Black-capped chickadees (Poecile atricapilla) convey predator-specific information in their "chick-a-dee" vocalizations

Christopher Neal Templeton

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Black-capped chickadees (*Poecile atricapilla*) convey predator-specific information in their “chick-a-dee” vocalizations

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B.S., Denison University, 1995

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for the degree of

Master of Science

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Black-capped chickadees (*Poecile atricapilla*) convey predator-specific information in their "chick-a-dee" vocalizations

Communicating specific information about potential predators may be adaptive if the predators differ in the degree of threat they represent. Although there has been considerable research on alarm signaling in response to different classes of predators (i.e., aerial vs. terrestrial), few studies have addressed whether animals transfer information about different predators from a single class with their anti-predator vocalizations. In this study, I systematically presented a wide variety of potential predators to three captive flocks of black-capped chickadees (*Poecile atricapilla*) living under semi-natural conditions in a large outdoor aviary. Predators included two species of live mammals (cat and ferret), numerous live, tethered raptors (3 species of hawks, 5 species of falcons, and 5 species of owls) and two controls (no predator and live bobwhite quail). These species varied in natural history, body size, and degree of risk they pose to chickadees. I recorded "chick-a-dee" mobbing vocalizations produced in response to different predators and analyzed acoustic features to determine if this call varied relative to specific predators. The number of certain syllable types (A and B) did not vary among treatments. However, chickadees reduced the number of one syllable (C) and increased the number of another syllable (D) per call when they encountered more dangerous predators. Chickadee calls produced in response to northern pygmy-owls (high risk) and great horned owls (low risk) also differed acoustically in many temporal and amplitude features. Because communication involves both a signal producer and a signal receiver, I conducted playback experiments to determine whether variations in "chick-a-dee" calls convey predator information to receivers. Chickadees strongly responded to playback of their "chick-a-dee" call as compared with a control. They responded differently to calls given to pygmy-owls than to calls given to great horned owls. Thus, acoustic variations in this vocalization are reliably produced in response to different species of predators and used by conspecifics to make behavioral decisions. These results indicate that chickadees communicate information about the degree of threat a predator represents through very subtle acoustic features of their "chick-a-dee" call. This appears to be one of the most sophisticated anti-predator communication systems documented to date.
ACKNOWLEDGMENTS

This project would not have been possible without the assistance of a number of people. I would especially like to thank Kate Davis and the Raptors of the Rockies for all of their time spent scaring helpless chickadees. Her assistance was invaluable throughout the entire course of this project. I would like to thank my committee, Erick Greene, Ken Dial, and Jon Graham for helpful guidance and for sticking with me after a slow start. Erick has served as a scientific inspiration, mentor, and friend over the past three years. I would like to thank Ken for many fruitful discussions about scaling and the allometry of behavior that greatly affected the scope of this project. Jon’s statistical expertise was extremely helpful as I continued to add more and more analyses. Nate Schwab was a skilled and reliable field assistant during many of the recordings. Charles Eldermire and Caleb Putman helped me catch birds, record vocalizations, and helped deal with too many other technical issues at “the fort” to name. Marchie’s Nursery and Caras Nursery both provided trees and shrubs to build a natural chickadee habitat inside the aviary. Swift Instruments donated a pair of high quality binoculars used to identify individual chickadees. Kim Hastings, Jamie Martin, and Tracey from the “Food Farm” let me use their pet ferrets in the name of science. I would also like to thank “kitty-cat” and “bud” the barn cat for their time. Members of the “white trash lab” provided feedback on my ideas and writing throughout the process. Last, I would like to thank my family and the many good friends I’ve met in Missoula for providing moral support and keeping my spirits high.
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ABSTRACT

Communicating information about the specific features of potential predators to conspecifics may be adaptive if the predators differ in the degree of threat they represent. Although there has been considerable research on alarm signaling in response to different classes of predators (i.e., aerial vs. terrestrial), few studies have addressed whether animals distinguish among different predators from a single class with their anti-predator vocalizations. In this study, I systematically presented a wide variety of potential predators to three different captive flocks of black-capped chickadees (*Poecile atricapilla*) living under semi-natural conditions in a large outdoor aviary. Predators included two species of live mammals (cat and ferret), numerous live, tethered raptors (3 species of hawks, 5 species of falcons, and 5 species of owls) and two controls (no predator and live bobwhite quail). Predator species varied in both natural history and morphology, indicating that they pose different risks to chickadees. I recorded the “chick-a-dee” mobbing vocalizations produced in response to different predators and analyzed several features to determine if aspects of this call varied relative to specific predators. The number of certain syllable types (A and B) did not vary among the treatments.
However, chickadees reduced the number of one syllable (C) and increased the number of another syllable (D) per call when they encountered more dangerous predators relative to the control. Chickadee calls also differed in several more subtle temporal and amplitude acoustic features when I compared the northern pygmy-owl (high risk) and great horned owl (low risk) treatments. These results indicate that chickadees assess different species of potential predators and encode information related to the degree of threat in variations of their “chick-a-dee” call. These results illustrate one of the first systems where this degree of information encoding occurs in such a subtle anti-predator vocal system.
INTRODUCTION

Many animals vocalize when they encounter potential predators, and there has been much interest in understanding both the evolution and adaptive significance (e.g., Marler 1955; Sherman 1977; Sherman 1981; Hoogland 1996) and the specific meanings (e.g., Seyfarth et al. 1980; Evans et al. 1993a; Ackers & Slobodchikoff 1999) of these signals. Anti-predator vocalizations often differ in acoustic structure depending on the situation in which they are produced. Understanding how this variation relates to the context in which the call is produced can provide insights into how an animal perceives its environment. If a given prey species experiences different predators that vary in hunting strategies, riskiness, or response urgency, selection should favor acoustic variations in anti-predator vocalizations that encode this information.

Species that produce different types of alarm calls may transmit information about the type of potential predator or the relative risk posed by the perceived danger. Specifically, vocalizations can vary in relationship to the class of predator, as in functionally referential alarm call systems, or in relationship to the degree of threat that a predator represents, as in urgency-based systems. Several species of small mammals produce anti-predator vocalizations that appear to encode information about the degree of risk, or response urgency, of a given predator encounter (reviewed by Fichtel & Kappeler 2002). For example, California ground squirrels, Spermophilus beecheyi, produce
“whistle” calls in high risk situations, usually involving aerial predators, and “chatter” calls in lower risk situations, usually involving terrestrial predators (Owings & Hennessy 1984). Because “whistles” are occasionally given to very close or unexpected terrestrial predators and “chatters” are sometimes given to non-threatening aerial predators, these calls appear to refer to the degree of threat, or response urgency, and not the specific type of predator.

Some species are faced with a suite of predators that vary sufficiently in hunting strategies to necessitate different escape strategies. In these situations, anti-predator vocalizations that convey information about the specific type of predator, not just the degree of threat, should be favored (Hauser 1996). Referential alarm call systems have been documented in several different species of primates (reviewed in Fichtel & Kappeler 2002). For instance, vervet monkeys, Cercopithecus aethiops, produce acoustically distinct vocalizations when they encounter a snake, an eagle, or a leopard, (Struhsaker 1967) and these calls are specific to the class of predator, not other contextual information such as the urgency of response (Seyfarth et al. 1980). Unlike the urgency-based anti-predator vocal systems found in some other mammals, the distinct vocalizations of vervet monkeys and other primates can be thought of as functionally referential.

Although alarm calling has been thoroughly studied in some mammals, little is known about the amount of information conveyed in avian anti-predator vocalizations.
Domestic chickens, *Gallus gallus*, produce acoustically different alarm calls to aerial and terrestrial predators and these calls appear functionally referential for the two classes or locations of predators (Gyger et al. 1987; Evans et al. 1993a).

Many species of passerine birds also have two different types of vocalizations associated with predators, a “seet” call and a “mobbing” call (Marler 1955). The “seet” call is a high frequency, low amplitude alarm call; it is typically produced when an aerial threat is first perceived and usually causes conspecifics to freeze in place or dive for cover. In contrast, the “mobbing” call is typically low frequency, high amplitude, and therefore, highly localizable; this call is used as a recruitment signal and is usually associated with the approach or harassment of a terrestrial predator or a stationary, perched raptor. Further, Arabian babblers, *Turdoides squamiceps*, use different vocalizations when they mob stuffed owls than when they mob cats, suggesting that they vocally discriminate between the two predator classes, terrestrial predators and perched raptors (Naguib et al. 1999).

In addition to discriminating among different classes of potential predators, discriminating among morphologically similar predators within a single class should be adaptive if the predators vary in the degree of threat they pose to a given prey animal. A few studies have suggested that some birds make even more fine-scaled discriminations among potential predators and encode this information in their alarm calls. For instance, chickens differentiate among overhead stimuli based on the size of the object (Evans et
al. 1993b), whereas other species, such as lapwings, *Vanellus spp.* (Walters 1990), black-capped chickadees, *Poecile atricapilla* (Ficken & Witkin 1977), and American coots, *Fulica americana* (Grubb 1977), may distinguish among different species of aerial predators.

