiguous. Statistical tests were conducted

using SPSS 18.0 for Windows. Because sample sizes were relatively small and normality could not be assumed, non-parametric statistical tests were used to analyze the data. Recordings were obtained from each of the 20 sites (Table 1).

CHAPTER III

RESULTS

To determine inter-observer reliability, an additional observer independently rescored the calls. Agreement for each of the three note types as well as for total notes was high for both before and after model flight (N=20 sites), as was agreement for latency (N=15 sites). Correlations for the two scorers range from 0.849 to 1.000 (Spearman's Rho: 0.961 Total notes before model, 0.880 Total notes after model, 0.849 A notes before model, 0.968 A notes after model, 1.00 C notes before model, 0.920 C notes after model, 0.946 D notes before model, 0.920 D notes after model, and 1.00 Latency to return to stand).

Presentation of moving blue jay and hawk models produced significant changes in chickadees' call structures. Chickadees produced more A notes (two-tailed sign tests: A Notes, $p < 0.001$; C notes, $p = 0.003$; and total notes, $p = 0.012$; in the 30 seconds after the model was released compared to the 30 seconds before the model was released, while D notes showed no such trend ($p = 0.607$; Figure 7). Notes produced during the four-second model presentation varied greatly between sites (Table 2).

Model type had a significant effect on the amount of C notes that chickadees produced, with the "hawk" models (N = 7) eliciting more C notes than "blue jay" models (N = 13) (Mann-Whitney Test, U=20, Z=-2.173, two-tailed p=0.028 (Figure 8). None of the other comparisons (A notes or D notes) were significantly affected by model type.

Latency to return to the feeding stand after model presentation was not significantly different between “hawk” models (N=7) and “blue jay” models (N=13) (Mann-Whitney Test, U=20, Z=-0.612, two-tailed p=0.594 (Figure 9).

CHAPTER IV

DISCUSSION

Individuals are subject to countless benefits as a result of being part of a social group, such as an increased foraging ability as well as a heightened vigilance against predation (Krause and Ruxton, 2002). This heightened defense is often manifested through an individual's alarm calling in the presence of a predatory threat, which can result in the group being alerted about danger (Krause and Ruxton, 2002).

By living in social groups, individuals may minimize their individual risk by surrounding themselves by conspecifics. For example, a "selfish herd" scenario might predict that individuals within a social group might each attempt to reduce their individual risk of predation. Hamilton (1971) provided an example of such a scenario by suggesting a hypothetical lily pond inhabited by frogs as well as by a predatory snake. Because each individual frog should seek to minimize its individual risk, the frogs would seek to stay away from the water where the snake would be a threat, while also avoiding the bank where conceivably, other terrestrial predators may exist. Using this model, Hamilton mathematically demonstrated how each frog should seek to position itself between two other frogs, thus creating a "selfishly" designed aggregation. Selfish motivations should therefore play a major role in why an animal might choose to engage in a potentially costly behavior like alarm calling. The increased threat associated with alarm calling must therefore carry some benefit through which one's individual fitness can be increased in a "selfish" manner (Sherman, 1977).

The selective advantage associated with the role of alarm caller must outweigh the potential threat in order for such a costly action to take place. Hamilton (1964) suggested that

certain genes must cause such cooperative behavior or “kin selection”. This theory suggested that such altruistic behavior manifests not as a function of the benefit to the individual, but instead on the gene’s benefit to itself. Hamilton’s rule predicts that an individual is likely to help another individual only if the benefit to the first individual, combined with the degree of relatedness between the two, outweighs the potential cost of the behavior. Alarm calling for the benefit of the group can act to increase the inclusive fitness of an individual if the group is largely related to the alarm caller. By alarm calling, an individual stands to maximize the reproductive success of its own offspring as well as the success of its relatives, thus maximizing its own inclusive fitness (Da Silva, Mahan & Da Silva, 2002).

Kin Selection has recently been the source of debate, since some researchers do not believe that its models adequately explain why alarm calling occurs in social groups (Nowak, Tarnita, & Wilson, 2010). These researchers go on to point out that natural selection as applied to individuals and/or groups may actually do more to explain alarm calling than would kin selection, with one example being “reciprocal altruism”. In groups composed of non-relatives, Trivers (1971) suggested that an individual caller’s altruistic actions will be noted and later reciprocated by the other members of the group. This reciprocation will then perpetuate the reversal of cooperative social roles, and promote altruistic behavior at the level of the group.

In this study, the structure of the chick-a-dee calls produced by Carolina chickadees was affected by the presence of specific flying models. After models flew through testing sites, each note type other than D notes showed significant increases. Chick-a-dee calls in hawk contexts were found to contain significantly more C notes than were calls produced in blue jay contexts. Since the model type had a significant effect on the number of C notes produced, it can be

concluded that the birds' reactions were not due simply to encountering a novel stimulus. The specific differences in how the models were painted elicited unique responses in the alarm calls of chickadees. These results suggest that chickadees can perceive salient predator-related visual stimuli in a relatively short time period (i.e., within 4 seconds), and adjust their calling behavior quickly (i.e. within 30 seconds) to signal different levels of threat.

Based on Templeton et al. (2005), I expected calls made in hawk contexts to have an increased number of D notes, as this increase would be proportional to the increase of the perceived threat associated with the model. It would seem however, that my results were more consistent with those found in Ficken et al. (1994) with Mexican chickadees, which also produced more C notes in the presence of a predator. Therefore, the Carolina chickadees in the current study were shown to react to predator stimuli with an increase in C notes, consistent with research done on Mexican chickadees (Ficken et al., 1994) rather than with research on black-capped chickadees (Templeton et al., 2005). Production of D notes remained consistent for both hawk and blue jay contexts. Previous research suggesting that chickadees produce more D notes due to a more imminent threat (Bartmess-LeVasseur et al., 2010) or that birds near the ground produce more D notes (Freeberg, 2008) were therefore not corroborated.

