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SEED TYPE, PREDATOR, AND SOCIAL INFLUENCES ON FORAGING BLACK-
CAPPED CHICKADEES (*POECILE ATRICAPILLUS*)

By

Sayako Iwanaga

THESIS

Submitted to
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ABSTRACT

SEED TYPE, PREDATOR, AND SOCIAL INFLUENCES ON FORAGING BLACK-CAPPED CHICKADEES (*POECILE ATRICAPILLUS*)

By

Sayako Iwanaga

Food quality, predator cues, and social interactions influence how an animal forages. The suburban environment exposes animals to artificial food sources (e.g., bird feeders) and different predators not usually encountered in the wild. Perhaps most notable of novel suburban predators is the domestic cat (*Felis catus*). I presented free-ranging chickadees and their mixed-species flock members a cat decoy and two different seed types, sunflower and safflower, in either single-feeder or dual-feeder presentations. Chickadees engaged in foraging behaviors rather than active anti-predator tactics. Chickadees preferred sunflower seeds over safflower seeds, and the social interactions were largely influenced by seed type. Chickadee contact calls increased around the less visited feeder, possibly to initiate collective movement to a different feeding site. Alarm calls may have been used as an aggressive behavior to eliminate competition, rather than as an anti-predator alarm or defense tactic. Presentation of a predator did not directly influence chickadee foraging activities, but chickadees gave slightly more high-alarm calls when a predator was presented. Future investigation should focus on intra- and interspecific interactions that vary based on different predators and how these predator cues affect a bird's foraging behavior in a suburban environment.

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The thesis was written in the format used in *Journal of Field Ornithology*.

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LISTS OF SYMBOLS & ABBREVIATIONS

AMGO: American Goldfinch

RBNU: Red-Breasted Nuthatch

S: Standard deviation

CHAPTER ONE: LITERATURE REVIEW

Optimal foraging theory predicts that animals will partake in feeding events with the highest net energy intake after paying the net cost of obtaining food (MacArthur and Pianka 1966; Schoener 1971; Charnov 1976; Stephens and Krebs 1987). Since this theory was first published, many studies found animals foraging in sub-optimal ways (for review, see Tversky and Simonson 1993). Environmental situations during foraging may influence an animal's heuristic decision making and lead them to make sub-optimal feeding choices (Emlen 1966; Norberg 1977; Charnov 1976). A breadth of laboratory studies (Houston et al. 1980; Levey and Karasov 1989; Bateson 2002) and studies under natural settings (Schneider 1984; Lima 1985; Quinney and Ankney 1985; Heinrich 1988; Brotons 1997; Dolby and Grubb 1999; Brotons and Herrando 2003) demonstrate how food choice, predator, and social interactions can influence foraging behaviors. My research focused on the suburban environment, which additionally exposes animals to artificial food sources (bird feeders) and a specific type of predator, the domestic cat (*Felis catus*). In this chapter, I provide background on the potential influences food types, predator cues, and social interactions have on avian feeding behavior.

FOOD CHOICE

Most wintering birds are generalists, feeding on variety of food types over the low-resource winter. For birds living within or near human communities, access to food and food choices can be greater than what their wild counterparts would encounter. The abundant food supply associated with human communities can increase bird abundance,

species diversity (Fuller et al. 2008), and fledging success (Robb et al. 2008). Although humans can unintentionally provide supplemental food to birds (e.g., garbage, compost, landscaping, etc.), they also intentionally provide food for birds in the form of feeder stations, almost exclusively near houses and other buildings. The most widely used supplemental feeding seed is black-oil sunflower seeds, followed by safflower, corn and millet seeds (FeederWatch 2011). With increased food abundance and increased food choice options, it is possible for birds to show preference behaviors in choosing certain food types over others.

Food choice can be influenced by direct and indirect information about the food. Birds and mammals use direct information such as food size (Houston et al. 1980; Quinney and Ankney 1985; Naef-Daenzer et al. 2000; Hayslette 2006) and nutritional value (Taghon 1981; Belovsky 1984; Willson and Comet 1993) when making food selections. In most avian foraging studies, the morphological characteristics, rather than nutritional content, were a larger factor in food selection (Díaz 1996). Indirect information such as previous history with a food source also plays a large role in foraging choices by birds (Bateson 2002). Gray jays (*Perisoreus canadensis*) ignored food traps with high-risk and varying reward (Waite 2001), and black-capped chickadees repeatedly chose “low-variance” (low-risk, low-reward) traps when they made choices on feeding sites (Barkan 1990).

PREDATOR INFLUENCE

The influence of food quality on foraging behavior is second only to anti-predator activities (Pyke 1984). Protection from predators defines how most animals behave

during feeding bouts. Studies across rodents (Lima and Valone 1986; Thorson et al. 1998; Orrock et al. 2004) and passerines (Schneider 1984; Walther and Gosler 2001) found the distance to cover as the most important feature in choosing where to forage. In white-crowned sparrows (*Zonotrichia albicollis*), the distance to cover out-weighed foraging efficiency; the sparrows cleared the food closer to maximum cover before they moved to the next available feeding ground (Schneider 1984).

Birds often have ability to distinguish predators by auditory (Chandler and Rose 1988; Adams et al. 2006; Whitear and Stehlik 2009) or visual (Klump and Shalter 1984; Montevecchi and Maccarone 1987; Leavesley and Magrath 2005; Griesser and Ekman 2005; Templeton et al. 2005; Hendrichsen et al. 2006) cues. Identifying the predator allows the birds to have flexible foraging tactics across various foraging situations because the amount of energy placed on anti-predator activities is situational (Templeton et al. 2005; Tvardíková and Fuchs 2011). For example, tit species foraged longer during the lower predator threat situations than in higher predator threat conditions (Tvardíková and Fuchs 2011).

Birds that live in urban and suburban environments must identify one of the most common and voracious predators, the domestic cat (*Felis catus*). In southeastern Michigan, free-ranging cats killed at least one bird a week, totaling over 10,000 birds taken during breeding season (Lepczyk et al. 2004). Although bird feeders attracted more avian predators than cats, cats preyed predominantly on small, ground feeding birds near the feeder (Dunn and Tessaglia 1994). Cats usually spend more time near human settlements and are less likely to go into the forest (Kays and DeWan 2004) than other predators. When small changes in the environment (e.g. external temperature, distance to

cover) can cause large changes in the predation risk (Brown and Kotler 2004), birds feeding at artificial feeders face increased risk from ground predators.

Being alert for predators is important, but anti-predator behavior takes attention away from foraging (Dukas and Kamil 2000). Therefore, a balance between vigilance and foraging is important. Some responsibilities of anti-predator monitoring are shared among group foragers, but a few vigilant individuals may lose valuable feeding time while keeping a watchful eye. In contrast, non-vigilant individuals may become easy prey items. This is especially true for ground-feeding birds, which become sitting targets for ground predators while attention is centered on foraging (Lima and Bednekoff 1999). Even if feeding at a feeder may not be a difficult task, social interactions within the foraging flock could also distract birds from anti-predator behaviors and foraging opportunities.

SOCIAL INTERACTIONS

Many resident winter birds will forage in temporary winter flocks. Sharing resources to reduce predation risk can be a more optimal feeding behavior than maximizing food intake (Winterhalder 1986). Large flocks can also deter larger birds away from a food source (Langley 2001). However, while flocking provides protection against predators, it can increase food competition among flock members. Niche partitioning between species (Alatalo and Moreno 1987) or between dominant and subordinate members within a species (Otter 2007) may limit competition. Dominant members often have preferential access to the best available food source (Desrochers 1989; Ficken et al. 1990; Otter 2007). Because exploratory behavior is dependent on

social context (Van Oers et al. 2005), the subordinate birds have secondary access to food and take higher predation risks when seeking other foods (Desrochers 1989; Fox et al. 2009). In mallards (*Anas platyrhynchos*), subordinate ducks had the same food intake but visited more patches than dominant ducks (Gyimesi et al. 2010). Furthermore, interspecific dominance by body size may also affect foraging behaviors (Kohda 1991; Smith 1991; Daily and Ehrlich 1994; Shelley et al. 2004; Borowske et al. 2012). The dominance status within a flock often dictates how an individual bird will behave at a food source, but foraging situations can influence the foraging success of subordinate birds more than they affect dominant birds.

The influence of competition is situational. When ruddy turnstones (*Arenaria interpres*) forage on a single food source, subordinate members showed a decrease in foraging success. However, when the food source was scattered, subordinates had equal foraging success as dominant individuals (Vahl et al. 2005). Other researchers have found food abundance can trump the influence of competition (Dolman 1995; Brotons and Herrando 2003). For example, increased numbers of competitors did not always decrease the food intake rate of socially foraging snow buntings (*Plectrophenax nivalis*; Dolman 1995) or common ravens (*Corvus corax*; Heinrich 1988) when food was plentiful. Birds show foraging behavior specific to varied food availability and social conditions. As such, areas with established bird feeders have high concentration of birds (Wilson 1994) and they are more likely to engage in foraging competition.

MODEL SPECIES: THE BLACK-CAPPED CHICKADEE

Black-capped chickadees (*Poecile atricapillus*) are year-around residents across most of northern North America. Most chickadee populations are non-migratory and form non-breeding season flocks from fall throughout winter (Smith 1991). The six- to eight-membered flock (Otter 2007) usually contains local pairs that were mated during the previous spring (Smith 1991). These multi-pair flocks dissolve again each spring into territorial mated pairs for the breeding season (Smith 1991). Non-paired immature birds will disperse to join other flocks consisting of other non-related individuals (Smith 1991). In the non-breeding winter season, chickadees, along with many other residential birds, often join a mixed species flock during the fall and stay within the flock until breeding season in April (Smith 2010).