Unfortunately, studies of how anti-predator vocalizations relate to different species within a class of predators have generally been conducted under unrealistic laboratory conditions or are based on sporadic, chance observations of predator encounters in the wild with limited sample sizes. No study has rigorously conducted controlled presentations of live predators to birds living under natural or semi-natural conditions that isolate vocal responses to the specific predator species from other features such as the location, behavior, or movement patterns of the predator.

In this study, I examined variation in the mobbing vocalizations of black-capped chickadees (*Poecile atricapilla*) when encountering different species of live predators under semi-natural aviary conditions. Chickadees are ideal for this type of study because they have a highly developed vocalization system where very subtle differences in the structure and use of their vocalizations can substantially affect their behavior (e.g., Nowicki 1983; Mennill et al. 2002). Chickadees form social flocks of 6-8 birds in the non-breeding season that consist of long-term, mated pairs (Ficken et al. 1981; Desrochers & Hannon 1989; Smith 1991). They are wide-ranging, and in many habitats encounter a large variety of potential predators. They produce “high zee” alarm calls
("seet") when aerial predators fly overhead, and "chick-a-dee" vocalizations ("mobbing") when they encounter a perched raptor or a terrestrial predator (Ficken et al. 1978). The "chick-a-dee" call is highly variable; it appears to be used for a variety of functions and encodes much information at several different acoustic levels (Smith 1991). Variations in this vocalization convey individual (Mammen & Nowicki 1981) and flock (Nowicki 1983; Nowicki 1989) identity, the direction the caller is facing (Witkin 1977), and perhaps even the motivational state of the caller (Hailman et al. 1985). A major function of the "chick-a-dee call" is to alert conspecific flock-mates to potential predators (Odum 1942), so variations in the acoustic structure of this call may also encode information about the specific identity of a potential predator.

To determine if variation in the acoustic structure of the "chick-a-dee" call depends on the species of predator encountered, I presented flocks of chickadees with live mammalian predators and live perched raptors that ranged in the degree of threat they represent to chickadees (Table 1). Features that may affect the degree of risk a given species of predator represents include the type (i.e., aerial vs. terrestrial), diet, activity patterns, and body size of the predator. In general, predators that hunt mostly small birds should be more dangerous than predators that hunt larger birds or mammals. Because chickadees are only active during daylight and roost in cavities at night, diurnal predators should be more dangerous than nocturnal predators. Because maneuverability is important in predator-prey interactions (Howland 1974) and small birds are more
maneuverable than large birds (Pennycuick 1989), predators that are closest to the size of a chickadee should pose a greater risk than larger predators. Therefore, small, maneuverable, diurnal, bird-feeding predators such as northern pygmy-owls, Cooper’s hawks, and merlins should be more dangerous to chickadees than small mammal-feeding, large sized, or nocturnal predators such as rough-legged hawks, great horned owls, and prairie falcons. If chickadees differentiate among different species of predators, they should respond most strongly to the predators that pose the greatest threat. In this study, I examine the amount of information about predators that chickadees encode in their “chick-a-dee” vocalization.
METHODS

Animals and Facilities

I captured four flocks of chickadees from areas surrounding Missoula, Montana during October 2000-March 2001 and October 2001-March 2002. The first flock contained 10 individuals and the other three flocks each had 6 individuals. I first aged the birds according to the specific markings on their tail (Pyle 1997). Then, I marked all of the birds with uniquely colored leg bands and released them into a large (16m x 6m x 4m), outdoor aviary at the University of Montana’s Field Research Station at Fort Missoula. In order to approximate a natural chickadee habitat, the aviary contained numerous live trees and shrubs and several snags containing natural cavities.

Mealworms (*Tenebrio molitor*) were the chickadee’s primary food source; numerous (c. 80-100) worms were hidden throughout the aviary each day. Chickadees were also provided with sunflower seeds *ad libidum*, and their diet was regularly supplemented with peanuts, hard-boiled eggs, and spotted knapweed (*Centaurea maculosa*) flowering heads (from which the birds obtained *Urophora* fly larvae, a commonly-used winter food source). A large heated bowl was kept filled with clean water for chickadees to drink and bath in.
Chickadees were allowed to acclimate to the experimental aviary and the human observers for approximately one week before I began the predator presentations. Chickadees took to captivity extremely rapidly (typically less than 30 minutes before they appeared to exhibit normal foraging behavior), and within a couple days they tolerated and foraged close to people in the aviary without giving alarm calls. Thus, I believe this period was sufficient for habituation to the aviary and human observers.

Predator Presentations

hawk, *Accipiter cooperii*, red-tailed hawk, *Buteo jamaicensis*, and rough-legged hawk, *B. lagopus*). Most of these raptors were rehabilitation birds that could not be released because of broken wings; although most could not fly, they were very healthy in all other respects and were alert and active throughout the experiments. Because most of the raptors were frequently used in educational programs, they were accustomed to sitting tethered on a perch and rarely moved from their perch (attempted flight) during the course of the trial.

Each predator treatment was replicated for three different flocks of chickadees (51 total presentations). For each flock, I presented the predators in a random order. Because the chickadees in the first flock seemed to respond in a similar fashion each time they encountered a particular predator, I presented each predator only once to a given flock thereafter. In order to minimize habituation, predator presentations were usually separated by at least two days.

Prior to each trial, an assistant and I entered the aviary with recording equipment and binoculars. Although the chickadees rapidly habituated to human observers, we remained stationary in the aviary for at least 5 minutes before introducing a predator to ensure that any response the chickadees displayed was not directed at us. Chickadees typically foraged during this period and did not give alarm calls prior to the predator presentations. A third person then slowly moved a predator into the aviary from an inside window by passing it through an opaque black screen that hid the window from the
chickadees. This ensured that the chickadees were responding to the predator and not to stimuli associated with the human handler. Each predator was presented on the same perch and in the same location in the aviary for a 15-minute period.

Once the predator was introduced into the aviary, we recorded the chickadees’ vocalizations on Maxell XL-II audio cassette tapes using Sennheiser shotgun microphones (ME66) connected to Mineroff Electronics pre-amplifiers (SME-BA6), and Sony TCM-5000 (“modified bird version”) analog tape recorders. Each observer recorded calls from one-half of the aviary. To avoid observer bias, we each recorded on the same side for all of the presentations. We were able to identify and note individual callers most of the time. If we were unsure of the caller’s identity, the call was classified as “unknown” for analyses. Avisoft-SASLab Pro version 3.93 (Specht 2001) was used to digitize each of the 5,440 “chick-a-dee” vocalizations we recorded throughout the experiment.

Calling Rates

To determine if vocalization rates varied in relation to different predators, I measured the average number of “chick-a-dee” calls given during each 15-minute presentation. I determined overall differences among the treatments using an ANOVA.
and conducted specific pair-wise comparisons of all the treatments using Tukey’s post-hoc comparisons which adjust for an experiment-wide alpha level (Ott 1993).

*Syllable Composition*

To determine if general patterns exist in the acoustic structure of the “chick-a-dee” call related to the type of predator, I measured the number of A, B, C, and D syllables (Ficken et al. 1978; Hailman et al. 1985), and the total number of syllables in each call (Figure 1a). I averaged the number of each syllable per call for each individual bird-predator combination, so that an individual bird was considered a sampling unit. I assumed that each bird responded primarily to the treatment instead of the behaviors of other birds, making this the appropriate choice of sampling unit. Using these averaged values, I then compared the number of each syllable per call among predator treatments. I used a natural log transformation for the C data to homogenize the variances (all other data sets met this assumption), and then used a univariate ANOVA to compare each syllable. I used Tukey’s post-hoc test (Ott 1993) to conduct pair-wise comparisons for each syllable where I detected an overall effect of the predator treatment.

To determine whether the size of the potential predator influenced the syllable composition of the calls, I obtained the average body length, body mass, and wingspan of
each raptor species (Sibley 2000) and compared these measurements with the mean number of D syllables per call using linear regression.

Temporal and Amplitude Measurements

Because the D note appears to be most important in encoding a wide variety of information (Mammen & Nowicki 1981; Nowicki 1983; Nowicki 1989; see syllable composition results), I also conducted more detailed analyses of the acoustic structure of D notes. For these analyses, I randomly selected calls only from the highest quality recordings. I analyzed 5 calls from 6 different individuals that were produced in the presence of a northern pygmy-owl, and 5 calls from the same individuals that were produced in the presence of a great horned owl (60 calls total).