Despite the hawk-specific effect for C note production, it was clearly the case that chickadees were generally responding strongly to both of the moving models. As predicted by Templeton et al. (2005) as well as Ficken et al. (1994), more overall notes were given in the 30 seconds after exposure and flight of the models, implying chickadees were attending to the threat rather than to feeding. Additionally, because there was a uniform latency to return to the feeder to

take seed after both types of stimuli, both must have been considered as similar threats, at least in the context of feeding.

These reactions may reveal the benefits of overly cautious behavior. As discussed in Haftorn (2000), such a “Better Safe Than Sorry” strategy may be far more advantageous than the potentially costly process of selectively alarm calling only during “true attacks”. Therefore, while many of the chickadees’ alarm calls were made in blue jay or non-predatory contexts, such “false alarms” may still have worked to protect and alert conspecifics to a potentially threatening situation (Haftorn, 2000), particularly if energetic costs of alarm calling are low, as should be the case with these calls.

Haftorn (2000) provides an example of how such a strategy may be advantageous within the willow tit (*Poecile montanus*). Playbacks were used to record the birds’ reaction to various threatening, as well as non-threatening, auditory stimuli. The researchers noted that the birds seemed to alarm call to some degree to nearly every stimulus, regardless of whether it was associated with a high level of threat. This observation led the researchers to conclude that such a “Better Safe Than Sorry” strategy would be advantageous in that situations occurring during a real attack can be very brief and therefore not provide considerable time to allow an appropriate reaction, and that such calls can thereby be helpful in the long run even if the threat is innocuous.

It should additionally be noted that this general lack of alarm specificity could have been a result of using moving stimuli rather than stationary ones. The ambiguity of the responses due to model may simply have been due to a simple threat response applied to all potentially threatening scenerios. As an example, chickadees were often observed “false” alarm calling in response to other stimuli such as the arrival of the researcher at the site.

The consistency of model stimuli used in this study proved to be one of its major strengths. Because each model was made of the same wooden construction and painted with the same ultraviolet paint, each stimulus was consistent with the next. Similar studies that have used combinations of man-made, mounted, or live predators (Naguib, Mundry, Ostreiher, Hultsch, Schrader, & Todt, 1999; Veen, Richardson, Blaakmeer & Komdeur, 2000) have suffered from the inability to make strong comparisons between stimuli. Additionally, the production of alarm calls as a result of each crudely painted model, which caused them to not to look exactly like live birds, provided support for the generality principle set forth in the "Better Safe Than Sorry" strategy (Haftorn, 2000). Such artificial models have also previously been used to elicit anti-predator behavior in other studies (Barash, 1976; Hanson and Coss, 1997; Gursky, 2006; Veen et al., 2000).

Because this study was done in the field, birds had more of an opportunity to escape than would captive populations. For example, similar studies that have been conducted with aviary-housed birds resulted in more anti-predatory behavior, conceivably because the birds' ability to escape had been greatly diminished (Baker & Becker, 2002; Templeton et al., 2005). By varying the distance of the cable from the feeding station, future studies could additionally work to see how much of a proximity effect the models had upon the birds. For example, Baker and Becker (2002) as well as Bartmess-LeVasseur (2010) found that chickadees reacted more strongly to closer predators than to those that were farther away, and it would be interesting to study whether these effects remain consistent for moving stimuli.

In conclusion, the current study supports the hypothesis (Ficken et al., 1994; Bartmess-LeVasseur et al., 2010) that the call structure of the Carolina chickadee can encode specific

information based on various predatory conditions. Because vocalizations are not always made in reaction to obvious cues (Owren, Seyfarth & Hopp, 1992), researchers should be conservative when making such assumptions. In this case however, given the research that has been done supporting this finding (Ficken et al., 1994; Nowicki, 1983; Baker & Becker, 2002; Templeton et al., 2005), it seems logical to assume that changes in predatory model stimuli directly elicited changes in chickadee call structure. By extending the findings of these previous studies to those involving moving predator models, the current study has provided an excellent avenue for future researchers to explore further.

Previous research has indicated that increases in specific note types can signal specific threat responses in Carolina chickadees. For example, increases in A notes in the context of threatening stimuli can indicate a more frightened response, and cause conspecifics to flee or freeze (Freeberg, 2008; Bartmess-LeVasseur, 2010). Differences in D notes due to a threatening situation can indicate varying levels of a “mobbing” or hostile response, based on the threat level of the stimulus (Templeton et al. 2005). Finally, the increases in C notes conceivably due to threatening stimuli found in this study may also indicate a heightened “mobbing” response (Ficken et al., 1994). Alternatively, increased C note production could be related to flight tendencies on the part of the caller (Smith, 1972; Freeberg, 2008). Finally, the role of C notes as “flight” notes could indicate that Mexican chickadees (Ficken et al., 1994) as well as Carolina chickadees in this case are responding to threatening stimuli while fleeing the area.

The call system of the Carolina chickadee may provide an excellent example of how complex vocal signals can be used in reciprocal altruism. Mobbing/alarm contexts of chickadees’ signals may relate directly to the specific motivations that caused them, thus providing an

excellent avenue through which to understand the animals' specific reasons for why they react to stimuli as they do (Marler, 1956; Morton, 1977). Additionally, by using these complex signals to warn conspecifics of an incoming threat, Carolina chickadees may be demonstrating a heightened quality of signalling, causing conspecifics to reciprocate the same level of specificity within their signals, in a clear example of reciprocal altruism (Trivers, 1971). Therefore, future research should aim to record not just the behaviors of the signaling individual, but also the longitudinal behavioral responses of conspecific receivers. Finally, by understanding potential audience effects among the other chickadees of the mixed flock, we can work towards understanding the mechanisms that allow reciprocal altruism to manifest in a social group.

Literature Cited

Ackers, S. H. & Slobodchikoff, C. N. (1999). Communication of Stimulus Size and Shape in Alarm Calls of Gunnison's Prairie Dogs, *Cynomys gunnisoni*. *Ethology, 105*,149-162.