Due to their semi-tame nature, black-capped chickadees have been the focus of various long-term studies on local populations. Chickadees are relatively well-studied, and therefore, make ideal models for a field study investigating multiple cues used for behavioral decisions during feeding events. Chickadees are adapted to the winter climate, both physiologically (Cooper and Swanson 1994; Grubb and Pravosudov 1994) and behaviorally (Smith 1991; Grubb and Pravosudov 1994; Otter 2007), allowing for continuous data collection throughout winter seasons.

Throughout winter, chickadees are a common backyard bird often found feeding on human-maintained bird feeders. They are opportunistic feeders, eating and gathering plant and animal matter (Bent 1988) throughout most of their waking hours. Chickadees prefer to forage in low-variance situations (Smith 1991), such as those found around bird feeders kept by bird enthusiasts. Bird feeders typically provide plenty of sunflower seeds

that have high fat content (USDA 2011), and thus help chickadees maintain energy reserves despite the hostile conditions of boreal winters. Because chickadees are often leader birds in finding new food sources (Smith 1991), other species often follow chickadees to bird feeders and thus chickadees are regularly required to participate in numerous interspecific interactions.

Chickadees often flock in a mixed-species flock in the winter (Smith 1991). The different species can establish new interspecific dominance relationships (feeding ranks) within and among flocks, which can provoke agonistic interactions between chickadees and other species. These interactions can also be understood through the chickadee's well-studied vocal communication. One such vocalization is the "chick-a-dee" complex. The complex is composed of four notes, in sequential order (Smith 1991). The "chick-a-dee" complex may convey flock identity (Nowicki 1983). Chickadees use the "chick-a-dee" complex during flock interactions; increased use of the complex also has been linked to decreased foraging activity (Nowicki 1983).

While social interactions between chickadee flocks may be characterized by use of the "chick-a-dee" vocalization complex, interactions between chickadees in the same flock are often characterized by a different call, the "tseet" call. "Tseet" calls are chickadee's contact calls (Smith 1991) which may convey information on individual identities (Guillette et al. 2010). The "tseet" calls could be used in initiating flock movement, since dominant members in bird flocks lead the group to a different foraging site (Radford 2004). The use of this contact call can be useful in determining the dominant chickadee's activity, and how it influences the foraging behavior of other chickadees.

Chickadees also have distinct alarm calls (Ficken et al. 1978; Apel and Ficken 1981; Ficken and Weise 1984; Hailman 1989; Clemmons and Howitz 1990; Ficken 1990; Hughes et al. 1998; Gammon and Baker 2004). When chickadees perceive extreme threat, they can utter the high pitched “zee” call (Smith 1991). The “zee” call is often uttered when a threat is approaching (Smith 1991). Another type of alarm call is the “chick-a-dee” call. The complex may have different meanings in various contexts (Smith 1991), and it can be also used as a “mild” alarm call (Ficken et al. 1978). The last note, “D-notes”, can indicate the perceived threat level by the caller (Templeton et al. 2005).

Other chickadee vocalizations include the territorial “fee-bee” song and the “gargle”. The “fee-bee” song is only sung by the males, most commonly during breeding season but can also be heard throughout the rest of the year (Smith 1991). The younger birds may utter the sub-song (Smith 1991), or half song, which is not the full “fee-bee” song. The other, and possibly the least understood vocalization is the chickadee “gargle”. The “gargle” is composed of randomized “A”, “B”, “C”, and “D” notes (Smith 1991). The call may be used during an agonistic interaction when two chickadees are in close proximity and its use commonly follows a confrontation (Ficken et al. 1978). However, the “gargle” is highly variable and as complex as the “chick-a-dee” call, making it difficult to confidently associate its use with contextual meaning.

Using the vocalizations described above, chickadees are ideal birds to quantify foraging behaviors. Chickadees are common feeder birds that may visit as a single-species flock or a mixed-species flock. The agonistic behaviors and vocal interactions are well-studied at feeding sites (Smith 1991). The chickadee alarm calls are also distinguishable from other vocalizations, making it possible to quantify one of their anti-

predator behaviors. My research investigated the influence of food choice, predator and social interactions on foraging chickadees in a suburban environment.

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CHAPTER TWO: SEED TYPE, PREDATOR, AND SOCIAL INFLUENCE ON FORAGING BLACK-CAPPED CHICKADEES (*POECILE ATRICAPILLUS*)

CHAPTER OVERVIEW

Non-migratory bird species that are resident in northern Michigan have various adaptations that allow them to withstand the harsh winters, where survival can be dependent on food accessibility (Brittingham and Temple 1988; Desrochers et al. 1988; Brittingham and Temple 1992). Supplemental feeders put up by humans may increase winter survival in birds (Brittingham and Temple 1988; Jones and Reynolds 2008); however, it also introduces them to urban predators, such as domestic cats (Lepczyk 2004; Beckerman et al. 2007; Sims et al. 2007). These predator contacts along with negative social interactions can decrease food intake (Desrochers 1989; Ficken et al. 1990). My research explores how food options, predator cues, and social interactions influence black-capped chickadees' (*Poecile atricapillus*) seed preferences, agonistic behavior, and vocalization behaviors in the suburban environment. Free-ranging chickadees and their mixed-species flock members were presented with two different seed types, sunflower and safflower, in video recorded trials where either a single seed type or both seed types were presented at known chickadee feeding stations. Additionally, the chickadees were subjected to the presentation of a cat decoy during their foraging activities. In general, chickadees preferred sunflower seeds over the safflower seeds. There was no clear relationship between the number of seeds taken per chickadee and the presentation of predator cues. Chickadees changed foraging behaviors depending upon available seed types and the social interactions between conspecifics and

heterospecifics; predator influence was minimal. In the context tested here, alarm calls may have an aggressive function, rather than a “predator-alarm” function. There also was an increase in contact calls as more sunflower seeds were taken by heterospecific individuals, which could be speculated to initiate flock movement. Future investigation on the effects of seed nutritional value, variable predator types and the change in use of vocalizations during interspecific interactions may provide better insight to the factors that influence chickadee foraging behavior.

INTRODUCTION

Winters in the Great Lakes region are relatively long. Major problems that many animals face are low temperatures and the dramatic drop in food abundance. They must evaluate conditions and alter foraging tactics to increase their chance of retrieving food. In this study, foraging black-capped chickadees were exposed to two different seed choices and a model cat to observe how their foraging behavior was influenced by different food types and the presence of predator cues. Interactions with conspecifics and heterospecifics were also recorded to investigate influence of social interactions on foraging activities. There were three main hypotheses tested in this experiment: (1) foraging activity will concentrate around the food with higher metabolic energy gain; (2) the presence of other birds will decrease chickadee’s foraging activities and increase agonistic behaviors and vocalizations; and (3) the presence of a potential predator will decrease foraging behaviors in chickadees and increase anti-predator behavior.

Food Choice

Food choice and the risk analysis for obtaining food are based on environmental stochasticity (Barkan 1990) and predictable seasonal changes. Food choice is dependent on the bird's surrounding environment, because they do not simply eat (and/or cache) any food that they find (Myton and Ficken 1967). For instance, Carolina chickadees (*Poecile carolinensis*), a closely related species to the black-capped chickadees, chose and ate larger seeds in cooler temperatures (Myton and Ficken 1967).

Food choice can be a result of food preference, which can be predicted by nutritional content. I focused on two commonly used bird feeder seeds, safflower (*Carthamus tinctorius*) and black-oil sunflower (*Helianthus annuus*) seeds. Sunflower seeds generally provide higher metabolic energy than safflower seeds (National Research Council 1994), and chickadees often feed on high fat containing foods (Smith 1991). The seed choice in chickadee, therefore, is predicted as the sunflower seeds with higher nutritional gain.

Social Interactions

Social flocks of chickadees develop dominance hierarchies, which often govern their feeding behavior and territory acquisition. Dominance hierarchy is best observed at feeding sites, where the alpha male chases away lower ranking birds (Otter 2007). This hierarchy is retained throughout the winter and the chickadees can recognize individual birds and their rankings (Smith 1991).

In chickadees, dominant members often have preferential access to the best available food sources and breeding sites, while the subordinate birds have secondary access (Desrochers 1989, Ficken et al. 1990, Otter 2007). In a close relative to the black-

capped chickadees, the mountain chickadees (*Poecile gambeli*), showed dominance when one chickadee supplanted or chased another bird away from a feeding area, or when a subordinate passively moved away from the feeder (Fox et al. 2009). Subordinate members may experience higher predation risks (Zanette and Ratcliffe 1994) due to foraging for supplementary food sources (mountain chickadees, Fox et al. 2009) and nesting in sub-par sites (Desrochers 1989). Subordinate birds also make earlier alarm calls than their dominant flock members, which could slightly increase their chance of being detected by their predators (Zanette and Ratcliffe 1994).

Winter flocks of black-capped chickadees often include other species, forming a mixed-species flock. White-breasted nuthatch (*Sitta carolinensis*), red-breasted nuthatch (*Sitta canadensis*), downy woodpeckers (*Picoides pubescens*) and hairy woodpeckers (*Picoides villosus*) are among the species that readily associate with black-capped chickadees (Smith 1991). Larger species generally dominate over the smaller species (Smith 1991; Daily and Ehrlich 1994; Shelley et al. 2004; Borowske et al. 2012), although this pecking order across species can change between situations (Morse 1970). Black-capped chickadees can make up the majority of the flock (Morse 1970) and can initiate the collective movement in these mixed-species flocks (Smith 1991).