For each call, I measured the duration of the “chick” section, the duration of the “dee” section, the interval between the “chick” and “dee” sections, and the duration of the first D note (Figure 1a). I subjectively categorized the first D note as “flat,” “wavy,” “ascending,” or “descending” depending on the overall shape (Figure 1b). Calls were classified by examining the frequency modulation of a single overtone throughout the note. Overtones of “flat” calls did not vary substantially in frequency; overtones from “ascending” notes increased by approximately 300-500 Hz from beginning to end;
overtones from "wavy" notes wavered up and down in frequency throughout the syllable. I also measured several acoustic features similar to those described by Nowicki (1989) using a power spectrum analysis (FFT=512) taken from the center of the first D note of each call (Figure 1c). These features were the lowest frequency peak above −30dB relative to the peak, the highest frequency peak above −30dB relative to the peak, the frequency of the first two peaks above −30dB (frequency 1 & 2; used to determine the distance between overtones), the number of peaks above −10dB, the peak frequency, the highest frequency peak above −10dB relative to the peak, and the lowest frequency peak above −10dB relative to the peak. I calculated the interval between overtones by subtracting frequency 1 from frequency 2. I also calculated the bandwidth at −10dB and −30dB.

To compare the overall shape of the D notes between calls produced in the presence of the pygmy-owl with calls produced in the presence of the great horned owl, I used a Chi-square test. I made similar comparisons with each of the continuous variables using a two-way ANOVA; calling individual was used as a random factor to account for variation in acoustic features among birds. Principle components analysis was used for data reduction to determine the degree of overlap among the fine-scale acoustic measurements (Ott 1993).
RESULTS

Calling Rates

Chickadee calling rates were significantly different among the trials (ANOVA: $F_{16, 34} = 5.167, p < 0.0001$). The calling rate was lowest for the control (28 calls per 15 minutes) and tended to increase in the following order of treatments: bobwhite quail, rough-legged hawk, gyrfalcon, prairie falcon, short-eared owl, great gray owl, ferret, cat, great horned owl, merlin, peregrine falcon, red-tailed hawk, kestrel, saw-whet owl, Cooper’s hawk, and pygmy-owl (322 calls per 15 minutes). Post-hoc tests indicate that only the Cooper’s hawk, saw-whet owl, and pygmy-owl treatments statistically differed from the control ($p = 0.028$, $p = 0.048$, and $p < 0.001$, respectively).

Syllable Composition

The total number of syllables per call differed among the treatments (ANOVA: $F_{16, 34} = 3.05, p < 0.0001$). No significant differences existed in the average number of A or B syllables per call ($F = 1.603, p = 0.066$ and $F = 1.092, p = 0.361$, respectively; Table 2), however, the average number of C notes per call differed among predator treatments.
(F = 4.735, p < 0.0001; Table 2). The average number of D notes per call also
substantially differed across predator treatments (F = 7.771, p < 0.0001; Table 2).

Chickadee’s vocal response to predators appears to be graded instead of clear-cut
and the large number of predators in this study prevents reporting results from all
possible post-hoc comparisons here. Therefore, for the purposes of demonstrating the
main patterns in the chickadee vocalizations, I will focus on some of the large-scale
differences instead of reporting the results from every pair-wise comparison.

When comparing the number of C notes per call, the treatments fell into two
groups (Figure 2). Treatments that were not statistically different from the control were
the bobwhite quail (procedural control), cat, ferret, rough-legged hawk, red-tailed hawk,
short-eared owl, great horned owl, great gray owl, American kestrel, merlin, prairie
falcon, peregrine falcon, and gyrfalcon (p > 0.1 for all). Chickadees used fewer C notes in
their calls for the cooper’s hawk, northern pygmy-owl, and saw-whet owl than during the
control (p = 0.007, p < 0.001, and p = 0.003, respectively).

There are three fairly distinct groups of predators based on the number of D
syllables per call (Figure 3). Predators that did not differ from the control were the
bobwhite, rough-legged hawk, short-eared owl, great gray owl, prairie falcon, and
gyrfalcon (p > 0.1 for all). Compared to the control, D note frequency per call increased
in response to the cat, ferret, red-tailed hawk, great horned owl, Cooper’s hawk, kestrel,
merlin, or peregrine falcon (p < 0.001, p < 0.001, p = 0.032, p = 0.017, p < 0.001, p =
Chickadees used the most D notes in their vocalizations when confronted with northern pygmy-owl and saw-whet owls ($p < 0.01$ for both).

The number of D notes per call was inversely related to predator size, with the smallest predators eliciting the calls with the most D notes (Figure 4: body length: $y = 4.3 - 0.04x, R^2 = 0.628, p = 0.001$; log body mass: $y = 5.9 - 1.2x, R^2 = 0.616, p = 0.001$; wingspan: $y = 4.4 - 0.02x, R^2 = 0.765, p = 0.001$).

**Temporal Measurements**

Many of the fine-scale acoustic features of the “chick-a-dee” vocalization varied with the predator treatment (Table 3). The duration of the “chick” section did not differ between the great horned owl and the pygmy-owl trials ($F = 0.872, p = 0.355$). However, the duration of the “dee” section (all D notes) was longer in calls given to the pygmy-owl than in calls given to the great horned owl ($F = 9.984, p = 0.003$). In contrast, the duration between the “chick” and “dee” sections of the call was significantly shorter in the pygmy-owl trials than the great horned owl trials ($F = 11.364, p = 0.001$). The first D note of each call was shorter in the pygmy-owl trials than the great horned owl trials ($F = 9.984, p = 0.003$). The duration between the first and second D notes was also significantly shorter in response to pygmy-owls ($F = 9.043, p = 0.004$).
Amplitude Measurements

Overall shape of the first D note was different between the two treatments (Chi-square: df = 3, p < 0.0001). During the great horned owl presentation, chickadees used mostly "flat," or normal D notes (68%) with few "ascending" (16%), "descending" (3%), or "wavy" (13%) notes. However, during the pygmy owl presentation, chickadees used primarily "ascending" (55%) and "wavy" (42%) D notes and very few "flat" D notes (3%).

There were no differences between treatments in the lowest frequency or highest frequency peaks above -30dB (F = 0.012, p = 0.914 and F = 1.393, p = 0.243, respectively; Table 3) or the bandwidth between these peaks (F = 1.370, p = 0.247). The peak frequency did not differ between the two predator treatments (F = 2.591, p = 0.113), nor did the highest or lowest frequency peaks above -10dB (F = 1.092, p = 0.715 and F = 1.947, p = 0.169, respectively).

Calls that chickadees produced during the great horned owl presentations tended to have D notes that contained more high-energy peaks above -10dB (F = 2.855, p = 0.097) spanning a wider bandwidth (F = 2.719, p = 0.105) than those produced during the pygmy-owl presentations (Table 3). D notes used during the great horned owl treatments
tended to have more widely-spaced overtones than D notes used during the pygmy-owl treatments ($F = 3.385, p = 0.071$).

Principle components analysis of the fine-scale measurements did not achieve substantial data reduction in the number of parameters (7 components with eigenvalues > 1); examining the first two principle components could not sufficiently explain the predator treatment. This indicates that most of the parameters are not strongly associated and each may explain different information.
DISCUSSION

Black-capped chickadees discriminate among different species of potential predators and change the acoustic structure of their "chick-a-dee" mobbing calls in several ways that appear to encode information about the predators. Calling rates increased for certain predators relative to control trials. The number of A and B syllables does not vary substantially, but for certain predators, chickadees use fewer C syllables and more D syllables in their calls than they do during control trials. Chickadees also change fine-scale acoustic features of their calls, in particular the D syllables, depending on which predator they encounter.

Calling Rate

Chickadees increased their calling rate in response to the Cooper's hawk, northern saw-whet owl, and northern pygmy-owl relative to the control. Differences in calling rate may reflect the urgency of response due to the relative risk posed by each predator. This result supports the idea that repetitions in chickadee alarm calls function to indicate the strength of the message (Hailman et al. 1985; Hurd 1996). Increased calling rates that correspond with more dangerous predators are also consistent with tonic communication theory, where repetitions of discrete signals serve to maintain or gradually increase the
behavioral response of the receiver (Schleidt 1973). By changing the calling rate, chickadees may convey information about the potential risk of the predator, and therefore, the urgency of the mobbing response. An alternative explanation of increased calling with increased danger is that adding vocal signals to mobbing behavior may help “move on” the predator through increased harassment levels or by advertising superior quality of the prey animal (Curio & Regelmann 1985).