Baker, M. C. & Becker, A. M. (2002). Mobbing Calls of Black-capped Chickadees: Effects of Urgency on Call Production. *Wilson Bulletin, 114(4),* 510-516.

Barash, D. P. (1976). Mobbing Behavior by Crows – Effect of Crow In distress Model. *The Condor, 78 (1),* 120.

Bartmess-LeVasseur, J., Branch, C. L., Browning, S. A., Owens, J. L., & Freeberg, T. M. (2010). Predator stimuli and calling behavior of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology & Sociobiology, 64*, 1187-1198.

Bildstein, K. L. & Meyer, K. (2000). Sharp-shinned Hawk (*Accipiter striatus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.proxy.lib.utk.edu:90/bna/species/482 doi:10.2173/bna.482.

Bloomfield, L. L., Phillmore, L. S., Weisman, R. G. & Sturdy, C. B. (2005). Note Types and Coding in Parid Vocalizations. III: The Chick-a-dee Call of the Carolina

Chickadee (*Peocile carolinensis*). *Canadian Journal of Zoology, 83*, 820-833.

Church, S. C., Bennett, A. T. D., Cuthill, I. C. & Patridge, J. C. (1998). Ultraviolet Cues Affect the Foraging Behaviour of Blue Tits. *The Royal Society*, *265*, 1509-1514.

Cockrem, J. F. & Silverin, B. (2002). Sight of a Predator Can Stimulate a Corticosterone Response in the Great Tit (*Parus major*). *General and Comparative Endocrinology, 125*, 248 –255.

Curio, E. (1978). Adaptive Significance of Avian Mobbing I. Teleonomic Hypotheses and Predictions. *Z. Tierpsychologie, 48(2)*, 175-183.

Da Silva, K.B., Mahan, C. & Da Silva, J. (2002). The Trill of the Chase: Eastern Chipmunks Call to Warn Kin. Journal of Mammology, 83, (2), 546–552.

Derim-Oglu, E.N., Maximov, V.V. (1993). Small Passerines Can Discriminate Ultraviolet Surface Colours. *Vision Res., 34(11)*, 1535-1539.

Dolby, A.S. & Grubb, T.C., Jr. (1998). Benefits to Satellite Members in Mixed-species Foraging Groups: An Experimental Analysis. *Animal Behavior, 56*, 501-509.

Ekman, J. (1989). Ecology of Non-breeding Social Systems of Parus. *Wilson Bulletin,*

101(2), 263-288.

Evans, C.S., Evans, L. & Marler, P. (1993). On the Meaning of Alarm Calls – Functional Reference in an Avian Vocal System. *Animal Behavior, 46* (1), 23-38.

Evans, C. S. & Marler, P. (1995). Language and animal communication: parallels and contrasts. In H. Roitblat & J. Arcady-Meyer (Eds*.) Comparative Approaches to Cognitive Science* (pp. 341–382). Cambridge, Massachusetts: MIT Press.

Ficken, M.S. (1981). Food Finding in Black-capped Chickadees – Altruistic Communication? *Wilson Bulletin, 93(3),* 393-394.

Ficken, M.S., Ficken, R.W. & Witkin, S. R. (1978). Vocal Repertoire of the Black-Capped Chickadee. *The Auk, 95*, 34-48.

Ficken, M.S., Hailman, E.D. & Hailman, J.P. (1994). The Chick-a-dee Call System of the Mexican chickadee. *The Condor, 96*, 70-82.

Ficken, M.S. & Witkin, S.R. (1977). Responses of Black-capped Chickadee Flocks to Predators. *The Auk, 96*, 156-157.

Forsman, J. T. & Mönkkönen, M. (2001). Responses of Breeding Birds to Heterospecific Song and Mobbing Call Playbacks Under Varying Predation Risk. *Animal Behaviour, 62,* 1067-1073.

Freeberg, T. M. (2008). Complexity in the chick-a-dee call of Carolina chickadees (*Poecile carolinensis*): associations of context and signaler behavior to call structure. *Auk, 125,* 896-907.

Freeberg, T.M. & Lucas, J. R. (2002). Receivers Respond Differently to Chick-a-dee Calls Varying in Note Composition in Carolina Chickadees, *Poecile Carolinensis. Animal Behavior, 63,* 837-845.

Gottfried, B. M., Andrews, K. & Haug, M. (1985). Breeding Robins and Nest Predators: Effect of Predator Type and Defense Strategy in Initial Vocalization Patterns. *Wilson Bulletin, 97(2),* 183-190.

Gursky, S. (2006). Function of Snake Mobbing in Spectral Tarsiers. *American Journal of Physical Anthropology, 129,* 601-608.

Haftorn, S. (2000). Contexts and Possible Functions of Alarm Calling in the Willow Tit, (*Parus montanus*); The Principle of ‘Better Safe Than Sorry”. *Behaviour, 137,* 437-449.

Hailman, J. P. (1989). The Organization of Major Vocalizations in the Paridae.

Wilson Bulletin, 101(2), 305-343.l

Hailman, J. P., Ficken, M. S. & Ficken, R. (1985). The ‘Chick-a-dee’ Calls of *Parus atricapillus*: A Recombinant System of Animal Communication Compared with Written English. *Semiotica, 56(3-4),* 191-224.

Hamilton, W.D. (1964). The Genetical Evolution of Social Behavior. I. *Journal of Theoretical Biology, 7,* 1-16.

Hamilton, W.D. (1971). Geometry for the Selfish Herd. *Journal of Theoretical Biology, 31,* 295-311.

Hanson, M.T. & Coss, R.G. (1997). Age Differences in the Response of California Ground Squirrels (Spermophilus beecheyi) to Avian and Mammalian Predators. *Journal of Comparative Psychology, 111(2),* 174-184.

Hegner, R.E. (1985). Dominance and Anti-predator Behaviour in Blue Tits (*Parus caeruleus*). *Animal Behaviour, 33,* 762-768.

