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I am submitting herewith a thesis written by Ellen Jolene Mahurin entitled “Feeding Behavior and Chick-a-dee Calls in the Presence of Predator Models: A Field Study of Carolina Chickadees (*Peocile carolinensis*).” I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts with a major in Psychology.

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FEEDING BEHAVIOR AND CHICK-A-DEE CALLS IN THE PRESENCE OF
PREDATOR MODELS: A FIELD STUDY OF CAROLINA CHICKADEES
(*POECILE CAROLINENSIS*)

A Thesis Presented for the Master of Arts Degree

The University of Tennessee, Knoxville

Ellen Jolene Mahurin

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Abstract

This study describes feeding and chick-a-dee calling behavior of Carolina chickadees (*Poecile carolinensis*) in the presence of predator models. Chickadees occur in stable social groups over much of the year, and birds in social groups often indicate the presence of predators through alarm calling and calling related to mobbing behavior. Research with two other chickadee species has found a relationship between predator stimuli and calling behavior, including the note composition of chick-a-dee calls.

Here, I presented Carolina chickadees with avian models, and a “no model” control. The species represented by the avian models were the Cooper’s hawk (*Accipiter cooperii*), a natural predator of chickadees; the great horned owl (*Bubo virginianus*), a bird of prey but not a predator of chickadees; and the American crow (*Corvus brachyrhynchos*), a non-bird of prey. Stimuli were initially covered with a cloth and then exposed during the experimental procedure. Audio recordings of flocks were obtained at 16 field sites in eastern Tennessee from October 2004 to March 2005.

Chickadees took significantly fewer seeds and produced more chick-a-dee calls during the post-exposure period than during pre-exposure for both the hawk and owl stimuli, but not for the crow and no model stimuli. I detected no effect of stimulus type on note composition of chick-a-dee calls, but note composition was affected by the proximity of the signaler to the seed stand for all four note types measured in this study.

Note composition in chick-a-dee calls in Carolina chickadees may not be strongly influenced by external referents like predator type. Instead, note composition may be influenced by the state of arousal of the signaler or its behavioral tendencies. An increase in calling rate in Carolina chickadees may serve a general recruitment function, though playback studies are needed to test these ideas.

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CHAPTER I

INTRODUCTION

Social groups bring numerous advantages to individual group members, including increased ability to find food, defend a territory and detect potential predators (S.M. Smith, 1991; Krause and Ruxton, 2002). Birds in social groups often indicate the presence of predators through alarm calling and calling related to mobbing behavior (Marler, 1955, 1956; Morton, 1977). Mobbing involves birds of one or more species gathering around a stationary or moving object, which is perceived as potentially dangerous, while giving low, loud calls and frequently changing locations and performing stereotyped wing and tail movements (Curio, 1978).

Individuals who call in the presence of predators risk being recognized and preyed upon. Alarm calling is common in many species; therefore, there must be some selective advantage for callers. Hamilton (1964) suggested that alarm calling plays a part in increasing the inclusive fitness of an individual. Inclusive fitness is the sum of direct fitness (the reproductive success of one's own offspring) and indirect fitness (the reproductive success of other relatives). If an individual's calls result in warning its offspring, siblings and other relatives of the presence of a predator, those relatives have a better chance of survival (Sherman, 1977; Da Silva, Mahan & Da Silva, 2002). Alternatively, Trivers (1971) suggested that alarm calling may evolve because of reciprocal altruism. A caller in a stable social group benefits from acting altruistically by warning non-relatives of the presence of a predator because those individuals will also give alarm calls to warn the individual (Trivers, 1971; Ficken, 1980; Krams & Krama, 2002; Krams, Krama & Igaune, 2006).

Stable social groups of birds composed of genetically unrelated individuals most likely benefit from alarm calling due to reciprocal altruism. Examples of birds forming this type of social structure can be found in the Paridae family, which includes species of tits, titmice and chickadees. Chickadee species use the chick-a-dee call, which is made up of distinct notes, to communicate among flock members and maintain social cohesion (S. T. Smith, 1972; S. M. Smith, 1991). This call has been particularly well studied in black-capped chickadees (*Poecile atricapilla*). Black-capped chickadees will call at an increased rate upon detection of a food source, which alerts other flock members (Ficken, 1980). In the presence of different types of predators, black-capped chickadees have been found to increase rates of chick-a-dee call production, and to vary the note composition of calls, based on predator characteristics (Templeton, Greene and Davis, 2005).

In the current study, Carolina chickadees (*Poecile carolinensis*) were presented with models of avian predators while feeding at field sites. The purpose of this study was to describe feeding and chick-a-dee calling behavior in the presence of predator models.

Alarm calls in animals

Alarm calling has been studied in many species of social animals, using a range of techniques. In general, as the amount of control exercised by the experimenter increases, the ability to infer causation increases, but the relation of the results to animals in the wild can often become less clear. At one end of the spectrum are unmanipulated field observations, where the observer makes an effort not to interact with the subjects at all (Ficken & Witkin, 1977; Freeberg, In Review). Such an observer can (if diligent) be confident that the behavior she records accurately represents the behavior of animals in

the wild. However, if the behavior of interest is rare, or if it causes the subjects to become more difficult to observe, field observations without observer interference are usually too inefficient for collecting reliable data. With unmanipulated studies, furthermore, it is difficult to determine the cause of observed behavior.

At the other end of the spectrum is the completely controlled experiment, where the subjects are kept in a laboratory and respond to well-defined stimuli (for examples of studies related to the questions posed here, see Baker & Becker, 2002; Evans, Evans & Marler, 1993). Control over every aspect of the subject's environment is an important tool, useful for mapping out behavior that might be observed in the wild. But the fine details of natural behavior are often influenced by subtle environmental cues that may be impossible to replicate in a laboratory setting. For example, captive birds might be predisposed to make alarm calls because they are trapped. The experimental approach taken in the present study, involving the presentation of stimuli to wild, unenclosed birds, is intermediate between these two approaches.

With any study technique, it is often difficult to determine the messages conveyed by and meanings perceived by detection of vocalizations (W. J. Smith, 1977). A correlation cannot always be made between the vocalizations of an individual and the behavior of the individual or environmental cues (Owren, Seyfarth & Hopp, 1992). Many attempts have been made to decipher meaning and causation. It has been found that some species give alarm calls with distinctly different sound features in different situations (Ackers & Slobodchikoff, 1999; Evans, Evans & Marler, 1993; Gottfried, Andrews & Haug, 1985; Marler, 1955, 1956; Naguib et al., 1999). Seyfarth, Cheney & Marler (1980) concluded from research that vervet monkeys referred to types of predators in the environment by using distinct calls. Evans and Marler (1995) present the idea that

the signals produced by animals in the presence of predators is influenced by predator factors like shape and distance from the caller and social factors like the presence or absence of conspecifics. Morton (1977) suggested that differences in call structure indicate different motivations on the part of the caller, such as alarm or hostility. Marler, Evans and Houser (1992) proposed that vocal signals lie along a continuum from purely arousal-based signals to those referential to external stimuli.

An excellent example of calls with different sound features given in different situations can be found in chaffinches (*Fringilla coelebs*). Marler (1955) found that chaffinches, in the field, have distinct calls and behavior in response to flying versus perching raptors. They respond to a flying raptor with a call that has a relatively pure tone, high frequency and an imperceptible beginning and end (Marler, 1955). These features make it extremely difficult for the raptor to determine the source of the sound (Jones and Hill, 2001). In the case of a perching raptor, chaffinches respond in an opposite manner to that described above. The call produced by chaffinches in this situation offers abundant location clues: a range of low frequencies and a harsh beginning and end. While calling in the presence of a perching raptor, chaffinches do not flee but make themselves conspicuous by mobbing the predator (Marler, 1955).

Seyfarth, Cheney and Marler (1980) found that predator type influenced call structure in wild groups of vervet monkeys (*Cercopithecus aethiops*). Monkeys gave acoustically different alarm calls to three different types of predators: leopards (*Panthera pardus*), martial eagles (*Polemaetus bellicosus*) and pythons (*Python sebae*). They write that “[l]eopard alarms were short tonal calls, typically produced in a series on both exhalation and inhalation. Eagle alarms were low-pitched, staccato grunts, and snake alarms were high-pitched ‘chutters’ ” (Seyfarth et al., 1980, p. 802). Monkeys hearing

playbacks of these three calls reacted in three different ways. Leopard alarms caused them to climb into trees, eagle alarms caused them to look up and/or run into dense brush and snake alarms caused them to look at the ground. These responses were very similar to responses given upon sighting the actual predators.

Manser, Seyfarth and Cheney (2002) suggested that in a southern African mongoose (*Suricata suricatta*), alarm calls carry information about both predator type and urgency. They found that suricates used some general alarm calls, which were given to many different predators. Specific alarm calls were given to the following: mammalian predators attacking from the ground, avian predators attacking from the air, and snakes. Manser et al. (2002) also defined situations of high, medium and low urgency for each of these three alarm situations. They found that mammalian, avian and snake calls were acoustically distinct. Additionally, within each category, high, medium and low urgency calls showed significant acoustical differences.

Evans, Evans and Marler (1993) found that domesticated roosters (*Gallus gallus*) produced distinctly different alarm calls in response to two different predators. Roosters were presented with video of a figure in the shape of a flying hawk and video of a live raccoon (*Procyon lotor*). They also found that hens gave different reactions to playbacks of these two calls. First, roosters' reactions to video of the two different predators were recorded. Video of a soaring hawk-shaped silhouette caused subjects to crouch, sleek their feathers, turn their heads to look up and give aerial alarm calls. Some subjects remained frozen in this position until the end of the video. When a raccoon was depicted on the screen, subjects moved to the other end of the cage, fixated on the monitor, adopted an erect posture, pivoted to and fro and gave ground alarm calls. Next, the rooster calls, recorded from the first experiment, were played back to hens. Subjects

hearing the aerial alarm calls ran toward cover, crouched, scanned horizontally and fixated upward. Subjects hearing the ground alarm calls adopted an erect posture and scanned horizontally. There was no effect on using cover or looking upward in the case of hearing ground alarm calls.