*Syllable Composition*

I presented both aerial (hawks, falcons, and owls) and terrestrial predators (cat and ferret) in this experiment. Many previous studies have indicated that birds give different anti-predator vocalizations for these two broad classes of predators. However, most of these studies have presented aerial predators in different ways than terrestrial predators (e.g., Greene & Meagher 1998; Blumstein 1999; Le Roux et al. 2001), potentially confounding the interpretation that the prey species distinguishes between the classes of predators and not their location or behaviors. Naguib et al. (1999) showed that mobbing Arabian babblers vocally discriminate among a stuffed short-eared owl and a caged cat when they were presented in similar ways (i.e., both close to the ground). However, it is not clear whether the vocalizations reflect specific classes of predators (i.e., raptor vs. mammal) or the intensity of the threat (i.e., low vs. high risk). My results
show that chickadees do not vocally discriminate between raptors and mammals when they are presented in very similar ways. This suggests that the “chick-a-dee” call as a whole does not refer specifically to the type of predator.

Instead of referring to the type of predator, variation in a vocalization may contain other information like the degree of threat a particular predator or situation represents. In my study, chickadees did not vary the number of A or B syllables in relationship to the treatment. This suggests that A and B syllables do not encode information regarding the degree of threat of a predator. Either type of syllable may be used to convey other information such as the behavioral state or movement patterns of the caller (Smith 1972; Ficken et al. 1994). In contrast, chickadees used fewer C notes and more D notes in their “chick-a-dee” calls in response to some predators than they did to others. The numbers of both C and D notes in a call appear to correspond with the degree of risk a specific predator represents.

There was a trend for chickadees to include fewer C notes in their calls when they encountered more dangerous predators. However, only the calls produced in response to the Cooper’s Hawk, pygmy-owl, and saw-whet owl were statistically different from the control. This finding suggests that chickadees may encode risk information in the number of C notes per call, with fewer C notes potentially indicating more threatening situations. An alternative explanation is that in more dangerous situations, such as encountering a threatening predator, chickadees may replace C notes with other syllables, like D notes.
The number of D notes per call was highly variable among predator treatments. Several potential predators did not elicit calls that differed from the control in the number of D notes. These were species that do not typically feed on small birds like chickadees. Some of these species, such as the rough-legged hawk (Johnsgard 1990), short-eared owl (Holt & Leasure 1993), great horned owl (Houston et al. 1998), and great gray owl (Bull & Duncan 1993), feed primarily on small mammals. Other species, such as the prairie falcon and gyrfalcon, focus most of their hunting efforts on both small mammals and medium-sized birds (Johnsgard 1990). In contrast, chickadees responded to the presence of some other predators by adding more D syllables to their calls. These predators were the red-tailed hawk, Cooper’s hawk, American kestrel, merlin, peregrine falcon, northern pygmy-owl, northern saw-whet owl, domestic cat, and ferret. Most of these species probably pose a major threat to chickadees in the winter.

Merlins and Cooper’s hawks feed almost exclusively on small birds like chickadees (Johnsgard 1990). Other species such as the red-tailed hawk, American kestrel, and peregrine falcon, usually focus on small mammals, insects, or larger birds and probably do not often eat chickadees. However, each of these species is known to prey on birds the size of chickadees under the right circumstances (Johnsgard 1990).

Chickadees added the greatest number of D notes to their calls when they encountered the pygmy-owl and the saw-whet owl. Small owls are highly maneuverable and represent one of the few predators that regularly catch small birds like chickadees.
Northern pygmy-owls are known to prey heavily on chickadees where their ranges overlap in the western U.S. (Holt & Petersen 2000). Saw-whet owls hunt small birds in the eastern U.S. (Smith 1991; Cannings 1993), but where their range overlaps with pygmy-owls in the west they are thought to focus mostly on small mammals (Cannings 1993). Three alternative explanations may explain the unexpected strong response of chickadees to this predator: 1) Saw-whet owls may hunt more avian prey in the west than was previously thought. 2) Even if they favor other prey, their small size means that they could capture chickadees, making them a real threat regardless of their primary diet. 3) chickadees may not discriminate between pygmy-owls and saw-whet owls. Perhaps pygmy-owls pose such a great threat that selection has favored a strong mobbing response to small owls encountered during daylight hours, regardless of the species.

The two mammalian predators also appear to be treated as dangerous threats. Near urban areas like Missoula, MT it is likely that domestic house cats kill considerable numbers of small birds (Crooks & Soulé 1999), making them a substantial threat to chickadees. Ferrets resemble mustelids that naturally occur with chickadees. The least (Mustela nivalis), short-tailed (M. erminea) and long-tailed (M. frenata) weasels are known to be nest predators on other species of chickadees and tits (Perrins 1979; Gold & Dahlsten 1983) and they may also opportunistically prey on adult birds in the winter.

Body size of the predator (measured by body length, body mass, or wingspan) is highly correlated with the strength of the chickadee’s response (number of D notes per
Because small birds are so agile, a predator must also be highly maneuverable in order to prey on chickadees. It is commonly thought that body size is inversely related to maneuverability in birds. This is because the mass-specific power required to fly is nearly independent of body size (Ellington 1991), but the mass-specific power available is inversely proportionate to body size (between $M^{2/3}$ and $M^{5/6}$). Thus, small birds have relatively more power available for energetically demanding maneuvers (Pennycuick 1989). Because turning radius (maneuverability) can be important in prey capture (Howland 1974), small predators are predicted to be most dangerous to small prey birds. Thus, small predators should actually pose a greater threat to chickadees than large predators. The regression models indicate that chickadees use more D notes in their vocalizations when responding to small predators than when responding to large predators.

While these models explain a large portion of the variation in the number of D notes per call (60-75%), closely examining the residuals indicates that chickadees are most likely using other cues than simply body size when assessing the threat of a potential predator (Figure 4). For instance, chickadees use many more D notes in their calls for the Cooper’s hawk, a medium-sized predator that feeds primarily on small birds, than the model predicts. Similarly, chickadees use fewer D notes than predicted for the American kestrel, a small predator that less frequently feeds on birds. Thus, it appears that chickadees are actually distinguishing among specific species of potential predators.
rather than simply using a rule based on the predator's body size (i.e., small predators are dangerous, large predators are not).

**Temporal and Amplitude Measurements**

Fine scale acoustic analyses of the "chick-a-dee" call indicate that in addition to varying the number of C and D syllables, chickadees also change several more subtle features of this call depending on which predator they encounter. Calls given to pygmy-owls had shorter "chick" sections, longer "dees" sections, shorter D notes, and shorter intervals between D notes. Furthermore, D notes differed in their overall shape and calls produced in response to a pygmy-owl tended to have fewer high-energy peaks and smaller frequency intervals between overtones than calls produced in response to a great horned owl. These results suggest that chickadees encode even more subtle information in this call than can be achieved by simply varying the number of syllables.

Chickadees may change all of these features of their vocalizations to encode specific information about the predator encounter or the urgency for subsequent behaviors (i.e., mobbing). Another explanation is that some of these features may vary as the result of changing any given acoustic feature of the call. For instance, spacing D notes closer together may impose time constraints on the formation of each D note, subsequently changing the other call features as a byproduct. Similarly, changing the
amplitude of the call (i.e., making the call louder so that it projects farther), may impose anatomical constraints on call production which affect other features of the call. For instance, D notes may not be perfectly formed in shape, number of overtones, or in the spacing of the overtones as a result of changing amplitude. Although the PCA results do not suggest that the acoustic features I measured were highly associated, other unmeasured features may affect the production of these acoustic features. However, regardless of which mechanism regulates the physical production of the call, several fine-scale features of the calls vary in predictable ways and could be used to transmit reliable information about the specific features of a potential predator to conspecifics.

**General Conclusions**

Chickadee anti-predator vocalizations appear to represent a new type of alarm-calling system. Unlike referential and risk-based alarm call systems, which use acoustically distinct calls or gradations between different calls (Macedonia & Evans 1993), chickadees use variations in a single type of call to convey information about potential predators. Because of the amount of information encoded in this single type of vocalization, the “chick-a-dee” call may represent a vocal anti-predator system that is unparalleled in its subtleties compared with other known examples.
Although I have presented evidence that chickadees respond differently to different species of predators, I can not distinguish whether this behavior is genetically-based or learned. The production of the other type of anti-predator vocalization ("High Zee") is innate rather than learned, however, chickadees must learn the appropriate context for its use over time (Apel & Ficken 1981). A similar scenario is also found in the development of alarm calls in vervet monkeys (Cheney & Seyfarth 1990). Further, one potential function of mobbing behavior may be to teach young birds which predators are dangerous (Curio 1978) suggesting that some degree of learning may take place. One of the flocks in my study did not respond strongly to the merlin, and learning may explain this unexpected result if these birds had not previously encountered this species. Because all of the captive flocks contained both juvenile (HY/SY) and adult (ASY) birds, it is impossible to know whether the observed predator discrimination is learned or instinctual. Future studies comparing naïve and experienced birds would be instructive.

