

INVESTIGATION OF TUFTED TITMOUSE (*Baeolophus bicolor*) ANTI-PREDATOR
VOCALIZATIONS

By

STACIA A. HETRICK

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Stacia A. Hetrick

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Abstract of Thesis Presented to the Graduate School
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By

Stacia A. Hetrick

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Chair: Kathryn E. Sieving

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Tufted titmice (*Baeolophus bicolor*) are reported to produce different types of anti-predator vocalizations in response to different predators and they are highly social with other species of birds. The goals of this study included investigation of the anti-predator vocalizations of the titmouse and determination of whether these calls contain information about the type of predator detected (predator-specific) and whether they contain information about the risk of the situation (risk-based). Additionally, I sought to determine whether sympatric bird species perceive and respond appropriately to the information about predators encoded in titmouse anti-predator vocalizations. In the first experiment I tested the hypothesis that titmice give predator-specific vocalizations (unique vocalizations denoting the specific predator species or class) in response to different species, including avian, mammalian, and reptilian classes of predators. Titmice produced a combination of vocalizations in response to the predators and there was no evidence that any particular vocalization denoted a specific predator species or class. Titmice varied the note composition, note duration and note structure of their 'chick-a-dee' mobbing calls with respect to predator type, which could indicate that they are producing risk-based mobbing calls (in which the call structure varies as a function of risk). In the second experiment, therefore, I designed a test to determine with certainty whether titmice produce risk-based mobbing calls.

The hypothesis tested addressed whether titmouse mobbing calls are situationally specific (call structure varies according to the situation) in response to predators that represent different levels of risk (i.e., high- and low-risk). The results indicated that titmice produce situationally specific risk-based mobbing calls in response to predators by varying their call rate, note composition, and frequency and temporal characteristics, as a function of predator risk. In a final experiment, I tested whether Carolina chickadees (*Poecile carolinensis*) respond to titmouse risk-based mobbing calls and alarm calls with perception specificity (calls alone elicit appropriate response in absence of original stimulus). Chickadees varied their behavior, note composition and temporal characteristics as a function of playback type in much the same way that titmice responded to the actual predators, indicating that the chickadees responded with perception specificity. Interspecific risk-based call systems, like the one characterized here, likely play an important role in decreasing predation risk in animal social groups and, more generally, the larger community of animal species. Interspecific communication systems represent potential mechanisms underlying positive interactions, such as ecological facilitation, that help to structure and maintain aggregations within vertebrate communities.

CHAPTER 1 INTRODUCTION

Tufted titmice (*Baeolophus bicolor*) are nuclear species in mixed species flocks of birds that form during the winter in eastern North America. In these flocks, predators are commonly encountered and titmice are thought to give different anti-predator vocalizations (in different situations) that are commonly identified as either ‘seet’ calls (also known as the ‘hawk’ or ‘flying predator’ calls) in response to aerial raptors or ‘chick-a-dee’ mobbing calls in response to terrestrial predators. The goal of this study was to investigate the anti-predator vocal behavior of the titmouse and to ascertain whether these calls contain information about the species or class (avian, mammalian, or reptilian) of predator detected (predator-specific) or whether they contain information about the risk of the situation (risk-based), or neither. Additionally, I sought to determine whether sympatric bird species perceive and respond appropriately to the information about predators encoded in titmouse anti-predator vocalizations.

First, I tested the hypothesis that titmice have predator-specific calls in response to different types of predators. In chapter 2, I present findings of predator presentations (of a hawk, an owl, a cat, and a snake) to individual, captive titmice, showing that they do not give unique calls for different predator species or predator classes (avian, mammalian, reptilian), but vary their vocal response to the different predators by altering note composition, call structure, and temporal characteristics of their ‘chick-a-dee’ calls. This type of response is characteristic of risk-based calls, where the calls vary in a graded manner according to the degree of risk. The degree of risk that each predator posed (or that titmice presented with each predator would perceive) in this first experiment was largely unknown, so I was unable to determine positively whether titmice give risk-based calls in response to different predators. To determine

experimentally whether titmice vary their calls according to risk, I conducted a second experiment, which I present in the third chapter.

The results from the first experiment led to the formation of two additional hypotheses, which I address in chapter 3. The situational specificity hypothesis states that titmice will vary the structure of their calls according to distinct situations, such as encounters with predators that represent different degrees of risk. The interspecific perception specificity hypothesis states that titmouse calls alone should elicit appropriate responses from heterospecifics in the absence of the original stimulus. To address the first hypothesis, I presented captive titmouse flocks with high- and low-risk predators and analyzed their behavioral and vocal response. To address the second hypothesis, I presented captive Carolina chickadee (*Poecile carolinensis*) flocks with playbacks of the titmouse vocalizations in response to the high- and low-risk predators as well as titmouse seet calls and analyzed their behavioral and vocal response. In this chapter, I present my findings that titmice do give risk-based calls to high- and low-risk predators by varying their call rate, note composition, call structure and temporal features of their ‘chick-a-dee’ mobbing calls. I also present findings that chickadees respond appropriately to these calls and to titmouse seet calls by altering their behavioral and vocal response. These experiments have led to a better understanding of how titmice communicate about the predation risk environment and how chickadees, and potentially other sympatric species respond to titmouse vocal signals. These signals may play a critical role in decreasing the predation risk environment for chickadees and other sympatric species in this system.

CHAPTER 2
ANTI-PREDATOR VOCALIZATIONS OF THE TUFTED TITMOUSE (*BAEOLOPHUS
BICOLOR*): DO THEY DENOTE PREDATOR SPECIES OR CLASS?

Many species respond to predator encounters with specific vocalizations. Some species have different calls that denote particular predator species or classes (predator-specific), while some vary one or more of their vocalizations according to the degree of risk a predator represents (risk-based). In this study, I wanted to determine whether Tufted titmice produce predator-specific vocalizations in response to different predator species or classes (avian, mammalian, reptilian). To reliably determine if titmice have calls that denote different predators, I presented captive, adult titmice with four predators- a hawk, an owl, a cat, and a snake- and a control, all in the same manner. I found that titmice most often produced a combination of different vocalizations, including ‘chick-a-dee’ mobbing calls (composed of chick and D notes), ‘seet’ alarm notes, contact (chip) notes, and song, none of which denoted a specific predator species or class. They did, however, vary their vocal responses to the different treatments in terms of note composition, note duration and note structure of their mobbing calls. The cat elicited the least chick notes and the most D notes per call, followed by the hawk and owl, with the snake and control eliciting the most chick notes and fewest D notes per call. In addition, the bandwidth and entropy of the D notes elicited by the hawk and cat were greater than those elicited by the owl, snake and control. These findings suggest that titmice may be responding according to the degree of risk that the predators represent, rather than the predator species or class, indicating that they may be producing risk-based calls.

Introduction

Predator-Specific and Risk-Based Anti-Predator Calls

Many animals give specific vocalizations when they encounter a predator. Some species give predator-specific calls in which different call types are used to denote particular predator species or classes. It has been well documented in the literature that many primate species give structurally-distinct alarm calls to different types of predators (Seyfarth et al. 1980a, b; Macedonia 1990; Pereira and Macedonia 1991; Zuberbühler 2001; Kirchhof and Hammerschmidt 2006). These calls have also been documented in some carnivore species, namely the suricate (*Suricata suricatta*), a social mongoose, which gives distinct alarm calls to terrestrial predators, avian predators and snakes (Manser 2001). Domestic chickens (*Gallus domesticus*) also label predator classes by giving qualitatively different vocalizations to aerial and terrestrial predators (Gyger et al. 1987; Evans et al. 1993).

In contrast, some animals vary their vocal response to predators according to the degree of risk (also called response urgency) that the predator poses. Some species vary the rate in which they call while others vary the quality of the calls they produce. Several species of marmot (*Marmota sp.*) vary the rate of their calls as a function of risk (Blumstein 1995a; Blumstein and Arnold 1995; Blumstein and Armitage 1997a). In particular, yellow-bellied marmots (*Marmota flaviventris*) increase their call rate and potentially give calls with a larger bandwidth in response to higher risk predator situations (Blumstein and Armitage 1997a). When presented with different degrees of risk, Mexican chickadees (*Poecile sclateri*) vary the pitch of a single kind of alarm call according to the degree of risk (Ficken 1989) and Black-capped chickadees (*Poecile atricapilla*) alter their call rate of ‘chick-a-dee’ calls (Baker and Becker 2002).

Consequences of Specific Anti-Predator Calls

Call specificity with respect to predator type might be adaptive if an animal has predators that require different escape reactions. For example, in vervet monkeys, which have both terrestrial and aerial predators, they run up into trees when they hear an alarm call denoting a terrestrial predator and they look up, run into dense bush, or both when they hear an alarm call denoting an aerial predator (Seyfarth et al. 1980a). In social species with different types of predators, having predator-specific calls may allow group members to respond appropriately to predator threats even if they themselves have not detected the predator. Contrastingly, risk-based calls may give group members an indication of the threat level, but they do not necessarily contain the predator-specific information that would allow for different specific escape responses. Many passerines are said to have different calls that are given to aerial and terrestrial predators (Marler 1957). If these calls are, in fact, predator-specific calls that label different predator classes (i.e., aerial and terrestrial; avian, mammalian, and reptilian), this would lead to receivers being able to choose specific escape responses. But if these calls denote the degree of risk that is associated with the different types of predators, receivers would not have the predator-specific information needed to choose a specific escape response. In animals that live in stable groups, as some mixed-species flocks of birds do, evolution might favor calls that provide predator-specific information to other flock members.

Additionally, some anti-predator signals may affect detected predators in different ways, with some call types being potentially more efficient at deterring or distracting different predators (Naguib et al. 1999). One possible function of anti-predator calls is to signal to the predator that it has been detected and receptive predators might terminate the hunt rather than expend their energy pursuing prey that are aware of its presence (reviewed in Smith 1986). Evidence that supports this idea comes from observations by Morse (1973) of foraging accipiters

that did not typically attack if tit flocks gave alarm calls but would attack before they called, although the specificity of the calls is unknown. Australian honeyeaters (*Phylidonyris novaehollandiae*) may be communicating with predators by producing loud aerial alarm calls that likely deter attacks from the predators by informing them that they have been sighted and that the prey birds have already gone into hiding (Wenzel 1997). It has been suggested that another important function of anti-predator calls, specifically mobbing calls, could be to warn predators that they are about to be harassed and therefore, should retreat before they suffer potential injury from the mobbers (Frankenberg 1981). The use of different types of calls by prey species in response to predators may serve different functions and may play an important role in influencing the subsequent behavior of the detected predator.

Therefore, it is important to understand these anti-predator calls because they may be a key factor in decreasing the predation risk environment for signalers and receivers. Predator-specific calls, in particular, are likely to exist in systems where animals are in stable groups and have predators that require different escape techniques. In this study, I address whether the Tufted titmouse, a common passerine that participates in mixed-species flocks that share different types of predators in common (avian, mammalian, reptilian), possesses predator-specific calls in response to these various predator types.

Study System

The subject of the present study is the Tufted titmouse (*Baeolophus bicolor*). The titmouse is a common songbird in deciduous forests in eastern North America and is a regular visitor at bird feeders, especially during the fall and winter. Titmice are year-round residents in the study area of North-central Florida and participate in mixed-species flocks in winter (Gaddis 1979; Farley et al. in review). These flocks typically contain one or more Tufted titmice, Carolina chickadees (*Poecile carolinensis*) and usually include several attendant or ‘satellite’ species.

Most flocks contain a pair of titmice, their offspring, and/or other unrelated juveniles (Pielou 1957; Brackbill 1970). Regular satellite species include: Black-and-white warblers (*Mniotilta varia*), Downy woodpeckers (*Picoides pubescens*), Ruby-crowned Kinglets (*Regulus calendula*), Blue-headed and White-eyed vireos (*Vireo solitarius*, *V. griseus*) and Blue-gray gnatcatchers (*Poliioptila caerulea*; Farley et al. in review).

Titmice and potentially Carolina chickadees play the role of the ‘nuclear’, or focal species, around which mixed-species foraging flocks form during the winter months and the other flock members play the role of ‘satellite’ species (Gaddis 1983; Grubb and Pravosudov 1994; Greenberg 2000). Nuclear species in mixed-species bird flocks are generally characterized by behavioral traits that include dominance, sociality, and a high level of vigilance (Munn and Terborgh 1979; Hutto 1994). In addition, parid nuclear species act as sentinels by readily giving vocalizations in response to predators, thereby potentially alerting flock members of danger (Gaddis 1983; Dolby and Grubb 1998).

Typical predators of titmice include feral and house cats (*Felis domesticus*), hawks, owls, and snakes (Bent 1946). In my study area, the most common predators of forest passerines in winter include Sharp-shinned (*Accipitor striatus*) and Cooper’s hawks (*A. cooperii*); Eastern screech-owls (*Megascops asio*); Red-shouldered (*Buteo lineatus*) and Red-tailed hawks (*B. jamaicensis*); American kestrels (*Falco sparverius*); and feral and house cats (Sieving et al. 2004; S. A. Hetrick, pers. obs.). Snakes, most commonly rat snakes (*Elaphe sp.*), typically prey on the eggs, nestlings and sometimes adults of titmice and other small birds during the summer months (Jackson 1978; Halliday and Adler 1986; S. A. Hetrick, pers. obs.). During the winter months in eastern North America, Sharp-shinned hawks are most likely the most important

predator of small woodland birds (Bent 1937; Morse 1970; Bildstein and Meyer 2000), including titmice and other flock associates (Gaddis 1979, 1980; S. A. Hetrick, pers. obs.).

Two main types of anti-predator vocalizations have been described for Tufted titmice: the ‘seet’ alarm call (also known as the high whistle, see-see-see, ‘hawk’ call, and ‘flying predator’ alarm call) and the mobbing or scold call (known as seejert, chick-a-dee; Dixon 1955; Marler 1955; Gaddis 1979, 1980). Titmouse mobbing calls are variants of the ‘chick-a-dee’ call, which is a complex call composed of combinations of introductory ‘chick’ notes, and subsequent ‘D’ notes (dee notes, churr notes), with the number and presence of each note type being variable (Latimer 1977; Hailman 1989). The broadband structure of the D notes in the mobbing calls causes them to be easily localizable, while the pure tone structure of seet calls causes them to be difficult to locate (Marler 1955). When mobbing calls are given in response to predators, many birds are attracted to the area and may harass the predator, whereas seet alarm calls result in the cessation of movement (freezing) by the caller and nearby birds or in rapid escape to cover (Gaddis 1980; Ficken 1989; Baker and Becker 2002; Howell 2006; S. A. Hetrick, pers. obs.).

Although many studies have focused on aspects of the vocal repertoire of birds in the family Paridae, surprisingly little attention has been devoted to the vocalizations of Tufted titmice, especially in the anti-predator context (Dixon 1955; Gaddis 1979, 1980, 1983; Hill 1986). It is not known whether titmice have specific vocalizations for different predators, although it is commonly stated that members of the family Paridae give ‘seet’ or ‘hawk’ calls to raptors flying overhead (Marler 1955; Latimer 1977; Harrap and Quinn 1995). Titmice could be giving seet calls to (1) denote the predator as a hawk or accipiter (predator-specific calls with respect to species); (2) denote the class of predator as avian (predator-specific calls with respect to class); (3) denote the class of predator as aerial (predator-specific calls with respect to class);

(4) signal the immediate degree of danger (risk-based calls); or (5) any combination of these. No study has yet to confirm whether titmice use the seet call to reliably denote accipiters, aerial or avian predators, or to denote a situation where the titmouse is in immediate risk of attack. As Templeton et al. (2005) noted, previous studies have presented aerial and terrestrial predators in different ways (Greene and Meagher 1998; Blumstein 1999b; Le Roux et al. 2001), which confounds the interpretation of responses given to predator type versus risk situation (i.e., predator proximity, location, or behavior). In order to determine if the titmice were able to distinguish between predator species or between avian, mammalian, and reptilian predator classes, all predators were presented in the same manner in this experiment.

Research Design

The purpose of this study was to investigate the anti-predator vocal behavior of the Tufted titmouse; specifically, whether titmice have specific vocalizations for different predators (predator-specific calls). This study dealt with the vocal responses of titmice to both stuffed predator mounts and live predators- avian, reptilian and mammalian. Wild-caught birds were tested in a captive situation with both the bird and the predator being in cages. I presented individual adult titmice with 4 different predators: an owl, a hawk, cat, snake and a control, all in the same manner.

Hypothesis

I tested the hypothesis that titmice have predator-specific calls (call type uniquely covaries with predator species or class). In order to have predator-specific vocalizations, the titmice must give different call types that are predictably associated with different predator classes or species (Blumstein 1999a). Titmice could separate the predators into classes in various ways. For example, they may separate them into classes according to whether the predator is aerial or terrestrial; whether the predator is avian, mammalian, or reptilian; or, they could be more

specific and separate them into species such as hawk, owl, cat, and snake. In this experiment, I tested the latter two of these possibilities.

I conducted a true experiment under controlled conditions by presenting four different predator species in a similar manner to individual adult titmice to obtain vocal recordings of titmouse calls in response to the presentations. Subsequent analyses of the recordings were conducted to determine whether titmice give specific vocalizations in response to the different predators. All predators were presented in a clear cage directly across from the cage containing the titmouse. If titmice give predator-specific vocalizations that label either predator species or predator class (avian, mammalian, or reptilian), then the manner in which the predators are presented should not matter. For example, if titmice have specific ‘hawk’ calls that denote hawks, they should respond with ‘hawk’ calls to aerial as well as perched hawks. On the other hand, if titmice respond according to the degree of risk, one or more of their calls would likely vary in response to an aerial versus a perched hawk (assuming that the two situations represent different degrees of risk).

Predictions

I predicted that the titmice would respond with different call types to the different types of predator being presented. I predicted that they would give predator-specific vocalizations that are associated either with predator class (avian, mammalian, or reptilian) or with individual predator species. In the first case, the titmice would have different vocalizations for the hawk and owl (avian) than for the cat (mammalian) and snake (reptilian) and in the second case, the titmice would have unique calls for one or more of the four different species.

Methods

I examined the responses of adult titmice to four different predator species and a control. Fifteen adult titmice were caught between November 6, 2004 and January 21, 2005 at various

locations in Florida--the Ordway-Swisher Biological Station in Melrose, the USDA/APHIS/WS/NWRC Florida Field Station (United States Department of Agriculture, Animal & Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center; USDA lab) in Gainesville, FL and various residences in the city of Gainesville. The birds were captured using mist-nets and transferred to the USDA lab. The birds were housed and tested in 0.5 x 0.5 x 0.5m cages containing several branches for perching. They were fed an ad-lib diet of mixed seed, mealworms, suet, and chopped fruit and vegetables.

In order to be sure of acquiring appropriate anti-predator responses, I used only adult titmice in the experiment. Chickadees acquire information about predator identity through learning from older birds in their social groups (reviewed in Smith 1991). Since titmice have a similar social system to chickadees, I expected that young-of-the-year may not give informative responses in this experiment. To determine if the birds were adults, I used the molt limit criteria in Pyle (1997) for aging.

At least 24 hours before the first predator presentation, the cage containing the bird was brought into the testing environment in order for the bird to acclimate. The testing environment was an outdoor aviary (9 x 3 x 2.3m) at the USDA lab that contained numerous branches and snags and was adjacent to forest, providing a semi-natural environment. Within the large aviary, the cage containing the test subject was placed on a 0.5m platform with the predator presentation cage 0.75m away from the test cage on a 0.5m platform (Fig. 2-1). The predator presentation cage was made of clear plexi-glass and a sheet covered it at all times except during the tests. A camouflage blind containing the researcher and a microphone were also within the aviary, 4.5-6m away from the test and predator cages.

Predator Presentations

Each bird underwent a series of 5 different treatments after the acclimation period. Each test consisted of one of 4 predator treatments - a stuffed Sharp-shinned hawk (*Accipiter striatus*), a live Eastern screech-owl (*Megascops asio*), a live domestic house cat (*Felis domesticus*), and a live red rat snake (*Elaphe guttata*) - or a control (an empty cage) being presented in random order (hereafter the treatments will be referred to as hawk, owl, cat, snake and control). The tests began at 0800 and were conducted every 2 hours until 1600. Each test consisted of one of the predators being placed into the cage 20 minutes before testing began. For the control, the researcher went through the steps as if they were placing a predator in the cage. Care was taken to ensure that the bird in the test did not view the predator until the test began. The test began when the sheet covering the predator cage was removed, allowing the bird to view the predator or empty cage. Recordings were made for 5min pre-stimulus and 7min post-stimulus; however, only the first 5min post-stimulus were included in the analysis. A Sennheiser shotgun microphone (ME 66) was used to record the vocalizations directly onto a laptop computer using Raven Interactive Sound Analysis Software Version 1.1 with a sampling rate of 44100 at 16-bit resolution.

Spectrographic Analyses

I analyzed vocal responses for 72 out of the 75 presentations for the adult titmice (n=14 for cat, n=15 for control, n=15 for owl, n=15 for snake, and n=13 for hawk); the titmice did not vocally respond in 2 of the presentations and one of the hawk recordings was lost due to equipment failure. Spectrographic analyses were performed on the vocal recordings using Avisoft SASLabPro 4.39. To edit out noise, each sound file was FIR low-pass filtered at 12kHz and high-pass filtered at 1.4kHz. The spectrogram parameters used were FFT=512, Frame Size=75%, Window=Hamming, Overlap=87.5%. I classified and labeled all vocalizations given

in response to the treatments, which included ‘chick-a-dee’ calls, songs, seet notes, and chip notes. The notes in each call, or ‘chick-a-dee’ complex, were visually classified as introductory ‘chick’ notes or subsequent ‘D’ notes. In titmice, the various introductory notes grade into each other and are not easily distinguished into natural categories; therefore, the introductory notes were classified together as ‘chick’ notes (Fig. 2-2a). On the other hand, D notes can be reliably classified (Bloomfield et al. 2005) due to their harmonic-like structure and little frequency modulation. D notes also have a higher entropy and lower frequency than the introductory chick notes, and D notes always occur at the end of the call, or are the only notes comprising a call, making them easily distinguished from introductory notes (Fig. 2-2a). Songs, seet notes and chip notes were also visually classified. Songs are unique and can be easily distinguished from other vocalizations (Fig. 2-2b). Seet notes were recognized by being high-pitched (around 8-10kHz for titmice) whistles with a narrow bandwidth that have no sharp onset or ending and cover only a narrow frequency range (Fig. 2-2c; Apel 1985; Marler 1955). Chip notes were recognized as being single-syllable notes that are typically chevron-shaped with a shorter duration than seet notes (Fig. 2-2d).