Naguib et al. (1999) found that Arabian babblers (*Turdoides squamiceps*) did not have acoustically different calls for different types of predators, but used two call types in different ways in two predator contexts. Subjects were presented with two different predators in the field: a stuffed short-eared owl (*Asio flammeus*) and a live caged cat (*Felis communis*). Subjects mobbed both predators using call type one (tzwick), which was always followed by call type two (trill). Subjects gave more tzwicks before beginning a trill when the cat was presented. In the presence of the owl, they gave more trills after initial tzwicks. Because tzwicks are given initially for both predators, before the situation is fully evaluated, these vocalizations may indicate babblers are more uncertain about the situation. Since tzwicks continue with the cat, which is alive and therefore a greater threat, these vocalizations may indicate a higher urgency. The combination of the two calls has the potential to provide graded information about differences in urgency in predator situations.

Mobbing can be an effective defense for flocks of birds because it often serves to drive off the predator (Curio, 1978; Pettifor, 1990). Ostreiher (2003) found that individual Arabian babblers exhibited mobbing-like behavior when alone but that mobbing was intensified when two babblers were present. Subjects were presented with a model of an ambushing sand viper (*Cerastes cerastes*), which is a common predator in the babbler's home, Israel. In trials with two-babbler groups, each bird showed a

mobbing reaction that was longer in duration and with a greater rate of calls, place changes, and wing raises relative to cases when the individuals were alone.

Mobbing can attract birds of the same species as the initial caller, and those of different species. In a study by Hurd (1996), a speaker playing black-capped chickadee mobbing calls attracted 24 non-chickadee species to within 6 m of the speaker, where they exhibited mobbing behavior typical for their species. While recording Carolina chickadees at field sites in the summer of 2003, prior to this study, I observed songbirds mobbing a barred owl (*Strix varia*). A few tufted titmice (*Baeolophus bicolor*) began the mobbing event with loud harsh calls. They kept in motion by hopping from branch to branch around the perching owl. After a minute or two, Carolina chickadees, northern cardinals (*Cardinalis cardinalis*) and dark-eyed juncos (*Junco hyemalis*) joined the titmice in mobbing. The juncos dived at the owl and, after a few more minutes, drove it off. The low sounding calls given by the mobbing birds were distinct from other vocalizations I had heard in other contexts.

Chickadees and the chick-a-dee call

The focal species for this study was the Carolina chickadee of the family Paridae. Carolina chickadees are small passerines (songbirds) that are common in the southeastern United States and often live in close proximity to humans (Mostrom, Curry and Lohr, 2002). Along with chickadees, the Paridae includes tits and titmice (Harrap and Quinn, 1995). Carolina chickadees are abundant in east Tennessee, where this study took place. They can be found deep in deciduous forests feeding on insects, spiders, seeds and fruit. They can also be found in suburban areas eating seeds from yard feeders (Mostrom et al.,

2002). Carolina chickadees are considered a resident species because they do not migrate at any time during the year (Mostrom et al., 2002).

This resident status may be related to the complexity of the social structure and vocal behavior observed in Carolina chickadees (Ekman, 1989). Social structure changes throughout the year. In the spring chickadees are found in male/female pairs and often form a group with their offspring into the summer. In the fall, young disperse to other areas and begin to form flocks with unrelated birds. During the winter, chickadees are typically found in flocks of 3-7 birds, which are composed of male/female pairs and unrelated young from the previous spring (Ekman, 1989; Mostrom et al., 2002). Winter flocks of Carolina chickadees often join other species (including other Parids) and forage together (Harrap and Quinn, 1995). The parids and non-parids that live in close proximity to chickadees may benefit from chickadee alarm calls (Sullivan, 1985; Dolby & Grubb, 1998; Forsman & Mönkkönen, 2001).

Chickadees can signal alarm (Ficken, Ficken & Witkin, 1978) and mobbing (Templeton et al., 2005) through the use of their chick-a-dee call. This call can be broken down into components, called notes. Distinct note types can be combined in a variety of ways, resulting in a large diversity of distinct calls. The chick-a-dee call follows rules of note ordering (S.T. Smith, 1972; Hailman, Ficken & Ficken, 1985; Hailman, Ficken & Ficken, 1987). For example, notes almost always occur in descending frequency over the course of a particular call. Any note may be left out, given once, or repeated a variable number of times (Hailman & Ficken, 1986; Hailman, 1989). This high level of complexity allows for the possibility of conveying large amounts of information. For example, S.T. Smith (1972) found that the chick-a-dee call was used to communicate about flock movement, mate interactions, and predator interactions.

The call of the black-capped chickadee, which has been well described, uses four note types called **A**, **B**, **C** and **D**, listed in order of descending frequency (Hailman et al., 1985; Ficken et al., 1978). Black-capped chickadees have been found to vary the notes used in their chick-a-dee calls depending on context. In a study using live predators, Templeton et al. (2005) found that aviary-housed black-capped chickadees gave more chick-a-dee calls and calls richer in **D** notes when a smaller predator was presented, compared to when a larger predator was presented. Small, quick moving birds like chickadees are prey for animals that are likewise small and quick. Therefore, it may be suggested that the smaller predator was perceived as a greater threat than the larger one. Changes in the chick-a-dee call are often accompanied by other changes in behavior in the presence of predators. A study by Desrochers, Bélisle & Bourque (2002) found that black-capped chickadees reduced visits to feeders that were far from forest cover when mobbing playbacks were presented. Furthermore, in the presence of a stuffed merlin (*Falco columbarius*), black-capped chickadees uttered alarm calls and refused to leave forest cover. Baker and Becker (2002) presented black-capped chickadees with a stuffed prairie falcon (*Falco mexicanus*) in the laboratory. They found that subjects responded more quickly with more chick-a-dee calls when the falcon was presented at a 1 m distance from their enclosures than at a 6 m distance. They also found that chick-a-dee calls contained more **A** notes and fewer **B** notes at the 6 m distance (Baker and Becker, 2002).

The present study

Similar note types to those defined for the black-capped chickadee have been defined for the Carolina chickadee (Bloomfield, Phillmore, Weisman & Sturdy, 2005).

In the present study, with Carolina chickadees, notes were classified as **Az**, **C**, or **D** or placed into a group called Introductory notes (**Figure 1**^{*}; Miller et al., In Review). Study subjects were presented with a model of an avian predator, and notes that may indicate alarm or hostility on the part of the caller were of particular interest (Marler, 1955; Morton, 1977). **Az** notes were a subset of the **A** note category, defined for the Carolina chickadee by Bloomfield et al. (2005). **Az** notes were distinguished from other **A** notes because they have characteristics similar to the alarm calls of other species (Marler, 1955; Morton, 1977). They have very little frequency modulation, an audibly imperceptible beginning and end and the highest frequency of any other chick-a-dee note. All other **A** notes and **B** notes were grouped together and labeled as Introductory notes. **C** and **D** notes were of interest in this study because they have characteristics similar to the mobbing calls of other species (Marler, 1955; Morton, 1977). They have a harsh beginning and end and cover a range of low frequencies.

In the present study, Carolina chickadees were presented with four stimulus types: 3 man-made, perching, avian models, and no model. The species represented by the avian models were the Cooper's hawk (*Accipiter cooperii*), great horned owl (*Bubo virginianus*), and the American crow (*Corvus brachyrhynchos*). The Cooper's hawk is a medium sized (39-45 cm in length) diurnal raptor whose prey includes small-to medium-sized adult birds like Carolina chickadees (Rosenfield & Bielefeldt, 1993; S.M. Smith, 1991). The great horned owl is a large (46–63 cm in length) nocturnal raptor, whose prey includes other birds that forage at night or that roost in open nests or on water, and is not a predator of the Carolina chickadee (Houston, Smith, & Rohner, 1998). The American crow is a medium to large sized (43–53 cm) diurnal omnivore whose diet includes the

^{*} All figures and tables appear in the appendix, which begins on page 38.

eggs and nestlings of a wide variety of birds (Verbeek & Caffrey, 2002). At the time of my study (October-March), the American crow is of no threat to Carolina chickadees.

When coming into contact with predators, prey animals typically devote more energy to anti-predator activity, including calling, and less energy to feeding (Baack & Switzer, 2000; Cockrem and Silverin, 2002; Lind, Jöngren, Nilsson, Alm, & Strandmark, 2005). Prey animals also may alter their calls in the presence of predators. Perching predators appearing at close range, like the hawk stimulus in this study, usually elicit calls associated with alarm or mobbing behavior (Baker & Becker, 2002). Stimuli in the present study were initially covered with a cloth, which was pulled away midway through data collection to expose one of the three models or no model. I predicted that the exposed hawk stimulus would cause subjects to take fewer seeds from the seed stand and give more calls, compared to when the hawk stimulus was unexposed and compared to the other stimulus types. I also predicted that the chick-a-dee calls given would suggest mobbing behavior. Specifically, I predicted that chickadees would use more **D** notes in their chick-a-dee calls in the presence of the hawk stimulus (Apel, 1985; Templeton et al., 2005).

To strengthen the test of these predictions, other stimulus types were included in this study. The owl stimulus differed from the hawk stimulus in being a bird of prey but not a natural predator of the chickadee. The crow stimulus differed from the hawk and owl stimuli in being a non-predator, non-bird of prey. There was also a stimulus where the cloth was removed to expose no model. This stimulus was meant to test for alarm calls that subjects may have given in response to the sudden movement of the cloth rather than to the models. Subjects were recorded while the model stand, supporting each stimulus type, was unexposed and exposed.

There were other potential expectations for note composition of calls recorded in this study. Subjects could have given more **C** notes in their chick-a-dee calls when the hawk stimulus was exposed, similar to mobbing calls in Mexican chickadees (*Poecile sclateri*) (Ficken, Hailman & Hailman, 1994). Based on my field observations in summer of 2003, it was reasonable to expect that the exposed owl stimulus could have caused subjects to take fewer seeds from the seed stand and give more calls, compared to when the owl stimulus was unexposed and compared to the other stimulus types. The exposed owl stimulus could have also elicited chick-a-dee calls rich in **D** notes, suggesting mobbing behavior. Alternatively, the surprising event of the appearance of a potential predator or the movement of the cloth could have elicited alarm calls from subjects. Specifically, they could have used more **Az** notes in their chick-a-dee calls in response to the exposed stimuli and/or the movement of the cloth covering.