Vocalizations

Black-capped chickadees have a variety of calls used in various social contexts (see chapter 1). I focused on eight distinct vocalizations: “tseet”, repeated “tseets”, “zee”, “D-notes”, “ABCD”, “fee-bee” song, half song and “gargle”. The associated context in which these calls are used can be found in Chapter One. The description to identify each call is described below.

The “tseet” calls are the most commonly used calls at a feeder. The “tseet” calls were characterized by a chevron shaped singular call (Fig. 1.a), which appeared between 6.0 to 8.5 kHz.

A call was classified as a repeated “tseet” call if there were repeated chevron-shaped “tseet” notes within 0.2 seconds of one another. The frequency range was similar to that of the “tseet” calls, but the number of repeated notes ranged from 2 to 20 notes (Fig. 1.c).

“Zee” calls had the repetition of the repeated “tseet,” but the fundamental frequency of a “zee” call spanned a much broader range of frequencies (2.0 to 14.0 kHz). “Zees” lacked the clear chevron shape of the “tseet” or repeated “tseet” calls. Each note extended its frequency well above the strongest portion of the note (Fig. 1.d). These calls also ranged in the number of repeated notes within a call.

Variability in “chick-a-dee” call complex was measured in two different categories. “Chick-a-dee” complex generally consist of “A-B-C-D” notes used in this order. “D-note” calls were classified by the varying repetition of the “D-notes” (Smith 1991; Fig. 1.f). Only the “D-notes” were counted because the number of “D-notes” specifically communicates the threat level perceived by other chickadees (Templeton et al. 2005), and the “chick-a-dee” complex ranged in the number of beginning notes used (Smith 1991). The frequencies of “D-note” calls were between 2.9 and 4.3 kHz.

The other category of the “chick-a-dee” complex is the “ABCD” call. Some “chick-a-dee” complexes used the whole sequence of “A-B-C-D” notes (or “B-C-D”) in rapid succession and ended in one D note. This call differed from the “D-note” calls due

to its repetition of the whole “ABCD” (sometimes “BCD”) at constant intervals. The time between this unique “ABCD” call was about 3 to 4 seconds (Fig. 1.g).

The “fee-bee” vocalization is the male chickadee’s two-note song. The first note is sung at a higher frequency (3.3 and 3.9 kHz) than the following note (2.9 to 3.3 kHz; Fig. 1.h). Each note lasted about 0.5 seconds, averaging 1 second for the whole call. A call was identified as a half song when it only consisted the first note of the “fee-bee” song (“fee”; Fig. 1.i).

A “gargle” was the most rapid and repetitious call, and also the most diverse of the calls in chickadee vocalizations. “Gargles” did not always follow a specific note pattern. Often, a note would differ in frequency from the note before, and the time between each note would be less than 0.2 seconds (Fig. 1.e).

MATERIALS AND METHODS

Experimental Design

This experiment evaluated the behavioral response of chickadees to two different food types (sunflower seeds or safflower seeds) along with varied presentations of a feline predator decoy at established feeder stations. The seed types were presented either independently (“single-feeder presentation”) or together (“dual-feeder presentation”) for the duration of the predator treatments. The experimental feeders were presented for ten minutes, and the predator model was either presented during the first five minutes or the second five minutes of feeder presentation, in randomized order. When the predator model was absent, it was hidden from the birds’ view (Fig. 4.a).

The experimental design included six different conditions defined by three different seed presentation categories and two types of predator cues (Table 1). Each five

minute presentation or absence of a predator was a session, and each video recorded two sessions - one right after another. Each site was visited at least once a month throughout the five-month study period, until each of the six combinations (Table 1) of seed and predator presentation had been tested once at each site. To further analyze other possible variables, I also recorded social influences from heterospecific individuals.

Since pre-established residential feeders were used for this research, the setup for each site had slight differences due to variable environments surrounding the feeders. Separate identical bird feeders (“Enchanted Garden Copper Tube Seed Feeder”; Model Number: MENTUBE7; Menards® SKU: 2661420) were used for seed presentations, made of clear plastic feeding holes with copper perches (Fig. 3). I used black-oil sunflower seed from Nature’s Beauty Wild Bird Food (minimum 14% protein, minimum 19% fat, maximum 30% fiber; Performance Seed, MN, USA) and the safflower seed was Performance Seed, (minimum 8% protein, minimum 12% fat, maximum 30% fiber). To begin each site visit and session, the homeowner’s established feeders were removed and/or covered by a sheet. The experimental feeders were then hung in place of the homeowner’s feeders. Feeder posts were not uniform across all sites, but all feeders hung at least one meter off the ground. When both feeders were presented, they were hung on the same feeder post. Most posts had two hooks for feeders, while some feeder posts had only one. In these cases, both feeders were hung from the single hook, with only the tops of the feeders touching each other. Feeder perches were always available for birds to land. The experimental setup was taken down after each site visit, and the site’s original feeding setup was restored.

The predator was presented using a model of a medium-sized black housecat enclosed within a box (the “catamatix”; Fig. 4). The cat (“Scary Cat” BC-Cat-87529; Wal-Mart Stores Inc.) could be moved in and out of the box by a pulley system, which was remotely operated from a distance of five meters. The “catamatix” was placed on the ground three meters from the experimental feeder during each site visit (Fig. 5).

The control for the predator presentation was not showing the predator decoy, “predator absent.” The “catamatix” was unopened during this “predator absent” phase. There was no actual decoy control used in this study.

Chickadee and heterospecific behavioral observations near the feeder were recorded using a video camera (Sony DCR-SX44) on a tripod placed five meters from the feeder and about eight meters from the “catamatix”. Wherever possible, the camera was set directly in line with the feeder and the “catamatix”. The recording session commenced when at least one chickadee landed and took a seed from the experimental feeder. The video recorded bird activity for approximately 13 minutes; five minutes with predator present and five minutes with predator absent (presentation order randomized), and with some additional time recorded before and after the presentations. In instances where no chickadees visited the feeder within an hour, the setup was taken down and the site was revisited at a later date.

Data Collected

I visited nine sites six times each, resulting in a total of 54 video records. Videos were reviewed and quantified for the following: (1) the number of each seed type taken, (2) the number of chickadees in the area (determined using both visual and aural cues), (3) the duration each chickadee perched at a feeder (as supporting measurement for seed

preference), and (4) movement between feeders (when both feeders were present). For the heterospecific individuals, the type and the number of seeds taken and the maximum number of non-chickadee species present were also recorded.

Social and agonistic interaction analyses: Heterospecific species were identified through visual and aural cues. I counted feeder visits and analyzed activity observations on American goldfinch (*Spinus tristis*) and red-breasted nuthatches (*Sitta canadensis*) due to their regular presence at the experimental feeders. Activity levels were estimated on a scale of 1-5, where 5 represented the highest activity. The highest activity rating was recorded when a species was seen or heard continuously near the feeder for the five-minute session. Activity levels were scored as a 1 when the heterospecific individuals were heard or seen for less than a minute.

Agonistic interactions were recorded as displacement between chickadees or heterospecifics, displacement across species, or tolerance by chickadees. A displacement was tallied when a bird on a feeder left without taking a seed as another bird landed on the feeder. When a chickadee on the feeder did not leave as another bird landed, it was recorded as tolerance. There were few instances of birds flying up to the feeder, hovering, and flying away without landing on the feeder. I separated these instances from other agonistic behaviors and labeled them as “missed landing” by a chickadee or heterospecific.

Vocalization Analyses: Double-channel recorded audio tracks (sampling frequency of video camera= 48 kHz) were extracted from the videos (AoA Audio Extractor Basic, v. 2.3.1), and visualized using Raven Lite v.1.0 (Cornell Lab of Ornithology). The analysis started from either the time the predator was displayed or 5

minutes before the predator display, and ended at the time the predator was retracted or 5 minutes after retraction.

Chickadee vocalizations were classified into eight separate categories: “tseet”, repeated “tseets”, “zee”, “D-notes”, “ABCD”, “fee-bee”, half song, or “gargle” (Ficken et al. 1978). The “tseet” and repeated “tseet” calls were measured for close-contact chickadees interactions. Because “tseets” are similar in structure to the A-note (Fig. 1.b) and often difficult to differentiate, any chevron shaped singular note was categorized as a “tseet” call. I separated the repeated “tseets” from the “tseets” to find possible differentiation in call usage because I did not separate between the A note and the “tseet” calls. The “D-notes”, “zee”, and potentially the “ABCD” and “gargle” calls, measured the perceived threats by the chickadees and also as measures for intra- and interspecific aggression (Ficken et al.1978). The territorial “fee-bee” song and the half song were indirect measures for distant chickadee interactions. The characteristics for each vocalization are described in chapter one. Each call was counted using visual and auditory confirmation.

Statistical Analyses

An index for bird foraging activity was calculated by dividing the number of seeds taken during a session by the maximum number of chickadees for each treatment. Similarly, vocalization activity was quantified by the number of calls produced by the maximum number of chickadees at the feeder (SPSS ver. 19.0.0.1, IBM 2010). Sessions with no birds activity (“0”) were excluded from statistical analyses, unless otherwise noted. Excluding the “no activity” sessions did not impact my results because there were no patterns to when the chickadees showed no foraging activity.

Although each treatment included two sessions from the same day, I treated the data as separate sessions (i.e. independent samples). This was due to the fact that most chickadee foraging events occurred in spurts of two to three minutes, and there were no sessions where chickadees fed continuously throughout the ten-minute recording.