This study has shown that chickadees produce mobbing vocalizations that vary at several different acoustic levels and appear to encode information that relates to the species of predator encountered as the call is produced. Whether a receiver is able to extract this degree of predator information from these acoustic differences is the topic of Chapter II.


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Table 1: Predator features, including type, average body size, time of activity, and primary diet, were used to predict the degree of risk each species poses to chickadees. Predators are presented in phylogenetic groupings.

<table>
<thead>
<tr>
<th>Predator Species</th>
<th>Type</th>
<th>Mass (g)</th>
<th>Length (cm)</th>
<th>Wingspan (cm)</th>
<th>Time Active</th>
<th>Primary Diet</th>
<th>Predicted Danger</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hawks</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cooper's Hawk</td>
<td>Accipiter cooperii</td>
<td>aerial</td>
<td>450</td>
<td>43</td>
<td>77</td>
<td>day small birds</td>
<td>High</td>
</tr>
<tr>
<td>Red-tailed Hawk</td>
<td>Buteo jamaicensis</td>
<td>aerial</td>
<td>1080</td>
<td>56</td>
<td>122</td>
<td>day small mammals, few birds</td>
<td>Medium</td>
</tr>
<tr>
<td>Rough-legged Hawk</td>
<td>B. lagopus</td>
<td>aerial</td>
<td>990</td>
<td>56</td>
<td>133</td>
<td>day small mammals</td>
<td>Low</td>
</tr>
<tr>
<td><strong>Falcons</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American Kestrel</td>
<td>Falco sparverius</td>
<td>aerial</td>
<td>117</td>
<td>27</td>
<td>55</td>
<td>day invertebrates, small mammals, small birds</td>
<td>Medium</td>
</tr>
<tr>
<td>Merlin</td>
<td>F. columbarius</td>
<td>aerial</td>
<td>190</td>
<td>31</td>
<td>60</td>
<td>day small birds</td>
<td>High</td>
</tr>
<tr>
<td>Peregrine Falcon</td>
<td>F. mexicanus</td>
<td>aerial</td>
<td>720</td>
<td>46</td>
<td>102</td>
<td>day medium-sized birds</td>
<td>Medium</td>
</tr>
<tr>
<td>Prairie Falcon</td>
<td>F. peregrinus</td>
<td>aerial</td>
<td>720</td>
<td>45</td>
<td>100</td>
<td>day small mammals, some birds</td>
<td>Low</td>
</tr>
<tr>
<td>Gyrfalcon</td>
<td>F. rusticolus</td>
<td>aerial</td>
<td>1400</td>
<td>38</td>
<td>117</td>
<td>day medium-sized mammals and birds</td>
<td>Low</td>
</tr>
<tr>
<td><strong>Owls</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Pygmy-owl</td>
<td>Glaucidium gnoma</td>
<td>aerial</td>
<td>70</td>
<td>17</td>
<td>30</td>
<td>day small birds, small mammals</td>
<td>High</td>
</tr>
<tr>
<td>Saw-whet Owl</td>
<td>Aegolius acadicus</td>
<td>aerial</td>
<td>80</td>
<td>20</td>
<td>42</td>
<td>night small mammals, some small birds</td>
<td>Medium</td>
</tr>
<tr>
<td>Short-eared Owl</td>
<td>Asio flammeus</td>
<td>aerial</td>
<td>350</td>
<td>38</td>
<td>95</td>
<td>both small mammals</td>
<td>Low</td>
</tr>
<tr>
<td>Great horned Owl</td>
<td>Bubo virginianus</td>
<td>aerial</td>
<td>1400</td>
<td>56</td>
<td>110</td>
<td>night small to medium-sized mammals</td>
<td>Low</td>
</tr>
<tr>
<td>Great Gray Owl</td>
<td>Strix nebulosa</td>
<td>aerial</td>
<td>1080</td>
<td>69</td>
<td>130</td>
<td>both small mammals</td>
<td>Low</td>
</tr>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cat</td>
<td>Felis domesticus</td>
<td>terrestrial</td>
<td>15000</td>
<td>60</td>
<td>NA</td>
<td>both birds, small mammals, insects</td>
<td>High</td>
</tr>
<tr>
<td>Ferret</td>
<td>Mustela putorius</td>
<td>terrestrial</td>
<td>1000</td>
<td>60</td>
<td>NA</td>
<td>day</td>
<td>Low</td>
</tr>
<tr>
<td><strong>Control</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>None</td>
</tr>
<tr>
<td>Bobwhite Quail</td>
<td>Colinus virginianus</td>
<td>170</td>
<td>24</td>
<td>32</td>
<td>day</td>
<td>grain</td>
<td>None</td>
</tr>
</tbody>
</table>
Table 2: Mean numbers and standard errors of A, B, C, and D syllables per call during each predator presentation. Depending on the number of birds calling, N = 18 or 20 for all treatment-syllable combinations.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>A mean</th>
<th>A SE</th>
<th>B mean</th>
<th>B SE</th>
<th>C mean</th>
<th>C SE</th>
<th>D mean</th>
<th>D SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1.828</td>
<td>.438</td>
<td>1.060</td>
<td>.276</td>
<td>0.526</td>
<td>.146</td>
<td>1.527</td>
<td>.232</td>
</tr>
<tr>
<td>Bobwhite Quail</td>
<td>2.209</td>
<td>.428</td>
<td>0.716</td>
<td>.141</td>
<td>0.947</td>
<td>.249</td>
<td>1.738</td>
<td>.236</td>
</tr>
<tr>
<td>Red-tailed Hawk</td>
<td>2.669</td>
<td>.497</td>
<td>0.743</td>
<td>.156</td>
<td>0.493</td>
<td>.136</td>
<td>2.454</td>
<td>.263</td>
</tr>
<tr>
<td>Rough-legged Hawk</td>
<td>1.589</td>
<td>.269</td>
<td>0.895</td>
<td>.254</td>
<td>1.004</td>
<td>.216</td>
<td>1.335</td>
<td>.254</td>
</tr>
<tr>
<td>Cooper's Hawk</td>
<td>2.356</td>
<td>.276</td>
<td>0.591</td>
<td>.074</td>
<td>0.266</td>
<td>.059</td>
<td>3.156</td>
<td>.201</td>
</tr>
<tr>
<td>American Kestrel</td>
<td>1.877</td>
<td>.241</td>
<td>0.701</td>
<td>.149</td>
<td>0.474</td>
<td>.116</td>
<td>2.762</td>
<td>.318</td>
</tr>
<tr>
<td>Merlin</td>
<td>1.452</td>
<td>.225</td>
<td>0.607</td>
<td>.136</td>
<td>0.353</td>
<td>.108</td>
<td>3.036</td>
<td>.254</td>
</tr>
<tr>
<td>Peregrine Falcon</td>
<td>2.296</td>
<td>.353</td>
<td>0.734</td>
<td>.124</td>
<td>0.277</td>
<td>.081</td>
<td>2.281</td>
<td>.305</td>
</tr>
<tr>
<td>Prairie Falcon</td>
<td>1.787</td>
<td>.225</td>
<td>0.707</td>
<td>.152</td>
<td>0.719</td>
<td>.300</td>
<td>2.196</td>
<td>.253</td>
</tr>
<tr>
<td>Gyrfalcon</td>
<td>1.758</td>
<td>.295</td>
<td>0.937</td>
<td>.183</td>
<td>0.485</td>
<td>.111</td>
<td>2.251</td>
<td>.343</td>
</tr>
<tr>
<td>Northern Pygmy-owl</td>
<td>2.029</td>
<td>.179</td>
<td>0.741</td>
<td>.217</td>
<td>0.199</td>
<td>.057</td>
<td>3.947</td>
<td>.346</td>
</tr>
<tr>
<td>Saw-whet Owl</td>
<td>1.179</td>
<td>.178</td>
<td>0.378</td>
<td>.069</td>
<td>0.271</td>
<td>.077</td>
<td>4.078</td>
<td>.288</td>
</tr>
<tr>
<td>Short-eared Owl</td>
<td>1.735</td>
<td>.376</td>
<td>0.996</td>
<td>.174</td>
<td>0.546</td>
<td>.166</td>
<td>2.273</td>
<td>.314</td>
</tr>
<tr>
<td>Great horned Owl</td>
<td>2.639</td>
<td>.414</td>
<td>0.496</td>
<td>.115</td>
<td>0.435</td>
<td>.129</td>
<td>2.555</td>
<td>.316</td>
</tr>
<tr>
<td>Great Gray Owl</td>
<td>2.063</td>
<td>.459</td>
<td>0.569</td>
<td>.147</td>
<td>1.035</td>
<td>.324</td>
<td>2.051</td>
<td>.332</td>
</tr>
<tr>
<td>Cat</td>
<td>1.833</td>
<td>.250</td>
<td>0.542</td>
<td>.143</td>
<td>0.219</td>
<td>.070</td>
<td>3.214</td>
<td>.242</td>
</tr>
<tr>
<td>Ferret</td>
<td>2.213</td>
<td>.278</td>
<td>0.694</td>
<td>.140</td>
<td>0.319</td>
<td>.169</td>
<td>3.552</td>
<td>.318</td>
</tr>
</tbody>
</table>

| F           | 1.603 | 1.092 | 4.735 | 7.771 |
| p           | 0.066 | 0.361 | <0.0001 | <0.0001 |