I measured several aspects of the notes and calls, including some that were based on measures used in previous studies of parids (Baker and Becker 2002; Freeberg et al. 2003; Templeton et al. 2005). For each treatment, I averaged the number of each type of vocalization (chick-a-dee, song, seet, chip). For the ‘chick-a-dee’ calls, I averaged the number of chick and D notes overall, the number and proportion of chick and D notes per call, and the duration of each chick and D note.

Spectrum-Based Measures

I also measured several fine-scaled acoustic parameters on the D notes in which I had high-quality recordings (not overlapping with outside noise). I measured the spectrum-based

parameters of the notes using a power spectrum with FFT length=512. For the D notes, the parameters were computed at the maximum spectrum of the entire D note (maxpeakhold) and are similar to those used by Nowicki (1989) and Templeton et al. (2005). The parameters were minimum and maximum frequency where the amplitude goes last below -30dB and where the amplitude goes last below -10dB (min and max frequency with the total option activated in Avisoft SASLabPro 4.39), bandwidth (calculated with min and max frequency described previously) and entropy.

For each factor that was measured, I used univariate analysis of variance (ANOVA) with the least significant difference (LSD) post-hoc test to conduct pairwise comparisons among the treatments. I transformed the data when appropriate to meet the assumptions of the analysis using arcsin(sqrt(n)) and log(n+1) transformations (Sokal and Rohlf 1995). All statistical analyses were performed using SPSS 11.5 for windows and significance in all statistical tests was set at the 0.05 alpha-level.

Results

Contrary to my predictions, the titmice did not give specific vocalizations to denote the different predator species or predator classes (avian, mammalian, reptilian). The titmice typically gave a combination of vocalizations in response to the predator and control treatments, usually consisting of chip notes and possibly ‘chick-a-dee’ calls, seet notes, or both. Their vocal responses were highly variable (see Fig. 2-3 a-e). Chip notes were by far the most common vocalization: 68 of the 74 five-min recordings contained chip notes (n=14 for control, n=15 for snake, n=13 for owl, n=13 for hawk and n=13 for cat). About an eighth to a quarter of the birds responded with ‘chick-a-dee’ calls to the control, snake and cat treatments and about half the birds responded with ‘chick-a-dee’ calls to the owl and hawk treatments (n=2 for control, n=3 for snake, n=7 for owl, n=8 for hawk and n=4 for cat). More titmice gave seet calls in response to

the hawk and cat than to the control, snake and owl treatments (n=4 for control, n=2 for snake, n=5 for owl, n=9 for hawk and n=7 for cat). Only a few birds responded with singing when presented with the predators (n=1 for control, n=1 for snake, n=3 for owl, n=2 for hawk and n=1 for cat). The means of each type of vocalization given to the different treatments are shown in Table 1.

Six out of 11 of the general spectrographic variables and all of the 7 fine-scale acoustic variables of the D notes varied significantly with treatment (ANOVA $p < 0.05$). In no case did the LSD pairwise comparisons indicate that titmice discriminated each predator from the other and the control. In most cases, the cat, hawk and owl were significantly different from the snake and control ((cat, hawk, owl) \neq (snake, control)) or the cat and hawk were significantly different from the owl, snake and control ((cat, hawk) \neq (owl, snake, control)).

Titmice did not give a significantly different number of 'chick-a-dee' mobbing calls to the different treatments (ANOVA $F_{4, 74} = 0.41$, $p = 0.798$), although the number of introductory chick notes per call and D notes per call differed significantly with treatment ($F_{4, 133} = 44.34$, $p < 0.001$; $F_{4, 133} = 21.96$, $p < 0.001$, respectively). The control and snake treatments elicited more chick notes per call and fewer D notes per call than the owl, cat and hawk. The cat treatment elicited the fewest chick notes and most D notes overall followed by the hawk and then the owl. The relationship can be clearly seen in Figure 2-4. The proportion of chick notes per call also differed significantly with treatment ($F_{4, 133} = 56.34$, $p < 0.001$), with the relationships between the treatments the same as above. The number of seet, song, chip, chick and D notes did not differ with respect to treatment ($p \geq 0.157$ in all cases, Fig. 2-5).

The duration of the chick and D notes was significant with respect to treatment ($F_{4, 134} = 3.69$, $p = 0.007$; $F_{4, 299} = 20.29$, $p < 0.001$). The pairwise comparisons revealed that the chick

notes in response to the cat were of greater duration than those given in response to the control and owl; the chick notes in response to the snake were of greater duration than those given in response to the control and owl; and the chick notes in response to the hawk were of greater duration than those given in response to the owl (with no other comparisons significant). The pairwise comparisons revealed that the D notes in response to the hawk were of greater duration than those given in response to all other treatments and the D notes in response to the cat were of greater duration than those given in response to the owl (with no other comparisons significant).

Of the 7 fine-scaled acoustic parameters that were measured, all were significant. The parameters that had multiple comparisons with a clear relationship between the treatments were maximum frequency where amplitude goes last below -10dB, bandwidth at -10dB and entropy. The titmice gave D notes with a larger bandwidth and higher maximum frequency at -10dB to the cat and hawk treatments than to the owl, control and snake treatments. Additionally, the D notes that the titmice produced in response to the hawk had a higher entropy than in response to the cat; both hawk and cat treatments elicited D notes with a higher entropy than the owl, control and snake treatments (Fig. 2-6).

Discussion

Contrary to my predictions, the results indicate that the titmice did not use different call types to label different predator species or predator classes (avian, mammalian, reptilian); therefore, they do not possess predator-specific calls in these contexts. They gave a variety of notes and call types during the predator presentations (chick-a-dee, seet, song, and chip), none of which were reliably associated with a particular predator. All of the predator presentations and occasionally the control presentation elicited seet notes from some of the titmice. Dixon (1955) and Marler (1955) have called the titmouse seet call the 'hawk' call or 'flying predator' call. But in this study titmice gave seet notes in response to other predators besides hawks and to predators

that were perched (not flying). The results from this experiment show that titmice do not vocally discriminate (by giving different call types) between predator species when they are presented in similar ways. In addition, the results indicate that set alarm calls are given in other circumstances besides just in response to aerial predators.

Although the titmice didn't give predator-specific vocalizations, they did vary the call and note structure of one specific vocalization, the 'chick-a-dee' mobbing call, in response to the different predators, which is characteristic of risk-based calls (Blumstein and Armitage 1997a). One way in which they varied their calls was by altering the note composition of the 'chick-a-dee' mobbing call. The cat treatment elicited the fewest chick notes and the most D notes, followed by the hawk and owl treatments. The snake and control treatments, which did not differ significantly from each other, elicited the most chick notes and the fewest D notes. Gompertz (1961) and Latimer (1977) noted that some parids decrease or drop the introductory notes of the mobbing call while extending the D note section as the level of risk increases. If this were true for Tufted titmice, then it would lead us to believe that the cat treatment represents the greatest risk, followed by the hawk and owl treatments, with the snake treatment representing the same amount of risk as the control. Evans et al. (1993) suggested that, under some conditions, terrestrial predators pose a greater threat than avian predators. Given that all birds used in this study were captured in or near suburban neighborhoods where outdoor cats are common around bird feeders frequented by titmice and other species (S. A. Hetrick, per. obs.), all test subjects would likely have experience with this species. Unlike a perched raptor (species dependent upon aerial attack to capture prey), a crouching cat in close proximity to a titmouse poses a very high risk to the adult bird. Therefore it is quite likely that the titmice in this study could have viewed the cat treatment as representing the greatest risk.

Encoding of Risk in Parid Anti-Predator Calls

Note composition may be particularly important in encoding information about predators and degree of risk. Studies of other birds in the family Paridae, namely chickadees, suggest that different variants of the ‘chick-a-dee’ call might encode information about the presence of different environmental stimuli (including predators) or the motivational state of the caller (Smith 1972; Gaddis 1985; Ficken et al. 1994). Hailman et al. (1985, 1987) suggested that note composition variation may encode information related to many factors, including potential predators, and the results from Ficken, Hailman, and Hailman’s (1994) study with Mexican chickadees supports that view. Black-capped chickadees altered the number of introductory A and B syllables in their ‘chick-a-dee’ calls in response to a predator mount presented at different distances, which represented different risk levels (Baker and Becker 2002). They also altered the number of D notes in the ‘chick-a-dee’ call in response to raptors of different sizes, with the smallest raptors eliciting the most D notes and the largest raptors eliciting the least (Templeton et al. 2005). The small raptors represented higher-risk situations to the chickadees and the large raptors represented lower risk situations, thus it is likely that the chickadees responded according to the degree of risk that they encountered.

Besides varying the note composition of the ‘chick-a-dee’ calls, I found that titmice also altered the structure of the D notes within the calls. Titmice gave D notes with a larger bandwidth and higher maximum frequency in response to the hawk and cat, while the owl, snake and control elicited D notes with a smaller bandwidth and lower maximum frequency. Other animals change their call structure in different predator situations. Yellow-bellied marmots vary several frequency characteristics of their calls, including bandwidth, as a function of distance to certain predators (Blumstein and Armitage 1997a). White-browed scrubwrens (*Sericornis frontalis*) vary the call structure of their aerial trill call by increasing the minimum frequency

(pitch) according to the distance from a suddenly appearing predator (Leavesley and Magrath 2005). In both of the aforementioned studies, the distance from the predator to the subject represents the amount of risk, with the closer distances representing higher risks; thus, we can conclude that both the marmot and the scrubwren vary the structure of their calls according to the degree of risk that they are presented with. In the present study, the hawk and the cat treatments elicited D notes from the titmice that had higher entropy than the D notes elicited from the owl, snake and control treatments. Entropy is a measure of the amount of randomness or ‘noise’ a note contains, with pure tones having no entropy and white noise having the most entropy; subsequently, entropy can be used as an indication of note harshness. Latimer (1977) noted that many birds in the family Paridae give calls that are harsher (higher entropy) as the level of aggression rises. Additionally, Morton (1977) documented that the motivational state of the caller influences signal structure and that harsh (high entropy), broadband (large bandwidth), low-frequency sounds are associated with aggressive behavior, whereas more tonal, high-frequency sounds are associated with non-aggressive or fearful behavior. Because the hawk and cat treatments elicited D notes with larger bandwidth and higher entropy (harshness), we can speculate that the titmice perceived a higher level of risk and had a higher level of aggressiveness in response to the hawk and cat than to the owl, snake and control treatments. Thus, I conclude that the level of risk according to titmice may be associated, at least in part, with the type of predator and not solely the proximity or location of a predator with respect to the test subject.

The results of both the note composition and D-note structure suggest that the titmice perceived the cat and hawk as having the most risk, followed by the owl and the snake and control had the least risk. In addition, more individual titmice responded with seet notes to the high-risk species; and the mean number of seet notes was highest in response to the cat and hawk

presentations. This evidence further supports the idea that the titmice viewed these two predators as posing the most risk. Apel (1985) concluded that Black-capped chickadees recognized the difference in the degree of danger between Sharp-shinned hawks and American kestrels by responding with more seet notes ('high sees') to the higher-risk Sharp-shinned hawk.

It is interesting to note that the titmice did not respond differently to the snake and control in terms of note composition and D-note structure, thus suggesting that the titmice did not perceive the snake as more of a risk than the control. There are several explanations as to why this occurred. The time of year that the study was conducted was winter, which could have affected the titmouse's response to the snake, as red rat snakes prey on birds and their eggs typically during the summer when most birds are nesting (Jackson 1978; Halliday and Adler 1986; S. A. Hetrick, pers. obs.). Another reason that the titmice may not have reacted differently to the snake and control could be due to the activity level and movements of the snake. The snake was stationary for the most part during the presentations and was not actively foraging, probably due to the cold outside temperature. On the other hand, the hawk in this study did not move because it was a stuffed mount and the titmice still responded as if it was a high-risk situation, suggesting that movement was not an important factor in determining their response.

Potential Biases

The responses of the individual titmice to the 4 predator treatments and control treatment were highly variable (as shown in Fig. 2-3). Some of this variation may be due to the existence of social dominance hierarchies within wild titmouse flocks (Brawn and Samson 1983). In these flocks, the alpha (most dominant) male possibly contributes the majority of the vocalizations in response to predators. This idea is supported by evidence in Pale-winged trumpeters (*Psophia leucoptera*), where the dominant male in the group gives the majority of the anti-predator vocalizations (Seddon et al. 2002). Older, and most likely more dominant, male Willow tits

(*Parus montanus*) give alarm calls more frequently than females or young males (Alatalo and Helle 1990). In the present experiment, all of the individuals were adults, but the sex could not be determined in most of the cases.

The mean number of ‘chick-a-dee’ mobbing calls given by titmice in response to the predators was lower than expected based on observations of natural encounters between titmice and their predators (S. A. Hetrick, pers. obs.). A factor that could have contributed to this could be that the titmice were housed alone and away from other titmice during the predator presentations. A few of the hypotheses as to why animals give anti-predator calls include alerting others and transmitting cultural information about predator characteristics (Klump and Shalter 1984). For either of these to occur, the caller must have an audience. Evans et al. (1993) found that domestic chickens (*Gallus domesticus*) rarely give aerial alarm calls unless they have an appropriate audience. My results show that not all of the titmice gave anti-predator vocalizations (seet or chick-a-dee mobbing calls) in response to the predator presentations. The most common and numerous vocalization given was the single syllable chip note, which is not typical of natural predator encounters (S. A. Hetrick, pers. obs.). Moreover, some individuals sang during trials, but primarily in response to the cat, hawk and owl, which likely represent the three highest-risk predators (Fig. 2-3). In the present experiment, the birds were held in a cage in an outdoor aviary. There were sometimes other birds such as cardinals and towhees in the area outside of the aviary that could have provided an audience for the titmice and wild titmice could occasionally be heard in the far distance. Even so, the titmice may have felt a reduced motivation to vocalize because they were not around their natural flock members.

Summary

In summary, my results clearly indicate that titmice do not produce predator-specific calls in response to different predator species or classes of predators (avian, reptilian, and mammalian)

when the predators are presented in the same manner. However, results do indicate that titmice may give risk-based calls in response to predators due to the fact that they varied their call structure and note structure in response to the different predators. Given that this experiment controlled for the situation under which predators were encountered, it is possible that the type of predator affected the amount of risk encoded in the calls of titmice; house cat and hawk elicited call structures typically associated with greater risk than either an owl or a snake. In chapter 3, I investigate further the nature of the risk-based communication system of titmice in response to predators.



Figure 2-1. Outdoor testing aviary showing the test cage containing the test bird on the left and the predator presentation cage on the right (with the sheet cover removed).

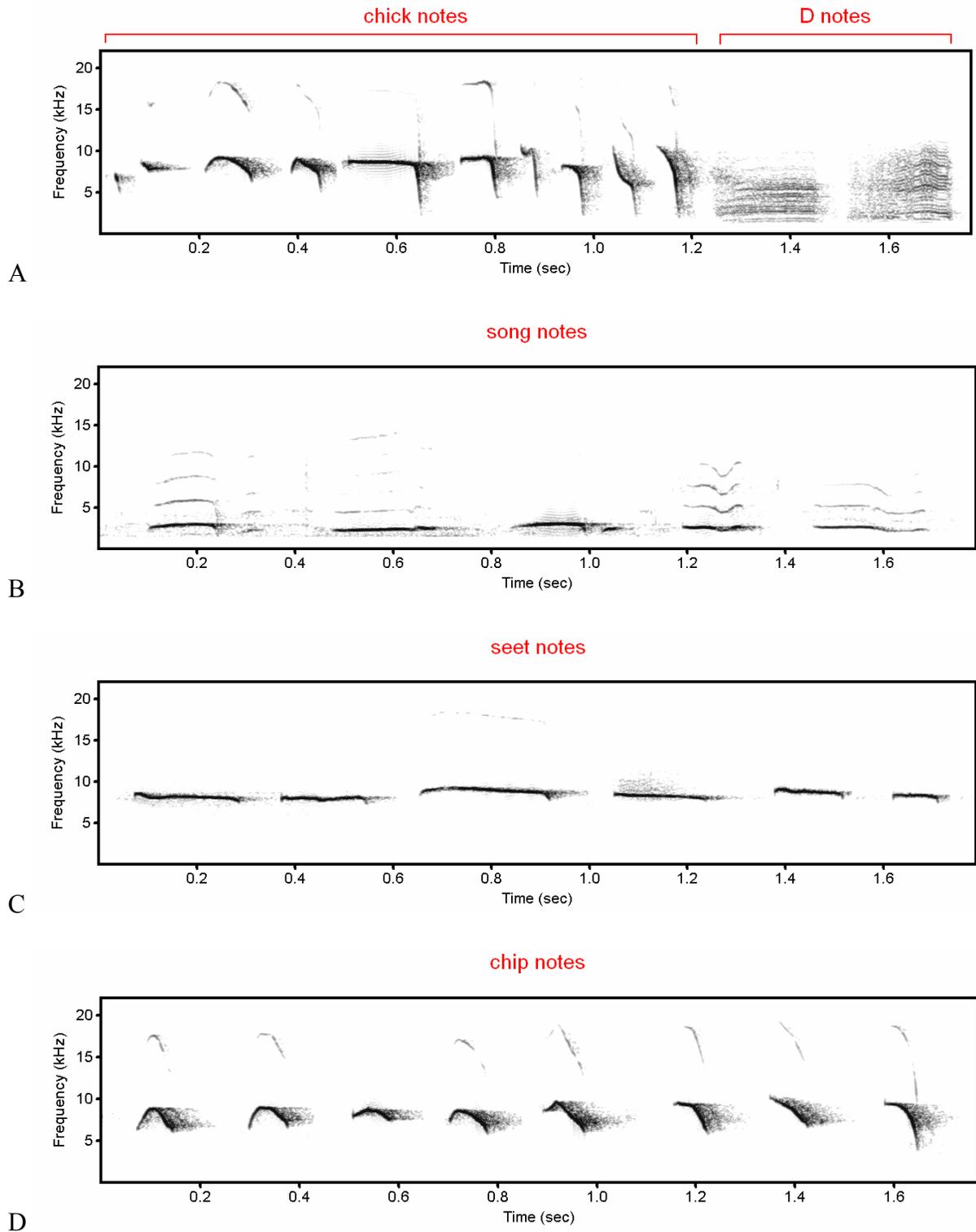
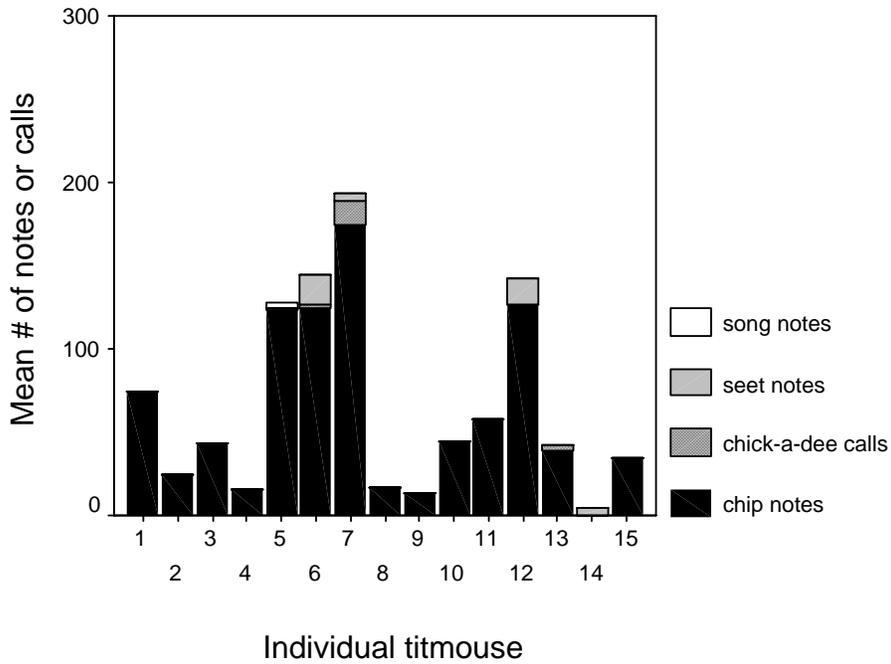
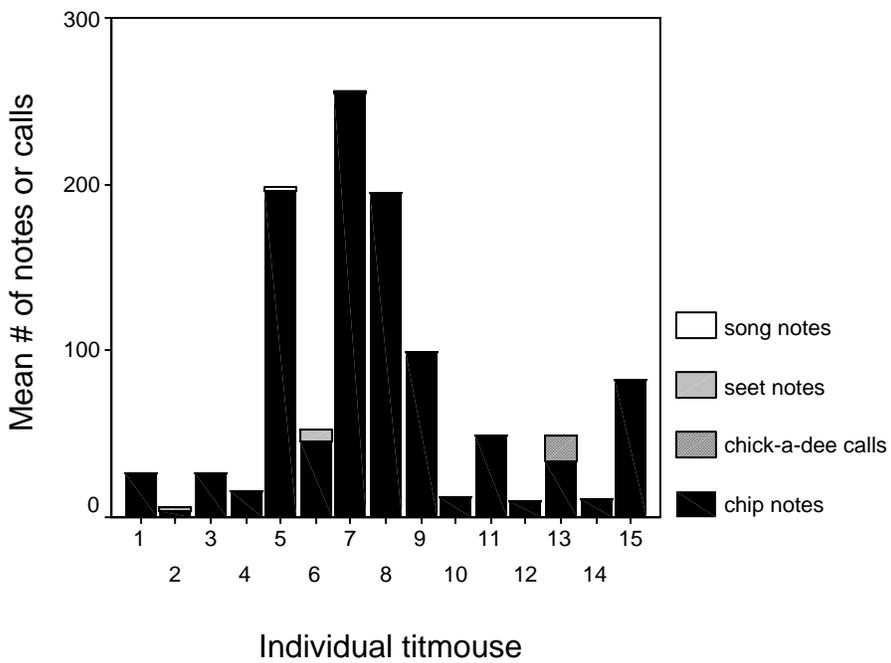


Figure 2-2. Examples of the variation within the main vocalizations of the Tufted titmouse in response to the 4 predator treatments and control. A) ‘Chick-a-dee’ call complex showing the variation in introductory chick notes and subsequent D notes. B) Variations of song notes. C) Variations of seet notes. D) Variations of chip notes.