CHAPTER II

METHODOLOGY

Subjects and field sites

The study subjects were wild Carolina chickadees living in deciduous forests of east Tennessee. Flocks of chickadees in this area had been observed and recorded prior to this study, beginning in fall of 2002. No birds were individually marked at the time of this study.

Recordings of flocks were obtained at 16 field sites in two locations: Ijams Nature Center (Ijams) in Knoxville, Tennessee (4 sites: I1, I2, I3 and I4) and The University of Tennessee Forest Resources, Research and Education Center (UTFRREC) in Oak Ridge, Tennessee (remaining 12 sites). Locations were separated by about 30 km. Adjacent sites within a location were separated by at least 400 m. Therefore, each site likely represented a different flock. In a study involving some banded Carolina chickadees, Freeberg & Lucas (2002) used a 250 m distance between sites to avoid repeating tests on the same individuals. The largest distance between sites in this study was 2.6 km between sites A and F at UTFRREC.

At each site's center stood a seed stand made of a wooden board (0.30 m x 0.46 m) atop a metal pole rising approximately 1.50 m from the ground. Four flags, positioned 10 m from the seed stand in four directions, defined the site boundaries. This made the site area roughly 14 m x 14 m (**Figure 2**). Each seed stand was stocked with approximately 50 g of a 1:1 mixture of black-oil sunflower seed and safflower seed two times a week to attract birds, from August 15, 2004 to October 1, 2004 (Miller et al., In Review).

Equipment and models

Calls of chickadees were recorded with a Sennheiser ME-64 microphone and a Marantz PMD-222 cassette recorder, using Maxell XL-II type II high bias tapes. Recordings were digitized using Cool Edit Pro 2.0 at a sample rate of 22,050 Hz and 16-bit resolution on a Windows XP platform. The resulting sound files were played back and visualized in spectrogram form using Cool Edit Pro 2.0 audio editing software. Spectrograms were viewed using the Blackmann-Harris windowing function and 256 bands of resolution. This program includes a counter with minutes, seconds and milliseconds for marking events within a recording.

Nine prefabricated models were used in this study (**Figure 3**). Three of each model type (crow, hawk and owl) were used. Models were made of plastic only (8 models) or plastic and synthetic feathers (crow 2) and some had additional paint added to make the models appear more realistic. Three variants of each model type were used to provide each recording site with a unique combination. Model sizes varied, as shown in Figure 3.

Recording procedure

Recordings began on October 1, 2004 and ended on March 10, 2005. Recording was attempted six days a week beginning 1 hour after sunrise (approximately 0800 EST) and ending no later than 1400 EST. Recordings were done in all weather conditions except for moderate to heavy rain. One to three observers[†], wearing dark clothing, were present at each recording session.

[†] This research was conducted with the help of 13 undergraduate students. When I was training the undergraduates, we recorded in groups of 2-3. Otherwise, single individuals or pairs did the recordings.

When the observers arrived at a site, they stocked the seed stand with approximately 50 g of the black oil sunflower/safflower seed mix. The microphone was placed on the ground within 1 m of the base of the seed stand. The 9 m microphone cable was stretched out, as straight as possible, allowing the cassette recorder to be placed on a cloth on the ground next to the observers. Observers set up small, dark colored camping chairs 9 m from the seed stand.

Models were placed atop a stand made of PVC pipe, which was painted brown for better camouflage (**Figure 4**). The stand was assembled from 9 pieces of pipe: three pipes 1 m in length, three pipes 0.30 m in lengths, two couplers and one 4-way connector. When assembled, the model was perched 3.05 m from the ground. It was secured to a tree 3 m from the seed stand with dark colored bungee cords. The model was covered with a camouflage cloth, which was attached to a 10 m string (**Figure 4**). From their location 9 m from the seed stand, observers could pull this string to expose the model at the appropriate time. When no model was presented, the set up and procedure was the same, including the model stand and removal of the camouflage cloth.

The goal was to obtain four recordings per site, one for each stimulus: crow, hawk, owl, and no model. After set up, observers waited for chickadees to appear within the site area to begin recording. Recording commenced after a waiting period of at least 10 minutes, in which two or more chickadees took seed from the seed stand (Miller et al., In Review). If no chickadees came to take seed from the stand and no chickadees were heard near the perimeter of the site 30 minutes after set up, recording at this site was abandoned for the day. If no chickadees came to take seed from the stand but chickadees were heard near the perimeter of the site, observers waited up to 1 hour before abandoning the site for the day. For each presentation, recording took place before and

after the model stand was exposed. One of the observers would verbally note the start of recording and state the time. The total recording time was 30 minutes. The first 15 minutes of recording took place with the model covered by a camouflage cloth. At the 15-minute mark, an observer would pull the string connected to this cloth, revealing the model. He or she would verbally note this and state the time. At the end of the 30-minute period, an observer would note the end of recording and state the time. The order in which stimulus presentations occurred at each site and the variants used were randomized with a simple computer program (**Table 1**). At least 24 hours passed between consecutive presentations at the same site. All four stimuli were presented at 15 sites. At the remaining site, B, the crow stimulus was not presented. Subjects did not appear at this site for the crow presentation before recordings were ceased on March 10.

During recording the following information was noted by observers: date, location, site, temperature, weather conditions, model being used, observers present, number of times Carolina chickadees took seeds from the stand, the location of calling chickadees in relation to the seed stand or the model (whichever was closest) and the number of chickadees present. The number of birds was estimated conservatively by reporting the maximum number of individuals visible at one point in time (Freeberg & Lucas, 2002). Estimation of maximum number of birds was done in each of the 5-minute blocks before and after the stimulus was exposed. I also noted instances of birds producing chick-a-dee calls in relation to feeding behavior on and near the seed stand. An earlier study with a smaller sample size suggested chick-a-dee calls produced within 1 m of a seed stand contained more **C** notes and fewer **Az** notes than calls produced at a greater distance from the stand (Miller et al., In Review.)

Data analysis

Twenty minutes out of each 30-minute recording were included in the analysis: 10 minutes before the stimulus was exposed and 10 minutes after the stimulus was exposed. For each recording, seed taking rates, calling rates and note composition of calls were determined. Only calls occurring within the site, the roughly 14 m x 14 m area around the seed stand, were included in the analysis.

The seed taking rates for each site and stimulus presentation were the number of times chickadees took seeds from the stand divided by the average number of birds observed during each 10-minute interval. Similarly, the call rates were the total number of chick-a-dee calls, occurring within the site area, divided by the average number of birds observed during each 10-minute interval.

For note composition of calls analysis, spectrograms of chick-a-dee calls were viewed in Cool Edit Pro 2.0 to determine note types (**Az**, **C**, **D**, and Introductory). Calls included in this analysis had the following characteristics: They occurred inside the 14 m x 14 m site area, contained two or more notes, were not obscured by another call, and the notes were clear enough on the spectrogram to be unambiguously typed. Because there were no calls of sufficient quality within the site area for the crow presentation at site Ar3, that presentation could not be included in the note composition of calls analysis. Extremely poor quality recordings (due to an incorrect setting on the recorder) of the crow presentation at site Ar4 and the hawk, owl and no model presentations at site C were not included in the analysis of note composition of calls because note types could not be determined.

All statistical tests were conducted with SPSS 13.0 for Windows. Analysis was done in two steps using Mixed Model ANOVAs with site as the random effect. First,

data from the pre-exposure period were examined for an effect of stimulus type on seed taking rates, calling rates and note composition of calls. Second, data from the post-exposure period were examined for an effect of stimulus type on seed taking rates, calling rates and note composition of calls. When post-exposure effects of the stimulus were detected, differences between the stimulus tests were assessed using the Bonferonni correction for multiple comparisons. Furthermore, recordings were grouped by stimulus type to compare the pre-exposure period to the post-exposure period in terms of seed taking rates, calling rates and note composition of calls. For stimulus type comparisons, log transformations were performed on seed taking rates, calling rates and numbers of **Az** notes, Introductory notes and **C** notes to normalize residuals in the ANOVA models (normality of residuals was tested using the Kolmogorov-Smirnov test).

CHAPTER III

RESULTS

Background to Data Set

Sixty-three recordings were obtained at 16 sites (**Table 1**). Assuming that each site represents one flock, the average flock size observed across the sites was 3.4 birds. The sum of individual birds comprising those flocks across all sites was 76. This count represents a conservative estimate of the number of different individuals involved in this study.

Observers noted 5,162 instances in which chickadees took seeds from the stands and 1,466 calls that were produced by chickadees within the field sites (including periods when stimuli were unexposed and exposed). From these data I determined seed taking rates and calling rates. In analyses of note composition of calls, some poor quality calls were eliminated from this set, leaving 1,394 calls. The total number of notes classified in the note composition of calls analysis was 10,996.

One additional observer, familiar with the characteristics I used to determine note type, independently scored 352 calls to determine inter-observer agreement on note type. I took a conservative approach to inter-observer agreement measures of each note type by only including calls in which one or both observers scored that note type. Agreement for each of the three note types and the introductory note group was high (Pearson correlation: 0.98 **Az** notes (N = 94 calls), 0.95 introductory notes (N = 191 calls), 0.99 **C** notes (N = 117 calls), and 1.00 for **D** notes (N = 287 calls); (Cohen's Kappas ranged from 0.870 to 0.99).

There were no significant effects of location (Ijams vs. UTFRREC) for any of the pre- or post-exposure dependent measures. There were no significant effects of stimulus type to report for the pre-exposure period. This indicates that subjects did not react differently to stimuli when they were covered with the camouflage cloth. Differences detected during the post-exposure period are reported below. The following results are reported in terms of stimulus type (crow model, hawk model, owl model or no model) and size of model (measurement in cm from head to tail of each model) (**Figure 3**).