Hurlbert, S.H. (1984). Pseudoreplication and the Design of Ecological Field Experiments. *Ecological Monographs, 54(2),* 187-211.

Jones, K.J. & Hill, W.L. (2001). Auditory Perception of Hawks and Owls for Passerine Alarm Calls. *Ethology, 107*, 717-726.

Krause, J. & Ruxton, G.D. (2002). Living in Groups. Oxford: Oxford University Press.

Lucas, J. R. & Freeberg, T. M. (2007). “Information” and the chick-a-dee call: communicating with a complex vocal system. In K. Otter (Ed.), *Ecology and Behavior of Chickadees and Titmice: An Integrated Approach,* (pp. 199-213). Oxford: Oxford University Press.

Manser, M.B., Seyfarth, R. M. & Cheney, D. L. (2002). Suricate Alarm Calls Signal Predator Class and Urgency. *Trends in Cognitive Sciences, 6(2),* 55-57.

Marler, P. (1955). Characteristics of Some Animal Calls. *Nature, 176,* 6-8.

Marler, P. (1956). Specific Distinctiveness in the Communication Signals of Birds. *Behaviour, 11*, 13-39.

Martin, P. & Bateson, P. (2007). *Measuring Behaivour: An Introductory Guide* (pp. 42-61). New York, NY: Cambridge University Press.

Morton, E.S. (1977). On the Occurrence and Significance of Motivational-structural

Rules in Some Bird and Mammal Sounds. *The American Naturalist, 111(981),* 855-869.

Mostrom, A. M., Curry R. L., & Lohr, B. (2002). Carolina Chickadee (*Poecile carolinensis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.proxy.lib.utk.edu:90/bna/species/636 doi:10.2173/bna.636.

Naguib, M., Mundry, R., Ostreiher, R., Hultsch, H., Schrader, L. & Todt, D. (1999). Cooperatively Breeding Arabian Babblers Call Differently When Mobbing in Different Predator-induced Situations. *Behavioral Ecology, 10(6),* 636-640.

Nowak, M. A., Tarnita, C. E. & Wilson, E.O. (2010). Inclusive fitness theory and eusociality. *Nature, 466,* 1057-1062.

Nowiki, S. (1983). Flock-specific Recognition of Chick-a-dee Calls. *Behavioral Ecology and Sociobiology, 12,* 317-320.

Owren, M. J., Seyfarth, R. M. & Hopp, S. L. (1992). Categorical Vocal Signaling in Nonhuman Primates. In H. Papoušek, U. Jürgens & M. Papoušek (Eds.) *Nonverbal Vocal Communication: Comparative & Developmental Approaches*

(pp. 66-86). New York, NY: Cambridge University Press.

Schleidt, W., Shalter, M.D., & Moura-Neto, H. (2011, February 21). The Hawk/Goose Story: The Classical Ethological Experiments of Lorenz and Tinbergen, Revisited. *Journal of Comparative Psychology*. Advance online publication. doi: 10.1037/a0022068.

Seyfarth, R. M., Cheney, D. L. & Marler, P. (1980). Monkey Responses to Three Different Alarm Calls – Evidence of Predator Classification and Semantic Communication. *Science, 210(4471),* 801-803.

Sherman, P.W. (1977). Nepotism and the Evolution of Alarm Calls. *Science, 197(4310),* 1246-1253.

Smith, S. M. (1991). The Black-capped Chickadee: Behavioral Ecology and Natural History. Ithaca, NY: Cornell University Press.

Smith, S. T. (1972). Communication and Other Social Behavior in Parus Carolinensis. Cambridge, MA: Nuttall Ornithological Club.

Sullivan, K. (1985). Selective Alarm Calling by Downy Woodpeckers in Mixed-species Flocks. *The Auk, 102,* 184-187.

Tarvin, K. A., & Woolfenden, G. E. (1999). Blue Jay (*Cyanocitta cristata*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.proxy.lib.utk.edu:90/bna/species/469 doi:10.2173/bna.469.

Templeton, C. N., Greene, E. & Davis, K. (2005). Allometry of Alarm Calls: Black-Capped Chickadees Encode Information About Predator Size. *Science, 308,*1934-1937.

Templeton, C.N. & Greene, E. (2007). Nuthatches Eavesdrop on Variations in Heterospecific Chickadee Mobbing Alarm Calls. *PNAS, 104(13),* 5479-5842.

Trivers, R.L. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology, 46,* 35-57.

Veen T., Richardson D.S., Blaakmeer K. & Komdeur, J. (2000). Experimental Evidence for Innate Predator Recognition in the Seychelles Warbler. *Proceedings of the Royal Society of London Series B – Biological sciences, 267 (1459),* 2253-2258.