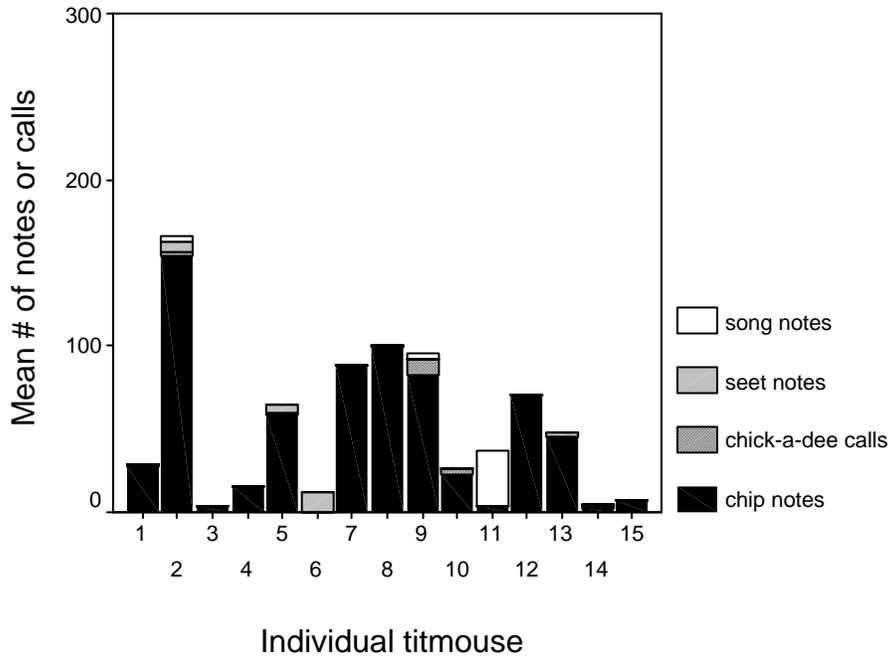


A

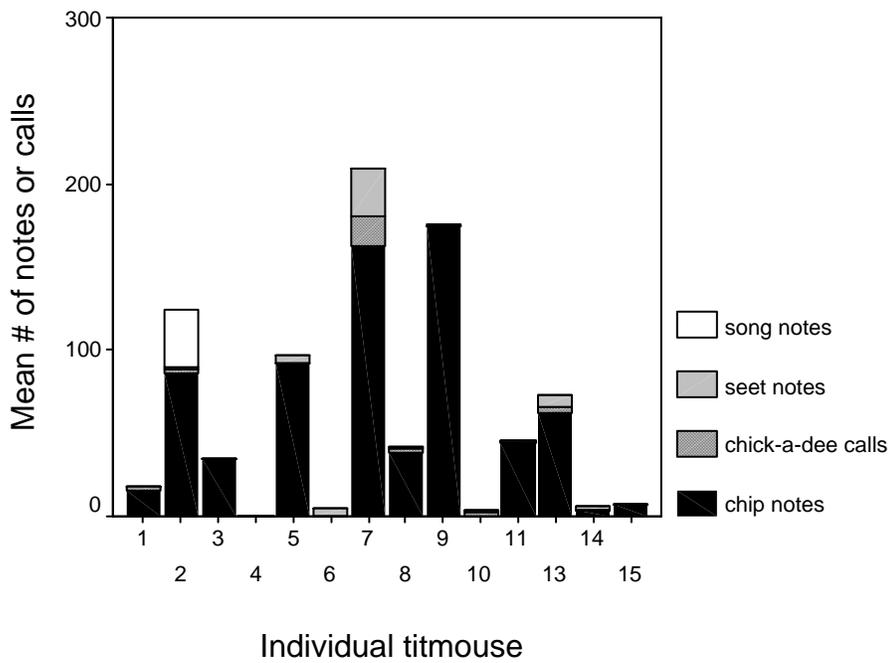


B

Figure 2-3. Number of each type of note or call given in the first 5min following presentation by the fifteen individual Tufted titmice in response A) to control, B) to snake, C) to owl, D) to hawk, E) to cat treatments.

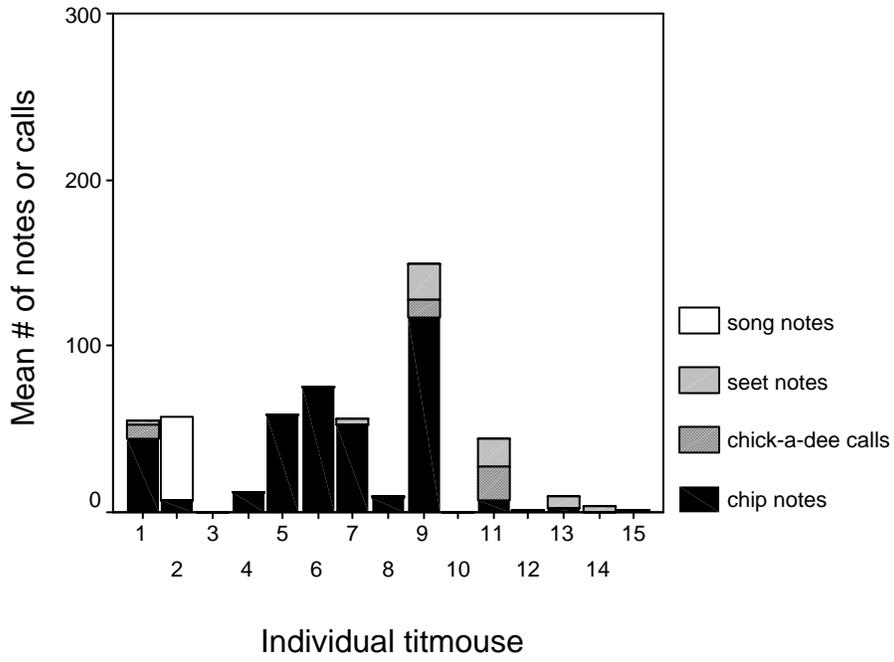


C



D.

Figure 2-3. (cont.)



E

Figure 2-3. (cont.)

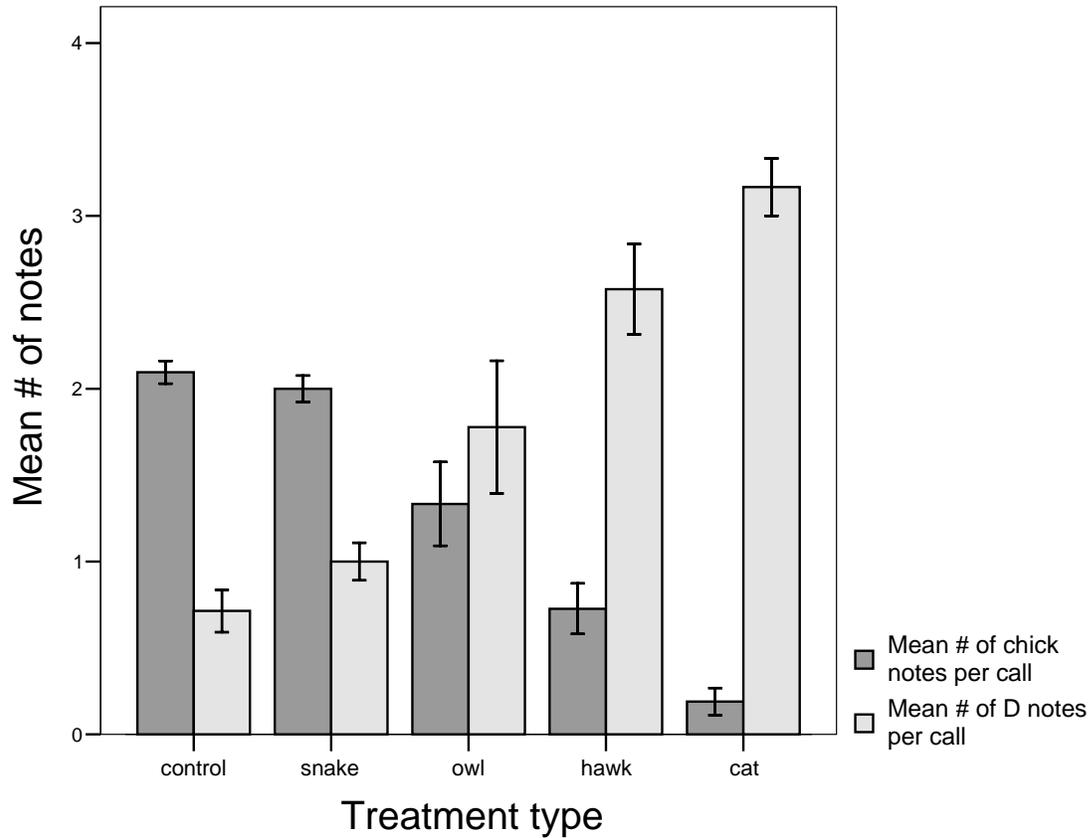


Figure 2-4. Number of chick and D notes per ‘chick-a-dee’ complex call given by Tufted titmice in response to predator treatments and control in the 5min following presentation. Both variables were significant with respect to treatment (ANOVA, $p < 0.001$). All pairwise comparisons were significant (LSD, $p < 0.05$) except for snake and control ($p = 0.647$, $p = 0.442$ for chick and D notes per call, respectively). Error bars: ± 1 SE.

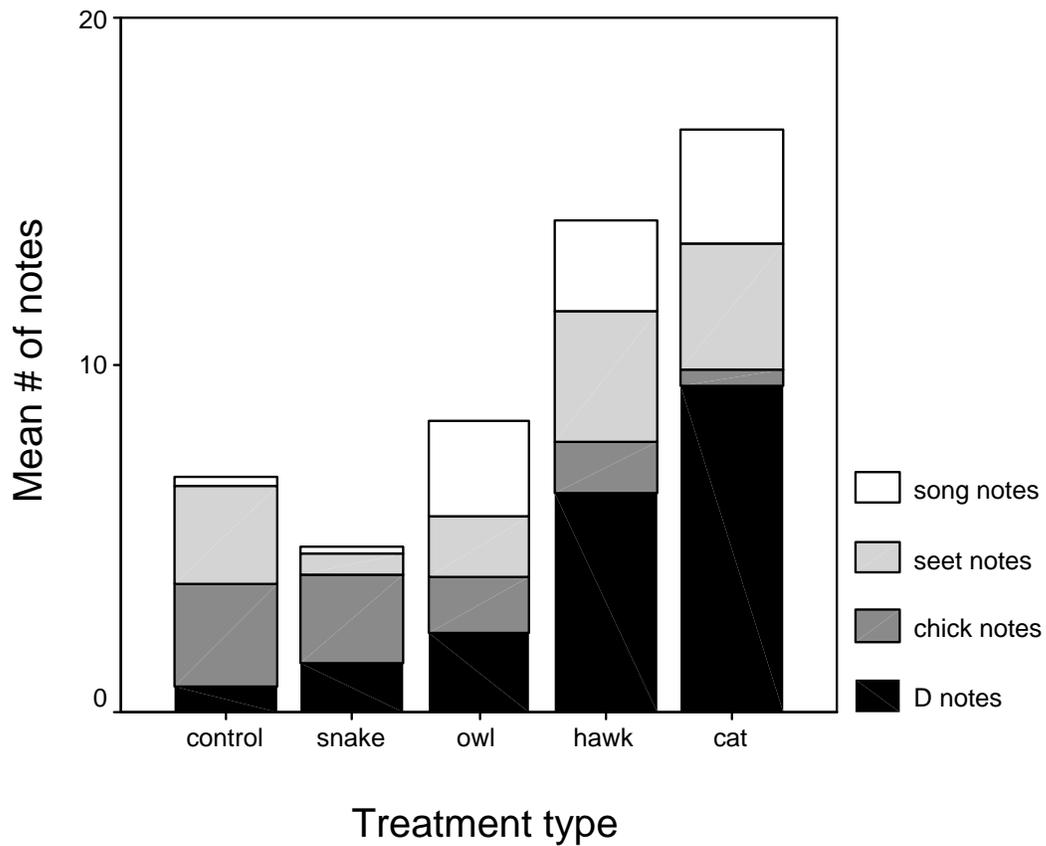


Figure 2-5. Mean number of overall song, seet, chick, and D notes that Tufted titmice gave in response to the predator treatments and control in the first 5min following presentation. None of the differences are significant with respect to treatment (ANOVA, $p > 0.05$).

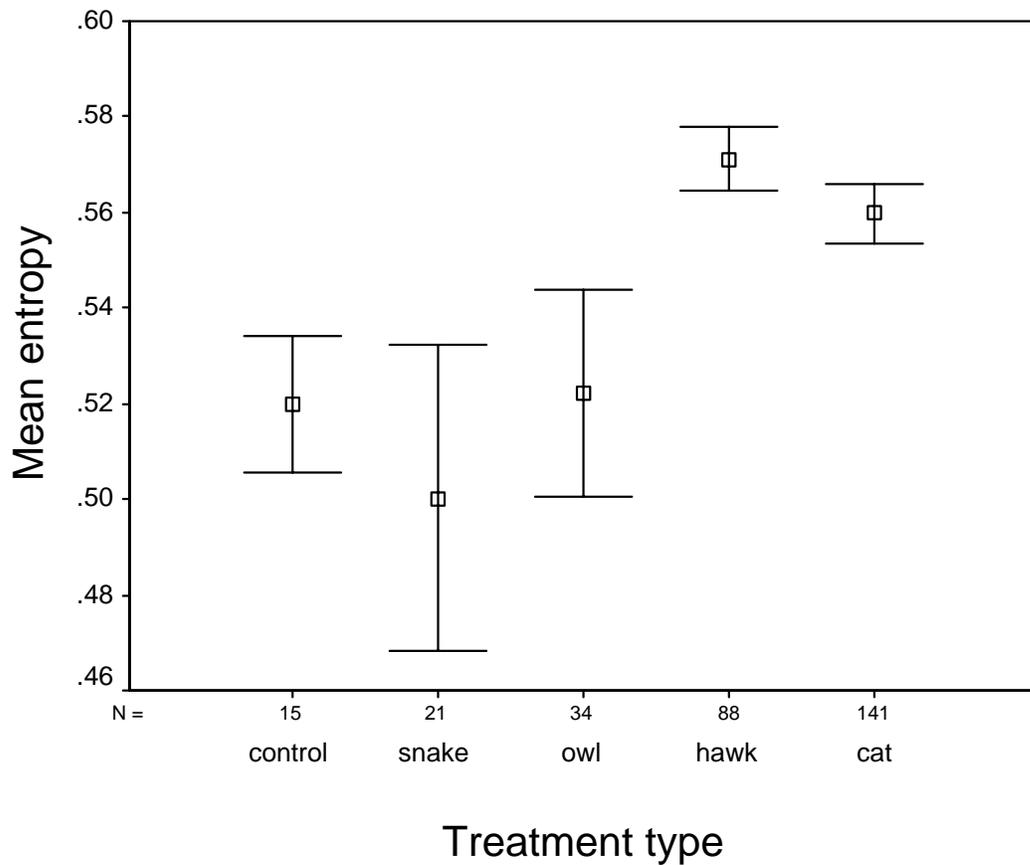


Figure 2-6. Mean entropy of the D notes of Tufted titmice in response to predator treatments and control in the first 5min following presentation. All pairwise comparisons were significant (LSD, $p < 0.05$) except between control and owl ($p = 0.868$), control and snake ($p = 0.166$), and snake and owl ($p = 0.061$). Error bars: ± 1 SE.

Table 2-1. Mean number of each note type given by individual Tufted titmice in response to predator and control presentations in the first 5min following presentation.

<u>Note type</u>	<u>Predator</u>	<u>N</u>	<u>Mean</u>	<u>SD</u>	<u>SE</u>
Chick	Control	15	2.93	7.53	1.94
	Snake	38	2.53	8.49	2.19
	Owl	24	1.60	4.87	1.26
	Hawk	21	1.50	3.78	1.01
	Cat	7	0.47	0.99	0.26
D	Control	7	0.73	2.15	0.56
	Snake	21	1.40	4.17	1.08
	Owl	34	2.27	3.41	0.88
	Hawk	21	6.29	10.06	2.69
	Cat	141	9.40	21.44	5.54
Seet	Control	43	2.87	5.78	1.49
	Snake	9	0.60	1.84	0.48
	Owl	27	1.80	3.43	0.88
	Hawk	43	3.79	7.60	2.03
	Cat	54	3.60	6.44	1.66
Song	Control	4	0.27	1.03	0.27
	Snake	3	0.20	0.78	0.20
	Owl	41	2.73	8.49	2.19
	Hawk	36	2.57	9.06	2.42
	Cat	50	3.33	12.91	3.33
Chip	Control	942	60.80	52.43	13.54
	Snake	1138	70.40	80.44	20.77
	Owl	713	45.60	45.71	11.80
	Hawk	809	51.36	58.32	15.59
	Cat	448	25.67	35.72	9.22

CHAPTER 3
INTERSPECIFIC RISK-BASED CALL SYSTEM OF TUFTED TITMICE
(*BAEOLOPHUS BICOLOR*) IN RESPONSE TO PREDATORS

Many animals give alarm vocalizations in response to predators but little work has focused on characterizing responses to such signals by sympatric heterospecifics. Tufted titmice (*Baeolophus bicolor*) and other members of family Paridae respond to predators that do not pose an immediate risk (e.g., perched predators) with complex mobbing calls that have been described as ‘chick-a-dee’ calls. Black-capped chickadee (*Poecile atricapilla*) mobbing calls vary with the degree of risk represented by different species of perched predators, and conspecifics, isolated from predator stimuli, will respond to these calls with risk-appropriate behaviors. Mobbing calls of the Tufted titmouse attract many bird species and generate vigorous interspecific mobbing flocks that harass and scold predators. I wanted to determine if titmice also vary their mobbing calls according to the degree of risk that predators pose and if other species respond to mobbing and other anti-predator calls of Tufted titmice with risk-appropriate behaviors. I presented captive flocks of titmice with live high- and low-risk predators and controls under semi-natural conditions to acquire vocal recordings. I then played these recordings and recordings of titmouse ‘seet’ alarm calls (given when the bird is startled or in a state of fear) to captive pairs of Carolina chickadees (*Poecile carolinensis*) without a predator stimulus. To the high-risk predator presentations, titmice approached the predator more closely and gave significantly more mobbing calls with different note composition and shorter note intervals and note bandwidths compared to vocalizations given to low-risk predator presentations and controls. In response to the playback of titmouse mobbing vocalizations to the high-risk predator, chickadees approached the speakers more closely, gave significantly more mobbing calls with different note composition and longer note

duration than calls given to the low-risk predator and control vocalizations of titmice and they froze and became silent in response to titmouse seet calls. Thus, titmice did vary their mobbing calls according to the degree of risk they experience, and chickadees responded appropriately to the various titmouse mobbing calls and alarm calls.

Possession of an interspecific risk-based call system provides one explanation for the socially dominant role that parid species play in interspecific associations (e.g., winter foraging flocks and predator-mobbing aggregations) involving multiple bird species.

Interspecific risk-based calls like those characterized here may underlie ecological facilitation in vertebrate communities more generally

Introduction and Background

Anti-Predator Vocal Signaling

Many vertebrate species respond to predator encounters by giving anti-predator vocal signals. Passerine birds typically have two main types of anti-predator vocalizations: alarm calls and mobbing calls. Typical passerine alarm calls are difficult to locate and are usually given when the birds are in a state of fear, such as when a predator poses an immediate threat of attack (Marler 1957; Ficken and Witkin 1977; Morton 1977; Apel 1985). Responses to alarm calls usually involve either the cessation of movement or abrupt flight to cover by the caller and other birds nearby (Marler 1955, 1957; Gompertz 1961; Ficken and Witkin 1977; Latimer 1977; Ficken 1989; Evans et al. 1993). In contrast, mobbing vocalizations are easily localizable and are usually given to perched predators posing little immediate risk, and these calls attract other species that often harass the predator, sometimes encouraging it to leave the area (Klump and Shalter 1984; Ficken and Popp 1996; Naguib et al. 1999; Baker and Becker 2002). The production and description of anti-predator vocalizations has commonly been presented as part of broader analyses of species' modes of communication and overall vocal complexity. Specific

focus on the production and context of individual species' anti-predator calls has shown that such calls can communicate information about predators, including the level or type of risk (Struhsaker 1967; Seyfarth et al. 1980b; Macedonia 1990; Dasilva et al. 1994; Blumstein and Armitage 1997a; Greene and Meagher 1998; Zuberbühler 2001). However, understanding when and how conspecifics and heterospecifics receive and respond to risks conveyed in anti-predator signals is just now coming to light (Naguib et al. 1999; Baker and Becker 2002; Templeton et al. 2005).

Predator-Specific and Risk-Based Call Systems

Different species' vocalizations in response to predators vary in complexity. Some vocalizations contain detailed information about the type of predator (predator-specific calls), while some contain information about the immediacy of threat that the caller faces (risk-based calls; Macedonia and Evans 1993; Greene and Meagher 1998). These two calling systems differ with respect to their production specificity. In production, both predator-specific and risk-based calls are referred to as 'situationally specific' because the call structure in some way varies with distinct situations. If the vocal response uniquely (or categorically) covaries with the stimulus type, as in predator-specific calls where a different type of call is associated with different predator species or classes, then there is a high degree of production specificity (Blumstein and Armitage 1997a). On the other hand, if the vocal response varies continuously, i.e., the same call type is produced with graded frequency or intensity according to the degree of risk, then there is not a high degree of production specificity. However, such a system is still considered to be situationally specific because higher and lower risk situations can be distinguished (Blumstein and Armitage 1997a,b; Blumstein 1999a). Risk-based (also called urgency-based) call systems have been found in several taxa including ground squirrels, marmots, scrubwrens, babblers and

chickadees (Robinson 1980, 1981; Sherman 1985; Ficken 1989; Blumstein 1995a,b; Blumstein and Arnold 1995; Naguib et al. 1999; Baker and Becker 2002; Leavesley and Magrath 2005).

Perception specificity refers to the nature of the signal-receivers' reaction to the immediacy of threat conveyed in anti-predator vocalizations. If a vocal signal produced under different situations elicits contextually appropriate responses from conspecifics and/or heterospecifics, in the absence of other cues, the vocal signals are said to generate 'perception specificity' (Evans et al. 1993; Macedonia and Evans 1993; Blumstein 1999a). Intraspecific perception specificity is common in vertebrates but work addressing interspecific perception specificity of signals is rare relative to the number of systems with sympatric heterospecifics that associate with one another (Fichtel and Kappeler 2002).

Species in the family Paridae are known to produce risk-based calls. Ficken (1989) demonstrated that Mexican chickadees (*Poecile gambeli*) vary their alarm or 'high zee' calls according to the degree of risk and Baker and Becker (2002) showed that Black-capped chickadees (*Poecile atricapilla*) vary their mobbing calls according to the immediacy of threat. Neither study conducted playbacks to address intra or interspecific communication to see if others were able to recognize the variation in the calls and respond appropriately. This is an important distinction because birds may produce situationally specific calls, but unless others are able to recognize them and understand their meanings, successful communication does not occur. Recently, Templeton et al. (2005) clearly demonstrated intraspecific communication among Black-capped chickadees. They found that the chickadees gave risk-based calls to different predators and that these calls elicited appropriate responses from conspecifics. In the present study, I tested for the presence of interspecific communication of predation risk between two species of parids that co-occur in the southeastern United States.