Number of birds

The average number of birds present, within the 14 m by 14 m site area during recordings, was not significantly different depending on stimulus type ($F(3, 44) = 1.883$, $p = 0.146$) or size of model ($F(5, 41) = 1.351$, $p = 0.263$). The number of observers (range: 1 to 3) present during recording also had no effect on the average number of birds present (Pearson correlation, $R = -0.168$, $p = 0.192$, $N = 63$).

Seed taking rates

The rate at which Carolina chickadees took seed from the seed stand was affected by stimulus type once the stimulus was exposed. (**Figure 5a**; $F(3, 44) = 4.999$, $p = 0.004$, on log-transformed data). In pairwise comparisons, chickadees took significantly fewer seeds when the hawk stimulus was revealed than when the crow stimulus ($p = 0.021$) or no model stimulus ($p = 0.012$) were revealed. Furthermore, there was no effect of stimulus exposure on seed taking rates for the no model stimulus ($F(1, 15) = 0.323$, $p = 0.578$) or crow stimulus ($F(1, 14) = 0.323$, $p = 0.579$), but chickadees took significantly fewer seeds once the stimulus was exposed than they did prior to stimulus exposure for

both the hawk stimulus ($F(1, 15) = 9.198, p = 0.008$) and the owl stimulus ($F(1, 15) = 6.802, p = 0.020$). There was no effect of model size ($F(5, 41) = 1.394, p = 0.247$) on seed taking rates.

Calling rates

The rate at which Carolina chickadees produced chick-a-dee calls within the site were affected by stimulus type once the stimulus was exposed (**Figure 5b**; $F(3, 44) = 3.382, p = 0.026$, on log-transformed data). Chickadees gave more calls to the exposed hawk stimulus than to the exposed crow stimulus. Chickadees tended to call more when the hawk stimulus was exposed compared to the no model stimulus. Significantly more calls were produced when the hawk stimulus was exposed than were produced prior to the hawk stimulus being exposed ($F(1, 15) = 10.675, p = 0.005$). Significantly more calls were produced when the owl stimulus was exposed than were produced prior to the owl stimulus being exposed ($F(1, 15) = 9.825, p = 0.007$). No effect of stimulus exposure on calling rates was detected for the no model stimulus ($F(1, 15) = 1.349, p = 0.264$) or the crow stimulus ($F(1, 14) = 1.626, p = 0.223$). There was no effect of model size ($F(5, 41) = 0.636, p = 0.673$) on calling rates.

Note composition of calls and stimulus type

I could detect no effect of stimulus type on note composition of chick-a-dee calls. Stimulus type had no discernible effect on the average number of **Az** notes (log-transformed $F(3, 24) = 1.086, p = 0.374$), Introductory notes (log-transformed $F(3, 24) = 0.500, p = 0.686$), **C** notes (log-transformed $F(3, 24) = 0.558, p = 0.648$), or **D** notes ($F(3, 24) = 1.441, p = 0.256$) given in the presence of each stimulus (**Figure 6**).

Note composition of calls and signaler proximity to seed stand

The note composition of chick-a-dee calls was significantly affected by the proximity of the signaler to the seed stand for all four note classes (**Figure 7**). When signalers were in close proximity to the seed stands (arriving to, on, or departing from the stand, as opposed to being perched in trees away from the seed stand but within the site), their calls contained significantly more **C** notes ($F(1, 15) = 13.561, p = 0.002$), and fewer **Az** notes ($F(1, 15) = 14.351, p = 0.002$), fewer Introductory notes ($F(1, 15) = 6.718, p = 0.020$), and fewer **D** notes ($F(1, 15) = 51.756, p < 0.001$), compared to when signalers were greater than 1 m from the seed stand.

CHAPTER IV

DISCUSSION

In this study, feeding and chick-a-dee calling behavior of Carolina chickadees was affected by the presence of predator models. Subjects responded to exposure of the hawk and owl stimuli with increases in calling rates and decreases in seed taking rates. An effect of stimulus type on note composition of chick-a-dee calls was not observed in subjects. However, an effect of proximity to the seed stand on note composition of chick-a-dee calls was observed.

As expected, for the pre-exposure period, no differences were found in chickadee seed taking rates, calling rates or note composition of calls across stimulus types. This indicates that the stimuli were adequately concealed from subjects' view before exposure. Because chickadees responded differently to different stimulus types for the post-exposure period (for seed taking and calling rates), the reaction is unlikely to be due simply to encountering a novel stimulus. Instead, it seems that the models were realistic enough to be recognized by chickadees and to elicit unique responses.

In agreement with my first prediction, significantly fewer seeds were taken and significantly more calls were given when the hawk stimulus was exposed vs. unexposed, which suggests that birds were spending less energy feeding and more energy calling in this situation. Subjects also took fewer seeds and gave more calls when the owl model was exposed vs. unexposed. The changes in calling rates may indicate that chickadees considered the hawk and owl stimuli as greater threats than the crow and no model stimuli (Templeton et al., 2005). Adult chickadees in this study may have had predatory experiences with large birds of prey that caused them to be more wary when the hawk

and owl stimuli were presented (Griffin & Galef, 2005). Alternatively, selection pressures may have favored chickadees that were more wary of birds of prey (Veen, Richardson, Blaakmeer & Komdeur, 2000). The changes in seed taking rates seem to indicate that chickadees reacted with more vigilance in the presence of the hawk and owl stimuli. Although I did not predict chickadees would show differences in calling and seed taking rates in the presence of the owl stimulus, it is not a surprising result given the observation I made in the field in summer 2003 in which chickadees and other species mobbed a barred owl. The similar response to the hawk and owl in seed taking and calling rates may mean that chickadees do not differentiate between a common predator, the hawk, and a common non-predator bird of prey, the owl. Chickadees may have identified both the hawk and the owl as potential predators due to similar body shapes, beak shapes and feather coloration.

The number of **Az**, **C**, **D** and Introductory notes given in chick-a-dee calls was not significantly different for any of the stimulus types. I expected chickadees to consider the hawk model threatening enough to show mobbing behavior and give calls associated with mobbing. However, production of **C** or **D** notes did not differ by stimulus or exposure. This finding differs from that of Templeton et al. (2005) with black-capped chickadees. Those chickadees uttered chick-a-dee calls richer in **D** notes in the presence of live predators, and the greater the perceived threat of the predator, the more **D** notes occurred in the calls. The findings of my study also differ from those of Ficken et al. (1994) with Mexican chickadees. During field observations, Mexican chickadees produced more **C** notes when a predator appeared. Production of **Az** notes, consistent with alarm, also did not differ by stimulus or exposure .

There were six recordings during which chickadees engaged in clear behavior characteristic of mobbing. These involved the exposed hawk stimulus at sites Ar1, Ar4, I2 and G, and the exposed owl stimulus at sites E and I. Mobbing was defined by the following behavior in subjects: orienting toward and coming within 2 meters of the stimulus and frequently changing where they were perched in nearby trees. There were too few observations of actual mobbing behavior to provide strong inference, but some general observations can be made. In all six recordings, there were fewer average **C** notes produced per call near the model, compared to calls given away from the model. In five of these recordings, there were more average **D** notes produced per call near the model compared to calls given away from the model. These observations suggest that when Carolina chickadees do engage in actual mobbing, they may use fewer **C** notes and more **D** notes in their chick-a-dee calls. If so, Carolina chickadees respond to predators more like black-capped chickadees than like Mexican chickadees. These interpretations must be taken with caution, however, because of the small sample of actual mobbing on which they are based.

The differences in note composition of calls in relation to feeding further supports work by Miller et al. (In Review), in which Carolina chickadees were recorded while foraging at seed stands. A variety of food types was offered during trials, including the black oil sunflower/safflower mix used in this study. Miller et al. (In Review) analyzed 1,101 calls across 10 sites and classified 7,627 notes. Their findings were that chickadees gave more **C** notes and fewer **Az** notes in close proximity to the seed stand compared to calls produced by birds farther from the stand. My study had the same findings with a larger data set. It appears that foraging is an activity in which Carolina chickadees vary

the note composition of their chick-a-dee calls in a specific way. Signalers may be communicating something specific about their feeding behavior to their flock members.

One of the major strengths of this study, over other similar studies, is the methodology concerning the models. All the models presented were man-made. Some studies use a combination of man-made models, stuffed predators and/or live predators to test for alarm calls and mobbing (Naguib et al., 1999; Veen, Richardson, Blaakmeer & Komdeur, 2000). It is difficult to make comparisons based on size or shape among stimuli that differ in level of realism as well. In addition, the presentation of a unique set of models for each site minimized pseudoreplication in this study. Although there was a small number (3) of each type of model, the model variants and the order in which they were presented at each site was randomized. Sample size was another strength of this study. Other field studies concerning the calls and flock behavior of Carolina or black-capped chickadees had smaller sample sizes and still resulted in significant effects (Nowicki, 1983; Freeberg & Lucas, 2002; Miller et al., In Review).

Methodological aspects of this study may have contributed to the lack of evidence for changes in note composition of chick-a-dee calls in the context of a predator. The threat posed by the hawk stimulus may have been significantly reduced by the numerous escape opportunities offered by the field setting. More anti-predator behavior was observed in the Baker and Becker (2002) study, which took place in the laboratory, and in the Templeton et. al (2005) study, which took place in aviaries. It is possible that the hawk model stimulus would have been more threatening if placed closer to where chickadees were feeding. However, I tried to set up a situation in which subjects could choose to flee from the predator, mob the predator, do nothing and cease eating, or continue eating. I chose a 3 m distance at which to reveal the predator model based on

Baker and Becker (2002), who found that black-capped chickadees had a much stronger reaction to predators presented at a 1 m distance than at a 6 m distance. My thought was that a model presented 6 m from the seed stand would not elicit a very strong reaction and a model presented at 1 m would be most likely to cause birds to flee, thus eliminating the possibility to gather data on mobbing and calling behavior.