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Table 3: Means and standard errors of several features measured from chick-a-dee calls produced in response to a great horned owl or a northern pygmy-owl. See Figure 2 for a description of the measurements. Durations are in seconds and frequency measurements are in Hz.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Great Horned Owl</th>
<th>Pygmy-owl</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N = 30</td>
<td>N = 30</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>SE</td>
</tr>
<tr>
<td>Duration of &quot;chick&quot;</td>
<td>0.2401</td>
<td>.031</td>
</tr>
<tr>
<td>Chick-dee interval</td>
<td>0.0289</td>
<td>.003</td>
</tr>
<tr>
<td>Duration of 1° D</td>
<td>0.1568</td>
<td>.004</td>
</tr>
<tr>
<td>Inter-D interval</td>
<td>0.0397</td>
<td>.002</td>
</tr>
<tr>
<td>Duration of &quot;dee&quot;</td>
<td>0.6444</td>
<td>.056</td>
</tr>
<tr>
<td>Frequency 1 &gt; -30dB</td>
<td>1347.4</td>
<td>60.6</td>
</tr>
<tr>
<td>Frequency 2&gt; -30dB</td>
<td>1661.8</td>
<td>62.9</td>
</tr>
<tr>
<td>Interval btw Freq. 1 &amp; 2</td>
<td>314.44</td>
<td>25.8</td>
</tr>
<tr>
<td>Max frequency &gt; -30dB</td>
<td>6428.8</td>
<td>175</td>
</tr>
<tr>
<td>Peak frequency</td>
<td>3535.4</td>
<td>63.8</td>
</tr>
<tr>
<td>Lowest peak &gt; -10dB</td>
<td>2924.2</td>
<td>105</td>
</tr>
<tr>
<td>Highest peak &gt; -10dB</td>
<td>4393.3</td>
<td>95.4</td>
</tr>
<tr>
<td>Bandwidth at -10dB</td>
<td>1469.1</td>
<td>112</td>
</tr>
<tr>
<td>Bandwidth at -30dB</td>
<td>5081.3</td>
<td>181</td>
</tr>
<tr>
<td>Number of peaks &gt; -10dB</td>
<td>4.71</td>
<td>.250</td>
</tr>
</tbody>
</table>

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FIGURE LEGENDS

Figure 1: a) The “chick-a-dee” vocalization usually contains both “chick” and “dee” sections. The call is composed of four different types of syllables: A, B, C, and D. The number of each type of syllable included can vary among calls. b) Examples of D syllables that were categorized as “flat,” “wavy,” or “ascending.” “Descending” shaped syllables were very uncommon and are not included. c) Power spectrum analysis from the center of a D note. The amplitude has been scaled relative to the highest energy overtone (dB = 0). Several acoustic features were measured including the frequency of the first and second peaks above –30 dB (F1 and F2, respectively), the lower and upper frequencies above –10 dB (L and U, respectively), the peak frequency (P), and the maximum frequency peak above –30 dB (M). Bandwidth at –10 dB (BW: -10) was calculated by subtracting L from U, and the bandwidth at –30 (BW: -30) was calculated by subtracting F1 from M. The interval between overtones was determined by subtracting F1 from F2.

Figure 2: The mean (± 1 S.E.) number of C syllables per “chick-a-dee” call recorded during the presentation of each predator. Predators are arranged in phylogenetic order with the control and procedural control treatments on the left. Black bars indicate predator treatments that are not statistically different from the control and white bars
indicate predator treatments that are different from the control (Tukey's post-hoc comparisons; \( p < 0.05 \)).

Figure 3: The mean (± 1 S.E.) number of D syllables per “chick-a-dee” call used during each treatment. Error bars represent 1 standard error of the mean. Predators are arranged by phylogeny with the control and procedural control treatments on the left. Black bars indicate treatments that are not different from the control; hatched and white bars indicate two classes that differ from the control and each other (Tukey's post-hoc comparisons; \( p < 0.05 \)).

Figure 4: The mean number of D syllables per call displayed as a function of predator body length, where \( y = 4.3 - 0.04x \) (\( R^2 = 0.628, p = 0.001 \)). The control, bobwhite quail, cat, and ferret treatments are excluded for this analysis.
Figure 1

(a) 

- “chick”
- “dee”

Time (s)

Frequency (kHz)

A B C C D D D

(b) 

- “flat”
- “wavy”
- “ascending”

Time (s)

Frequency (kHz)

(c) 

Relative Amplitude (dB)

F1 F2 L P U M

Frequency (kHz)

BW: -10

BW: -30

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Figure 2

Number of C Syllables Per Call

control
bobwhite
rough-legged
red tail
coopers
kestrel
merlin
peregrine
prairie
gyrfalcon
pygmy
saw whet
short eared
great horned
great gray
ferret
cat

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Figure 4

A graph shows the relationship between Predator Length (cm) and Number of D Syllables Per Call. The graph includes data points for various bird species, such as saw-whet, pygmy-owl, merlin, Cooper's, kestrel, peregrine, red tail, great horned, gyrfalcon, great gray, and rough-leg. The data suggests a negative correlation between length and syllable count. Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
CHAPTER II: Responses of black-capped chickadees to playbacks of predator-specific variations in their “chick-a-dee” call

ABSTRACT

Many animals appear to change their anti-predator vocalizations in relationship to features of the potential predator they encounter. Acoustic variations may even strongly correlate with the presence of certain types or distinct species of predators. However, understanding any communication system involves not only knowing about the production of the signals, but also how encoded information is used to make behavioral decisions by receivers. Black-capped Chickadees (*Poecile atricapilla*) produce consistent acoustic variations in their “chick-a-dee” mobbing call that appear to reflect the degree of risk represented by certain species of predators. However, it is not known if this information is used by conspecific chickadees. I conducted playback experiments with three flocks of six chickadees living under semi-natural aviary conditions to determine how chickadees respond to different “chick-a-dee” calls in the absence of other contextual information. Chickadees responded strongly to playbacks of “chick-a-dee” mobbing calls compared to control (pine siskin, *Carduelis pinus*, call) trials. Based on predator locomotor performance, natural history features, and the way chickadees respond to live predators (Chapter 1), I predicted that chickadees should treat “chick-a-
"chick-a-dee" calls given in response to a northern pygmy-owl (*Glaucidium gnoma*) differently than calls given in response to a great horned owl (*Bubo virginianus*). Chickadees increased their calling rates and approached the speaker more closely in response to playbacks of mobbing calls given to a northern pygmy-owl as compared to calls given to a great horned owl. Thus, acoustic variations in this vocalization are used by signal receivers in addition to being reliably produced in response to different predators. These results indicate that chickadees communicate information about the degree of threat a predator represents through very subtle acoustic features of their "chick-a-dee" call.
INTRODUCTION

Anti-predator benefits that result from group living are a major factor promoting sociality in animals. Many animals use anti-predator vocalizations that vary in acoustic structure with the context in which they are given. The conditions necessary to evoke a given variant of a call have been studied in a number of different systems using both models and live predators (e.g., Grubb 1977; Seyfarth et al. 1980; Gyger et al. 1987; Greene & Meagher 1998; Blumstein 1999). These studies indicate that many different animals change their vocalizations with respect to different predator behaviors (Owings & Hennessy 1984; Evans et al. 1993), locations (Alatalo & Helle 1990; Stone & Trost 1991), or body sizes (Klump & Curio 1983; Evans et al. 1993; Ackers & Slobodchikoff 1999). Vocalizations may also contain information that reflects the degree of threat (and associated urgency of response) of a predator (Owings & Hennessy 1984; Macedonia & Evans 1993; Blumstein & Arnold 1995) or the type (Greene & Meagher 1998; Naguib et al. 1999) or particular species (Grubb 1977; Walters 1990) of predator encountered.

Species that produce vocalizations that vary predictably in relation to the type or species of potential predator may provide information about the specific class of predator ("referential"), or the degree of risk a given predator represents ("urgency-based"). For instance, vervet monkeys (Cercopithecus aethiops) produce acoustically distinct vocalizations when different types of predators (e.g., leopard, eagle, snake) are nearby,
and these calls are independent of the location or behavior of the predators (Seyfarth et al. 1980; Cheney & Seyfarth 1988). In contrast, many small mammals, like ground squirrels, have an urgency-based alarm call repertoire with “whistles” given in situations of immediate danger and “chatters” given in lower risk situations, regardless of the type of predator (Owings & Hennessy 1984; Macedonia & Evans 1993).