Food preference and predator influence: To detect chickadee preference in seed type, I used the Scheirer-Ray-Hare test (SRH test) to perform two-way non-parametric ANOVA tests on the number of seeds taken per chickadee and the perched time at each feeder. I applied the non-parametric ANOVA test because log₁₀, LN, square-root or cube-root transformations did not transform the safflower seed data into a normal distribution for regular ANOVA tests. For the SRH tests, the H-value is listed instead of the F-value because the SRH test found differences in associated ranks. Because the SRH test can only compare two variables per test and I had three independent variables (i.e. seed types, feeder presentation styles, and predator present or absent), each independent variable was paired with another variable across three tests. Sessions without chickadees taking seeds from the feeders were excluded from these tests.

Social interactions and food preference: To find the overall species diversity, I counted the number of sessions each species was observed (through audio or visual cues) near the experimental feeders. I found the most commonly observed heterospecific species by calculating the proportion of each species from the total observed heterospecific individuals.

I examined the influences of three independent variables on foraging behaviors of heterospecific individuals, and relationships between heterospecific individuals behavior with chickadee behavior. To find the influence of seed type, predator and feeder

presentations for heterospecific individuals, I divided the number of sunflower/safflower seeds taken by the maximum number of heterospecific individuals (all heterospecific individuals combined) to find the number of seeds taken per heterospecific individual. The influences from the three independent variables were then found by SRH tests.

The numbers of seeds taken per heterospecific were analyzed against chickadee behavior to find whether foraging behaviors between species influenced one another. I used bivariate non-parametric correlation analyses (Spearman's Rho correlations) to compare the number of sunflower/safflower seeds taken per heterospecific individual with each quantified chickadee behavior. All tests excluded sessions with no seeds taken by any heterospecific (i.e. "0" data); the "0" for other dependent variables were also excluded.

To find the whether the heterospecific activity levels reflected foraging success in heterospecific individuals, the number of seeds taken per heterospecific individual were also compared against the different heterospecific activity levels. I ran Kruskal-Wallis independent samples test to find the association between heterospecific activity level and chickadee behaviors. I analyzed for distribution of the number of seeds taken per chickadee and the number of calls made during various AMGO and RBNU activity levels. Outliers in the dependent variables and sessions without AMGO or RBNU activity were excluded from the analyses.

Influence of predator, social and food cues on vocal behaviors: The influence of the seed types and predator presentations on repeated "tseets", "D note", "ABCD", "tseet" and "zee" calls were analyzed using SRH tests. When comparing the seed type effects on the calls, the dual-feeder presentation data were excluded; only the single-feeder

presentation data (i.e. sunflower feeder only against safflower feeder only) were used. The exclusion of dual-feeder presentation data strictly found the seed type influence, and not the influence by the feeder presentation styles. The “fee-bee” song, half song, and “gargle” calls were not analyzed due to small sample size ($n < 8$).

To find associations between chickadee foraging activities and chickadee vocalizations, I used bivariate non-parametric correlation analyses (Spearman’s Rho correlations) to compare the number of five different calls made per chickadee with each quantified chickadee behaviors. Similar comparison tests were used to find associations between heterospecific foraging activity and chickadee vocalizations. AMGO and RBNU activity levels were also compared against the five vocalization types. Each comparison between vocalization and dependent variable excluded the “no visit” sessions. When there was a strong correlation between a seed type and vocalization, further correlation analyses compared the vocalization against single- and dual feeder presentations.

RESULTS

Food Choice and Vigilance

Across 54 feeding trials I recorded 540 minutes (54 trials of 10 minutes each) of chickadee feeding behavior. The number of seeds taken per chickadee was significantly affected by seed type ($H_{1,1} = 14.8$; $P < 0.001$) and feeder presentations ($H_{1,1} = 10.6$; $P = 0.001$). Chickadees took significantly more sunflower seeds ($\bar{x} = 2.10$, $s = 1.58$) than safflower seeds ($\bar{x} = 1.22$, $s = 1.23$; $P < 0.001$; Fig. 6). They also took significantly more

seeds from a single feeder presentation ($\bar{x}= 2.10$, $s= 1.67$) than dual-feeder presentation ($\bar{x}= 1.24$, $s= 1.07$; $P= 0.001$).

Seed type and feeder presentations also affected the average time chickadees were at the feeder. The average perched time at the safflower feeder was significantly longer ($\bar{x}= 5.52$, $s= 4.54$) than at the sunflower feeder ($\bar{x}= 3.77$, $s= 4.68$; $H_{1,1}= 12.4$; $P< 0.001$; Fig. 7). The time at a feeder during dual-feeder presentation was longer ($\bar{x}= 5.05$, $s= 5.73$) than during single-feeder presentation ($\bar{x}= 4.32$, $S= 3.66$; $H_{1,1}= 8.12$; $P< 0.001$).

The third independent variable, predator presentation, did not have a significant effect on either the number of seeds taken per chickadee or the average perched times. When tested with the influence of seed type or feeder presentations, the SRH test did not find predator presentation to be influential with either combination (both $H_{1,1}< 0.09$; $P> 0.70$).

The numbers of times chickadees switched between feeders were not compared between seed type or predator presentation due to small sample size. There were few instances when both feeders were presented (19 sessions). Chickadees were found to switch from one feeder to another during a dual-feeder presentation at a lower rate than birds of other species (chickadees: 8 sessions out of 19 total; heterospecifics: 10 sessions out of 19 total). The sample sizes for these behaviors were too small to run meaningful statistical analyses.

Heterospecific interactions and food preference

Within the 54 sessions, there were 10 heterospecific species sighted or heard near the feeders (Fig. 8), but only American goldfinch (*Spinus tristis*; AMGO) and red-breasted nuthatches (*Sitta canadensis*; RBNU) took seeds from the experimental feeders

during trials. The AMGO was the most commonly observed heterospecific species (39% out of total heterospecific species observations). The RBNU visited the feeders more often ($n= 32$) than AMGO ($n= 24$), although RBNU were observed half as many times (20% out of total heterospecific species observations) as the AMGO (Fig. 8).

The activity levels for AMGO (sunflower: $n= 49$; $r_s= -0.101$; $P= 0.490$; safflower: $n= 36$; $r_s= -0.176$; $P= 0.303$) and RBNU (sunflower: $n= 49$; $r_s= 0.061$; $P= 0.675$; safflower: $n= 36$; $r_s= -0.139$; $P= 0.417$) were not associated to the number of seeds taken per chickadee, or with the chickadee's average perched time (AMGO sunflower: $n= 50$; $r_s= 0.118$; $P= 0.413$; AMGO safflower: $n= 47$; $r_s= 0.026$; $P= 0.893$; RBNU sunflower: $n= 50$; $r_s= -0.103$; $P= 0.476$; RBNU safflower $n= 47$; $r_s= 0.069$; $P= 0.646$).

The seed types did not influence activity levels of AMGO and RBNU. The activity levels for AMGO (Kruskal-Wallis test $P= 0.298$) and RBNU (Kruskal-Wallis test $P= 0.289$) did not significantly differ in the number of sunflower seeds taken per heterospecific individual. The number of safflower seeds taken also did not differ between activity levels (Kruskal-Wallis tests AMGO: $P= 0.191$; RBNU: $P= 0.611$).

Although the activity levels did not change between the numbers of seeds taken, the seed type presented was more influential than the predator presentation on the number of seeds taken per heterospecific. The heterospecifics had preference towards the sunflower seeds ($\bar{x}= 6.06$, $s= 10.7$) over safflower seeds ($\bar{x}= 0.971$, $s= 0.627$; $H_{1,1}= 3.44$; $P= 0.063$). Feeder presentation did not influence the number of seeds taken ($H_{1,1}= 0.002$; $P= 0.962$).

There were no associations between the numbers of seeds taken per heterospecific against number of seeds taken per chickadee. There were not enough sessions in which

the heterospecific took safflower seeds while chickadees took sunflower or safflower seeds ($n < 8$). When heterospecifics took sunflower seeds, there were no associations between the number of seeds taken per chickadee ($n = 18$; $r_s = -0.253$; $P = 0.311$).

The influences of the three independent variables were not analyzed against agonistic and tolerance behaviors as had been planned because they were observed infrequently. Out of the 108 sessions analyzed, most sessions (79 out of 108 sessions) did not show any social interaction at the feeder. During the sessions with social interactions, there were more instances of chickadees displacing one another ($n = 13$) than chickadees displacing heterospecifics ($n = 3$). Displacement of chickadees by heterospecifics ($n = 6$) occurred slightly more than the displacement of one heterospecific ($n = 4$) by another. Chickadee tolerance toward other birds was also uncommon ($n = 7$). When chickadee and heterospecifics came near the feeder, they often landed on the feeding perch; there were few instances where chickadees ($n = 4$) and heterospecific ($n = 5$) approached but did not perch on the feeder. Due to small sample size, I was unable to statistically analyze agonistic behaviors among chickadees or between species.

Chickadee Vocalizations

The most frequently recorded chickadee call was the “tseet” call ($n = 104$; $\bar{x} = 21.4$, $s = 18.0$), followed by the repeated “tseet” call ($n = 95$; $\bar{x} = 14.4$, $s = 21.2$), D note call ($n = 73$; $\bar{x} = 6.22$, $s = 6.76$), “zee” calls ($n = 30$; $\bar{x} = 5.85$, $s = 14.0$) and “ABCD” call ($n = 53$; $\bar{x} = 2.11$, $s = 4.43$). Most calls were not associated with the number of chickadees in the area; the number of chickadees was only inversely associated with the repeated “tseets” ($n = 95$; $r_s = -0.280$; $P = 0.006$).