It is possible that the models were not realistic enough, being plastic, to elicit strong anti-predator reactions from chickadees. In opposition to this possibility is the fact that chickadees' seed-taking rates and calling rates were clearly affected by the stimuli presented. The hawk and owl models were the only stimuli to which more calls were given when exposed versus unexposed. The hawk and the owl models were the only two stimuli that caused chickadees to take less seeds when they were exposed vs. unexposed. Also, other studies that used predator models composed of man-made materials (plastic, wood or rubber) found them to be effective in eliciting anti-predator responses from birds and mammals (Barash, 1976; Hanson and Coss, 1997; Gursky, 2006; Veen, Richardson, Blaakmeer & Komdeur, 2000).

Chickadees may show great individual variation in vocal responses to predators. In a study of non-vocal anti-predation behavior of the chaffinch, Quinn and Cresswell (2005) suggested that such behavior is part of a behavioral syndrome, correlated to personality. This means that some individuals will respond to predators with more fear and others with more hostility, for example. Note composition of chick-a-dee calls may be affected by such differences.

It may be that Carolina chickadees simply do not encode information about predators with the note composition of their chick-a-dee calls, unlike what is seen in black-capped and Mexican chickadees (Apel, 1985; Ficken, Hailman & Hailman, 1994).

Alternatively, Carolina chickadees may respond to predators in a way similar to how black-capped chickadees respond to foreign flocks. Nowicki (1983) found that black-capped chickadees responded to playbacks of the chick-a-dee calls of foreign flocks with an increased rate of calling and decreased rate of seed taking. Increased calling rates in the presence of a threat may be a more powerful mode of signaling for Carolina chickadees than changes in note composition. Social factors may influence chickadee calling behavior (see Evans & Marler, 1995 for discussion of social influence on animal alarm calls). The increased rate of calling may serve a general recruitment function. It is also possible that recruiting is the first step in the mobbing process. Perhaps if more birds had been recruited, in this study, more mobbing behavior would have been observed. The average number of chickadees present during recordings was 3.4 (range 2-7). This range is similar to the numbers of birds observed in the field by Ficken and Witkin (1977). Animals who encounter predators as a group can benefit from the dilution effect (Cresswell, Lindt, Kaby, Quinn & Jakobsson, 2003). That is, the more potential prey animals around a predator, spaced relatively evenly, the lower the risk of any one individual being attacked. In a smaller group, chickadees may refrain from giving conspicuous calls so as not to draw attention to themselves. In a larger group, the risk of giving conspicuous calls is likely decreased and the chance of successfully driving off the predator may be increased.

To test the interpretations of data from this study, future studies could alter the methods. To avoid pseudoreplication completely, each model variant could be presented at each site. The stimuli could have been presented at two different distances, like 6 m and 1 m as in the Baker & Becker (2002) study. This methodology might show significant differences in seed taking and calling rates between the two distances. Having

a more flexible recording schedule might also result in more calls. Observers could wait until at least two birds were present at the seed stand before exposing the stimulus. The use of live predator models could elicit a stronger response than plastic models.

To conclude, the structure of the chick-a-dee call of Carolina chickadees is complex, being made up of distinct note types, which can be combined in a variety of ways. Call structure may not be strongly influenced by external referents like predator type. Animal vocalizations, in general, cannot always be directly linked to behavior or obvious environmental cues (Owren, Seyfarth & Hopp, 1992). The notes of the chick-a-dee call may encode the state of arousal of the signaler (S.T. Smith, 1972). Such arousal may be evident in differences in call structure in different foraging situations (Miller et al., In Review). Note composition of chick-a-dee calls may also be influenced by individual behavioral tendencies. If so, this could explain the variation in the types of notes produced by chickadees in the context of a predator. The rate of calling and rate of seed taking by Carolina chickadees appears to be affected by predator type. An increase in Carolina chickadee calling rate may serve a general recruitment function, though playback studies are needed to test these ideas.

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Appendix

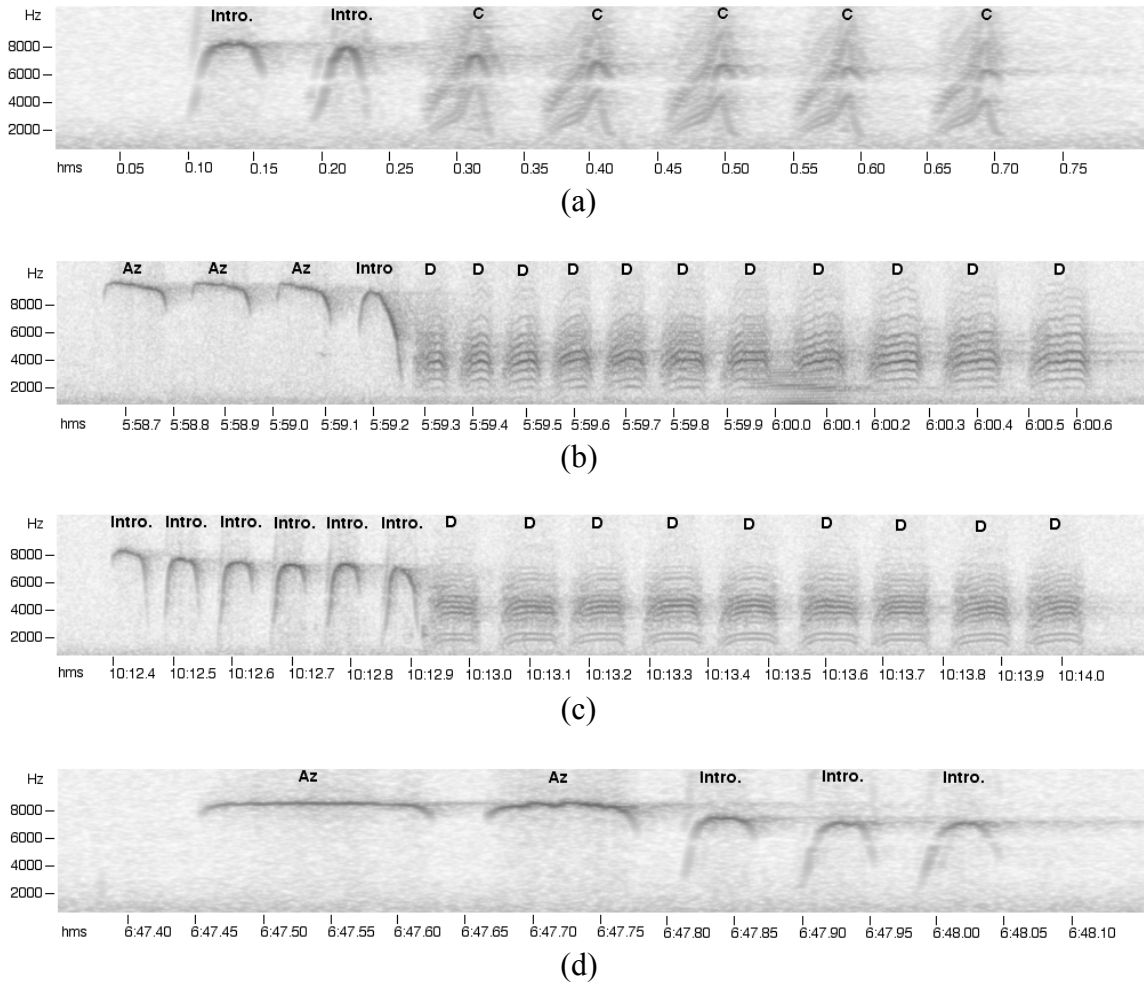


Figure 1. Examples of chick-a-dee calls of Carolina chickadees in this study.

Calls are presented as spectrograms with frequency (hertz) on the y-axis and time (minutes, seconds and fractions of a second) on the x-axis. Note type appears above each note. (a) Caller departing from seed stand at site Ar2 after owl 2 exposed. (b) Caller ~2 m from seed stand at site Ar3 before hawk 2 exposed. (c) Caller arriving to seed stand at site I3 after “no model” exposed. (d) Caller on ground below seed stand at site Ar2 after hawk 3 exposed.