Understanding the function and adaptive significance of alarm call systems requires knowing not only how signals are produced in relation to the caller’s environment, but also how variations in signals are perceived by conspecific receivers (Marler et al. 1992; Hauser 1996). In both of the above systems, playback studies have shown that conspecifics use anti-predator calls to make behavioral decisions independent of the environmental context in which they hear the call. However, in other systems, variations in call structure are reliably produced in relation to the degree of risk presented during a predator encounter, but these variations do not appear to communicate risk information to conspecifics. For example, Brant’s whistling rats, *Parotomys brantsii*, produce short calls in high-risk situations and long calls in low-risk situations, but playback experiments have shown that conspecifics do not respond to these two types of alarm calls as though they convey different information (Le Roux et al. 2001; Le Roux et al. in press). Thus, testing the perception of specific signals is equally as important to understanding an anti-predator communication system as testing the production of the signals.
Black-capped chickadees (*Poecile atricapilla*) encounter a wide variety of potential predators that range in body size, degree of risk, and hunting strategy (Smith 1991). Many predators are actively mobbed when they are encountered perched in the chickadee’s territory (Ficken et al. 1978; Shedd 1983; Smith 1991; Zanetter & Ratcliffe 1994). When mobbing potential predators, chickadees produce a complex recruitment vocalization termed the “chick-a-dee” call (Odum 1942; Ficken et al. 1978) that is highly variable in acoustic structure (Mammen & Nowicki 1981; Hailman et al. 1985). In a previous study (Chapter 1), I systematically presented captive flocks of chickadees with a wide variety of live predators and showed that the “chick-a-dee” call varies in several subtle, but important acoustic features in relation to the degree of threat that a potential predator represents. For example, calls produced in response to high-risk predators, like a northern pygmy-owl (*Glaucidium gnoma*), are statistically distinguishable from the calls given to lower risk predators, like a great horned owl (*Bubo virginianus*). In this study, I present results of playback experiments designed to test whether conspecific receivers derive information about potential predators from acoustic differences in the vocalizations of a signaler. Chickadees should respond more strongly to playback of calls produced in response to a pygmy-owl compared to calls produced in response to a great horned owl if information related to the species or degree of threat is conveyed in the “chick-a-dee” call.
METHODS

Experimental Aviary

I conducted playback experiments from November 2001 to February 2002 with three flocks of six individual black-capped chickadees captured from different locations surrounding Missoula, MT. Each flock of chickadees was housed in an outdoor, experimental aviary at the University of Montana’s Field Research Station at Fort Missoula, in Missoula, MT. The aviary was large (16m x 6m x 4m) and contained numerous live trees, shrubs, and snags to approximate natural conditions. In a previous study, I recorded “chick-a-dee” mobbing vocalizations of individual chickadees when the flock was exposed to many different predators including a great horned owl and a northern pygmy-owl (Chapter 1). I used these mobbing calls to construct playback stimuli.

Playback stimuli

I tested the response of chickadees to three general types of stimulus (Figure 2): calls produced in response to great horned owls, calls produced in response to northern pygmy-owls, and control calls of a pine siskin (Carduelis pinus). Chickadees have a
subtle and complex communication system, and individuals in captivity rapidly habituate to playback stimuli (personal observation). For these reasons, I had to design the intricate playback experiment described below in order to isolate the chickadees' responses to the playback stimuli (see Figure 1 for design summary).

Because chickadees encode information about flock membership in their “chick-a-dee” calls and respond differently to calls given by members of other flocks than they do to calls given by members of their own flocks (Mammen & Nowicki 1981; Nowicki 1983), I only used calls recorded from members of the same flock that would experience the playback stimulus. To control for differences in the acoustic structure of different individual’s calls or the likelihood that other birds would differentially respond to certain individuals (i.e., dominant vs. subordinate birds), I constructed playback tapes using calls recorded from known individuals and I used a single bird’s great horned owl and pygmy-owl calls as paired playback stimuli.

Each playback treatment consisted of 15 seconds of “chick-a-dee” calls from a single individual. In order to avoid pseudoreplication of playback stimuli (Kroodsma 1989; McGregor et al. 1992), every vocalization used in this experiment was a unique exemplar. Because the calling rate and the length of “chick-a-dee” calls vary in response to the two different predators (Chapter 1), I standardized for the total length of the playback stimulus (15 sec) instead of the absolute number of calls. A typical pygmy-owl stimulus tape contained approximately seven separate “chick-a-dee” calls, whereas a
Typical great horned owl stimulus tape contained approximately four calls during the 15 seconds of playback. These averages approximate the normal calling rates observed when chickadees encounter these predators under semi-natural conditions.

To mimic a natural predator encounter, I first played one of three different "high zee" aerial predator alarm calls for five seconds (14 syllables). Each "high zee" exemplar was synthesized from the same initial call, thus, similar predator information should have been coded in each playback (Ficken 1990). The three "high zee" variants were rotated to diminish habituation; each variant was equally presented for all treatments. Playback of the "high zee" typically caused the chickadees to freeze for several seconds. "High zees" were followed by 30 seconds of silence, and then 15 seconds of one of the experimental treatments.

Experimental Design

Because chickadees rapidly habituate to playback experiments in captivity (personal observation), I blocked the three treatments by the time of day and the calendar date relative to the start of the playback experiments to assure that any differences in response were not due simply to habituation (Figure 1). On each day of experiments, three total playbacks (one of each treatment) were conducted. To diminish habituation, each playback was separated by at least 3 hours and I did not conduct playback.
experiments on subsequent days. Three days of experiments (9 total playbacks) were conducted for each flock. On each day a different bird's calls were used for the pygmy-owl and great horned owl treatments (e.g., “red” on day 1, “blue” on day 2, and “green” on day 3).

For each trial, the speaker was hidden in one of three different places in the aviary to reduce habituation. The speaker location coincided with the time of day, so that the speaker was located at the same position for the first, second, and third trials of each day. This ensured that the speaker location did not influence the overall behavioral response to the playback because each treatment was broadcast from each location the same number of times.

Behavioral Responses

To characterize the behavioral responses of chickadees, I recorded the following variables during and immediately after the 15-second playback. I measured the closest distance that any bird approached the speaker (“closest approach”), the number of birds that came within 3 meters of the speaker, the number of birds that came within 1 meter of the speaker, the approximate time that the birds returned to displaying normal behavior (i.e., reduced calling rates, moved away from the speaker, and resumed foraging; “return time”), and the number of “chick-a-dee” calls that were produced by the flock during the
first 90 seconds after the playback began. I also assessed the overall strength of the response on a subjective 1-5 scale ("overall strength"): 1 represented no visible or vocal response; 5 represented the strongest response with most of the birds either approaching the speaker or calling rapidly; 2, 3, and 4 represented intermediate responses with some birds either approaching the speaker or increasing calling rates.

Statistical Analyses

To determine if any of the behavioral variables differed among the three playback treatments, I used a Kruskal-Wallis non-parametric test for all comparisons. This test was preferable to the parametric equivalent (ANOVA) because the variances of several of the variables were somewhat heterogeneous (Ott 1993). I used one-tailed, post-hoc Mann-Whitney U tests to compare each variable between the great horned owl and pygmy-owl treatments because my a priori expectation was that the chickadees would respond more strongly to the pygmy-owl treatment than the great horned owl treatment. I also used a varimax-rotated principle components analysis (PCA) with all of the response variables included as factors to examine the relationship between overall approach and call-rate features among the different playback treatments.
RESULTS

There were strong differences among treatments in each of the behavioral variables I measured (Table 1). Chickadees approached more closely to playback of calls given to a pygmy-owl ("pygmy-owl treatment") than to those given to a great horned owl ("great horned owl treatment") or control pine siskin calls ("control treatment"; $X^2 = 14.69, p = 0.001$). More individuals approached within 3 meters ($X^2 = 14.40, p = 0.001$; Figure 3) and within 1 meter ($X^2 = 11.34, p = 0.003$) of the speaker in response to the pygmy-owl treatment than the great horned owl or control treatments. Chickadees displayed the longest mobbing response (later return time) to the pygmy-owl treatment, followed by the great horned owl and control treatments ($X^2 = 12.69, p = 0.002$).

Chickadees produced the most "chick-a-dee" mobbing calls during the pygmy-owl playback, followed by the great horned owl and control playbacks, respectively ($X^2 = 11.50, p = 0.003$; Figure 4). The overall strength of the response was greatest for the pygmy-owl treatment, followed by the great horned owl and the control treatments ($X^2 = 19.61, p < 0.001$).