Appendix

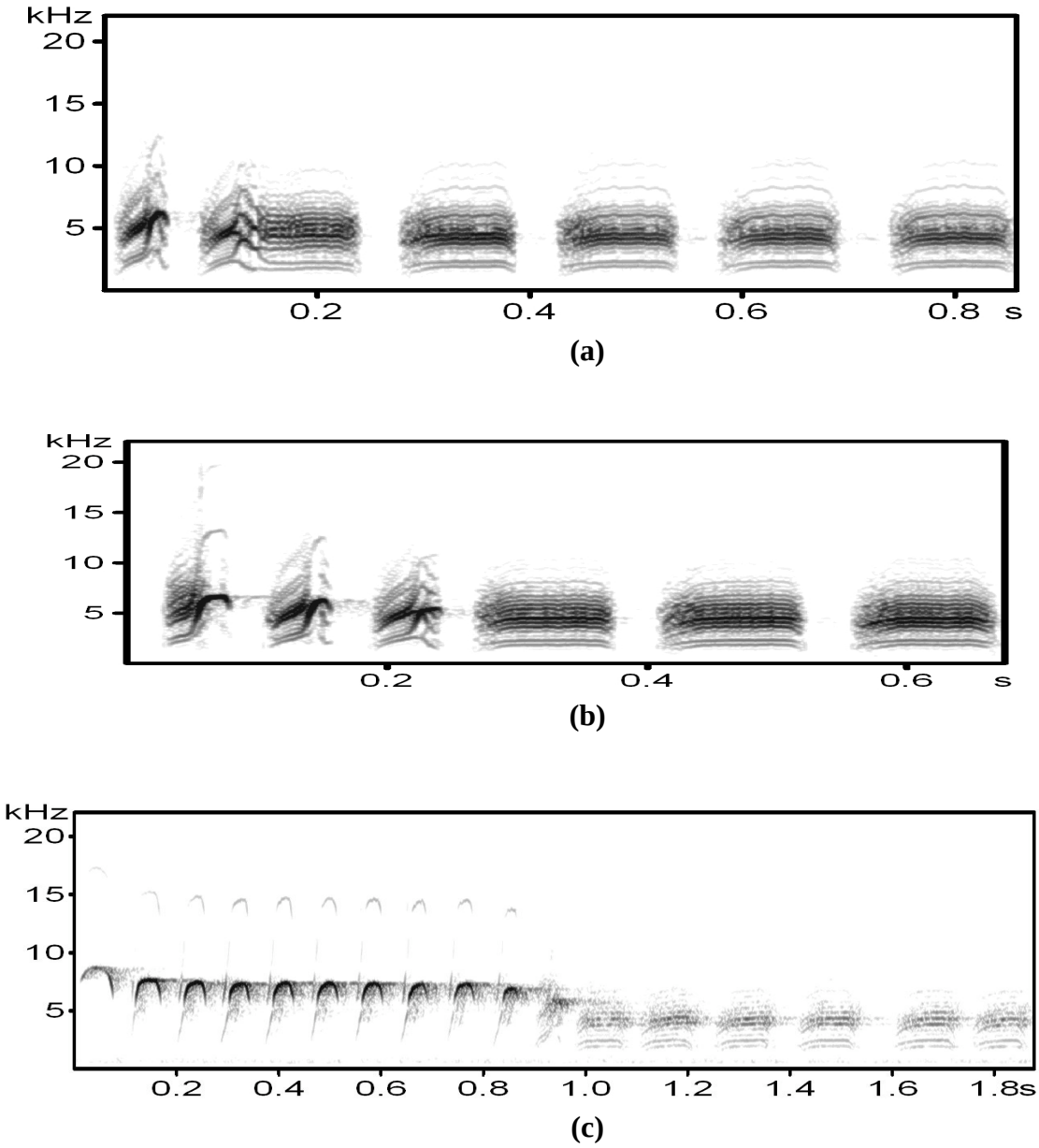


Figure 1. Examples of chick-a-dee calls of Carolina chickadees in this study. Spectrograms have frequency (hertz) on the y-axis and time (min) on the x-axis.

(a) Notes: C, D Hybrid, 4D

(b) Notes: 3C, 3D

(c) Notes: A, 9E, C, 6D

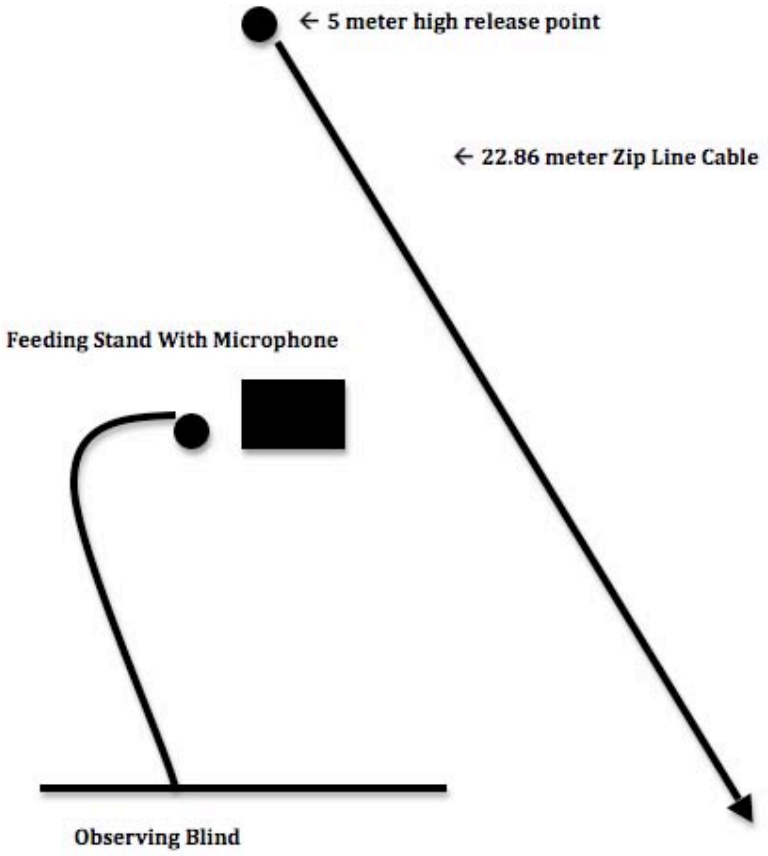


Figure 2. Schematic of general study site layout.

An aerial schematic view of sample study site that is not to scale. The 75’ (23 m) cable extended through the site alongside the feeding stand, with one end attached to a tree at 16’ (5 m) and the other attached at ground level. Observing blind was placed 10 m from stand.



Figure 3. View of sample study site from feeding stand.

Zip-line cable is visible in the right diagonally extending to tree, while the microphone and microphone stand can be seen to the left of the feeding stand.



Figure 4. Close up of models.

“A” sized models with hawk on left side and blue jay on right.