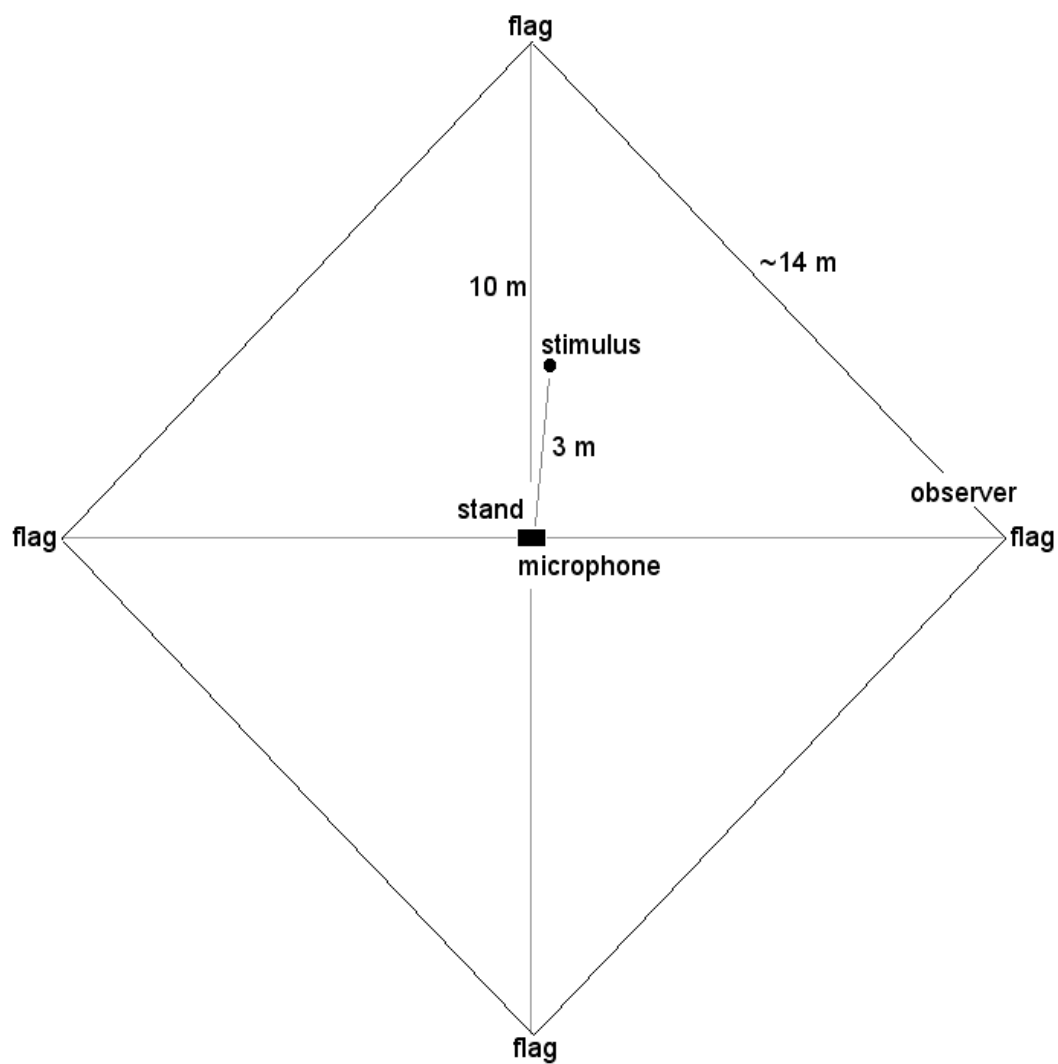


Figure 2. Study site layout.

A view of a sample study site from above. Four flags, each 10 m from the seed stand, created a roughly 14 m x 14 m site area. The microphone was positioned under the seed stand, the stimulus was placed 3 m from the seed stand and observers sat approximately 9 m from the seed stand.

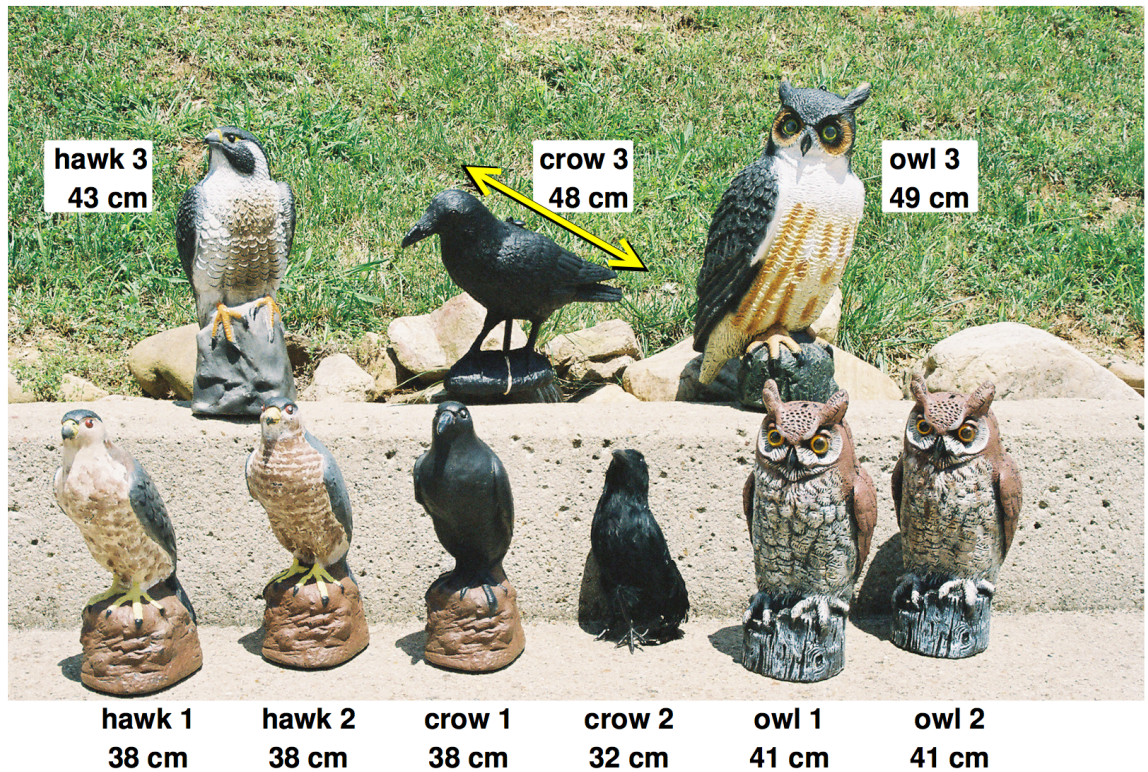


Figure 3. Models.

The nine models used in this study: 3 hawk variants, 3 crow variants and 3 owl variants.

Model size was measured from head to tail, as indicated on crow 3. There were six model size classes (32, 38, 41, 43, 48 and 49 cm).



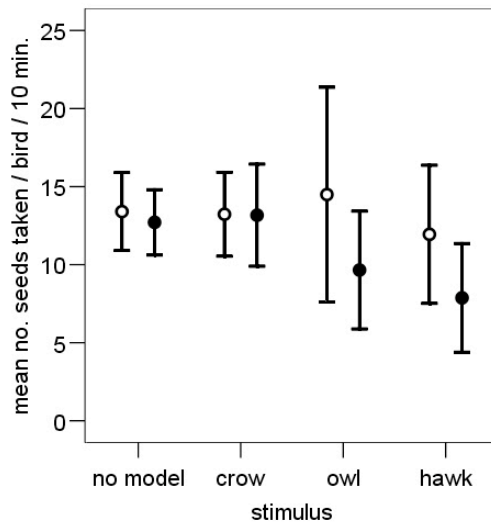
Figure 4. Model stand with unexposed and exposed stimulus.

An observer attaches the model stand, supporting owl model 3, to a tree within the area of site F. (left) Owl model 3 unexposed, covered with the camouflage cloth, and (right) exposed.

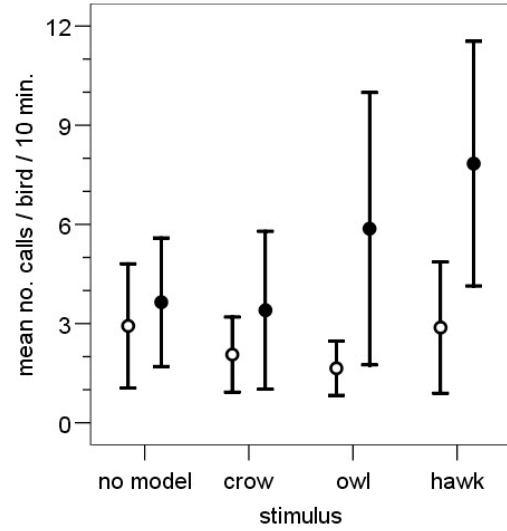
Table 1. Stimulus presentations for all study sites.

Site	First presentation		Second presentation		Third presentation		Fourth presentation	
<i>I2</i>	1-Nov	Hawk 1	2-Nov	No model	5-Nov	Crow 1	22-Dec	Owl 1
<i>Ar4</i>	10-Nov	Owl 1	15-Nov	Hawk 1	18-Nov	Crow 1	22-Nov	No model
<i>II</i>	13-Nov	Owl 1	17-Jan	Crow 3	24-Jan	Hawk 3	26-Jan	No model
<i>Ar1</i>	16-Dec	Crow 2	20-Dec	Hawk 3	1-Feb	No model	17-Feb	Owl 3
<i>Ar2</i>	10-Jan	No model	16-Feb	Owl 2	18-Feb	Hawk 3	22-Feb	Crow 2
<i>B</i>	18-Jan	Owl 2	25-Feb	Hawk 3	3-Mar	No model		
<i>C</i>	21-Jan	Crow 2	25-Jan	No model	30-Jan	Hawk 1	1-Feb	Owl 1
<i>I3</i>	24-Jan	Hawk 3	31-Jan	Crow 1	2-Feb	No model	7-Feb	Owl 3
<i>Ar3</i>	25-Jan	Owl 3	28-Jan	Crow 2	11-Feb	No model	17-Feb	Hawk 2
<i>D</i>	28-Jan	Owl 3	4-Feb	Crow 2	17-Feb	No model	19-Feb	Hawk 3
<i>E</i>	28-Jan	No model	12-Feb	Owl 2	15-Feb	Crow 1	17-Feb	Hawk 1
<i>I4</i>	7-Feb	Crow 3	9-Feb	No model	23-Feb	Owl 3	25-Feb	Hawk 3
<i>A</i>	12-Feb	No model	18-Feb	Owl 2	25-Feb	Crow 1	3-Mar	Hawk 2
<i>F</i>	12-Feb	Owl 1	15-Feb	No model	18-Feb	Hawk 1	24-Feb	Crow 1
<i>G</i>	19-Feb	Owl 3	24-Feb	No model	26-Feb	Hawk 2	4-Mar	Crow 3
<i>I</i>	24-Feb	No model	26-Feb	Hawk 3	2-Mar	Owl 2	4-Mar	Crow 3

Note that there was no crow stimulus presentation for site B. There were no chickadees present at this site during several attempts to record with the crow stimulus.



(a)



(b)

Figure 5. Seed taking and calling rates.

Plotted are means and 95% confidence intervals of non-transformed (a) seed taking rates and (b) calling rates. For each stimulus, empty points are pre exposure and solid points are post exposure.