Study System

The Role of Tufted Titmice in Mixed-Species Foraging and Mobbing Flocks

Tufted titmice (*Baeolophus bicolor*) and (potentially) Carolina chickadees (*Poecile carolinensis*) play the role of the ‘nuclear’, or focal species, around which mixed-species foraging flocks form during the winter months. In these flocks, chickadees are socially subordinate to titmice (Waite and Grubb 1988) and are frequently found outside of foraging flocks (Contreras unpubl. data; Farley et al. in review). Other species (more than 12-15) that associate regularly with titmouse flocks play the role of ‘satellite’ species (Gaddis 1983; Grubb and Pravosudov 1994; Greenberg 2000). Regular satellite species in North-central Florida include a diverse set of species: Black-and-white warblers (*Mniotilta varia*), Downy woodpeckers (*Picoides pubescens*), Ruby-crowned kinglets (*Regulus calendula*), Blue-headed and White-eyed vireos (*Vireo solitarius*, *V. griseus*) and Blue-gray gnatcatchers (*Poliophtila caerulea*; Farley et al. in review). Contreras (unpubl. data) has shown that heterospecific flock members follow titmice around the flock territory, providing direct evidence that titmice are likely to play an active leadership role as the dominant nuclear species in this system. Nuclear species of mixed-species bird flocks are generally characterized by behavioral traits that lend themselves to interspecific communication; including interspecific dominance, a high level of vigilance, and intraspecific sociality (Munn and Terborgh 1979; Hutto 1994). While not often tested effectively, nuclear species in bird flocks are thought to facilitate flock formation and sometimes food-finding, initiate and guide flock movements, and reduce predation risk for satellite species (Mönkkönen et al. 1996; Dolby and Grubb 2000). In addition, parid nuclear species act as sentinels by giving anti-predator vocalizations in response to predators, thereby alerting other flock members to danger (Gaddis 1983; Dolby and Grubb 1998).

Tufted titmice serve as nuclear species in mobbing aggregations of birds as well as in foraging flocks. Mobbing aggregations, where one or more bird species gather around and harass a predator, are relatively common in North-central Florida. These aggregations, that can include more than 20 or 30 species of forest birds (Sieving et al. 2004), are formed when a predator is spotted that is not an immediate mortality threat (e.g., a perched predator). Titmice are the most vigilant and aggressive species in mobbing aggregations and these aggregations appear to form around them (Greenberg 2000; S. A. Hetrick, pers. obs.). In North-central Florida, up to half of the forest bird community responds to titmouse mobbing calls (more than to other common local species' mobbing or alarm calls in this system) by approaching the sounds and engaging in mobbing behavior (Sieving et al. 2004). Thus, it is likely that a complex interspecific communication system exists between the Tufted titmouse and sympatric heterospecifics involving both the production of situationally specific anti-predator calls and contextually appropriate responses to these calls by others (Morse 1973; Sullivan 1984; Zimmerman and Curio 1988).

Anti-Predator Calls of the Tufted Titmouse

The Paridae have two main anti-predator vocalizations in their repertoire: the 'seet' alarm call (Fig. 3-1a; also known as the high zee, high see, 'aerial' predator call) and the mobbing or scold call (known variously as, churring, seejert, chick-a-dee; Smith 1972; Ficken and Witkin 1977; Gaddis 1979). Mobbing calls are variants of the 'chick-a-dee' call, which is a complex call composed of combinations of introductory 'chick' notes and subsequent 'D' notes (dee notes, churr notes), with the number and presence of each note type being variable (Fig. 3-1b, c; Latimer 1977; Hailman 1989). The 'chick-a-dee' call complex (or portions of it) is produced in many non-predator situations in addition to being the dominant mobbing vocalization (Latimer 1977; Hailman 1989; Grubb and Pravosudov 1994). Which call is given depends on the

situation; for example, an alarm call (seet) will typically be given to a raptor in flight that poses an immediate threat of attack, while mobbing calls are typically given to perched raptors representing much less risk of attack (Ficken 1989, S. A. Hetrick, pers. obs.). Mobbing calls are easily localizable and are given when other birds are attracted to harass the perched predator, whereas alarm calls are difficult to locate and result in the cessation of all vocalizations and movement (freezing) by the caller and nearby birds or in rapid escape to cover (Ficken 1989; Baker and Becker 2002; Howell 2006).

While it seems clear that interspecific risk-based signaling is likely to be quite common in vertebrate communities, based on the diverse studies showing perception specificity among heterospecific receivers of anti-predator calls (Nuechterlein 1981; Sullivan 1984; Seyfarth and Cheney 1990; Hurd 1996; Shriner 1998; Windfelder 2001), the degree to which most of these signaling systems are risk-based and/or predator-specific is unknown.

Research Design

I conducted two experiments to address whether Tufted titmice possess an interspecific risk-based call system in response to predators. Experiment 1 involved presenting high- and low-risk predators and controls to titmouse flocks to address the *situational specificity* of the titmouse's vocal responses. Experiment 2 was a playback study that addressed the *perception specificity* of Carolina chickadee pairs to titmouse anti-predator vocalizations in response to the high- and low-risk predators (obtained in Exp. 1) and titmouse seet vocalizations.

Hypotheses

I propose that Tufted titmice have an interspecific risk-based call system in response to predators. This type of call system is composed of 2 parts, which represent 2 distinct hypotheses and I conducted a separate experiment for each hypothesis. The first experiment tested the *situational specificity hypothesis* that titmice will vary the structure of their mobbing calls

according to the situation (Blumstein 1999a; Blumstein and Armitage 1997a,b). One way to do this is to vary the structure of the calls according to the degree of risk that they are presented with. Titmice can vary their mobbing calls in many ways. They can vary the number of mobbing calls given, and within a mobbing call they can vary the type of notes given (introductory chick notes or D notes), how many times a note is given, the temporal parameters of the notes and calls (e.g., note duration, interval between notes and calls) and the acoustic structure of notes (e.g., bandwidth, entropy). Titmice may use all or some of these ways to vary their mobbing calls with respect to threat level. Several researchers have found that parids respond to higher threat levels by increasing their call rate and increasing the number of D notes within the calls (Apel 1985; Baker and Becker 2002; Templeton et al. 2005). Some parids decrease or drop the introductory notes of the mobbing call while extending the D note section as the level of risk increases (Gompertz 1961; Latimer 1977). In addition, Templeton et al. (2005) found that Black-capped chickadees (*Poecile atricapilla*) vary certain temporal measures and the acoustic structure of certain notes when presented with predators of different risk levels. I tested for all of these possible variations across different risk situations.

I also conducted an analysis of the behavioral responses of the titmice to the predators and controls as a standard for determining whether the chickadee responses in the next experiment were ‘appropriate’. Parids are known to mob perched predators, which do not pose an immediate predation risk (Langham et al. in press, S. A. Hetrick, pers. obs.). To characterize a mobbing response in Black-capped chickadees, Templeton et al. (2005) observed the number of chickadees that came within certain distances of the stimulus and the closest distance that any bird approached the stimulus. Since one of the accepted hypotheses for mobbing is to drive the predator out of the territory (Shedd 1982; Klump and Shalter 1984), it would make sense that

birds would have a greater motivation for mobbing higher-risk predators more intensely. One way to mob more intensely would be for more birds to approach the predator and to approach closer.

In the second experiment, I tested the *interspecific perception specificity hypothesis* that titmouse anti-predator calls should elicit appropriate responses from heterospecific flock members who hear the calls in the absence of the original stimulus (Macedonia and Evans 1993). For chickadees to give appropriate responses, I would expect them to respond to the playback of titmouse vocalizations to predator stimuli in the same way they would if the stimuli were present— in this case, indicated by the responses of titmice to the actual predator situations in Exp. 1.

Predictions

Experiment 1: Titmice produce risk-based mobbing calls that are situationally specific.

I predict that Tufted titmice will produce situationally specific mobbing calls that vary according to the degree of risk to which they are exposed. Specifically, I predict that titmice will vary their mobbing calls according to one or more of the parameters listed in Table 1.

To the Eastern screech-owl presentation, which represents a high-risk predator situation, I predict that the titmice will respond with greater mobbing intensity than to the Great horned owl presentation, which represents a low-risk predator situation. To respond with greater mobbing intensity to the Eastern screech-owl, I predict that the titmice will increase their mobbing call rate, approach the owl closer, and a greater proportion of titmice will come within 1m and 3m of the owl. I also predict that titmice will change their note composition by decreasing the number of chick notes and increasing the number of D notes as the risk level increases (Latimer 1977). In addition to call rate and note composition, variation in mobbing calls according to degree of

risk will be identified using the parameters listed in Table 1 (Apel 1985; Baker and Becker 2002).

Experiment 2: Chickadees exhibit interspecific perception specificity to titmouse anti-predator calls.

In addition, I predict that Carolina chickadees will respond to the titmouse anti-predator calls with some degree of perception specificity. I predict that the behavioral and vocal responses of chickadees will vary in response to playbacks of titmouse seet calls and calls for high- and low-risk predator situations. More specifically, in response to the playback of titmouse vocalizations given to a high-risk predator situation, I predict that the chickadees will respond with more intense mobbing by approaching the speaker more closely and giving a relatively larger number of ‘chick-a-dee’ calls (higher call rate) compared to the response to the playback of titmouse vocalizations elicited from a low-risk predator situation. A similar response was elicited from Black-capped chickadees when they were played conspecific mobbing calls in response to different predators (Templeton et al. 2005). Mobbing calls, in general, attract birds to the area of the caller to participate in mobbing (Hurd 1996; Baker and Becker 2002; S. A. Hetrick, pers. obs.); therefore, playbacks of titmouse mobbing calls would likely attract chickadees to the area of the speaker. I also predict that chickadees will alter their note composition as described for the titmice in Exp.1, as well as possibly varying other parameters listed in Table 1 in response to the different playback treatments. In response to titmouse seet calls, I predict that the chickadees will not generate mobbing, but will dive to cover and freeze while remaining silent without approaching the area of the speaker (Gaddis 1980; Ficken 1989).

Methods I: Situational Specificity Hypothesis

Five flocks consisting of 3 Tufted titmice were captured in Gainesville, Florida between 13 October 2005 and 5 January 2006. All 3 birds in each flock were captured at the same time from

the same location to ensure that the three birds knew each other. The birds were captured around suburban seed feeders using mist-nets and/or baited walk-in potter traps and then all birds were banded with uniquely colored leg bands. Immediately following capture the birds were transferred to a 12 x 8 x 4m outdoor aviary containing numerous live trees and snags, providing a semi-natural habitat at the USDA/APHIS/WS/NWRC Florida Field Station (United States Department of Agriculture, Animal & Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center; USDA lab) in Gainesville, Florida (Fig. 3-2). The aviary was constructed of ½ inch plastic mesh attached to 4 x 4in. posts. After the 24 hr habituation period, during which they were monitored for normal feeding activity and general health, flocks were tested for each of 4 mornings in a row while being fed *ad-libitum* from a feeder in the aviary. Birds were held for up to 7 days before being released back at their original capture site.

Predator Presentations

Each titmouse flock was presented with 4 treatments- a live Eastern screech-owl (high-risk predator, *Megascops asio*), a live Great horned owl (low-risk predator, *Bubo virginianus*) and 2 controls- a procedural control with a live Northern bobwhite quail (*Colinus virginianus*) and an experimental control with no stimulus (an empty perch). The owls were non-releasable, rehabilitated owls that were borrowed from Florida Wildlife Care, Inc. The 4 presentations were made in randomized order for each flock and spaced approximately 24 hours apart. Most hunting by both owls is nocturnal, but both owls occasionally hunt during the day (Packard 1954; Spendlow 1979; Gehlbach 1994). Diet studies have shown that both the Eastern screech-owl (screech owl) and the Great horned owl (great horned) prey on birds, but small songbirds comprise a much greater proportion of the diet of the small, maneuverable screech owl than the larger, less maneuverable great horned (reviewed in Gehlbach 1995 and Houston et al. 1998;

Gehlbach 1994; Turner and Dimmick 1981), thus making the screech owl a higher risk predator to the titmice (reviewed in Templeton et al. 2005).

I placed one of the stimuli in the aviary on a 1.2 m perch or platform (for the quail) under a removable cover and for the experimental control, I placed an empty perch under the cover, approximately 10min before the trial began and then retreated to a camouflaged blind just outside the aviary. Care was taken to ensure that the titmice did not view the stimulus until it was uncovered. The flock was given 5min or longer after the observer exited the aviary to resume normal behavior. Audio and video recordings and behavioral observations were then made for 5 minutes pre-stimulus and 7 minutes post-stimulus; however, only the first 2 minutes post-stimulus were included in the analysis. A Sennheiser omni-directional microphone (ME 62) was used to record vocal responses of the titmice directly onto a laptop computer using Raven Interactive Sound Analysis Software Version 1.1 with a sampling rate of 44100 at 16-bit resolution. Behavioral responses within the first 2min post-stimulus were characterized using the following behavioral variables adapted from Templeton et al. (2005): a) the closest distance any bird approached the stimulus (in m); b) the proportion of birds that came within 3m of the stimulus; c) the proportion of birds that came within 1m of the stimulus; and d) whether the birds were frozen in place during the entire treatment (Table 1). For the behavioral variables (a-c), I used Kruskal-Wallis non-parametric test with one-tailed Mann-Whitney U (MWU) post-hoc tests to conduct pairwise comparisons among the treatments.

Spectrographic Analyses

I analyzed vocal responses in 13 of the 20 presentations (n=5 for the screech, n=4 for the great horned, n=4 for the controls) because titmice did not vocally respond in 7 of the presentations. Due to the low instance of vocal response to the procedural control (n=2) and experimental control (n=2), the controls were lumped together in the analyses, resulting in n=4

control samples. Spectrographic analyses were performed on the vocal recordings using Avisoft SASLabPro 4.39. To edit out noise, each sound file was FIR low-pass filtered at 12kHz and high-pass filtered at 1.8kHz. The spectrogram parameters used were FFT=512, Frame Size=75%, Window=Hamming, and Overlap=87.5%.

The notes in each call, or ‘chick-a-dee’ call complex, were visually classified as introductory ‘chick’ notes or subsequent ‘D’ notes. The various introductory notes grade into each other and are not reliably distinguished into natural categories; therefore, they were classified together as ‘chick’ notes (Fig. 3-3). On the other hand, D notes can be reliably classified (Bloomfield et al. 2005) due to their harmonic-like structure and little frequency modulation. D notes also have a higher entropy and lower frequency than the introductory chick notes, and D notes always occur at the end of the call, or are the only notes comprising a call, making them easily distinguished from introductory notes (Fig. 3-3). Seet calls given by responding titmice were omitted from analysis because the recording equipment could not pick them up due to their extremely low amplitude. Single A or ‘chip’ notes were omitted in the analysis due to their prevalence and predominantly low amplitude and ‘peter’ songs were omitted in order to include only vocalizations used in the anti-predator context (Latimer 1977; Gaddis 1979).

For the predator treatments, there was only one titmouse contributing to the majority of the vocal mobbing in 4 out of the 5 flocks. This may be explained by the existence of social dominance hierarchies within the flock, with the alpha male possibly contributing the majority of the anti-predator vocalizations (Brawn and Samson 1983), as occurs in the closely related Willow tit (*Parus montanus*; Hogstad 1993) and in Pale-winged trumpeters (*Psophia leucoptera*; Seddon et al. 2002). In 3 of the 5 flocks, it was a known adult male that responded; in 1 flock, it

was a hatch year male; and in 1 of the flocks it was an adult of unknown sex (likely a male). Age and sex were determined according to the molt limit and wing chord criteria established by Pyle (1997). If more than one titmouse responded vocally to the treatment, the calls of the dominant titmouse responding were isolated and measured.

I measured several aspects of the notes and calls in the 2min post-stimulus recordings, including some that were based on measures used in previous studies of parids (Baker and Becker 2002; Freeberg et al. 2003; Templeton et al. 2005). For each treatment, I averaged the number of calls, the number of chick and D notes overall, the number of notes per call, the number and proportion of chick and D notes per call, the duration of each chick and D note, the call duration, the duration of the 1st D note per call, the interval between notes, the interval between the chick and D section, and the interval between calls (Table 1).

Spectrum-Based Measures

I also measured several fine-scaled acoustic parameters on a sub-sample of 10 D notes that were randomly chosen from each 2min post-stimulus recording. If there were fewer than 10 D notes in the 2min post-stimulus recording, as was frequently the case for the controls, I chose as many D notes as possible from the recording. In all cases, the D notes were chosen from high-quality recordings. I measured the spectrum-based parameters of the D notes in the sub-sample using a power spectrum with FFT length=512. The parameters were computed at the maximum spectrum of the entire D note (maxpeakhold) and are similar to those used by Nowicki (1989) and Templeton et al. (2005). The parameters were minimum and maximum frequency where the amplitude goes last below -30dB and where the amplitude goes last below -10dB (min. and max. frequency with the total option activated in Avisoft SASLabPro 4.39), bandwidth at -30dB and -10dB (calculated with min and max frequency described previously), entropy, and the number of peaks above -10dB.

For each acoustic factor that was measured, I used univariate analysis of variance (ANOVA) with the least significant difference (LSD) post-hoc test to conduct pairwise comparisons among the treatments. I transformed the data when appropriate to meet the assumptions of the analysis using \sqrt{n} , $\arcsin(\sqrt{n})$, and $\log(n+1)$ transformations (Sokal and Rohlf 1995). All statistical analyses were conducted using SPSS 11.5 for windows.

Because many of the variables were correlated with each other, I performed a Principal Components Analysis (PCA) on all 14 general spectrographic measures and 3 behavioral measures (excluding the measure of whether the birds froze in place). I used the uncorrelated composite variables generated from the PCA in a Discriminant Function Analysis (DFA) to determine if the discriminant functions could correctly classify the flock responses to one of the three treatments. Significance in all statistical tests was set at the 0.05 alpha-level.

Results I

The results of the univariate ANOVAs showed that all of the behavioral variables and 13 out of 14 of the general spectrographic variables that were measured varied with treatment ($p < 0.05$). I determined which treatments differed from the others with the LSD pairwise comparisons test. In some cases, the Eastern screech-owl treatment was significantly different from the Great horned owl, which were both significantly different from the lumped (procedural and experimental) controls (hereafter referred to as control). All transformations and the results for all pairwise comparisons are shown in Appendix A (Table A-1, A-2). Means, SD and SE for all measures taken are presented in Appendix B (Table B-1).

Titmice exhibited more intense mobbing behavior when presented with the screech owl than with the great horned or controls. Titmice approached the screech owl more closely and more of the titmice came within 1m and 3m of the screech owl than of the great horned or control (Kruskal-Wallis $\chi^2_2=7.057$, $p=0.029$; $\chi^2_2=8.670$, $p=0.013$; $\chi^2_2=7.355$, $p=0.025$,

respectively, Fig. 3-4, 5), although the pairwise comparisons between the great horned and control were not significant. None of the titmouse flocks froze in place during any of the treatments.

The titmice gave different numbers of mobbing calls to the different treatments (ANOVA $F_{2,20}=12.2$, $p=0.001$; Fig. 3-6), with the high-risk screech owl eliciting a higher call rate than the low-risk great horned or control treatments (LSD $p=0.006$, $p<0.001$, respectively) and the great horned eliciting a higher call rate than the control, although the difference was not significant (LSD $p=0.200$). In particular, the high-risk screech owl elicited fewer chick notes per call ($F_{2,266}=378.4$, $p<0.001$; Fig. 3-7), more D notes per call ($F_{2,266}=837.8$, $p<0.001$; Fig. 3-7), and a greater number of D notes overall ($F_{2,20}=16.2$, $p<0.001$; Fig. 3-8) than the great horned or control treatments. The overall number of notes per call ($F_{2,266}=359.9$, $p<0.001$) and the duration of the entire call ($F_{2,266}=280.0$, $p<0.001$) were greater and the interval between notes ($F_{2,1313}=7.7$, $p<0.001$) was shorter for the screech owl treatment than the great horned or control treatment.

Of the fine-scaled acoustic parameters that were measured, bandwidth at -30dB was different between the D notes in each treatment, with the screech owl treatment eliciting titmice to give D notes with a lower bandwidth than the great horned and control ($F_{2,105}=10.7$, $p<0.001$; all pairwise comparisons were significant). The screech owl treatment also elicited D notes with a higher minimum frequency (where amplitude goes last below -30dB) than the great horned or control ($F_{2,105}=13.1$, $p<0.001$; all pairwise comparisons were significant except between the screech and great horned treatment, $p=0.065$).

The results of the PCA on the 17 measures are summarized in Table 2. Four components with eigenvalues >1 were extracted from the data set. The first principal component (PC1) was

determined mostly by behavioral variables, call rate, and note composition variables. The second, third, and fourth principal components (PC2-4) were determined mostly by temporal features of the notes and calls. After varimax rotations, the first four principal components explained 85.3% of the variance, with PC1 accounting for 48.6% and PC2, 3 and 4 accounting for 15.7%, 10.8%, and 10.2% of the variance, respectively. The 17 variables are depicted in a bivariate plot that shows their respective values for PC1 and PC2 (Fig. 3-9). The DFA using the PCA factor scores led to 92.3% correct classification of the variables with the eliciting stimuli. The first of the two discriminant functions (DF1) accounted for 91.9% of the variation, and the second (DF2) accounted for 8.1 % of the variation. The resulting graph (Fig. 3-10) shows the separation of flock responses into three basic groups with clearly separated group centroids between the three treatments. The only misclassification was one of the flock's response to the great horned treatment classified as a response to the screech owl treatment.

Methods II: Interspecific Perception Specificity Hypothesis

Ten pairs of Carolina chickadees were captured in Gainesville, Florida between 10 January 2006 and 5 March 2006. The birds were captured, banded, and housed in the same manner as the titmice in Exp. 1. In the study region, observations of normal group sizes at feeders indicated that while titmice normally travel in groups of 3 or more, chickadees are nearly always in pairs. Thus the number of birds per 'flock' was different for the two species but was determined to be the most natural combinations of individuals likely to be related to, or at least familiar with, each other (flock members were always captured within a few minutes of each other at the same feeder – in the same mist net or in adjacent or same potter traps).

Playback Presentations

Playback recordings (2min duration) were constructed from recordings of titmouse mobbing calls, alarm (seet) calls and control vocalizations to make 5 independent replicates of

each of 4 playback treatment types. Two of the playback treatment types were of titmouse vocalizations acquired in Exp. 1 in response to the screech owl and the great horned. The control playback was constructed from pre-stimulus recordings of titmouse vocalizations (containing mostly contact vocalizations) acquired in Exp. 1. For each playback treatment type, there were 5 unique exemplars (5 different titmouse flock responses, recorded in Exp. 1). The fourth playback treatment type was of titmouse 'seet' calls acquired from other sources. Five unique seet call recordings (2min each, 123 to 217 seet calls per min) were made using seet calls recorded from one flock of free-living Tufted titmice responding to unknown stimuli (by Lang Elliot; <http://www.naturesound.com/>) and from a previous experiment with captive titmice responding to presentations of predators in close proximity (hawk, owl or cat; n=4 different birds, by S. A. Hetrick; see Chapter 2). Each of the 20 playback recordings (5 variants of each of 4 treatment types) was used twice for a total of 40 playbacks (n=40). Each of ten chickadee pairs received 4 of the playbacks (one each of the 4 treatments). The 4 treatments were presented in random order for each pair and spaced approximately 24 hours apart.