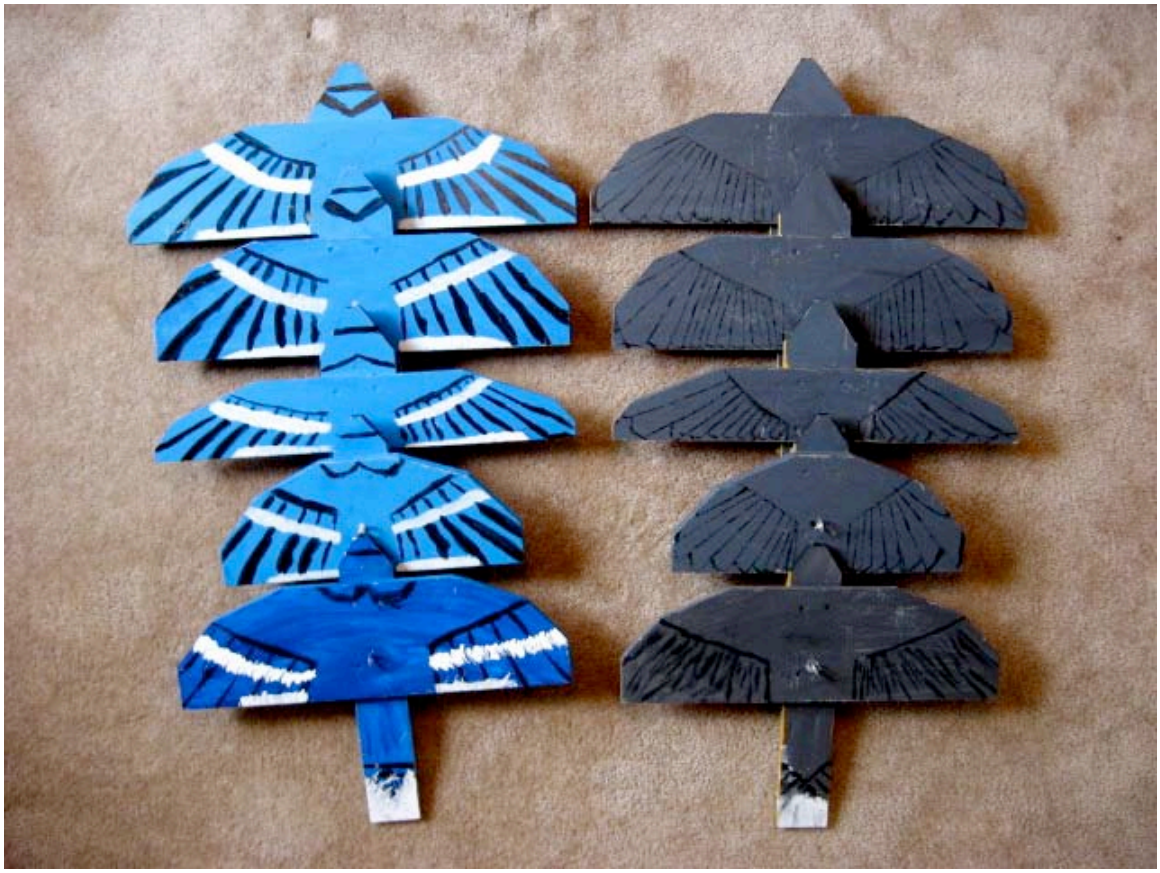


Figure 5. Top view of all models.

Blue jay models are on left and hawk models are on right, arranged sequentially with “A” models as the first (top-most) row and “E” models as the last (bottom-most) row.

A. 
L = 42 cm W = 63 cm

B. 
L = 42 cm W = 49 cm

C. 
L = 29 cm W = 59 cm

D. 
L = 31 cm W = 32 cm

E. 
L = 35 cm W = 45 cm

Figure 6. Model size variants.

Each of the five model size types is provided in hawk form, with the blue jay stimuli following the same size progression, making up ten models in all.