Seed type significantly affected the number of “D-notes” ($H_{1,1} = 9.54$; $P = 0.002$) and “zee” calls made per chickadee ($H_{1,1} = 13.2$; $P < 0.001$). “D-notes” were recorded more often during the sunflower feeder only presentation ($\bar{x} = 6.14$, $s = 5.27$) than safflower feeder only ($\bar{x} = 5.54$, $s = 6.67$). Contrastingly, the “zee” calls were more common during the safflower feeder only presentation ($\bar{x} = 21.38$, $s = 36.44$) than the sunflower feeder only presentations ($\bar{x} = 3.88$, $s = 4.87$; Fig. 9).

The different seed types also showed varying association with the “tseet” calls and numbers of each seed type taken. “Tseet” calls had a positive relationship with the number of safflower seeds taken per chickadee ($n = 35$; $r_s = 0.691$; $P < 0.001$), but did not have a significant relationship with the number of sunflower seeds taken per chickadee ($n = 49$; $r_s = 0.148$; $P = 0.311$; Fig. 10). When “tseet” calls were correlated with the number of safflower seeds taken during the single safflower feeder presentation and the number of safflower seeds taken during dual-feeder presentation, the single safflower presentation showed a strong association with “tseets” ($n = 22$; $r_s = 0.780$; $P < 0.001$) while the dual-feeder presentation did not ($n = 13$; $r_s = 0.078$; $P = 0.801$).

The “tseet” calls showed a positive relationship with the number of sunflower seeds taken per heterospecific ($n = 22$; $r_s = 0.445$; $P = 0.038$), and no relation with the number of safflower seeds taken per heterospecific ($n = 8$; $r_s = -0.233$; $P = 0.578$; Fig. 11). No correlation analyses of feeder presentation were run between “tseets” and the number of sunflower seed taken per heterospecific due to small sample size ($n = 5$). Although both sunflower taken per heterospecific and safflower taken per chickadees had positive correlations with the “tseet” calls, the sunflower taken per heterospecific and safflower taken per chickadee were uncorrelated with each other ($n = 13$; $r_s = -0.381$; $P = 0.199$).

The feeder presentation had significantly stronger influence on the number of “tseet” calls than the predator presentation ($H_{1,1} = 4.14$; $P = 0.042$). There were more “tseet” calls during the single-feeder presentation ($\bar{x} = 23.9$, $s = 19.2$) than during dual-feeder presentations ($\bar{x} = 16.8$, $s = 14.6$).

The “zee” alarm call was influenced more by the predator presentation (SRH test $H_{1,1} = 2.85$; $P = 0.09$) than the feeder presentation ($H_{1,1} = 0.806$; $P = 0.369$). There were more “zee” calls recorded during the predator presence ($\bar{x} = 6.80$, $s = 10.2$) than predator absence ($\bar{x} = 2.64$, $s = 3.98$), although the difference was not significant. However, when the outlier was removed, the predator influence was not significant in the number of “zee” calls made per chickadee ($H_{1,1} = 0.170$; $P = 0.192$; Fig. 12).

Aside from intraspecific interactions, the social environment also influenced chickadee vocalizations. The RBNU activity level positively correlated with the number of “D-notes” made per chickadee ($n = 27$; $r_s = 0.408$; $P = 0.035$; Fig. 13). However, none of the calls associated with the activity levels of AMGO (all $P > 0.100$). The maximum number of heterospecifics also did not correlate with the any vocalization types (all $P > 0.100$).

Out of the eight vocalization types observed, four types were not found to be significantly influenced by the independent factors presented in this study. The “ABCD” calls occurred in half of the sessions (50%, $n = 54$ out of 108 sessions), but showed no influence from the seed type, feeder or predator presentations. The “fee-bee” song, half song and “gargles” occurred in few sessions ($n < 10$), and therefore, no meaningful statistical tests for these vocalization types were conducted. The same three vocalizations were also omitted from the correlation analyses between vocalizations.

DISCUSSION

The foraging behavior of black-capped chickadees was predominantly influenced by seed type (see Fig. 6) while vocalizations were influenced by social interactions (see Figs. 11 and 13) and possibly by predator influence (Fig. 12). Being opportunistic feeders, chickadees took seeds from any feeder that was available; however, there was a distinct preference towards taking more sunflower seeds than safflower seeds.

There were associations between heterospecific foraging activities and chickadee alarm calls (“D-notes” and “zee” calls) and contact calls (“tseet” calls) usage. Both types of calls have been associated with social interactions in various avian studies (Radford 2004 b.).

The major assumptions for this discussion are that there is a dominance ranking established at the feeders, and the chickadee vocalizations reflect these social interactions. Ficken et al. (1978), Smith (1991), and Templeton et al. (2005) propose functions or specified context for various chickadee vocalizations (see introduction). Those assumed contexts are based on extensive field and laboratory analysis, and for the sake of this discussion I will assume they are valid. The associated contexts of each call should probably be taken with varied degrees of support, as there is always a degree of variability in contexts associated with particular vocalizations.

Food choice in black-capped chickadees

Chickadees showed a preference for the sunflower seeds, which supported the hypothesis that foraging activity will concentrate around the food with the higher

metabolic energy gain, the sunflower seeds. The chickadees took more sunflower seeds than safflower seeds in both single-feeder and dual-feeder presentations. Even when they were given an alternate seed choice, the higher number of sunflower seeds taken during the dual-feeder presentation demonstrated chickadee's preference for sunflower seeds.

The preference for the sunflower seeds was also shown by the shorter perched time (Fig. 7). Perched time at the feeder was used as another measurement for seed preference. The chickadees showed a shorter perched time at the sunflower feeder than at the safflower feeder. The shorter perched time could signify higher chickadee rotation rate at the feeder, and perhaps the reason for more sunflower seeds taken per chickadee. My study did not find whether the slightly higher metabolic energy gain from the sunflower (National Research Council 1994) or the slight difference in seed nutrition or familiarity in handling the seed influenced the chickadee's preference for sunflower seeds.

Social context and chickadee vocalizations

Changes in chickadee foraging behavior did not fully support the hypothesis that the presence of other species will decrease chickadee's foraging activities and increase agonistic behaviors. Chickadees did not significantly change their foraging behavior under different social conditions. However, social interactions may have influenced chickadee's vocalization behavior. The number of seeds taken per chickadee did not change between the number of sunflower or safflower seeds taken per heterospecific individual; however, chickadees used different vocalizations during different seed types taken by heterospecifics. The dominance interaction may have played a role when chickadees used the two alarm calls during their foraging events.

More “D-note” calls were recorded during the single sunflower feeder presentation. Because avian alarm calls can be used to threaten flock members (Satischandra et al. 2010), the “D-notes” could be viewed as aggression towards other birds taking the higher-valued sunflower seeds. Birds can become more vocal with increasing conspecific competitors (Radford 2004 a.), and smaller food sources with higher competition can decrease food intake in the subordinates (Vahl et al. 2005). In my study, “D-notes” were recorded more often during the single sunflower feeder presentation ($\bar{x}= 6.14, s= 5.27$) than single safflower feeder ($\bar{x}= 5.54, s= 6.67$; Fig. 9). The “D-notes” may have been used primarily by the chickadees that attempted to gain access to the preferred food. The birds in this study were not individually marked for identification, which is what would be required to assess the effect of dominance on vocalization behavior.

The “zee” calls were recorded more often during the single safflower feeder presentation (Fig. 9). The different number of “zee” calls between seed types (safflower: $\bar{x}= 21.38, s= 36.44$; sunflower: $\bar{x}= 3.88, s= 4.87$) could result from the younger, inexperienced birds calling from the safflower feeder. It is possible that the safflower feeder was open for the inexperienced subordinates because most chickadees infrequently fed from this feeder (Fig. 6). Subordinates generally are young birds and more likely to take risks venturing out to different feeding sites (Smith 1991). The open feeding site may also have been more exposed to predators (Desrochers 1989), especially because they were perched at the safflower feeder longer than they would be at the sunflower feeder (Fig. 7). Subordinates may have foraged at the less-occupied feeders and possibly used more high-alarm calls as an anti-predator tactic when they were exposed.

The study had insufficient sample size to determine if there was a direct association between heterospecific and chickadee feeding behaviors. I did not find the feeding behavior of heterospecifics to directly influence chickadee's seed choice because there was lack of association between the number of sunflower seeds taken per chickadee and the number of seeds taken per heterospecific individual ($n= 18$; $r_s= -0.253$; $P= 0.311$).

There were, however, differences in the use of "D-notes" (Fig. 13) during different RBNU activity levels. The activity levels of RBNU correlated positively with the "D-notes" usage, which can function as alarm calls (Smith 1991). Avian alarm calls can be used for "aggressive intent" against interspecific species (Satischandra et al. 2010). Supporting this idea, I also recorded more "D-notes" (Fig. 9) during the single sunflower feeder presentation (the preferred food source, Fig. 6), which may suggest that the chickadee attempted to protect the higher-valued food source. The possible protection of sunflower seeds may not have affected chickadee's foraging behavior, because there was no correlation between the number of sunflower seeds taken per chickadee and "D-note" usage. The presence of the smaller heterospecific, the RBNU (Ghalambor and Martin 1999), did not directly change the chickadee foraging behavior, but may have influenced the chickadee's use of an alarm call.