At the beginning of each playback treatment, SAH placed a pair of camouflaged RadioShack speakers (Model 40-1431) in the aviary on a 1.2m platform approximately 10min before the trial began and then retreated to a camouflaged blind just outside the aviary. For each treatment, the speakers were randomly placed in one of three locations in the aviary in order to reduce habituation to a particular direction. The pair was given 5min or longer after the observer entered the aviary to resume normal behavior. Recordings and behavioral observations were then made for 5min pre-playback, during the 2min playback of the titmouse vocalizations and for 5 additional min post-playback. The methodology from Exp. 1 was followed to record and

video-tape the chickadees' behavioral and vocal responses. This methodology was also used to analyze the behavioral variables associated with the chickadees' response.

Spectrographic Analyses

For each treatment, I analyzed 3min of behavioral responses and conducted spectrographic analyses of 3min of recordings. Some chickadee pairs gave strong responses during the 2min playback while some waited until the playback had finished to begin responding, so analysis of 3min total (2min during the playback and 1min post-playback) was deemed the most appropriate. Chickadee behavioral responses and acoustic parameters were characterized as in Exp.1. I did not analyze fine-scale acoustic measures on the chickadee vocalizations because most of the chickadee vocalizations overlapped with the titmouse vocalizations in recordings of the playback trial. The acoustic data were analyzed using univariate ANOVA with the LSD post-hoc tests to conduct pairwise comparisons among the treatments. The 'seet' playback was only considered in the analysis of the behavioral responses and excluded from the spectrographic analyses of vocalizations due to the low instance of calling during the playback treatment. Significance in all statistical tests was set at the 0.05 alpha level.

Results II

The results of the univariate ANOVAs showed that all of the behavioral variables and 9 out of 10 of the general spectrographic variables that were measured varied with playback treatment ($p < 0.05$). The LSD pairwise comparisons showed that in some cases, the chickadee's response to the screech mobbing playback (playback of the titmouse vocalizations elicited from a screech owl) differed from the response to the great horned mobbing playback (playback of titmouse vocalizations elicited from a great horned), which both differed from the response to the control playback (playback of pre-stimulus titmouse vocalizations). In other cases, one or more of the playback treatments did not differ from the other playback treatments. The details of the

transformations and the results for all pairwise comparisons are shown in Appendix A (Table A-3, A-4). Means, SD and SE of all measures taken are presented in Appendix B (Table B-2).

Chickadees exhibited more intense mobbing behavior when they heard the screech mobbing playback than when they heard the great horned mobbing and control playbacks. Chickadees approached the speakers that broadcast the vocalizations more closely and both members of the pair were more likely to come within 1m and 3m of the camouflaged speaker in response to the screech mobbing playback than to the great horned mobbing, control, or seet playbacks (Kruskal-Wallis $\chi^2_3=23.666$, $p<0.001$; $\chi^2_3=24.118$, $p<0.001$; $\chi^2_3=16.687$, $p=0.001$, respectively; Fig. 3-11, 3-12), although some pairwise comparisons were not significant (see Appendix A, Table A-3). The chickadee pairs did not freeze in place during any of the playbacks except the seet playback in which they each froze for 100% of the 3min experimental periods (and for long periods afterwards).

The screech mobbing playback elicited an overall greater number of notes per call (ANOVA $F_{2, 338}=9.1$, $p<0.001$) with a fewer number of chick notes per call ($F_{2, 338}=32.3$, $p<0.001$; Fig. 3-13) and a greater number of D notes per call ($F_{2, 338}=27.6$, $p<0.001$; Fig. 3-13) than the great horned mobbing or control playbacks. All of the pairwise comparisons were significant for these three variables except for the number of chick notes per call for the great horned mobbing playback and control playback (LSD $p=0.108$). The call duration and the average duration of each D note were greater for the screech mobbing playback than the great horned mobbing or control playbacks ($F_{2, 335}=27.8$, $p<0.001$; $F_{2, 775}=119.9$, $p<0.001$, respectively).

Discussion

Situational Specificity of Titmouse Mobbing Calls with respect to Risk

The results of the predator presentation experiment confirmed that Tufted titmice have situationally specific mobbing calls in that their calls varied according to the situation. These calls are risk-based because the calls varied according to risk. More specifically, the results confirmed my prediction that titmice would exhibit a stronger mobbing response to the higher risk predator. Behavioral responses of titmice to the predator presentations showed that titmice clearly distinguished high and low degrees of risk by exhibiting a more intense mobbing response to the high-risk Eastern screech-owl. They approached it more closely (within 1m) and gave a greater number of ‘chick-a-dee’ mobbing calls than to the low-risk Great horned owl (Fig. 3-4, 3-6). These results are consistent with the results of other researchers who found that other species in the family Paridae increase their mobbing call rate as the level of risk increases (Latimer 1977; Apel 1985; Baker and Becker 2002; Templeton et al. 2005). Black-capped chickadees (*Poecile atricapilla*) altered their rate of calling in response to a stuffed falcon at near and far distances (Baker and Becker 2002) and in response to different predator species (Templeton et al. 2005), by calling at higher rates in the higher risk situations. Many species of rodent also increase their rate of calling as risk increases (Nikol'skii and Pereladova 1994; Blumstein and Armitage 1997a; Randall and Rogovin 2002).

Titmice also varied their note composition in response to the different predators by decreasing the amount of introductory chick notes per call and increasing the amount of D notes per call as risk increased (Fig. 3-7). These findings agree with the observations of past authors who noted that as the level of fear or risk increases, titmice drop the prefix (chick) notes and increase the churr (D) notes (Odum 1942; Gompertz 1961; Latimer 1977). Variation in note composition was previously thought to encode information related to many factors, including

information about predators (Hailman et al. 1985, 1987; Ficken et al. 1994). Black-capped chickadees alter the number of introductory A and B notes in their ‘chick-a-dee’ mobbing calls in response to predators presented at different distances (Baker and Becker 2002) and vary the number of D notes in the calls in response to raptors of different sizes, with the smaller, higher risk raptors eliciting the most D notes (Templeton et al. 2005). According to my findings and the findings of the authors listed above, it appears that call rate and note composition, in particular, are important for titmice and chickadees in communicating about risk.

I also found that titmice varied the note interval and the bandwidth of the D notes according to the level of risk, which the chickadees could be cueing in on to help them interpret the content of the titmouse calls. Other birds and mammals have also been documented to change the structure of their call notes in different predator situations. White-browed scrubwrens (*Sericornis frontalis*) vary the structure of their aerial trill call by increasing the minimum frequency (pitch) of their calls according to the distance from a suddenly appearing predator (Leavesley and Magrath 2005). Yellow-bellied marmots also vary several frequency characteristics of their calls, including bandwidth, as a function of distance to certain predators (Blumstein and Armitage 1997a). In both of these studies, the distance from the predator to the subject represents the amount of risk, with the closer distances representing higher risk of being caught or attacked by a predator; thus, we can conclude that both the scrubwren and the marmot vary the structure of their calls according to the degree of risk that they perceive. As Templeton et al. (2005) noted, variation in the structure of calls in response to different predators, reflecting the degree of risk perceived, likely occurs in many species, but few researchers have tested for this.

The results of the DFA indicate that the high- and low-risk predator treatments and control treatment can be reliably (in 92.3% of the cases), and potentially uniquely, distinguished by the combined behavioral and general spectrographic variables that were measured in this experiment (Fig. 3-10). The combination of variables measured clearly discriminate between the titmouse responses to the treatments, raising the possibility that the production of anti-predator signals could be predator-specific. Davis (1991) made a similar argument that yellow-bellied marmots had predator-specific calls based on results from a multivariate DFA. If the titmouse's response were predator-specific, this would mean that while individual acoustic and behavioral parameters may vary in a graded fashion across predator situations (e.g., more and fewer D notes), the combination of multiple acoustic characteristics encoded in titmouse anti-predator signals could (together) uniquely identify distinct predator species or classes. It is impossible to conclude this, however, without further study of the nature of call production in Tufted titmice.

Some variation was evident in the vocal responses between the different titmouse flocks, and this could be attributed to the predator's movement and behavior at the time of presentation. Many authors have observed that the behavior of a predator affects birds' reactions to it. Increased call rates and more intense mobbing as a result of predator movement were reported in several species of birds including Carolina wrens (*Thryothorus ludovicianus*; Morton and Shalter 1977), Eurasian blackbirds (*Turdus merula*; Frankenberg 1981), and Pied flycatchers (*Ficedula hypoleuca*; Shalter 1978; reviewed in Apel 1985). It has also been suggested that some passerines can even detect differences in posture and behavior that are associated with how hungry a predator is, and mob more frequently if the predator is hungry (Hamerstrom 1957). In the present study, we did not detect that the two owls exhibited differences in posture or that their movement differed at different times, but we did not examine this, since they were tethered

to the perch and were generally calm during experiments. I did observe that the owls were sometimes looking in the direction of the titmice and sometimes looking in the opposite direction. On one occasion, the great horned owl jumped down from the perch to the ground and this seemed to evoke a momentary increase in titmouse call rate.

In general, it is well accepted that parids give alarm calls in response to predators that pose an immediate threat, such as an aerial predator in a low attack flight, and that they give mobbing calls to predators that do not pose an immediate threat, such as a perched predator (Gaddis 1980; Ficken 1989). Having different calls for different classes of predators suggests that titmice may be giving predator-specific calls, although this argument is weakened because there are many exceptions as to when titmice give these calls (see below). Here, I show that mobbing calls given by titmice to high- and low-risk (but all perched) predators and no-risk controls are also clearly situationally specific. Whether they are categorically different (predator-specific) or graded into one another (risk-based) may depend on how the calls are perceived by receivers. For example, if a receiver is listening to only the number of D notes given per minute (Fig. 3-8) then the level of risk being communicated will be graded across the range of numbers of notes given – and these can vary among individuals presented with the same stimulus. In these cases, the communication would be risk-based and not predator-specific by standard definitions (Macedonia and Evans 1993; Blumstein and Armitage 1997a; Blumstein 1999a). However, if a receiver is basing its assessment of risk on more than one parameter characterizing the titmouse mobbing calls, then 3 distinct (non-overlapping) classes of risk could be represented in the titmouse vocal responses to the three types of stimuli (2 owls vs. control). In either case, titmice are giving vocal signals that distinguish between high- and low-risk predators (both perched and not of immediate threat) and no-risk controls (quail or empty perch). More work is needed to

determine whether single or multiple call characteristics generate the most ‘appropriate’ responses in receivers.

Some bird species possess predator-induced calls that are functionally referential- that is the calls are predator-specific with respect to predator species or class (e.g., high degree of production specificity) and they produce appropriate responses in the individuals hearing them (e.g., high degree of perception specificity; Klump and Shalter 1984; Evans et al. 1993; Blumstein 1999a; Seddon et al. 2002). Within this framework, titmouse anti-predator calls appear to be functionally referential in that they usually give seet alarm calls to aerial predators and ‘chick-a-dee’ mobbing calls to perched and terrestrial predators (Gaddis 1980; Ficken 1989). In purely experimental situations used here (Chapters 2 and 3), I have found that this is not always the case, as perched predators and terrestrial predators presented to titmice in captivity sometimes elicited seet calls. This would imply a lower degree of production specificity for the seet call than is generally supposed. Seet call use may be more related to the level of fear or surprise that an individual experiences (Marler 1957; Apel 1985) and in captivity, fear levels could be generally higher than in the wild. ‘Chick-a-dee’ calls also appear to have a low degree of production specificity because they are given in a variety of non-predator situations as well as being the main mobbing vocalization (S. A. Hetrick, pers. obs.). Because one of the main requirements for functional reference is high production specificity, there is weak evidence that titmouse anti-predator calls are functionally referential because both calls appear to have low production specificity.

Perception Specificity of Chickadees Exposed to Titmouse Anti-Predator Calls

The results of the playback experiment confirmed my prediction that chickadees would respond with greater mobbing intensity to titmouse calls given in response to the high-risk screech owl and with freezing and silence to the titmouse seet playback. In other words,

chickadees that heard the titmouse calls were able to interpret them and respond appropriately. When the chickadees heard the screech mobbing playback, they responded (as the titmice did in response to the screech owl) by approaching the stimulus more closely (within 1m) than to the great horned mobbing playback (Fig. 3-11). Black-capped chickadees respond in a similar way to conspecific vocalizations elicited by high- and low-risk predators by altering their approach distance to the stimulus (Templeton et al. 2005).

In the present study, chickadees responded to the screech mobbing playbacks by altering the note composition of their ‘chick-a-dee’ mobbing calls. They decreased the amount of introductory chick notes and increased the amount of D notes per call (Fig. 3-13). I was unable to examine more subtle variations in call and note structure of the chickadee calls in this study (see methods) but it is likely that these varied in other ways similar to those of Black-capped chickadees and titmice (e.g., bandwidth, frequency; Templeton et al. 2005; Exp. 1). But by documenting that the relative frequency of chick versus D notes per call varied by treatment, my conclusions about risk-appropriate responses by chickadees are supported by the findings of others (Apel 1985; Baker and Becker 2002; Templeton et al. 2005). And responses of the chickadees clearly paralleled those of the titmice (Exp.1), indicating that chickadees responded to the titmouse calls, in the absence of other cues, in much the same way that the titmice responded to the actual predators.

When the chickadees heard playbacks of titmouse seet alarm calls, they froze in place every time and were almost totally silent for 5min or longer. This is similar to the observations of Ficken and Witkin (1977) who found that Black-capped chickadees immediately became motionless or moved to cover if in the open and froze upon hearing the alarm (e.g., high zee) calls of another chickadee. Several other authors have observed that recipients stop moving and

become silent upon hearing these calls (Ficken et al. 1978; Gaddis 1980; Waite and Grubb 1987; Ficken 1989). These responses make sense because seet calls are thought to be given when birds are fearful and/or perceive imminent attack, as with the sudden emergence of any potential predator including (especially) flying or low-cruising raptors (Latimer 1977; Ficken et al. 1978; Apel 1985; Ficken 1989). Smith (1972) suggested that seet calls probably function to alert recipients to danger. If the message that titmice are giving with their seet calls is extreme danger, it seems appropriate that the chickadees would respond by freezing in place and becoming silent. These behaviors would allow an individual to remain inconspicuous in the face of potential immediate danger, for example, to lessen the risk of being detected by a cruising predator that had not been located by the prey. In sum, responses to the situationally specific anti-predator calls of the titmouse suggest a high degree of perception specificity in chickadees.

Titmice Give Interspecific Risk-Based Mobbing Calls in Response to Predators

Although many researchers have demonstrated that anti-predator calls can communicate specific predator information to conspecifics (intraspecific communication), few have shown that these calls can also have meaning to heterospecifics (interspecific communication). Mixed species groups of lemurs, (*Eulemur fulvus rufus* and *Propithecus verreauxi verreauxi*) have evolved an interspecific functionally referential alarm system for diurnal raptors where both species respond to the calls of conspecifics and heterospecifics in the group (Fichtel and Kappeler 2002). Western grebes (*Aechmophorus occidentalis*) that nest in association with Forster's terns (*Sterna forsteri*) respond to the alarm calls of the terns by leaving their nests and swimming to open water (Nuechterlein 1981). Other primate, rodent, and avian groups may have interspecific anti-predator calling systems as well (Marler 1957; Francis et al. 1989; Shriner 1998; Windfelder 2001; Langham et al. in press). Compared to the large proportion of vertebrates that join mixed species groups (reviewed in Greenberg 2000), and the pervasive

evidence that most animal groups form, at least in part, to gain anti-predator advantages (Caro 2005), a lack of interspecific communication related to predator avoidance may be more surprising than its presence – but more work is needed to survey for the prevalence of these communication systems.

Most researchers that have found risk-based (or urgency-based) call systems in response to predators have focused on typical alarm calls as opposed to mobbing calls (Robinson 1980; Blumstein 1995a; Blumstein and Armitage 1997a; Leavesley and Magrath 2005). This distinction is important because alarm calls are associated with a flight or freeze response while mobbing calls are associated with approach and harassment of the predator. Many species' mobbing calls, as well as their alarm calls, may also be able to communicate differences in the risk environment.

It is likely that perception specificity of titmouse risk-based mobbing calls occurs among many other species, besides the closely related chickadees, that associate with titmice in foraging and mobbing flocks and that simply share habitats with titmice. Downy woodpeckers, for example, respond with risk-averse behaviors when they hear titmouse alarm calls (Sullivan 1984) and this makes sense because they spend a great deal of time with titmice in winter foraging flocks (Farley et al. in review). More telling are the results of an experiment by Howell (2006) in which the same playback recordings of titmouse calls that I used in Exp. 2 (for chickadees) were presented to free-living Northern cardinals (*Cardinalis cardinalis*) that were feeding at platform feeders in the open. The cardinals responded with risk-appropriate behaviors (e.g., freezing to seeet calls, and diving for cover more often in response to mobbing calls to high-risk predators than to mobbing calls to low-risk predators). Northern cardinals will join mobbing flocks but not titmouse-led foraging flocks, so are not classified as a mixed-flock joiner.

However, they are sympatric with titmice in many habitats throughout their common range and so are exposed to titmouse anti-predator calls very frequently. Most surprising yet, is the evidence found by Schmidt (unpubl. data) that squirrels feeding in trays in the open also respond appropriately to titmouse alarm (seet) and mobbing calls. These results suggest that a wide range of species that are and are not associated with, or taxonomically related to, titmice may perceive titmouse anti-predator calls with a high degree of perception specificity.

Finally, though I conclude based on findings presented here that both production and perception of titmouse anti-predator calls are risk-based (graded, or continuous), the near-complete separation in multivariate space achieved by the DFA between the titmouse vocal and behavioral responses to control, great horned and screech owl presentations (Fig. 3-10) raises a second possibility. If receiving species are able to discern multiple acoustic characteristics of titmouse anti-predator signals (i.e., hear the calls in a multivariate fashion), they could be discriminating among predator-risk situations according to class, as in a predator-specific (categorical) call system rather than a risk-based (continuous) system of perception (Davis 1991). If so, then the anti-predator signaling system of titmice may actually be interspecifically functionally referential (Evans et al. 1993; Blumstein 1999a). However, it is impossible to draw this conclusion without further study of the nature of call perception in species that exhibit appropriate responses to titmouse anti-predator calls.

Potential Functions of Interspecific Risk-Based Mobbing Calls of Titmice

My study revealed characteristics of risk-based mobbing calls of titmice that could be used by chickadees and other species to assess situation-specific risks, and clearly shows what risk-appropriate behaviors are when mobbing and alarm calls are given. But why should titmice possess a complex communication system with interspecific risk-based mobbing calls? Alarm calls (for extreme danger) are produced in many species that are intraspecifically social, and

have been reasonably explained on the basis of kin selection (Hamilton 1963, 1964; Maynard Smith 1965; Sherman 1977; Woolfendon and Fitzpatrick 1984). Researchers have formulated many hypotheses as to why birds give mobbing calls to perched predators (Curio 1978, 1980; Smith 1991). One hypothesis that seems to make sense for our particular system is the “move-on” hypothesis where individuals seek to drive the predator from the area (Curio 1978).

Titmouse flocks hold stable winter territories and therefore would benefit by moving a predator out of their territory to decrease the risk of future predation (Brawn and Samson 1983). By giving interspecific risk-based mobbing calls, titmice can alert others to the specific situation and induce them to join in the mobbing of the predator. Risk-based calls in response to higher risk predators would likely generate a more intense mobbing response because titmice and the receivers would have a greater motivation for driving these predators out of the area. A more intense response would likely result in a greater chance of moving the predator out of the area, which would benefit all flock members.

Most of the birds that participate in foraging and mobbing flocks with titmice share the same predators. Shriner (1998) noted that when species have predators in common, they might be able to obtain important information about predation risk from the anti-predator calls of the other species, and so natural selection would drive the evolution of interspecific perception specificity. It has been shown that more birds are attracted to titmouse mobbing calls than other local forest species' mobbing calls (Sieving et al. 2004) and my work shows that this could happen, in part, because the titmice are providing detailed information about the risk environment in their calls that may help reduce the predation risk for other species that evolve to use that information. The possession of such calls by titmice suggests a mechanism underlying their socially dominant role in mixed-species foraging flocks. Tufted titmice give information-

laden vocalizations according to the risk environment and Carolina chickadees and potentially other flock members are able to interpret and exploit this information, which may be an incentive for them to join these mixed-species flocks (Gaddis 1980; Sullivan 1984; Howell 2006). Other flock members may also benefit from the titmouse' high rates of vigilance, which allows them to reduce their own vigilance and put more of their energy into foraging (Cimprich and Grubb 1994). Therefore, there are many reasons to associate with titmice, and the specific information about predation risk that titmice provide, in addition to their high vigilance and aggressiveness towards predators, may each play a role in decreasing the predation risk for other species that associate, or merely live, with titmice.

Summary

In summary, this study clearly demonstrates that titmice possess an interspecific risk-based call system with respect to predators. I have described many call characteristics that could be used to communicate situational specificity and I have shown that chickadees respond to titmouse anti-predator calls with a high degree of perception specificity. Other work is showing that the risk-based anti-predator calls of titmice are perceived by, and generate situationally specific responses in, a wide range of unrelated species. If most of the species that share predators with titmice participate in an interspecific risk-based communication system, then this suggests a mechanism that could underlie interspecific facilitation via predation-risk reduction among diverse sympatric vertebrate species. The majority of species in the family Paridae, that are distributed throughout the Holarctic, exhibit highly conserved (similar) mobbing calls and a high proportion of passerine species that live with titmice respond to titmouse mobbing calls by exhibiting typical predator-mobbing behaviors (Langham et al. in press). This study (and others) suggests that heterospecifics respond appropriately to parid anti-predator calls with a high degree of perception specificity. Therefore, parid anti-predator vocalizations support a system of

interspecific communication about risk in which many species that share their predators may participate. The existence of such a broad-based communication system suggests that interspecific facilitation within bird communities of the Holarctic (where parids are distributed) may be as common as other, more widely-studied, ecological interactions in organizing bird communities (e.g., predation and competition).