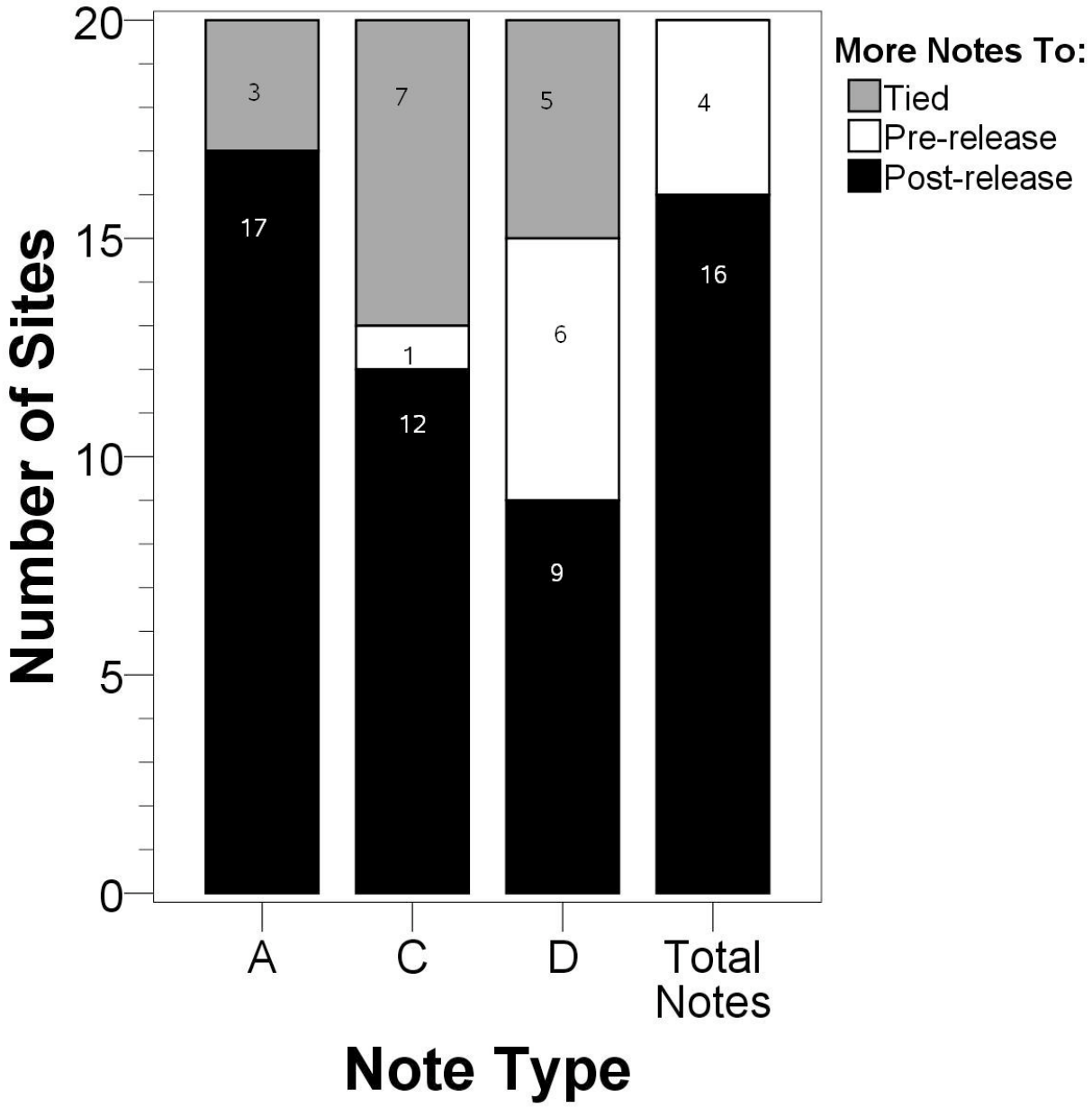


Figure 7. Note composition of all calls before and after model presentation.

Significantly more A and C notes and total notes were produced following presentation of both hawk and blue jay models, while no significant change was found for D notes.

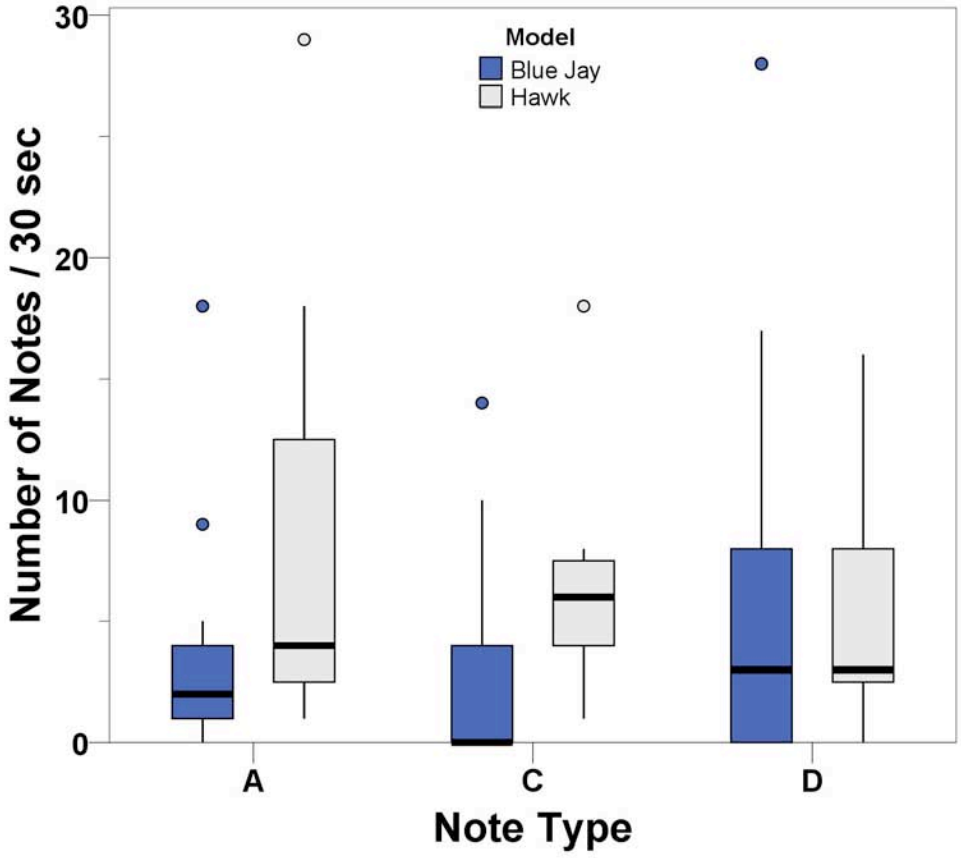


Figure 8. Note frequencies of calls by stimulus type.

In the 30-second interval following stimulus presentation, C notes were found to occur significantly more frequently for hawk stimuli than for blue jay stimuli.