Social context and the use of contact calls

Contact calls can be used to initiate group movement, which helps protect the dominant individual from foraging alone at the new site (Radford 2004 b.). The "tseet" calls may have communicated group movement among chickadees, although my study did not investigate changes in chickadee density over time. The single safflower feeder presentations were the least preferred food and patch quality (Fig. 6). However, there

was a strong association between the number of safflower seeds taken per chickadee from the single safflower feeder and the number of “tseet” calls made per chickadee ($n= 22$; $r_s= 0.780$; $P< 0.001$). The poor feeding site may have driven the chickadee flock to change foraging sites and use the group movement signal, the contact call. For black-billed gulls, noisy leaders attracted more followers (Evans 1982); the increase in contact calls during a single, safflower feeder presentation may have signaled the movement of a chickadee flock.

The movement of the flock would have opened the feeder for the risk-taking (Zanette and Ratcliffe 1994) lower-ranked chickadees. Subordinate birds are less likely to gain access to food at the new foraging sites (Radford 2004 b). Instead of moving with the flock, the subordinate chickadees may have stayed at the poor feeding site to use the available low quality food. This behavior may be the indirect reason for the strong association of “tseet” calls with the number of safflower seeds. In support to this idea, I found no association with “tseet” calls and the sunflower seeds taken (Fig. 10). It is possible that the strong positive association ($n= 35$; $r_s= 0.691$; $P< 0.001$) between the number of “tseet” calls and the number of safflower seeds taken may have been a result of indirect association between the two variables.

“Tseet” calls may also have moved chickadees away from a feeder occupied by heterospecific individuals. Both chickadees (Fig. 6) and heterospecifics preferred the sunflower seeds over the safflower seeds, although there were no direct association between the number of seeds taken per chickadee and the number of sunflower seeds taken per heterospecific individual ($n= 18$; $r_s= -0.253$; $P= 0.311$). However, when there were heterospecific individuals foraging with the chickadees, the “tseet” calls associated

positively with the number of sunflower seeds taken per heterospecific individual ($n= 22$; $r_s= 0.445$; $P= 0.038$). The positive association between “tseet” calls and the number of sunflower seeds taken per heterospecific individual may imply the chickadee flock moved away from a feeding site. Species dominance by a larger heterospecific species (Kohda 1991) may be associated with the chickadees’ use of “tseet” calls during interspecific interactions. Although my study did not differentiate between heterospecific individuals to directly support this possibility, the larger bodied AMGO may have deterred the smaller chickadees from approaching the feeder (Daily and Ehrlich 1994).

If chickadees moved away from the feeders due to AMGO presence, then just as with the poor feeding site condition, the chickadees could have used the contact calls to move the flock to a new feeding site. As further evidence of this, I found no association between “tseet” calls and the number of safflower seeds taken per heterospecific individual (Fig. 11). The lack of association may suggest the chickadee’s lesser need for changing feeding sites because the sunflower feeder was available for chickadees. The relationship between “tseet” calls and the number of sunflower seeds taken by heterospecific may be due to indirect association between heterospecific behavior and chickadee vocalizations.

Alternatively, the “tseet” calls could have attracted more chickadees (Sullivan 1984) in an attempt to deter interspecific species competition. However, the number of “tseet” calls did not associate with the maximum number of chickadees or heterospecifics. Contact calls may not always be used to gather birds; the increase of contact calls in pied babblers (*Turdoides bicolor*) did not gather more group members to a foraging site (Radford and Ridley 2008). The “tseet” contact call did not bring more chickadees

together or deter heterospecifics, and may more likely be a way to communicate collective movement.

Predator and Foraging behaviors

My hypothesis that the presence of a potential predator will decrease foraging time and increase anti-predator behavior in chickadees was not supported. This study found did not find “D-notes” or “zee” calls to be influenced by either presence or absence of a ground predator. The slight, but not significant, difference in “zee” calls may suggest that chickadees were slightly more alarmed when the predator model was presented. However, the “zee” calls did not associate with the number of seeds taken, which could suggest the cost of making “zee” calls was not great enough to induce changes in feeding behavior. If the “zee” calls were used primarily by younger, naïve chickadees, the cat model may have alarmed only the younger birds. The chickadee flock usually has a few young, low-ranking individuals (Smith 1991). The rest of the flock was most likely unalarmed, and the overall number of seeds taken was not affected by the predator presentation.

The lack of significant changes in feeding behavior during predator presentation and absence may have resulted from the use of a model ground predator. Predation studies on Paridae species found stuffed predators were less likely seen as a threat than live predators (Smith 1991). Nest predators also provoked less alarm among the birds in winter (Smith 1991). Additionally, terrestrial predators elicited fewer alarm calls than aerial predators (Templeton et al. 2005). Future studies should investigate which predator cues most influence the use of anti-predator vocalizations.

CHAPTER CONCLUSION

The higher number of sunflower seeds taken and the shorter perched time at the sunflower feeder suggested the chickadee's preference for this seed over safflower seeds. Because the costs and benefits were not directly tested in this study, it is unknown whether the slight differences in the metabolic energy gain had played a role in seed preference.

The presence of other birds did not decrease chickadees foraging activity, which was measured through the number of seeds taken per chickadee. However, I may have found increased agonistic vocalization behaviors in chickadees during the presence of heterospecific individuals. Some aggressive chickadees may have tried to dominate the RBNU by using alarm calls. The larger heterospecific individuals, the AMGO, may have deterred even the aggressive chickadees from approaching the feeders and forced the chickadee group to find a different foraging site.

The predator presentation also did not deter chickadees from foraging at the feeder. Engaging in vocal anti-predator behavior, such as making the "D-note" or "zee" calls, did not diminish chickadee foraging activities. The chickadees showed a change in the number of high alarm "zee" calls between predator presentations, but making anti-predator vocalizations was not strong enough to affect the number of seeds taken. The lack of change in foraging activity in the presence of a predator model may be due to the use of a non-aerial predator, or the unrealistic model of a ground predator. The chickadees invested time in taking sunflower seeds and deterring competition at the feeder, and anti-predator behavior appeared to be secondary when foraging at a bird

feeder. Future studies should focus on various predator models and cues to find what influences foraging chickadees to invest more time in anti-predator vocalizations.

Fig. 1: Sonogram images of chickadee vocalizations: (a) “tseet” call; (b) “A-note”; (c) repeated “tseets”; (d) “zee” calls followed by repeated “tseets”; (e) “gargle”; (f) “chick-a-dee” complex followed with “D-notes”; (g) chickadee complex as “ABCD” call; (h) “fee-bee” song; and (i) half song. The generally accepted context for each call is shown in parentheses (Ficken et al. 1978; Smith 1991). All vertical axes show frequency in kHz and the horizontal axes show the video time as an indicator of duration. All images were produced using Raven Lite v.1.0.

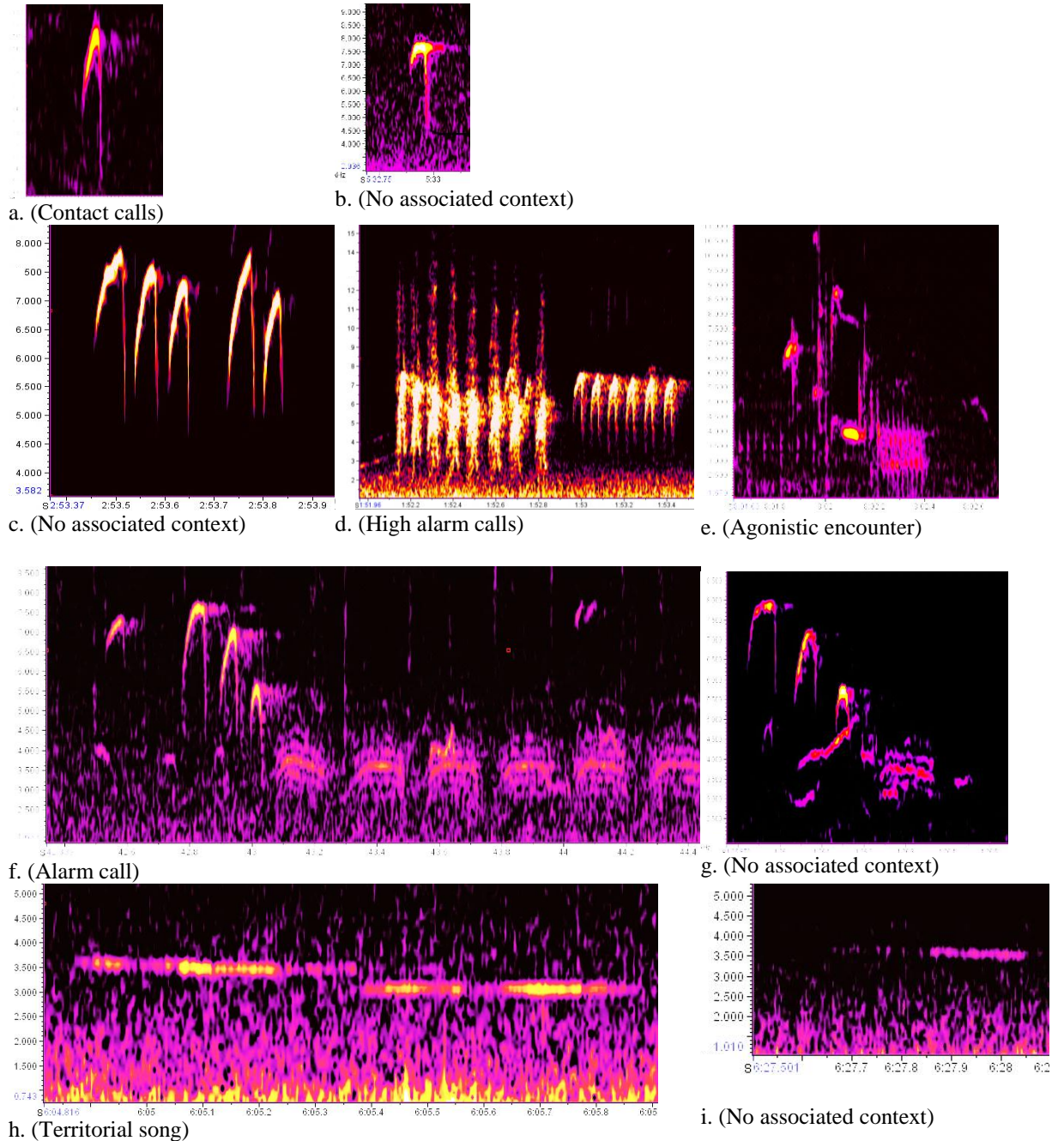


Fig. 2: Map of experimental sites in Marquette county, Michigan. The sites are marked with arrows (imagery ©2012 TerraMetrics; map data ©2012 Google). Five sites are within downtown Marquette; four sites are within Marquette county.