Chickadees responded more strongly to the playback of calls given to the pygmy-owl than they did to calls given to the great horned owl in all of the variables I measured. However, not all of these variables were statistically different in the post-hoc
comparisons. The closest approach to the speaker, the number of birds approaching within three meters of the speaker, and the return time were all marginally significant ($N_1 = 9; U = 22, p = 0.056, U = 22, p = 0.056, U = 23, p = 0.068$, respectively). The number of birds approaching within one meter of the speaker was not different for the two predator treatments ($U = 27, p = 0.129$). Chickadees produced significantly more “chick-a-dee” calls in response to the pygmy-owl treatment compared to the great horned owl treatment ($U = 17, p = 0.020$), and the overall strength of the response was greater for the pygmy-owl than the great horned owl playbacks ($U = 11, p = 0.004$).

All of the factors were organized along two primary axes in the PCA analysis (Figure 5). These two components accounted for 88.1% of the variation in the data. Approach behavior was positively associated with principle component axis one (PC1); calling rate was positively associated with principle component axis two (PC2). Thus, as values increased along PC1, the number of birds approaching the playback speaker increased. Increased values along PC2 indicated higher calling rates and longer return times.
Chickadees responded to playbacks of their "chick-a-dee" mobbing calls by approaching the speaker and increasing their calling rate. Similar behaviors were exhibited in response to playback of both "chick-a-dee" calls given to a northern pygmy-owl and "chick-a-dee" calls given to a great horned owl. However, the degree of response varied in strength between the treatments. Chickadees responded more strongly to pygmy-owl playbacks, by approaching closer, calling more, and responding for longer, than they did to great horned owl playbacks.

These results indicate that the "chick-a-dee" call conveys a message that initiates mobbing behavior and recruits conspecifics. Further, differential responses related to specific call variants show that receivers use variation in the acoustic structure of the call to make behavioral decisions independent of other context information. Because chickadees produce reliable variations in their "chick-a-dee" call in response to different species of predators and they respond differently to these variations without other contextual information, it appears that the "chick-a-dee" call may be similar to a functionally referential signaling system (Macedonia & Evans 1993; Hauser 1996). However, instead of signaling different types of potential predators, gradations in the "chick-a-dee" call probably reflect the degree of threat a given predator represents. Thus,
the mobbing vocalization of chickadees is unique in that it combines aspects of both referential and urgency-based anti-predator vocalization systems.

Although chickadees encode sufficient information in their “chick-a-dee” calls to convey predator risk to conspecific receivers, it is difficult to know which feature(s) of the call are being used for this purpose. In the previous chapter, I showed that a number of vocal features vary in relation to the threat of a potential predator, including the calling rate, average number of C and D syllables per call, duration of the “chick” and “dee” sections, interval between D notes, and the number of high energy overtones per D syllable (Chapter 1). Because chickadees habituate so rapidly to playback experiments, I chose to construct playback stimuli as they would naturally be given in an actual predator encounter, instead of attempting to vary each acoustic feature to determine what specific cues are used by receivers. Chickadees convey information specific to the predator, however, this information may be derived from any one, several, or all of the acoustically variable features of the “chick-a-dee” call.

The adaptive value of this type of signaling system in chickadees seems clear. Because most chickadee predators rely on an element of surprise to catch their prey (e.g., Cooper’s hawk and merlin, Johnsgard 1990), mobbing a potential predator and advertising that it has been detected may discourage hunting in that area (Curio 1978). Harassing a potential predator through active mobbing may also help “move on” the predator (Curio 1978). However, not all potential predators found in a chickadee flock’s
winter home range pose the same degree of threat (Ficken 1990; Smith 1991). Because chickadees may be food-limited in the winter due to low prey abundance and high energetic demands (Brittingham & Temple 1988; Smith 1991), discriminating among different species of potential predators and mobbing dangerous predators most intensely may be adaptive. It is reasonable to assume that the longer chickadees harass a potential predator and the closer they approach it, the more effective they will be at moving it on (Curio & Regelmann 1985). In my study, more chickadees approached the speaker more closely and stayed for longer periods when the “pygmy-owl” signal was broadcast than when the “great horned owl” signal was broadcast, suggesting that it is more important to actively mob pygmy-owls than great horned owls. A signaling system that encodes information about the degree of risk a given predator represents allows chickadees to selectively mob predators depending on the perceived risk.

My results suggest that chickadees encode and convey a large amount of information in their anti-predator vocalizations. Not only do they use different types of vocalizations for different classes of predators (i.e., flying aerial vs. perched raptor or terrestrial, Ficken et al. 1978), but they also convey more sophisticated predator information using very subtle variations within a single type of vocalization. This is one of the few systems where this level of information sharing has been demonstrated in anti-predator vocalizations.


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Table 1: Means and standard errors for each behavior measured in response to the playback experiments. The three treatments were “chick-a-dee” calls given in response to a great horned owl (N = 9), “chick-a-dee” calls given in response to a northern pygmy-owl (N = 9), and a pine siskin call as a control (N = 9).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Pine Siskin (Control)</th>
<th>Great Horned Owl</th>
<th>Northern Pygmy-Owl</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>mean</td>
<td>SE</td>
<td>mean</td>
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<tr>
<td>Closest approach to speaker (m)</td>
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<td>1.44</td>
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<td>Birds 3 m from speaker (#)</td>
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<td>.29</td>
<td>2.67</td>
</tr>
<tr>
<td>Birds 1 m from speaker (#)</td>
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<td>.11</td>
<td>1.22</td>
</tr>
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<td>“chick-a-dee” calls (#)</td>
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<td>.39</td>
<td>6.00</td>
</tr>
<tr>
<td>Return time (s)</td>
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<td>10.0</td>
<td>78.3</td>
</tr>
<tr>
<td>Overall strength</td>
<td>1.00</td>
<td>.00</td>
<td>3.00</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

Figure 1: Representative playback design used in this experiment for each flock. Three playback trials were conducted each day (at least 3 hours apart), on three different days (separated by at least 2 days). The first playback of each day was conducted in location a, with “high zee” 1 (HZ-1). The second and third playbacks of each day used location b with HZ-2 and location c with HZ-3, respectively. Treatments were blocked by both trial number and trial day, and during each day of trials, the great horned owl (GHWO) and northern pygmy-owl (NOPO) treatments were composed of “chick-a-dee” calls produced by a single individual (e.g., “red”).

Figure 2: Representative sonograms for each of the three playback treatments used in this experiment: “chick-a-dee” calls produced in response to a northern pygmy-owl (NOPO), “chick-a-dee” calls produced in response to a great horned owl (GHOW), and calls from a pine siskin (PISI). Each treatment was preceded by 5 seconds of “high zee” (aerial predator seet alarm call) and 30 seconds of silence.
Figure 3: Mean number (± 1 S.E.) of birds approaching within 3m of the speaker after each treatment: control pine siskin call (PISI), “chick-a-dee” calls in response to a great horned owl (GHOW), and “chick-a-dee” calls in response to a northern pygmy-owl (NOPO). Different letters signify statistically different groups (Mann-Whitney U test, p ≤ 0.05).

Figure 4: Mean number (± 1 S.E.) of “chick-a-dee” calls produced during the first 90 seconds after the start of each playback treatment: “chick-a-dee” calls in response to a northern pygmy-owl (NOPO), “chick-a-dee” calls in response to a great horned owl (GHOW), and control pine siskin call (PISI). Different letters signify statistically different groups (Mann-Whitney U test, p ≤ 0.05).

Figure 5: Principal components biplot for the three playback treatments. Approach features (number of birds 1 and 3m from speaker, closest approach) increase along the x-axis (PC1) and primarily vocal features (calling rate and return time) increases along the y-axis (PC2). Ellipses represent 95% confidence areas around the mean of each treatment.
<table>
<thead>
<tr>
<th>Playback Day</th>
<th>Trial Number</th>
<th></th>
<th></th>
<th></th>
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<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(location a, HZ-1)</td>
<td>(location b, HZ-2)</td>
<td>(location c, HZ-3)</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>NOPO (&quot;red&quot;)</td>
<td>PISI</td>
<td>GHOW (&quot;red&quot;)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>PISI</td>
<td>GHOW (&quot;blue&quot;)</td>
<td>NOPO (&quot;blue&quot;)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>GHOW (&quot;green&quot;)</td>
<td>NOPO (&quot;green&quot;)</td>
<td>PISI</td>
<td></td>
</tr>
</tbody>
</table>
Figure 2

Frequency (kHz)

NOPO

GHOW

PISI

Time (s)

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Figure 4

The figure shows a bar chart comparing the number of "chick-a-dee" calls across different treatments: PISI, GHOW, and NOPO. The NOPO treatment has the highest number of calls, followed by GHOW, with PISI having the lowest. The chart indicates significant differences between the treatments, with different letter annotations (a, b, c) suggesting post hoc comparisons.