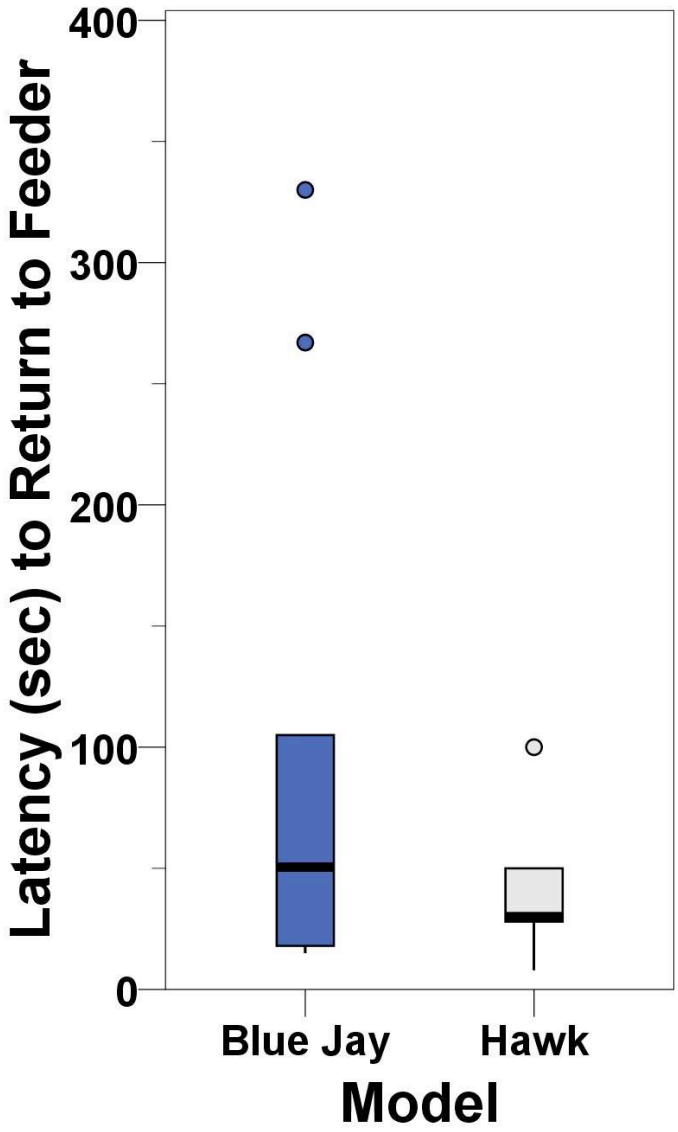


Figure 9. Latency to return to feeder following stimulus presentation.

No significant difference was found for latency to return to stand between hawk presentations and blue jay presentations.

Table 1. Stimulus presentations for study sites.

Site	Model Type	Model Size	Species Present*
UTFRREC			
A	Blue Jay	B	**CACH, ETTI**
B	Blue Jay	D	**CACH, ETTI**
C/D	Blue Jay	E	**CACH, ETTI**
E	Hawk	A	**CACH, ETTI, WNUT**
F	Blue Jay	B	**CACH, ETTI**
G	Blue Jay	C	**CACH, ETTI, WNUT**
I	Blue Jay	A	**CACH, ETTI, WNUT**
J	Blue Jay	E	**CACH, ETTI, WNUT**
K	Hawk	A	**CACH, ETTI**
Ar1	Blue Jay	C	**CACH, ETTI, WNUT**
Ar2	Blue Jay	C	**CACH, ETTI, WNUT**
Old Ar4	Hawk	C	**CACH**
New Ar4	Hawk	E	**CACH, ETTI**
Ar5	Blue Jay	B	**CACH**
NDSP			
A	Blue Jay	B	**CACH, ETTI, WNUT**
B	Hawk	A	**CACH, WNUT**
C	Hawk	D	**CACH**
E	Blue Jay	E	**CACH, WNUT**
IJAMS			
A	Hawk	C	**CACH, ETTI**
B	Blue Jay	D	**CACH, ETTI**

This schedule was randomly generated resulting in 7 Hawk trials and 13 Blue Jay trials.
* CACH = Carolina chickadee, ETTI = Eastern tufted titmouse, WNUT = White-breasted nuthatch

Table 2. Note Composition of Calls by Context.

Site	-30 to -4 sec	-4 to 0 sec	4 sec model 'flight'	+4 to +30 sec
Blue Jay Model				
FS A	3C3D		call, not scored*	1B3D
FS B			2A	
FS C/D		2A	3A	1A8D
FS F	3 gargles**			2A1B1D
FS G	3A		5A	1A5D, 1A3D, 1A5D, 1A4D
FS I	1B2D, 6E1B, 1B3D, 1B2D, 1B2D, 1B2D, 1B3D, 1B2D, 1B2D	1B3D	6E1D	
FS J	6C, 1A2D		1E1B3C, 4C5A	7C8D
FS Ar1	1B9D, 1B4D		11A2C	1B4D, 6A, 1A9E2C
FS Ar2			3A	
FS Ar5	12D, 1A2B, 1A9D, 10D, 1A10D, 13D		1A3E1A	
Ijams B	6E1C4D, 6E1C2D, 2D		2E10C3D	2E9D, 9D, 1A1E7D
NDSP A			2C, 1C	
NDSP E	4D, 1E2D		6C	1A4D, 2A4D
Hawk Model				
FS E	3B11E, 10D, 2A7D, 7D, 5D, 1A1Dh3D, 9D	7D	4A2E8C	2A3D, 1A4E
FS K	2A2D, 1E1Dh17D	7D	1E3C, 2E4C1D	15A, 1A1B6D
FS newAr4	1E6D, 1E6D, 1Dh4D, 1A7D, 1Dh2D		3A5E1C, 3A	11A, 3A, 3A, 3A, 3A
FS oldAr4		3E1C7D	2A1E	2C7D
Ijams A			3A, 10C	8C2D
NDSP B		2B1D	3C	1A1E3C3D
NDSP C	1B5D	3D	1E, 3E	2A1E1A1B3E3C, 1A5D, 3C4D

Calls produced during the 30-sec pre-stimulus period and 30-sec post-stimulus period, including the 4-sec period of model 'flight' and 4-sec pre-model exposure period for comparison.
* could not distinguish note types of chick-a-dee call due to background noise
** gargles are agonistic vocalizations of Carolina chickadees

Vita

Christopher Erik Zachau, son of Reinhard and Sharon Zachau, was born in Sewanee, TN on November 3, 1985. He graduated with a Bachelor of Arts in Psychology in 2008 from Hendrix College in Conway, AR. His interest in animal behavior was peaked by the Island Ecology Program, presented by the University of the South. Through this program, he was able to study social groups of ring-tailed lemurs (*Lemur catta*) on St. Catherine's Island, GA, causing him to immediately become interested in studying animals.

He also took part in a year-long position on board Marine Corps. Base Camp Lejeune in Jacksonville, North Carolina, where he worked to improve the habitats of the endangered red-cockaded woodpecker (*Picoides borealis*). This position also involved efforts to protect the nests of endangered sea turtles from the effects of military training.

After completion of his M.A. in experimental psychology, Chris plans to pursue a career in wildlife management. His primary interest is in predator-prey relationships, and how associated behaviors can provide valuable indications about environmental threat.