Table 1: Experimental design. All possible combinations for feeder, seed, and predator presentations are displayed between tables (a) and (b). The order in which the combination was presented at a site was randomized. Each “Cat-No Cat” combination was tested at all nine sites.

	Single Sunflower Presentation	Dual-feeder presentation	Single Safflower Presentation
1st 5 min	Cat	Cat	Cat
2nd 5 min	NO Cat	NO Cat	NO Cat

a.

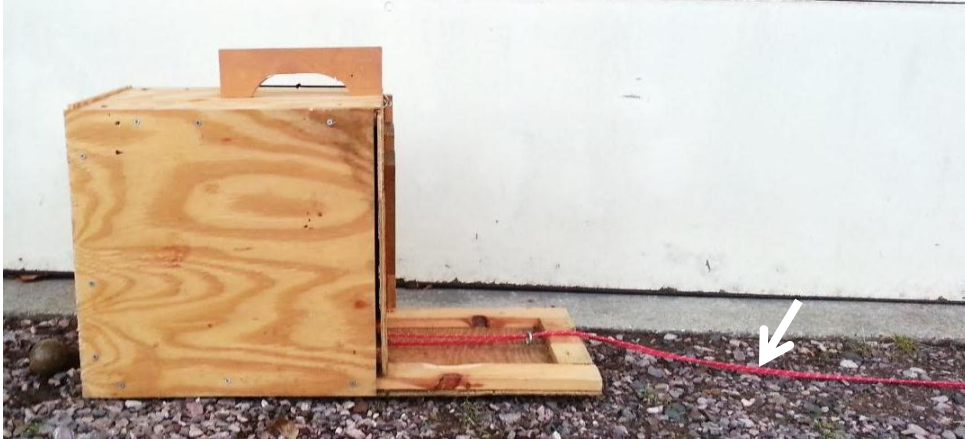
	Single Sunflower Presentation	Dual-feeder presentation	Single Safflower Presentation
1st 5 min	NO Cat	NO Cat	NO Cat
2nd 5 min	Cat	Cat	Cat

b.

Fig. 3: Image of experimental feeders. There are two holes on opposite sides, and two more holes below it, 90° from the holes above. The image displays a dual-feeder presentation, with both sunflower feeder (left) and safflower feeder (right).



Fig. 4: Image of the “Catamatix.” The rope (5m; arrows) on the right moves the cat in (a.) and out (b.) of the wooden box. (Dimensions for width × length × height × base: 31.75 × 31.27 × 31.33 × 80.65cm).



a.

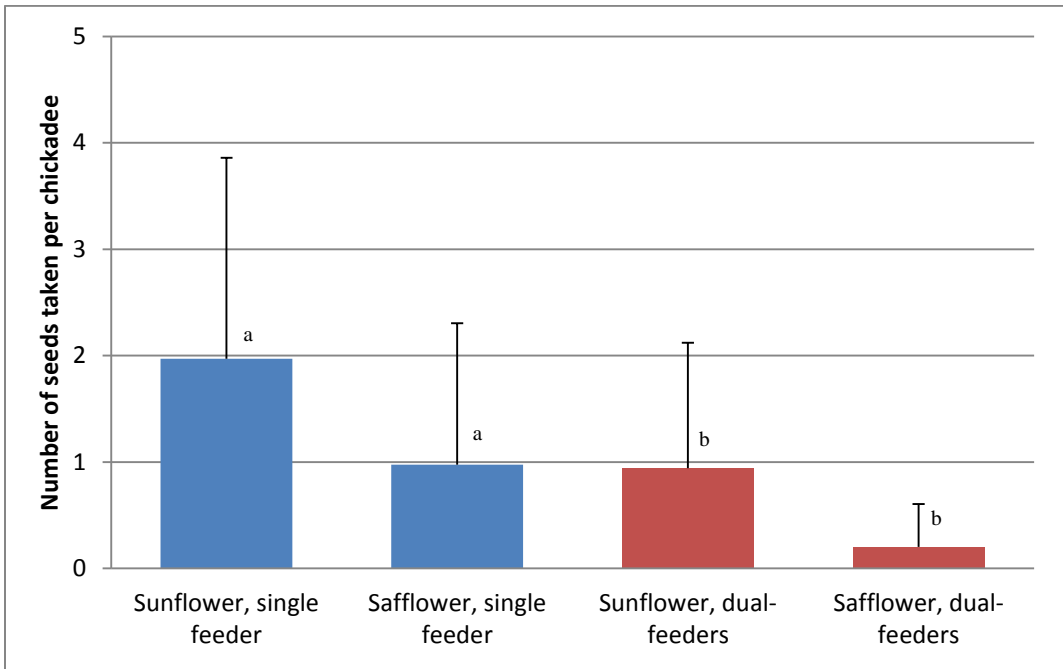


b.

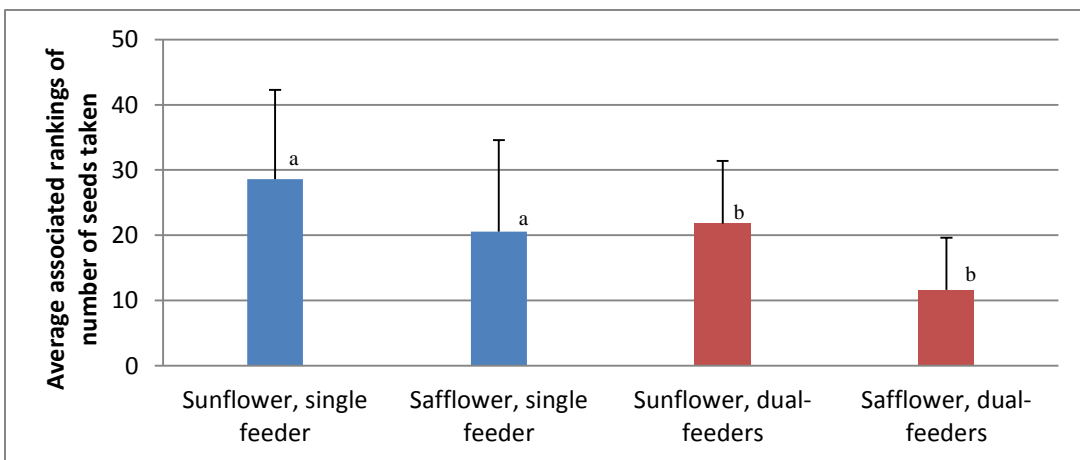
Fig. 5: Example of experimental setup during a visit. Photo capture from video taken during experimental visit is shown. Catamatix was three meters from the feeder post. The camera (not in view) was five meters from the feeder post and approximately eight meters from the Catamatix.



Fig. 6: Chickadee food choice. (a) Comparison between the average number of sunflower and safflower seeds taken per chickadee across single- (left two bars) and dual-feeder presentations (right two bars) shown. (b) Comparison between the average associated ranks for the number of sunflower and safflower seeds taken per chickadee across single- and dual-feeder presentations are shown. The error bars in both graphs indicate the standard deviation from the mean. The same letters indicate which two are significantly different from each other. When seed types were combined, more sunflower were taken than safflower ($H_{1,1} = 14.8$; $P < 0.001$).

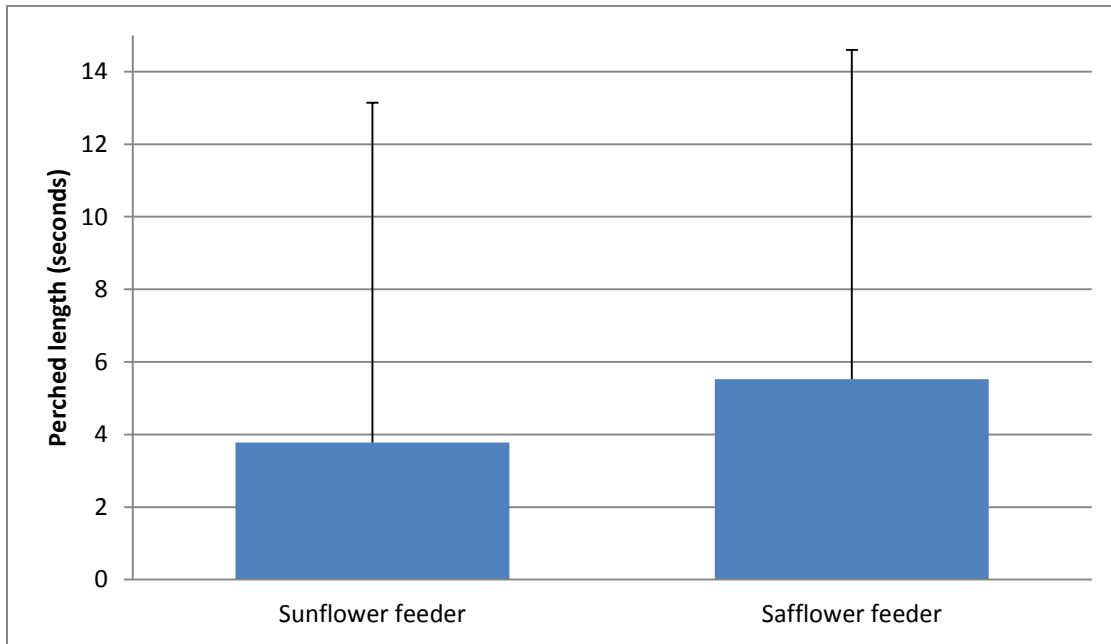


a.