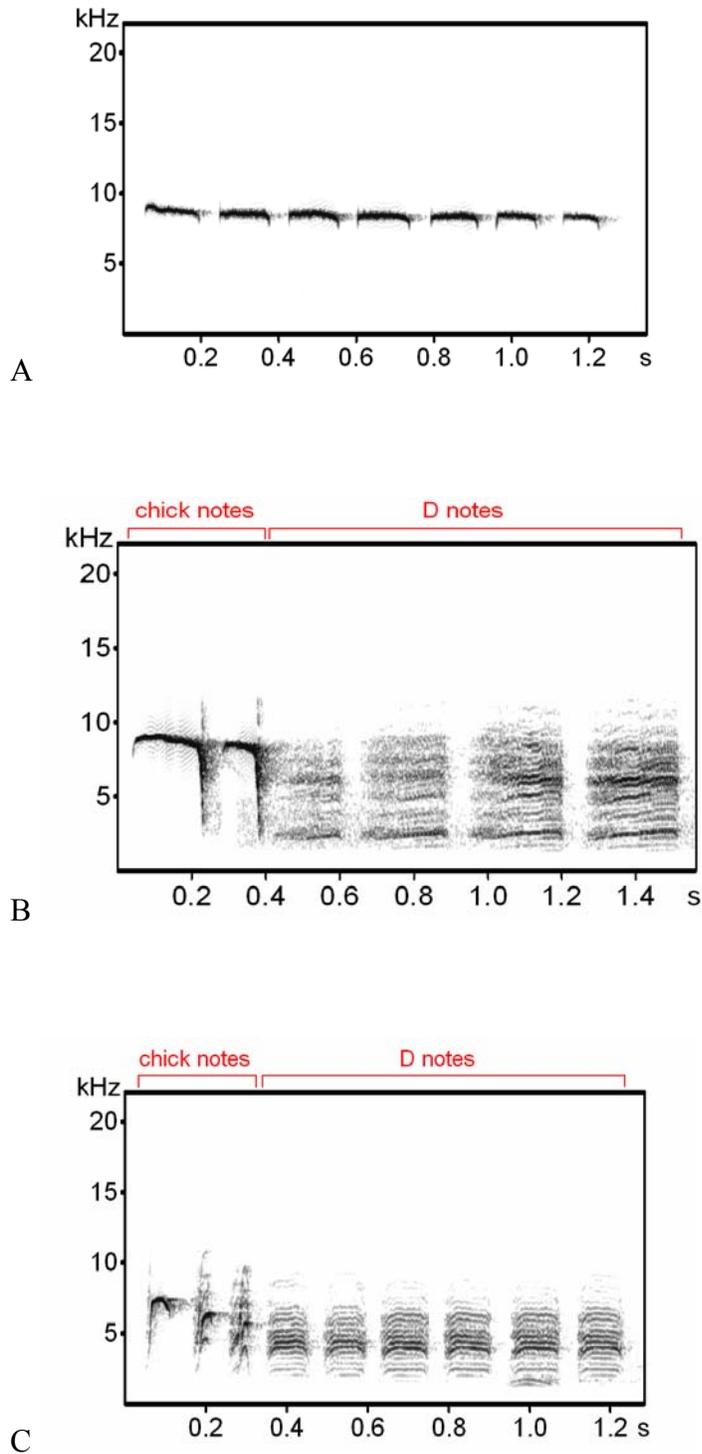


Figure 3-1. Examples of the major anti-predator vocalizations of the Paridae. A) Seet call of the Tufted titmouse. B) ‘Chick-a-dee’ mobbing call of the Tufted titmouse with introductory chick notes and subsequent D notes. C) ‘Chick-a-dee’ mobbing call of the Carolina chickadee with introductory chick notes and subsequent D notes.



Figure 3-2. Outdoor aviary at the USDA/APHIS/WS/NWRC Florida Field Station in Gainesville, Florida. Top picture: Platform with removable cover is in the center of the picture with camouflaged blind in background. Bottom picture: Another view of aviary with cover removed, revealing the Great horned owl on the perch.

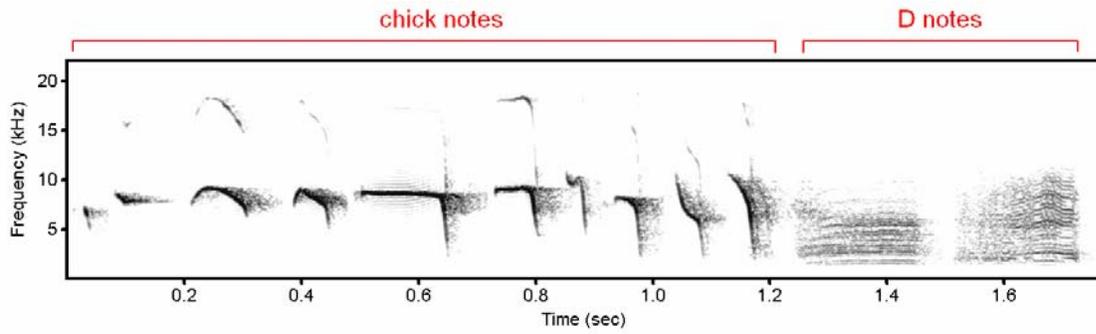


Figure 3-3. Examples of the variation in the chick notes and the less variable D notes in the 'chick-a-dee' call complex of the Tufted titmouse. The chick notes grade into each other and are not reliably distinguished into natural sub-categories.

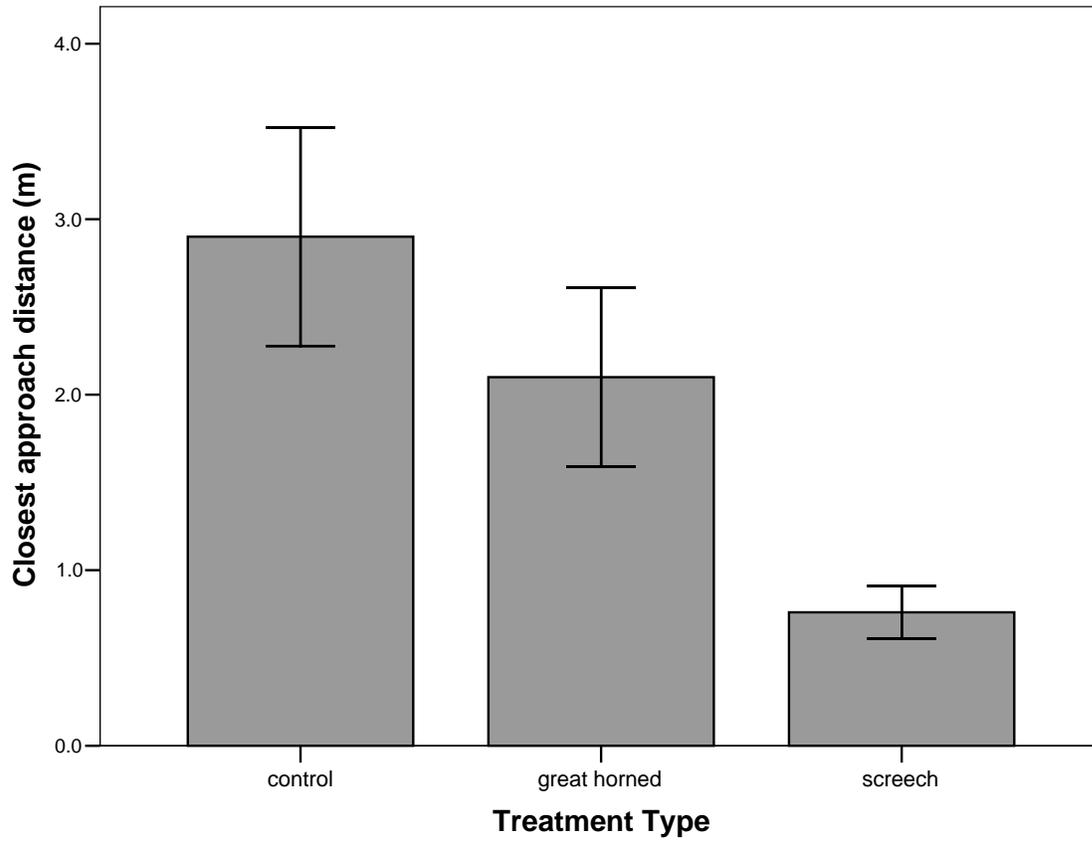


Figure 3-4. Closest approach distance of Tufted titmice to the stimuli during the predator and control treatments in the first 2min following presentation. All pairwise comparisons were significant (MWU, $p < 0.05$) except between the great horned and control treatments ($p = 0.594$). Error bars: ± 1 SE.

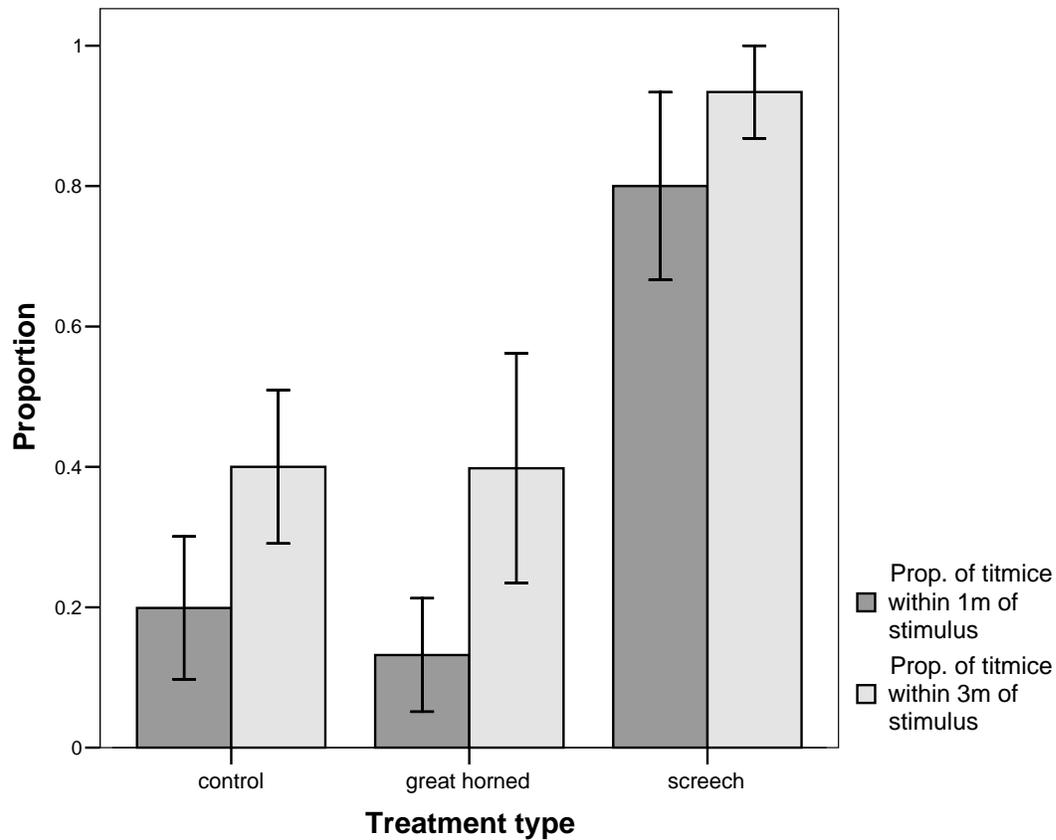


Figure 3-5. The proportion of Tufted titmice that approached within 1m and 3m of the stimuli during the predator and control treatments in the first 2min following presentation. For the proportion of titmice within 1m and 3m of the stimuli, respectively, all pairwise comparisons were significant (MWU, $p < 0.05$) except between great horned and control ($p = 0.953$, $p = 0.953$). Error bars: ± 1 SE.

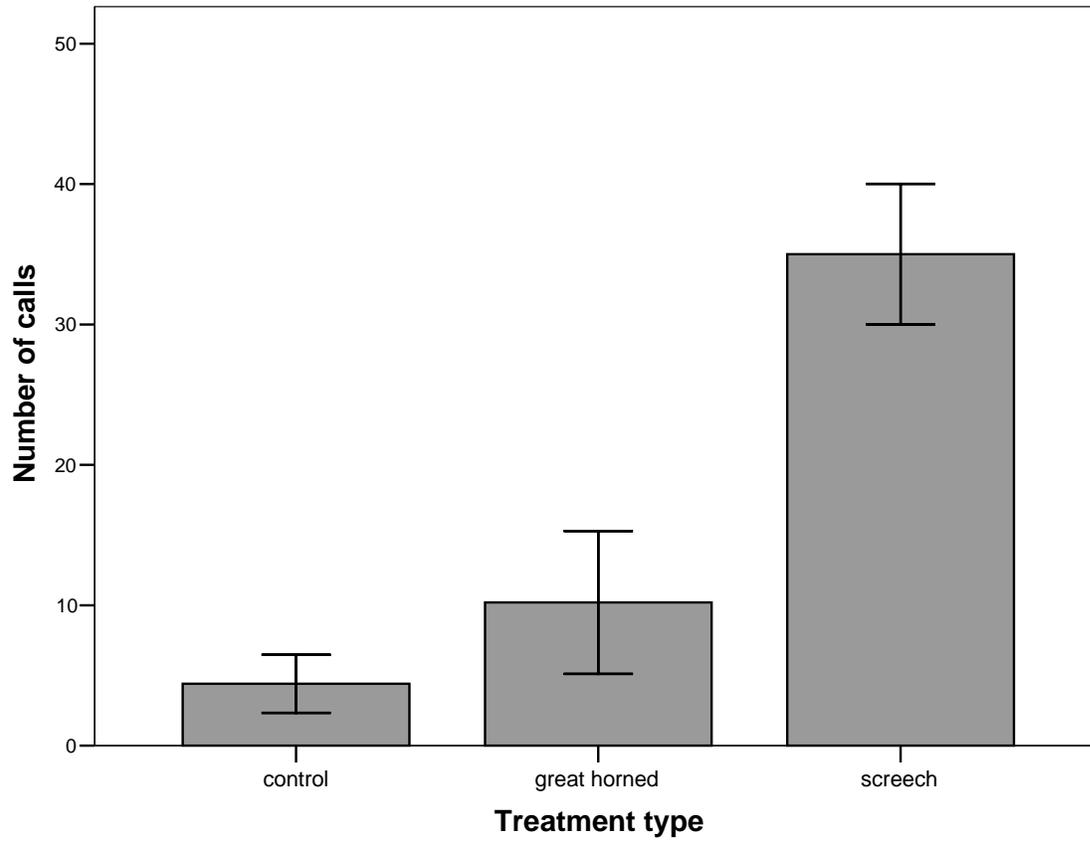


Figure 3-6. Number of 'chick-a-dee' complex calls given by Tufted titmice in response to the predator and control treatments in the first 2min following presentation. All pairwise comparisons were significant (LSD, $p < 0.05$) except between the great horned and control treatment ($p = 0.200$). Error bars: ± 1 SE.

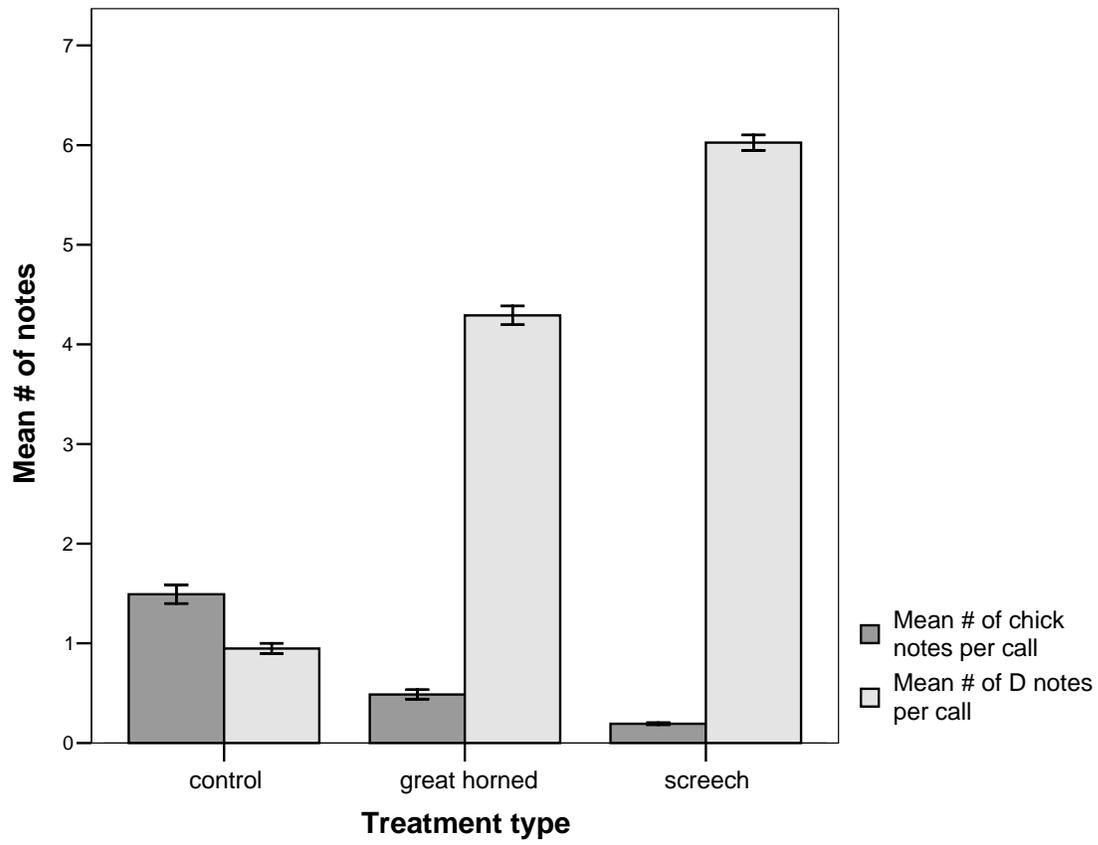


Figure 3-7. Number of chick and D notes per ‘chick-a-dee’ complex call given by Tufted titmice in response to the predator and control treatments in the first 2min following presentation. All pairwise comparisons were significant (LSD, $p < 0.05$). Error bars: ± 1 SE.

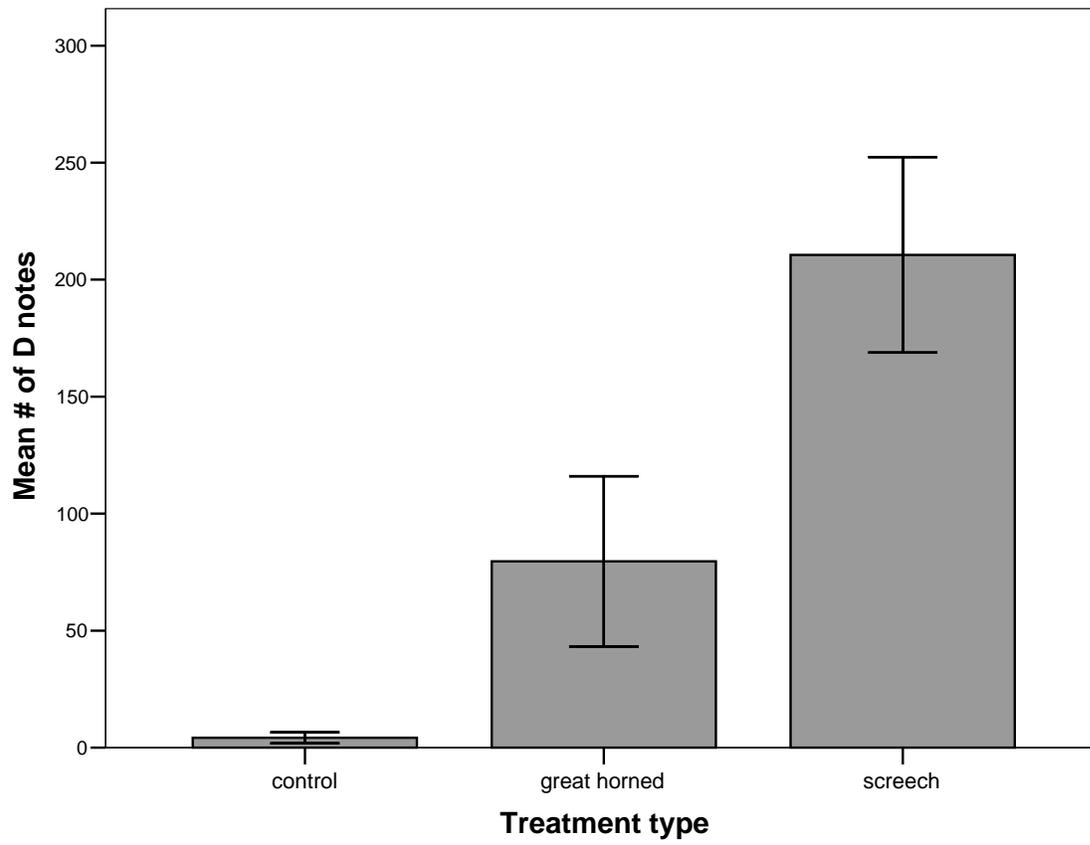


Figure 3-8. Mean number of D notes given by Tufted titmice in response to the predator and control treatments in the first 2min following presentation. All pairwise comparisons were significant (LSD, $p < 0.05$). Error bars: ± 1 SE.

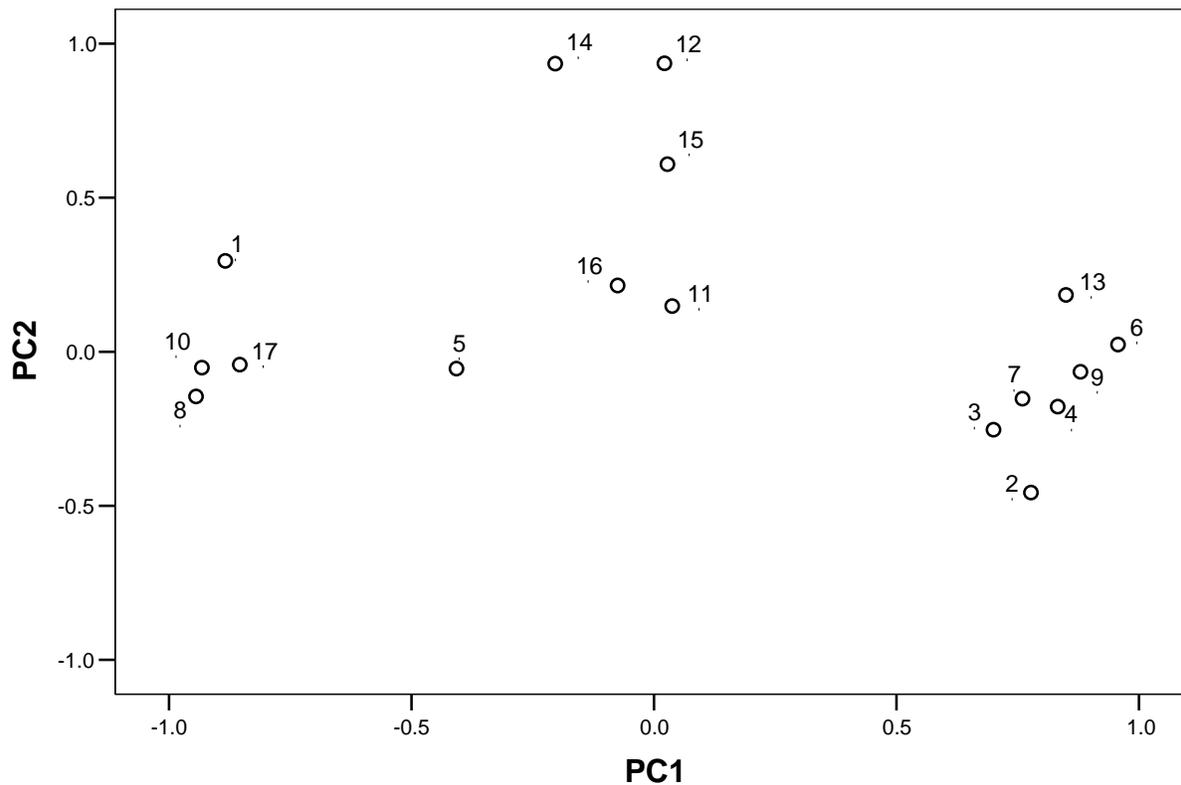


Figure 3-9. Plot of 17 behavioral and general spectrographic variables of Tufted titmouse calls in two-dimensional space defined by two principal components. PC1 is determined mostly by behavioral variables, call rate, and note composition variables, and PC2 is mostly by temporal features of notes and calls. The variables corresponding to the numbers in the plot are listed in Table 3-2.