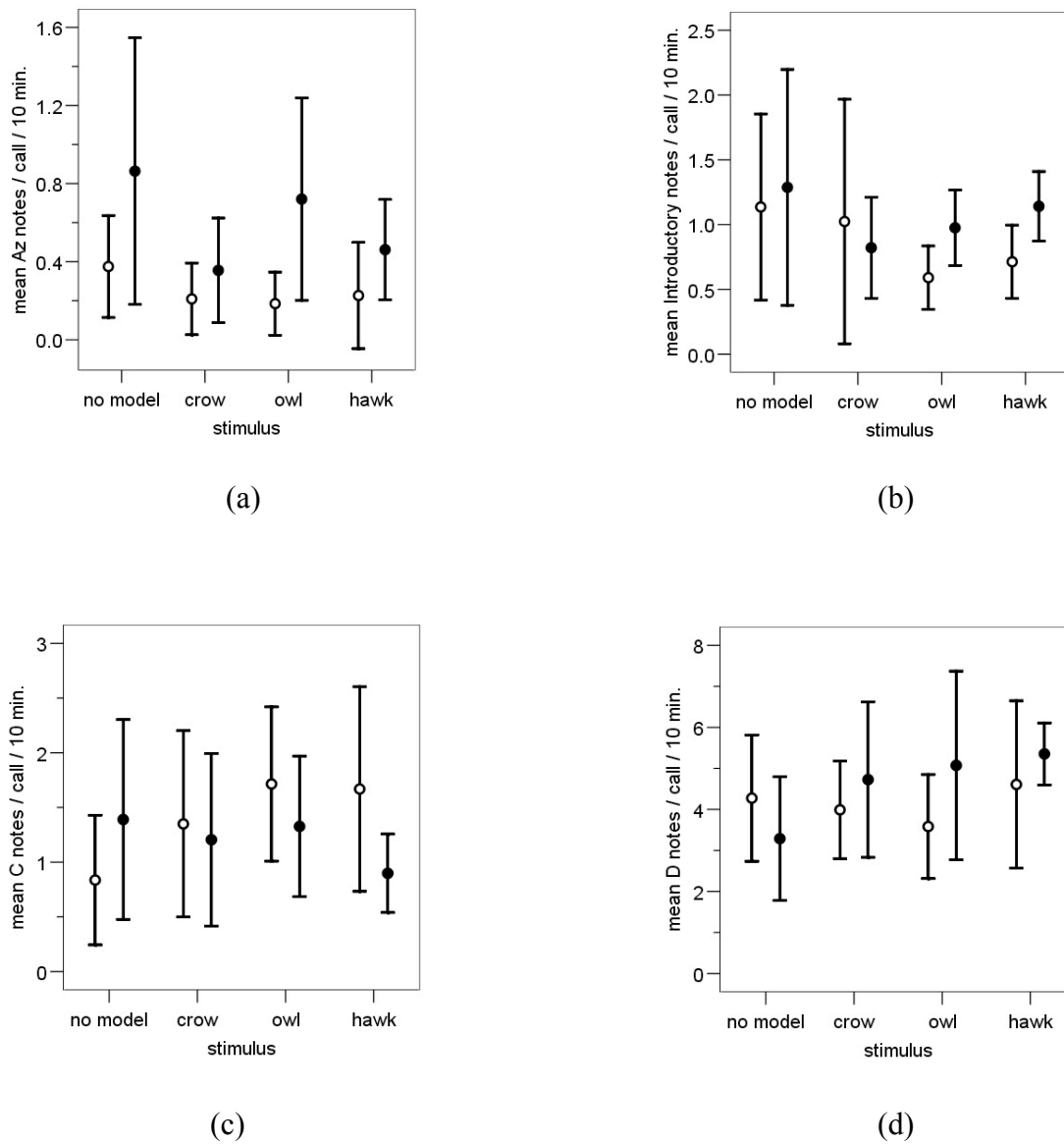


Figure 6. Note composition of calls and stimulus type.

Plotted are means and 95% confidence intervals of non-transformed (a) **Az** notes (b) Introductory notes (c) **C** notes and (d) **D** notes. For each stimulus, empty points are pre exposure and solid points are post exposure. There were no significant differences in the number of note types given in the presence of stimulus types for either exposure period.

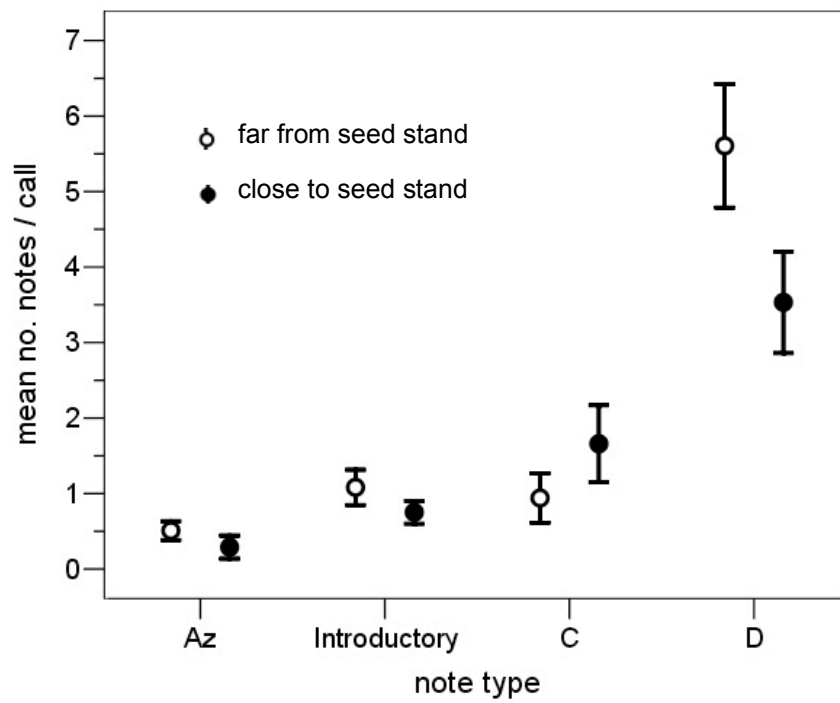


Figure 7. Note composition of calls and signaler proximity to seed stand.

Plotted are means and 95% confidence intervals for **Az**, Introductory, **C** and **D** notes given far from and close to the seed stand.

Table 2. Raw data: numbers of birds, seeds taken, calls and observers.

Shown for each site, stimulus (Stim.), model number (No.) and exposure period (Expos.) are the average number of birds counted, number of seeds taken, number of calls given and number of observers present (Obs.).

Site	Stim.	No.	Expos.	Birds	Seeds	Calls	Obs.
A	Crow	1	Pre	5.0	63	1	1
			Post	3.5	36	3	1
	Hawk	2	Pre	3.0	50	4	2
			Post	3.0	56	4	2
	None		Pre	5.0	56	2	3
			Post	5.5	60	7	3
	Owl	2	Pre	5.5	71	0	1
			Post	5.5	71	0	1
Ar1	Crow	2	Pre	3.0	44	3	1
			Post	2.0	43	0	1
	Hawk	3	Pre	1.0	4	2	1
			Post	3.0	10	45	1
	None		Pre	2.0	3	2	2
			Post	2.0	22	19	2
	Owl	3	Pre	2.0	15	10	2
			Post	2.0	12	6	2
Ar2	Crow	2	Pre	3.0	39	4	2
			Post	3.0	35	12	2
	Hawk	3	Pre	2.0	13	4	2
			Post	2.0	7	3	2
	None		Pre	3.0	49	0	2
			Post	4.0	47	1	2
	Owl	2	Pre	2.5	17	4	1
			Post	3.0	15	11	1
Ar3	Crow	2	Pre	1.5	30	0	3
			Post	2.0	38	1	3
	Hawk	2	Pre	2.5	16	25	2
			Post	3.0	19	14	2
	None		Pre	2.0	44	3	2
			Post	2.5	37	1	2
	Owl	3	Pre	2.0	23	0	2
			Post	2.0	22	6	2

Table 2. Continued.

Site	Stim.	No.	Expos.	Birds	Seeds	Calls	Obs.
Ar4	Crow	1	Pre	2.0	43	0	1
			Post	2.0	45	0	1
	Hawk	1	Pre	2.0	74	3	1
			Post	3.0	40	13	1
	None		Pre	2.0	41	9	1
			Post	3.0	52	3	1
	Owl	1	Pre	5.0	27	3	1
			Post	5.0	34	10	1
B	Crow		No recording				
	Hawk	3	Pre	3.0	35	1	1
			Post	3.0	15	23	1
	None		Pre	3.0	34	7	2
			Post	2.0	30	8	2
	Owl	2	Pre	1.5	18	1	2
			Post	1.0	7	29	2
C	Crow	2	Pre	6.0	107	26	1
			Post	6.0	104	20	1
	Hawk	1	Pre	6.0	67	0	1
			Post	7.0	7	2	1
	None		Pre	5.5	68	0	1
			Post	4.5	89	0	1
	Owl	1	Pre	6.0	169	0	1
			Post	7.0	101	8	1
D	Crow	2	Pre	4.5	87	32	2
			Post	3.5	67	55	2
	Hawk	3	Pre	6.0	69	17	3
			Post	2.0	42	51	3
	None		Pre	5.0	44	64	1
			Post	5.0	69	48	1
	Owl	3	Pre	2.0	113	7	3
			Post	5.0	66	53	3
E	Crow	1	Pre	5.0	45	9	1
			Post	4.0	41	2	1
	Hawk	1	Pre	4.0	44	4	3
			Post	3.5	38	6	3
	None		Pre	3.0	33	19	3
			Post	3.0	39	11	3
	Owl	2	Pre	6.0	70	11	3
			Post	6.0	51	19	3

Table 2. Continued.

Site	Stim.	No.	Expos.	Birds	Seeds	Calls	Obs.
F	Crow	1	Pre	4.0	23	9	2
			Post	3.5	27	11	2
	Hawk	1	Pre	3.0	31	3	2
			Post	4.0	42	13	2
	None		Pre	4.0	49	1	1
			Post	4.0	54	1	1
	Owl	1	Pre	3.0	32	3	3
			Post	3.0	19	9	3
G	Crow	3	Pre	3.0	47	0	2
			Post	2.5	42	1	2
	Hawk	2	Pre	2.5	55	0	2
			Post	4.0	12	60	2
	None		Pre	4.0	82	0	2
			Post	4.0	77	2	2
	Owl	3	Pre	4.0	54	1	3
			Post	5.0	37	26	3
I	Crow	3	Pre	3.0	32	11	2
			Post	3.0	20	9	2
	Hawk	3	Pre	2.0	6	20	2
			Post	2.0	0	17	2
	None		Pre	1.5	18	0	1
			Post	2.0	23	1	1
	Owl	2	Pre	2.5	18	3	2
			Post	2.5	7	48	2
II	Crow	3	Pre	3.5	43	13	1
			Post	5.0	38	10	1
	Hawk	3	Pre	4.0	61	3	3
			Post	4.0	63	10	3
	None		Pre	4.0	57	15	2
			Post	4.0	40	26	2
	Owl	1	Pre	6.0	81	8	1
			Post	5.0	83	6	1
I2	Crow	1	Pre	3.0	21	2	2
			Post	3.0	11	27	2
	Hawk	1	Pre	3.0	13	6	2
			Post	3.0	2	35	2
	None		Pre	3.0	17	20	2
			Post	3.0	20	16	2
	Owl	1	Pre	5.0	120	12	1
			Post	4.0	122	8	1

Table 2. Continued.

Site	Stim.	No.	Expos.	Birds	Seeds	Calls	Obs.
I3	Crow	1	Pre	3.5	29	12	1
			Post	3.0	27	22	1
	Hawk	3	Pre	1.5	16	16	2
			Post	2.0	10	16	2
	None		Pre	3.0	25	16	3
			Post	3.0	22	28	3
	Owl	3	Pre	3.0	17	9	3
			Post	1.0	0	2	3
I4	Crow	3	Pre	4.0	39	4	2
			Post	2.5	36	3	2
	Hawk	3	Pre	4.5	43	3	2
			Post	2.0	16	29	2
	None		Pre	3.5	38	7	2
			Post	4.0	31	25	2
	Owl	3	Pre	3.5	17	14	2
			Post	4.0	24	23	2

Table 3. Raw data: mean number of each note type per call.

Shown for each site, stimulus (Stim.), model number (No.) and exposure period (Expos.)

are number of calls analyzed for note composition and the mean number of each note

type per call. Three poor quality recordings at site C were not used.

Site	Stim.	No.	Expos.	Calls	Az	Intro	C	D
A	Crow	1	Pre	1	.000	.000	4.000	.000
			Post	3	.000	.667	.000	5.333
	Hawk	2	Pre	4	.250	1.250	1.750	2.250
			Post	4	.000	1.750	2.750	2.250
	None		Pre	2	.000	.000	.000	6.000
			Post	6	.333	1.667	.167	2.000
	Owl	2	Pre	0				
			Post	0				
Ar1	Crow	2	Pre	3	.000	1.000	.000	2.667
			Post	0				
	Hawk	3	Pre	2	.000	1.000	1.000	6.500
			Post	41	.341	.610	.049	6.537
	None		Pre	1	1.000	3.000	.000	.000
			Post	16	1.188	1.313	.375	2.625
	Owl	3	Pre	9	.667	.889	2.000	2.333
			Post	6	.167	.333	2.833	.833
Ar2	Crow	2	Pre	4	.250	1.000	1.250	4.750
			Post	10	.500	.400	1.600	2.900
	Hawk	3	Pre	4	.000	.000	5.500	1.000
			Post	3	.000	1.000	.333	5.333
	None		Pre	0				
			Post	1	.000	7.000	4.000	.000
	Owl	2	Pre	4	.250	.250	4.500	6.000
			Post	9	3.222	1.111	3.444	.000
Ar3	Crow	2	Pre	0				
			Post	0				
	Hawk	2	Pre	25	.280	.520	1.360	6.800
			Post	13	.308	1.077	1.077	5.769
	None		Pre	3	.000	.333	2.667	2.667
			Post	1	.000	1.000	3.000	.000
	Owl	3	Pre	0				
			Post	6	.333	.167	.000	12.500

Table 3. Continued.

Site	Stim.	No.	Expos.	Calls	Az	Intro	C	D	
Ar4	Crow	1	Pre	0					
			Post	0					
	Hawk	1	Pre	2	.000	.000	3.000	6.500	
			Post	13	.385	.692	.692	5.769	
	None		Pre	8	.125	.750	.125	6.750	
			Post	3	.000	.667	.000	7.000	
	Owl	1	Pre	3	.000	.333	.333	8.000	
Post			10	.400	.600	.800	11.500		
B	Crow		No recording						
	Hawk	3	Pre	1	.000	1.000	3.000	.000	
			Post	23	.609	1.435	.652	5.261	
	None		Pre	7	.000	.571	1.000	5.286	
			Post	8	.500	1.375	4.625	1.500	
	Owl	2	Pre	1	.000	.000	2.000	.000	
			Post	29	.655	1.241	.414	6.276	
	C	Crow	2	Pre	26	.385	.615	1.308	6.346
				Post	20	.250	.700	1.500	6.900
Hawk		1	Pre	0					
			Post	0					
None			Pre	0					
			Post	0					
Owl		1	Pre	0					
			Post	0					
D		Crow	2	Pre	32	.094	.969	.750	5.813
				Post	55	.345	1.218	.400	6.509
	Hawk	3	Pre	17	.353	1.471	3.588	2.059	
			Post	51	.235	.608	1.255	4.333	
	None		Pre	64	.516	1.156	2.031	5.266	
			Post	48	.250	1.021	1.500	4.646	
	Owl	3	Pre	7	.000	1.000	1.857	2.143	
			Post	52	1.538	1.385	.712	5.000	
	E	Crow	1	Pre	9	.333	1.000	3.222	4.556
				Post	2	.000	.000	4.500	.000
Hawk		1	Pre	4	.250	.750	.000	8.000	
			Post	6	1.500	.667	1.167	6.500	
None			Pre	19	.526	3.737	.474	.895	
			Post	11	.455	.909	.455	5.727	
Owl		2	Pre	5	.800	.800	2.000	2.600	
			Post	19	1.000	.474	1.105	3.474	

Table 3. Continued.

Site	Stim.	No.	Expos.	Calls	Az	Intro	C	D
F	Crow	1	Pre	6	.000	.500	.000	3.000
			Post	10	.000	1.000	.500	7.800
	Hawk	1	Pre	3	.000	.333	.000	13.000
			Post	13	.154	1.000	1.462	5.385
	None		Pre	1	.000	.000	.000	4.000
			Post	1	.000	.000	4.000	.000
	Owl	1	Pre	3	.000	1.000	2.667	1.333
			Post	8	.750	.875	1.500	2.875
G	Crow	3	Pre	0				
			Post	1	.000	.000	2.000	.000
	Hawk	2	Pre	0				
			Post	60	.883	2.117	.933	6.583
	None		Pre	0				
			Post	2	3.500	.500	.000	1.000
	Owl	3	Pre	1	.000	.000	.000	5.000
			Post	26	.077	1.231	.615	5.385
I	Crow	3	Pre	11	.909	5.545	.091	1.818
			Post	9	.778	1.111	1.667	2.333
	Hawk	3	Pre	20	.050	1.250	.450	4.850
			Post	16	.375	1.750	.688	5.000
	None		Pre	0				
			Post	1	4.000	.000	.000	2.000
	Owl	2	Pre	3	.000	.667	1.333	2.667
			Post	48	.542	1.729	1.021	5.479
I1	Crow	3	Pre	13	.538	1.077	1.077	4.769
			Post	9	.667	.889	.111	6.889
	Hawk	3	Pre	3	.000	.667	.000	4.000
			Post	7	1.429	1.000	.571	3.286
	None		Pre	15	.467	1.000	.000	5.267
			Post	23	.348	1.043	.565	5.478
	Owl	1	Pre	8	.000	.875	2.000	4.000
			Post	6	.000	1.000	1.833	7.500
I2	Crow	1	Pre	2	.000	.000	2.500	3.500
			Post	25	.360	.680	.440	7.720
	Hawk	1	Pre	5	1.800	1.000	.400	2.200
			Post	30	.333	.700	.667	7.567
	None		Pre	19	1.053	1.211	.579	6.789
			Post	15	.933	.933	.933	4.200
	Owl	1	Pre	12	.250	1.167	1.500	3.583
			Post	8	.375	1.625	2.625	.875

Table 3. Continued.

Site	Stim.	No.	Expos.	Calls	Az	Intro	C	D
I3	Crow	1	Pre	12	.000	.583	2.000	4.667
			Post	22	1.364	.864	.409	7.682
	Hawk	3	Pre	16	.188	.750	1.313	6.375
			Post	16	.125	1.063	1.000	6.250
	None		Pre	16	.813	.875	1.875	6.813
			Post	27	.444	.889	.407	8.852
	Owl	3	Pre	9	.222	.556	1.889	4.000
			Post	0				
I4	Crow	3	Pre	2	.000	.000	.000	6.000
			Post	3	.000	2.333	1.333	2.667
	Hawk	3	Pre	2	.000	.000	2.000	1.000
			Post	29	.241	1.655	.172	4.483
	None		Pre	7	.000	1.000	1.286	1.571
			Post	17	1.000	1.000	.824	4.294
	Owl	3	Pre	14	.214	.143	.214	4.929
			Post	23	.304	.913	.348	4.261

Vita

Ellen J. Mahurin has earned a B.S. in biology (2000) and a B.A. in psychology (2003) from the University of Tennessee in Knoxville. She was the recipient of an undergraduate summer research grant from The University of Tennessee in 2003. She presented a poster on this work titled “Vocal Communication in the Context of Food: The Chick-a-dee Call of the Carolina Chickadee (*Poecile carolinensis*)” at the Exhibition of Undergraduate Research and Creative Achievement in 2003. She is an author on a manuscript submitted for publication called “Food-Related Behavior Influences Note Composition of Chick-a-dee Calls in Carolina Chickadees (*Poecile carolinensis*).”

After completion of her M.A. in psychology, Ellen will work as an animal behavior consultant and trainer. Her primary interest is with species kept as pets such as dogs, cats and birds. Ellen plans to work with pet owners, animal rescue groups, pet product manufacturers and others through her business, Clever Critters.