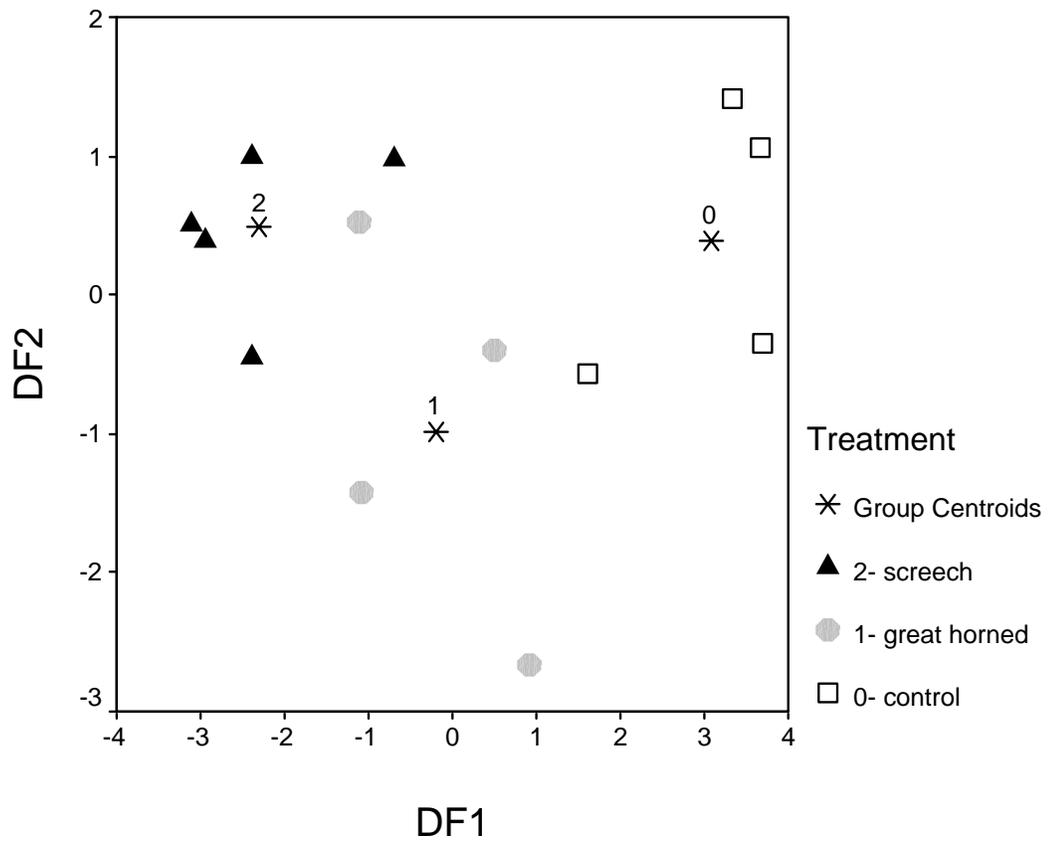


Figure 3-10. Graph of the results of the Discriminant Function Analysis for Tufted titmice with 4 PCA factor score input variables generated from 17 original behavioral and acoustic variables listed in Table 3-2.

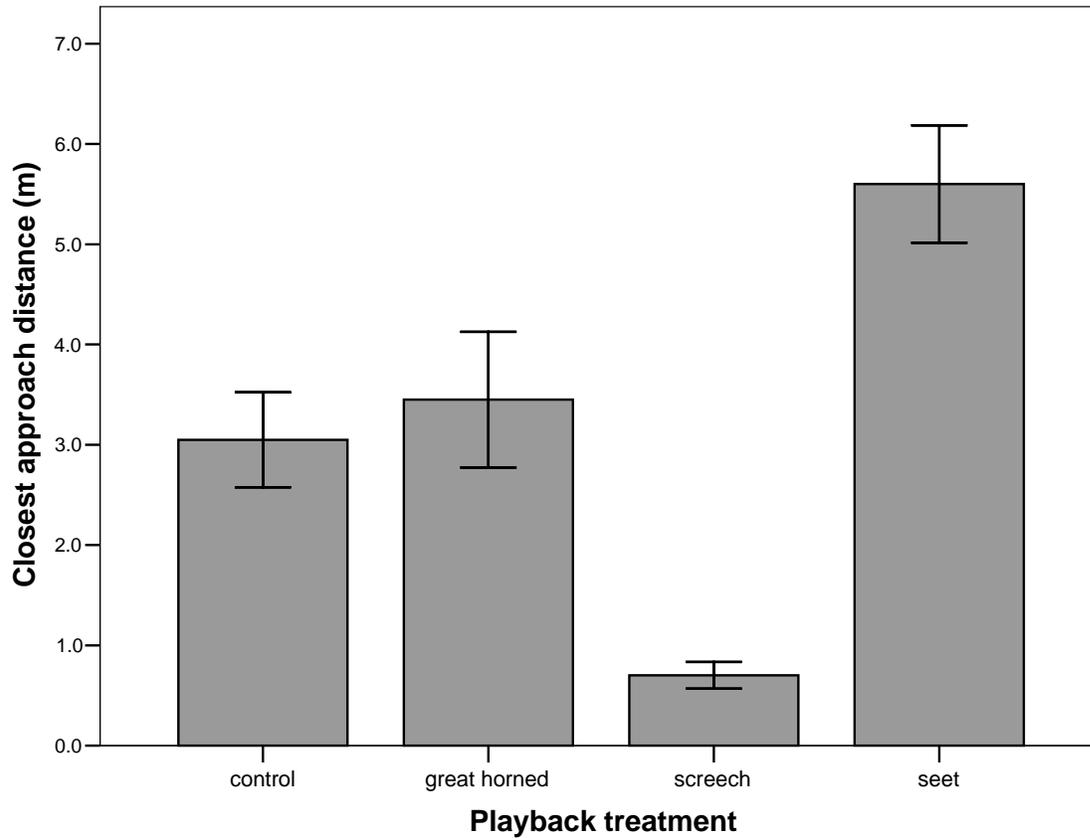


Figure 3-11. Closest approach distance of Carolina chickadees to the speakers during the playback treatments of Tufted titmouse vocalizations in the first 3min after the start of each playback. All pairwise comparisons were significant (MWU, $p < 0.05$) except between great horned and control ($p = 0.538$). Error bars: ± 1 SE.

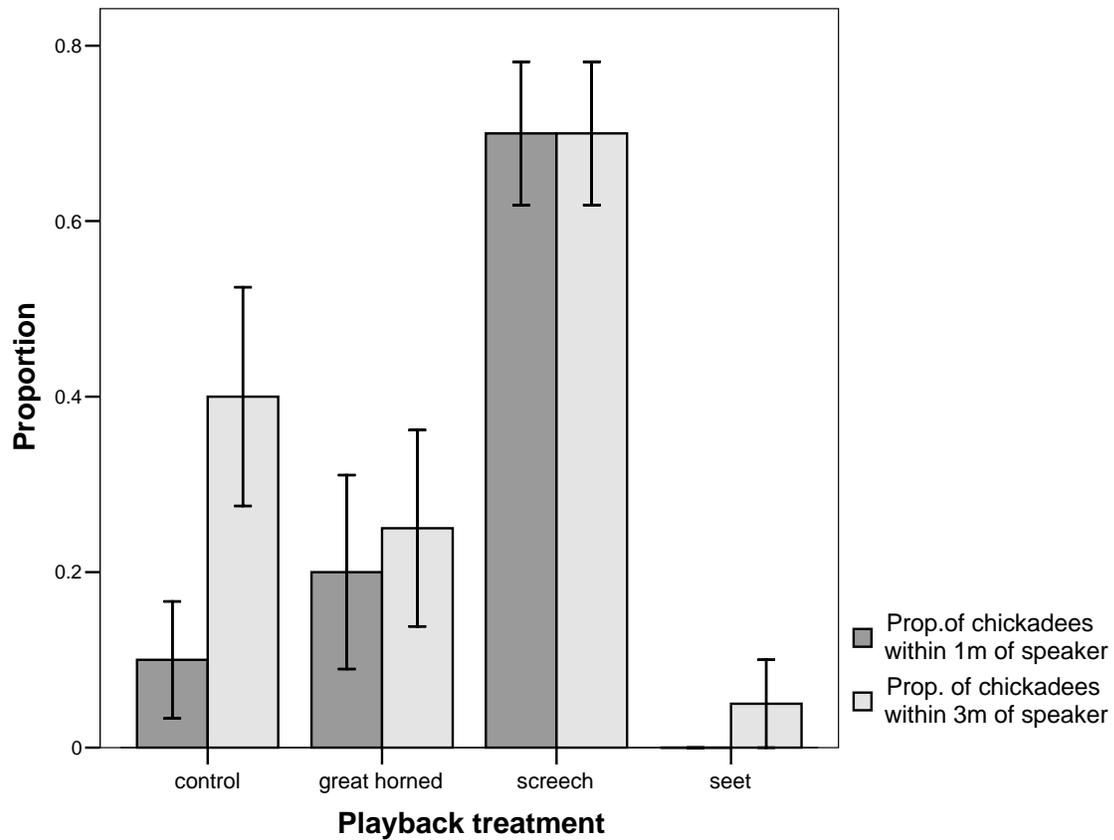


Figure 3-12. The proportion of Carolina chickadees that approached within 1m and 3m of the speakers during the playback treatments of Tufted titmouse vocalizations in the first 3min after the start of each playback. Not all pairwise comparisons were significant (see Appendix A, Table A-4). Error bars: +/- 1 SE.

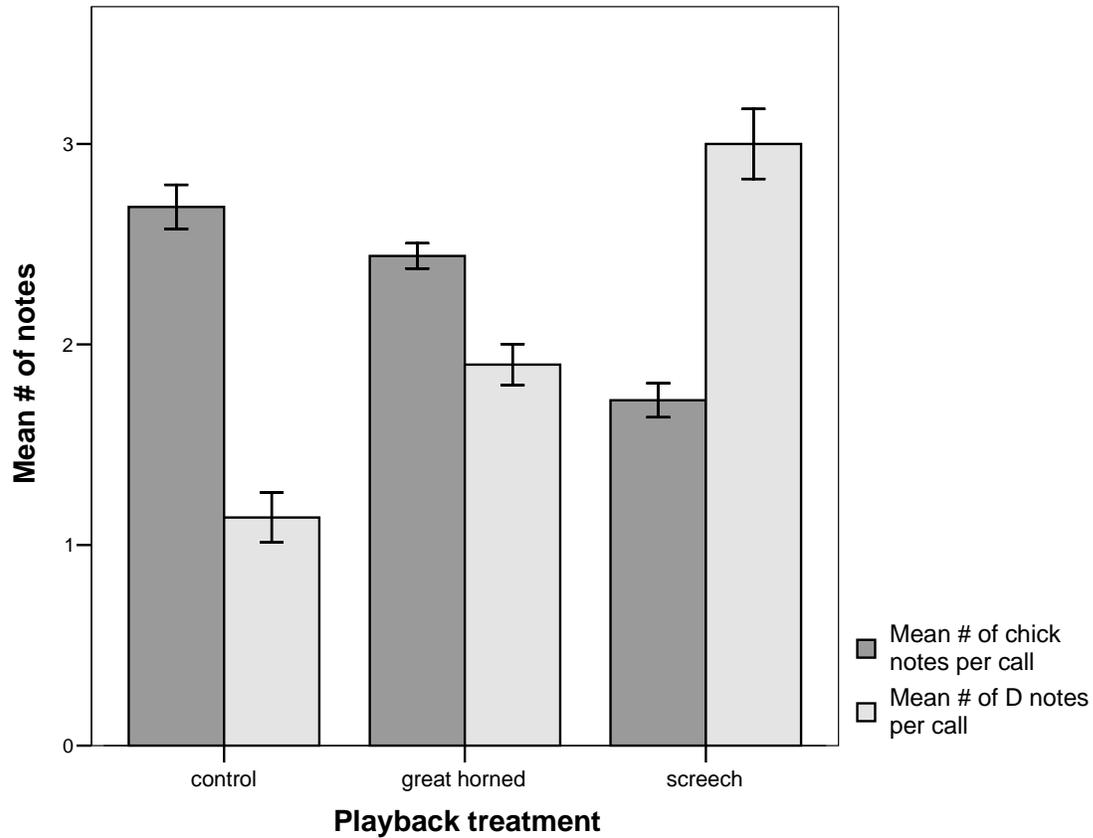


Figure 3-13. Number of chick and D notes per ‘chick-a-dee’ call given by Carolina chickadees in response to the different playback treatments of Tufted titmouse vocalizations in the first 3min after the start of each playback. All pairwise comparisons were significant (LSD, $p < 0.05$) except for the number of chick notes per call between the great horned mobbing and control playback ($p = 0.108$). Error bars: ± 1 SE.

Table 3-1. Acoustic (first two columns) and behavioral parameters (3rd column) used in analyzing the response of Tufted titmouse flocks to high-risk and low-risk predator presentations and control presentations.

<u>General spectrographic measures</u>	<u>Measures of acoustic structure of D notes</u>	<u>Behavioral measures</u>
*call rate- number of calls	minimum frequency where amplitude goes last below -10dB	*closest distance any bird approached the stimulus
*number of chick notes overall	maximum frequency where amplitude goes last below -10dB	*proportion of birds that came within 3m of stimulus
*number of D notes overall	minimum frequency where amplitude goes last below -30dB	*proportion of birds that came within 1m of stimulus
*number of notes per call	maximum frequency where amplitude goes last below -30dB	*whether the birds were frozen in place during the entire treatment
*number of chick notes per call	bandwidth at -10dB	
*number of D notes per call	bandwidth at -30dB	
*proportion of chick notes per call	entropy	
*duration of each chick note	number of peaks above -10dB	
*duration of each D note		
*call duration		
duration of 1 st D note of each call		
interval between notes		
interval between chick and D sections in each call		
interval between calls		

* parameters also used in Experiment 2 with Carolina chickadee pairs

Table 3-2. Factor loadings of the 17 behavioral and general spectrographic parameters on the four principal components after varimax rotation. Eigenvalues and amount of variance explained by the respective components are given at the bottom of the table.

	<u>Parameter</u>	<u>PC1</u>	<u>PC2</u>	<u>PC3</u>	<u>PC4</u>
1	close approach	-0.884	0.295	-0.142	0.230
2	prop. in 1m	0.777	-0.457	0.150	-0.021
3	prop. in 3m	0.700	-0.253	-0.046	0.071
4	call rate	0.833	-0.178	0.177	0.151
5	number of chick notes overall	-0.407	-0.055	0.274	0.616
6	number of D notes overall	0.957	0.023	-0.151	-0.047
7	number of notes per call	0.760	-0.152	-0.557	-0.014
8	number of chick notes per call	-0.944	-0.145	0.000	0.186
9	number of D notes per call	0.880	-0.065	-0.395	-0.190
10	prop. of chick notes per call	-0.932	-0.051	0.168	0.250
11	duration of each chick note	0.038	0.148	0.015	-0.861
12	duration of each D note	0.022	0.936	0.017	-0.227
13	call duration	0.850	0.184	-0.429	-0.099
14	duration of 1 st D note of each call	-0.203	0.935	0.157	-0.060
15	interval between notes	0.028	0.609	0.308	0.515
16	interval between chick and D sections in each call	-0.075	0.215	0.889	0.145
17	interval between calls	-0.854	-0.042	0.275	0.193
	Eigenvalue	8.26	2.67	1.83	1.73
	% variance explained	48.6	15.7	10.8	10.2

CHAPTER 4 CONCLUSION

The Tufted titmouse is a vocally complex species that possesses a sophisticated anti-predator call system (Gaddis 1979, 1980, this study). I conducted several experiments to investigate characteristics of this system and summarize the results in Figure 4-1. In the figure, I present titmouse vocal and behavioral responses to high- and low-risk predators and heterospecific responses to playbacks of the titmouse vocalizations (in the absence of the original predator stimulus). In response to high- and low-risk perched predators, titmice exhibited mobbing behavior (Fig. 4-1a) and produced ‘chick-a-dee’ mobbing calls with the high-risk Eastern screech-owl (screech owl) eliciting more intense mobbing (closer approach to the predator and more mobbing calls) than the low-risk Great horned owl (great horned) or control (see Fig. 3-4, 3-6). When Carolina chickadees (a heterospecific associate of titmice in the wild) heard playbacks of these calls in the absence of the predator stimuli, they responded in a similar manner as the titmice by exhibiting mobbing behavior and producing ‘chick-a-dee’ mobbing calls. Playbacks of titmouse mobbing calls produced in response to the high-risk screech owl elicited more mobbing calls and closer approaches by the chickadees than playbacks of titmouse calls given in response to the great horned (Fig. 4-1a, second box; see Fig. 3-11; Chapter 3). In response to aerial predators (Gaddis 1980) or when startled by the sudden emergence of a potential predator (Chapter 2), which represent extremely high-risk situations, titmice sought cover or froze in place and produced ‘seet’ alarm calls (Fig. 4-1b). When chickadees heard playbacks of titmouse seet calls in the absence of the original stimuli, they also responded by seeking cover or freezing in place and becoming silent (Fig. 4-1b, second box; Chapter 3).

It appears that titmice give more mobbing calls and exhibit more intense mobbing behavior as risk increases up to a point. But if the risk is too great, as is the case in an aerial predator encounter, mobbing is no longer appropriate and titmice exhibit fearful behavior (giving alarm calls, freezing in place and becoming inconspicuous). The fact that titmice, in general, give mobbing calls and exhibit mobbing behavior in response to high- and low-risk perched predators that do not pose an immediate threat and give alarm calls and become still and inconspicuous in response to aerial predators that do pose an immediate threat, can be explained by Morton's (1977) motivation- structural rules. The rules state that low-frequency, broadband sounds (like titmouse mobbing calls) will be produced when the caller is in an aggressive state and is likely to attack; whereas high-frequency, pure tones (like titmouse alarm calls) will be produced when the caller is non-aggressive or fearful.

In my first experiment, I found that titmice do not produce predator-specific vocalizations that denote predator type or predator class (Chapter 2). They gave a combination of different vocalizations in response to the control and predator treatments, which included avian, mammalian and reptilian predators (see Fig. 2-3). Seet alarm calls were occasionally given upon the removal of the cover from the presentation cage, and were most often given when the cage contained a hawk or a cat, which were likely the highest risk predators presented (explained in Chapter 2; see Fig. 2-5). The sudden emergence of these predators in close proximity to individual titmice in this experiment represents an extremely high-risk situation. It makes sense that titmice would produce seet alarm calls to all the predators presented in the manner used, but more of them in response to the predator species that represent the most risk. In this experiment the cat

and hawk likely represented the highest risk (see Chapter 2) and these were also the predator treatments that elicited the highest mean number of seet calls. Additionally, ‘chick-a-dee’ calls were given by titmice in response to all the treatments, but were most often given in response to the cat and hawk. According to Morton’s (1977) motivation-structural rules, these combined results likely indicate that titmice were most fearful (more seet calls were produced) in response to the cat and hawk treatment at first, as the seet calls were mostly elicited at the very beginning of the presentation. After their initial response, the titmice were most aggressive (more mobbing calls were produced) in response to the hawk and cat treatments. Overall, the results of this experiment clearly show that titmice do not produce predator-specific vocalizations in response to predator species or predator class (avian, mammalian, reptilian), but instead may be producing risk-based anti-predator calls.

Therefore, in the second experiment, I tested for and found that titmice produce situationally specific risk-based mobbing calls that vary according to the degree of risk that a predator represents (Chapter 3). In addition to producing more ‘chick-a-dee’ mobbing calls (see Fig. 3-6) and approaching the stimulus closer in response to the high-risk screech owl (see Fig. 3-4), titmice also varied the note composition of their mobbing calls (see Fig. 3-7) and varied several temporal and frequency characteristics of their vocal response with respect to risk. Chickadees that heard playbacks of titmouse mobbing calls in response to high- and low-risk predators responded in much the same way that titmice responded to the actual predators (Fig. 4-1a). In addition to producing more mobbing calls and approaching closer (see Fig. 3-11) when they heard titmouse calls in response to the high-risk screech owl, chickadees also varied the note

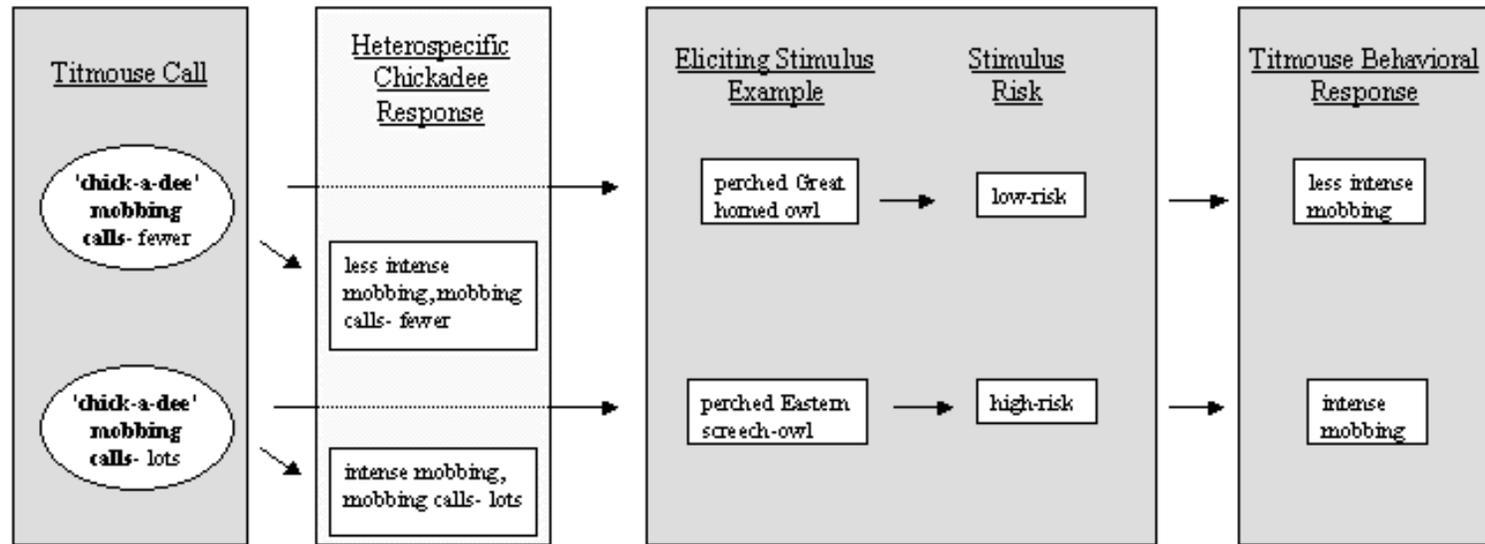
composition of the mobbing calls (see Fig. 3-13) and varied a few temporal note and call characteristics as a function of playback type. These combined results indicate that titmice possess an interspecific risk-based call system in response to predators (Fig. 4-1a).

The ‘chick-a-dee’ mobbing call and the seet alarm call appear to be functionally referential in terms of the type of predator encounter, as noted by Templeton et al. 2005, because, in general, titmice give mobbing calls in response to perched and terrestrial predators and seet calls in response to aerial predators (Gaddis 1980; Evans et al. 1993; Blumstein 1999a). For Tufted titmice, the evidence for this claim is weak because neither of these call types has a high degree of production specificity (a requirement for functional reference) because both calls are given in a variety of situations, including some non-predator situations. For example, the seet call is often given in any situation in which the bird experiences alarm and can be evoked by the sudden emergence of any potential predator, either aerial or terrestrial (Ficken and Witkin 1977; Latimer 1977), as I found in Chapter 2. In this study, titmice sometimes gave seet calls during the control treatment in response to the removal of the cover from an empty cage (Chapter 2). Even though no predator was present, the movement of the cover likely startled the titmouse and resulted in the titmouse producing seet calls. Additionally, the ‘chick-a-dee’ call of titmice is multifunctional and is given as a contact call, in coordinating group movements, and is also the primary predator mobbing call (Gaddis 1979; S. A. Hetrick, pers. obs.). Therefore, both call types have low production specificity and there is weak evidence for functional reference.

In summary, I present my four central conclusions. First, I documented that titmouse anti-predator calls are not predator-specific with respect to predator species or predator class (avian, mammalian, reptilian; Chapter 2), and this dispels some confusion in the literature about the production of seet alarm calls and ‘chick-a-dee’ mobbing calls. Seet calls have been described as ‘hawk’ or ‘aerial predator’ calls, and while they usually are given in response to a flying hawk, they are also given in other situations. Therefore, they are not reliably associated only with flying predators. Second, I documented that titmouse ‘chick-a-dee’ mobbing calls should be classified as risk-based in their production because the number and quality of the this call varied in a graded fashion as a function of risk. The third conclusion is that the nature of risk encoded in titmouse calls can be used by other species, as evidenced by appropriate behavioral responses by heterospecifics upon hearing the calls. This study was the first to document interspecific communication about such fine-scale differences in predation risk; i.e., that chickadees discern differences between calls given in response to two different species of perched owls. Finally, the last two conclusions taken together indicate that titmice possess an interspecific risk-based call system- a more sophisticated interspecific communication system with respect to predation risk than was previously known. Previous work showed that many species respond to titmouse mobbing calls, but we have improved understanding of these interactions by documenting that both the production and the perception of the calls by other species are risk-based. Titmice give specific information about different risk situations and heterospecific responses indicate that other species tailor their responses according to the specific level of risk being communicated. Many species that are sympatric with titmice respond to their anti-predator calls and may be

benefiting from the specific information that they contain. The positive benefits gained by receivers of predation risk information suggest that titmice may be playing an important facilitative role in animal communities.

95 A



B

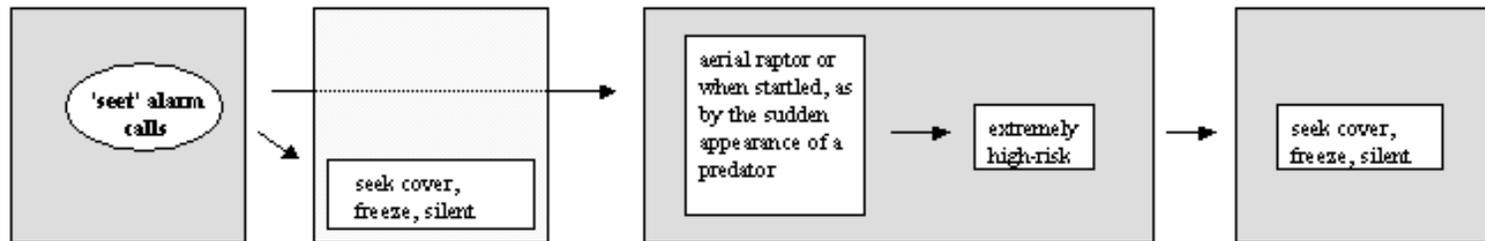


Figure 4-1. The flow diagram summarizes the vocal and behavioral responses of Tufted titmice to predators representing varying degrees of risk and heterospecific responses to playbacks of titmouse anti-predator vocalizations. The two shaded rows demonstrate the production of and responses to A) titmouse 'chick-a-dee' mobbing calls, and B) titmouse seet alarm calls.

APPENDIX A
SUMMARY TABLES OF STATISTICAL TESTS FOR RESPONSES OF TUFTED TITMICE
TO PREDATORS AND RESPONSES OF CAROLINA CHICKADEES TO PLAYBACKS

Table A-1. Behavioral responses of Tufted titmouse flocks to high- and low-risk predators and controls in the 2min following presentation. One-tailed Mann-Whitney U tests were used to generate pairwise comparisons. scr = Eastern screech-owl, gh = Great horned owl, cont = control

Measure	Kruskal-Wallis χ^2	df	Asymp. Sig.* p-value	screech versus great horned p-value	screech versus control p-value	great horned versus control p-value	Multiple Comparisons at p<0.05
closest approach (m)	7.057	2	0.029	0.053	0.019	0.594	scr<(gh=cont)
prop. in 1m	8.670	2	0.013	0.016	0.013	0.953	scr>(gh=cont)
prop. in 3m	7.355	2	0.025	0.053	0.008	0.953	scr>(gh=cont)

*- Asymp. Sig.= Asymptotic significance

Table A-2. General spectrographic measures and measures of acoustic structure of D notes of Tufted titmouse calls elicited in response to high- and low-risk predators and controls in the 2min following presentation. scr = Eastern screech-owl, gh = Great horned owl, cont = control

Measure	Transformation	ANOVA p-value	*F _{df}	Adjusted r ²	screech versus great horned p-value	screech versus control p-value	great horned versus control p-value	Multiple Comparisons at p<0.05
call rate (#/2min)	sqrt	0.001	12.2 _{2, 20}	0.540	0.006	<0.001	0.200	scr>(gh=cont)
chick notes overall (#/2min)	log(n+1)	0.384	1.0 _{2, 20}	0.001	0.706	0.198	0.381	scr=gh=cont
D notes overall (#/2min)	log(n+1)	<0.001	16.2 _{2, 20}	0.616	0.045	<0.001	0.007	scr>gh>cont
notes per call (#/2min)		<0.001	359.9 _{2, 266}	0.726	<0.001	<0.001	<0.001	scr>gh>cont
chick notes per call (#/2min)	sqrt	<0.001	378.4 _{2, 266}	0.740	<0.001	<0.001	<0.001	scr<gh<cont
D notes per call (2min)	sqrt	<0.001	837.8 _{2, 266}	0.863	<0.001	<0.001	<0.001	scr>gh>cont
prop. of chick notes per call	arcsinsqrt	0.001	16.3 _{2, 14}	0.702	0.260	<0.001	0.002	scr<gh<cont
duration of each chick note (s)		<0.001	17.8 _{2, 131}	0.205	0.001	0.034	<0.001	gh>scr>cont
duration of each D note (s)	sqrt	<0.001	63.7 _{2, 1492}	0.078	<0.001	0.499	0.001	gh>(cont=scr)
call duration (s)		<0.001	280.0 _{2, 266}	0.679	<0.001	<0.001	<0.001	scr>gh>cont
duration of 1 st D note in each call (s)		<0.001	52.0 _{2, 298}	0.256	<0.001	<0.001	0.199	scr<(gh=cont)
interval between notes (s)	sqrt	<0.001	7.7 _{2, 1313}	0.010	0.011	0.001	0.049	scr<gh<cont
interval between chick and D sections in each call (s)	sqrt	<0.001	13.8 _{2, 87}	0.229	0.409	<0.001	<0.001	(scr=gh)<cont
interval between calls (s)	sqrt	0.000	597.0 _{2, 293}	0.803	<0.001	<0.001	<0.001	scr<gh<cont
min. freq. where amplitude goes last below -10dB (Hz)		0.044	3.2 _{2, 105}	0.041	0.778	0.025	0.019	(scr=gh)>cont
max. freq. where amplitude goes last below -10dB (Hz)		0.021	4.0 _{3, 105}	0.054	0.552	0.019	0.007	(scr=gh)>cont
min. freq. where amplitude goes last below -30dB (Hz)		<0.001	13.1 _{2, 105}	0.189	0.065	<0.001	0.001	(scr=gh)>cont
max. freq. where amplitude goes last below -30dB (Hz)		0.734	0.3 _{2, 105}	-0.013	0.530	0.821	0.480	scr=gh=cont
bandwidth at -10dB (Hz)		0.279	1.3 _{2, 105}	0.006	0.668	0.195	0.119	scr=gh=cont
bandwidth at -30dB (Hz)		<0.001	10.7 _{2, 105}	0.157	0.047	<0.001	0.006	scr<gh<cont

Table A-2 (cont)

Measure	Transformation	ANOVA p-value	*F _{df}	Adjusted r ²	screech versus great horned p-value	screech versus control p-value	great horned versus control p-value	Multiple Comparisons at p<0.05
entropy		0.607	0.5 _{2, 105}	-0.010	0.524	0.619	0.329	scr=gh=cont
peaks above -10dB (#/D note)		0.988	0.0 _{2, 105}	0.019	0.915	0.944	0.879	scr=gh=cont

*- F_{df} = F_{df treatment, df total}

Table A-3. Behavioral responses of Carolina chickadee pairs to playbacks of Tufted titmouse vocalizations in response to high- and low-risk predators and controls and titmouse seet alarm calls in the 3min following the start of each playback. One-tailed Mann-Whitney U tests were used to generate pairwise comparisons. scr = Eastern screech-owl, gh = Great horned owl, cont = control

Measure	Kruskal-Wallis χ^2	df	Asymp. Sig.* p-value	screech versus great horned p-value	screech versus control p-value	great horned versus control p-value	screech versus seet p-value	great horned versus seet p-value	control versus seet p-value	Multiple Comparisons at p<0.05
closest approach (m)	23.666	3	<0.001	0.001	<0.001	0.579	<0.001	0.043	0.004	scr<(gh=cont)<seet
prop. in 1m	24.118	3	<0.001	0.005	<0.001	0.684	<0.001	0.280	0.481	scr>(gh=seet=cont)
prop. in 3m	16.687	3	0.001	0.011	0.105	0.436	<0.001	0.247	0.052	scr>gh scr=cont gh=cont scr>seet gh=seet cont>seet

*- Asymp. Sig.= Asymptotic significance

Table A-4. General spectrographic measures of Carolina chickadee calls elicited in response to playbacks of Tufted titmouse vocalizations in response to high- and low-risk predators and controls and titmouse set alarm calls in the 3min following the start of each playback. scr = Eastern screech-owl, gh = Great horned owl, cont = control

Measure	Transformation	ANOVA p-value	*F _{df}	Adjusted r ²	screech versus great horned p-value	screech versus control p-value	great horned versus control p-value	Multiple Comparisons at p<0.05
call rate (#/3min)	sqrt	0.027	4.1 _{2, 30}	0.178	0.609	0.012	0.037	(scr=gh)>cont
chick notes overall (#/3min)	sqrt	0.075	2.9 _{2,30}	0.113	0.693	0.077	0.034	scr=gh scr=cont gh>cont
D notes overall (#/3min)	sqrt	0.044	3.5 _{2, 30}	0.148	0.381	0.015	0.097	scr=gh scr>cont gh=cont
notes per call (#/3min)		<0.001	9.1 _{2, 338}	0.046	0.009	<0.001	0.051	scr>gh>cont
chick notes per call (#/3min)		<0.001	32.3 _{2, 338}	0.157	<0.001	<0.001	0.108	scr>(gh=cont)
D notes per call (#/3min)	sqrt	<0.001	27.6 _{2, 338}	0.137	<0.001	<0.001	0.010	scr>gh>cont
prop. of chick notes per call	arcsinsqrt	0.053	3.3 _{2, 27}	0.152	0.374	0.018	0.096	scr=gh scr<cont gh=cont
duration of each chick note (s)	sqrt	<0.001	11.2 _{2, 723}	0.028	<0.001	0.001	0.762	scr>(gh=cont)
duration of each D note (s)		<0.001	119.9 _{2, 775}	0.235	<0.001	<0.001	<0.001	scr>gh>cont
call duration (s)	sqrt	<0.001	27.8 _{2, 335}	0.138	<0.001	<0.001	0.008	scr>gh>cont

*- F_{df treatment, df total}

APPENDIX B
SUMMARY TABLE OF MEAN RESPONSES OF TUFTED TITMICE TO PREDATORS
AND CAROLINA CHICKADEES TO PLAYBACKS

Table B-1. Mean responses, standard errors, and standard deviations of Tufted titmice to predator and control presentations in the 2min following presentation.

Measure	Predator	N	Mean	SE	SD
closest approach (m)	control	10	2.90	0.62	1.969
	great horned	5	2.10	0.51	1.140
	screech	5	0.76	0.15	0.336
prop. in 1m	control	10	0.20	0.10	0.322
	great horned	5	0.13	0.08	0.181
	screech	5	0.80	0.13	0.299
prop. in 3m	control	10	0.40	0.11	0.345
	great horned	5	0.40	0.16	0.366
	screech	5	0.93	0.07	0.148
call rate (#/2min)	control	10	4.40	2.07	6.552
	great horned	5	10.20	5.08	11.367
	screech	5	35.00	5.01	11.203
chick notes overall (#/2min)	control	10	6.50	3.09	9.767
	great horned	5	6.60	2.09	4.669
	screech	5	6.80	1.16	2.588
D notes overall (#/2min)	control	10	4.20	2.32	7.345
	great horned	5	79.60	36.40	81.402
	screech	5	210.60	41.80	93.466

Table B-1 (cont.)

Measure	Predator	N	Mean	SE	SD
notes per call (#/2min)	control	43	2.19	0.1195	0.8283
	great horned	51	4.69	0.1357	0.9784
	screech	172	6.21	0.0722	0.9469
chick notes per call (#/2min)	control	43	1.49	0.0934	0.6126
	great horned	51	0.49	0.4683	0.3344
	screech	172	0.19	0.0100	0.1314
D notes per call (#/2min)	control	43	0.95	0.0527	0.3459
	great horned	51	4.29	0.9446	0.6746
	screech	172	6.02	0.0775	1.0158
prop. of chick notes per call	control	5	0.68	0.1053	0.2355
	great horned	4	0.16	0.0850	0.1699
	screech	5	0.04	0.0138	0.0307
duration of each chick note (s)	control	64	0.0221	0.000599	0.004792
	great horned	33	0.0278	0.000969	0.005564
	screech	34	0.0241	0.000303	0.001768
duration of each D note (s)	control	42	0.1860	0.00511	0.03311
	great horned	398	0.2048	0.00200	0.03993
	screech	1052	0.1821	0.00839	0.02722
call duration (s)	control	43	0.3340	0.00618	0.04050
	great horned	51	1.0617	0.01710	0.12215
	screech	172	1.5200	0.02796	0.36556

Table B-1 (cont.)

Measure	Predator	N	Mean	SE	SD
duration of 1 st D note of each call (s)	control	34	0.1830	0.00660	0.3847
	great horned	88	0.1927	0.00565	0.5303
	screech	176	0.1454	0.00197	0.2607
interval between notes (s)	control	62	0.0858	0.00210	0.01828
	great horned	339	0.0812	0.00398	0.01179
	screech	912	0.0791	0.001397	0.01480
interval between chick and D sections in each call (s)	control	27	0.0641	0.56963	0.010897
	great horned	26	0.0510	0.06375	0.020275
	screech	34	0.0472	0.03606	0.008144
interval between calls (s)	control	38	8.23	0.56963	3.5114
	great horned	85	1.74	0.06374	0.5876
	screech	170	1.37	0.03606	0.4701
min. freq. where amplitude goes last below -10dB (Hz)	control	21	1864.00	85.05	380.227
	great horned	36	2161.11	84.78	508.695
	screech	50	2133.40	60.44	427.382
max. freq. where amplitude goes last below -10dB (Hz)	control	21	6140.00	296.30	1357.501
	great horned	36	6854.72	113.64	681.823
	screech	50	6730.60	129.66	916.850

Table B-1 (cont.)

Measure	Predator	N	Mean	SE	SD
min. freq. where amplitude goes last below -30dB (Hz)	control	21	668.95	29.54	128.750
	great horned	36	841.94	34.90	209.391
	screech	50	914.40	23.79	168.210
max. freq. where amplitude goes last below -30dB (Hz)	control	21	7407.00	22.86	102.243
	great horned	36	7426.11	17.50	104.970
	screech	50	7412.80	12.44	87.971
bandwidth at -10dB (Hz)	control	21	4242.00	282.70	1264.277
	great horned	36	4688.89	144.65	867.877
	screech	50	4593.20	142.88	1010.305
bandwidth at -30dB (Hz)	control	21	6736.84	32.24	140.517
	great horned	36	6580.00	38.93	233.556
	screech	50	6494.00	26.01	183.937
entropy	control	21	0.4347	0.00557	0.0255
	great horned	36	0.4278	0.00504	0.0298
	screech	50	0.4314	0.00310	0.0219
peaks above -10dB (#/D note)	control	21	2.19	0.18	0.814
	great horned	36	2.17	0.07	0.447
	screech	50	2.18	0.07	0.523

Table B-2. Mean responses of Carolina chickadees to playbacks of Tufted titmouse vocalizations in response to predator and control presentations in the 3min following the start of each playback.

Measure	Playback	N	Mean	SE	SD
closest approach (m)	control	10	3.05	0.47	1.499
	great horned mobbing	10	3.45	0.68	2.140
	screech mobbing	10	0.70	0.13	0.420
	seet	10	5.60	0.59	1.852
prop. in 1m	control	10	0.10	0.07	0.211
	great horned mobbing	10	0.20	0.11	0.350
	screech mobbing	10	0.70	0.08	0.258
	seet	10	0.00	0.00	0.000
prop. in 3m	control	10	0.40	0.12	0.394
	great horned mobbing	10	0.25	0.11	0.354
	screech mobbing	10	0.70	0.08	0.258
	seet	10	0.05	0.05	0.158
call rate (#/3min)	control	10	4.90	1.62	5.109
	great horned mobbing	10	12.10	2.47	7.795
	screech mobbing	10	16.50	3.97	12.563
chick notes overall (#/3min)	control	10	13.70	4.53	14.330
	great horned mobbing	10	30.00	5.50	17.404
	screech mobbing	10	28.60	6.96	22.006

Table B-2 (cont.)

Measure	Playback	N	Mean	SE	SD
D notes overall (#/3min)	control	10	5.70	3.42	10.822
	great horned mobbing	10	22.20	6.74	21.327
	screech mobbing	10	49.80	24.43	77.270
notes per call (#/3min)	control	51	3.80	0.17	1.222
	great horned mobbing	121	4.27	0.09	1.040
	screech mobbing	166	4.72	0.13	1.710
chick notes per call (#/3min)	control	51	2.69	0.110	0.784
	great horned mobbing	121	2.44	0.062	0.689
	screech mobbing	166	1.72	0.085	1.092
D notes per call (#/3min)	control	51	1.137	0.125	0.899
	great horned mobbing	121	1.900	0.103	1.124
	screech mobbing	166	3.000	0.174	2.249
prop. of chick notes per call	control	8	0.86	0.061	0.172
	great horned mobbing	10	0.66	0.072	0.229
	screech mobbing	9	0.58	0.108	0.323
duration of each chick note (s)	control	137	0.0377	0.000524	0.00613
	great horned mobbing	300	0.0376	0.000386	0.00669
	screech mobbing	286	0.0398	0.000339	0.00573

Table B-2 (cont.)

Measure	Playback	N	Mean	SE	SD
duration of each D note (s)	control	55	0.0849	0.000416	0.00308
	great horned mobbing	222	0.0907	0.000369	0.00549
	screech mobbing	498	0.0994	0.000463	0.01034
call duration (s)	control	49	0.3510	0.018360	0.12852
	great horned mobbing	121	0.4279	0.010797	0.11877
	screech mobbing	165	0.5782	0.021590	0.07700

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BIOGRAPHICAL SKETCH

Stacia Ann Hetrick was born and raised in southwest Florida. She is the youngest of three children and has two older brothers. Stacia was a curious youngster and loved the outdoors. Her early pursuits in wildlife involved chasing lizards and frogs, raising gerbils, cats, dogs, guinea pigs and, as might be predicted, a parakeet she called “Peety”. She took a keen interest when her father, who enjoyed watching and photographing long-legged waders, would stop at a pond or canal alongside the road to snap pictures of wood storks and herons. Family boating trips also afforded her frequent opportunities for observing ospreys, eagles, and colonies of ibis as well as the occasional manatee, gator or water moccasin. Her interest in animals from an early age evolved to her pursuit of a major in wildlife ecology and conservation. It was during her years as an undergraduate at the University of Florida that she consciously began to realize her life’s passion would be ornithology.

Stacia graduated from UF with a BS degree in the spring of 2002 after which she felt fortunate to be able to take on a master’s project studying birds. In addition to her studies, discretionary time was spent volunteering, working bird-related field jobs, and making frequent scouting trips to the woods just to enjoy the simple wonders of nature. During her time as a master’s student, she worked as a Teaching Assistant and helped teach several wildlife classes to undergraduates. This led her to discover a second passion in teaching. Stacia intends to pursue a career in environmental education and hopes to never stop teaching others about the wonderful world of birds.