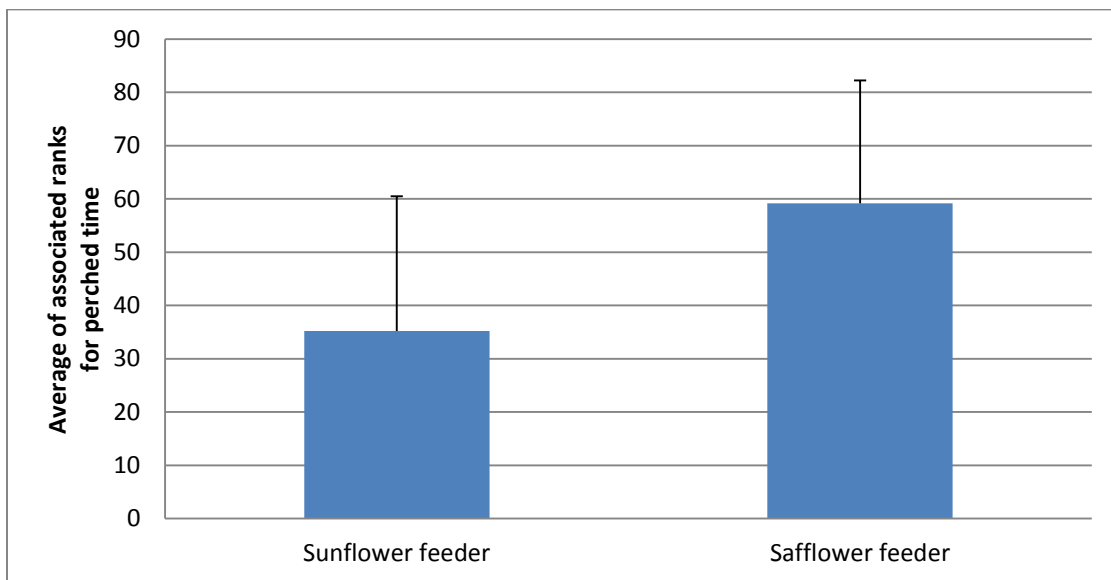


b.

Fig. 7: Chickadee feeder perching behavior. (a) Comparison of average perched times (in sec) between sunflower and safflower feeders are shown ($H_{1,I} = 12.4$; $P < 0.001$). (b) Comparison of average associated ranks for the perched times between sunflower and safflower are shown. In both graphs, the error bars indicate the standard deviation from the mean.



a.



b.

Fig. 8: Encounter rates of heterospecific individuals, shown as proportions of sessions where different heterospecific individuals were recorded.

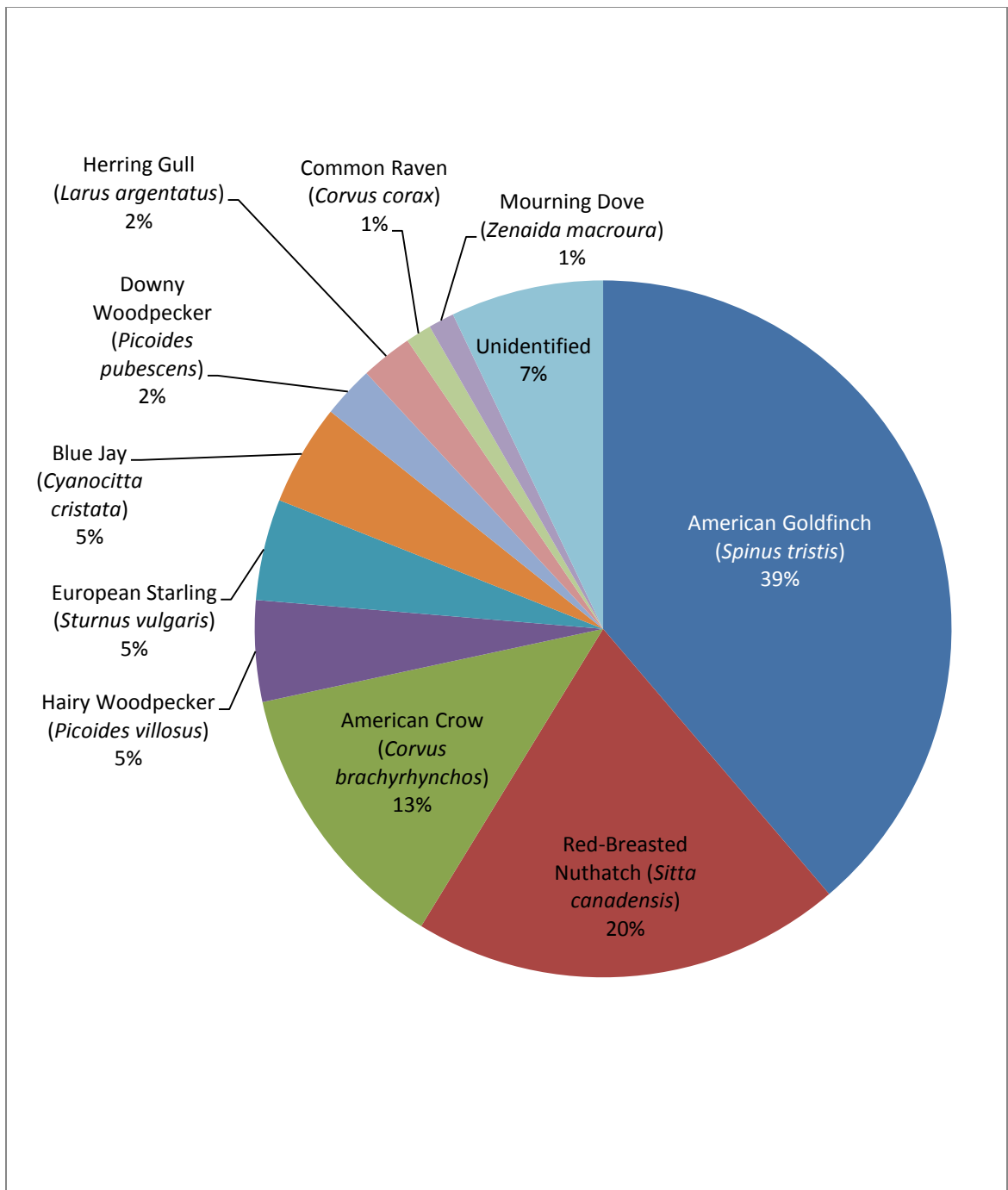
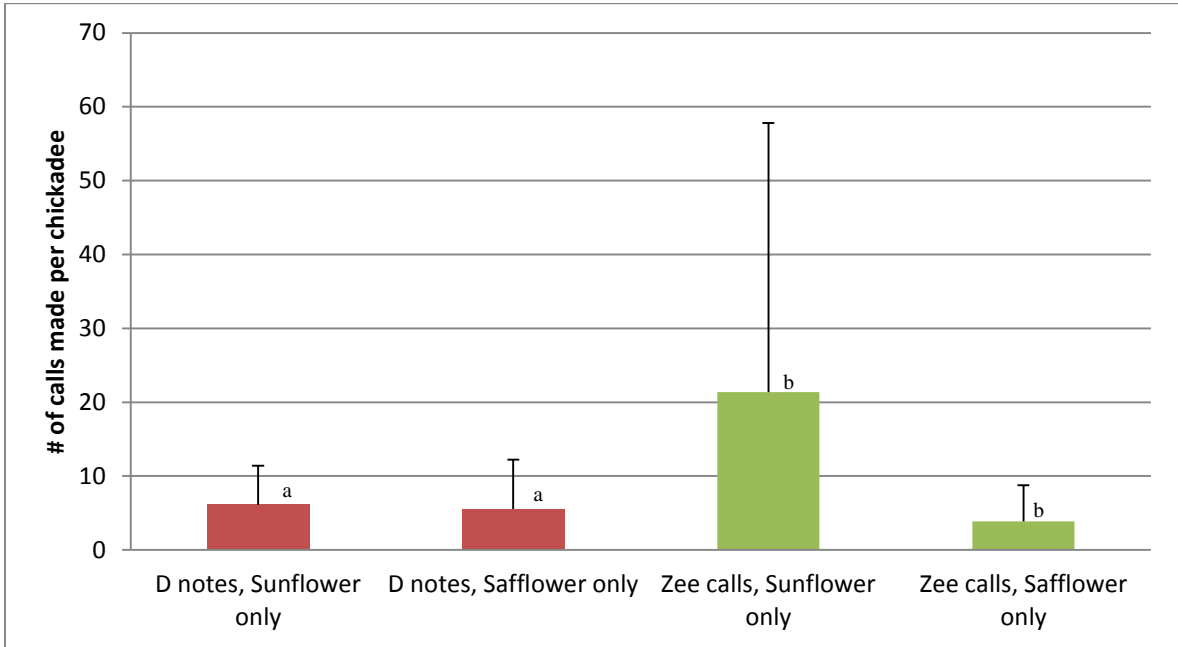
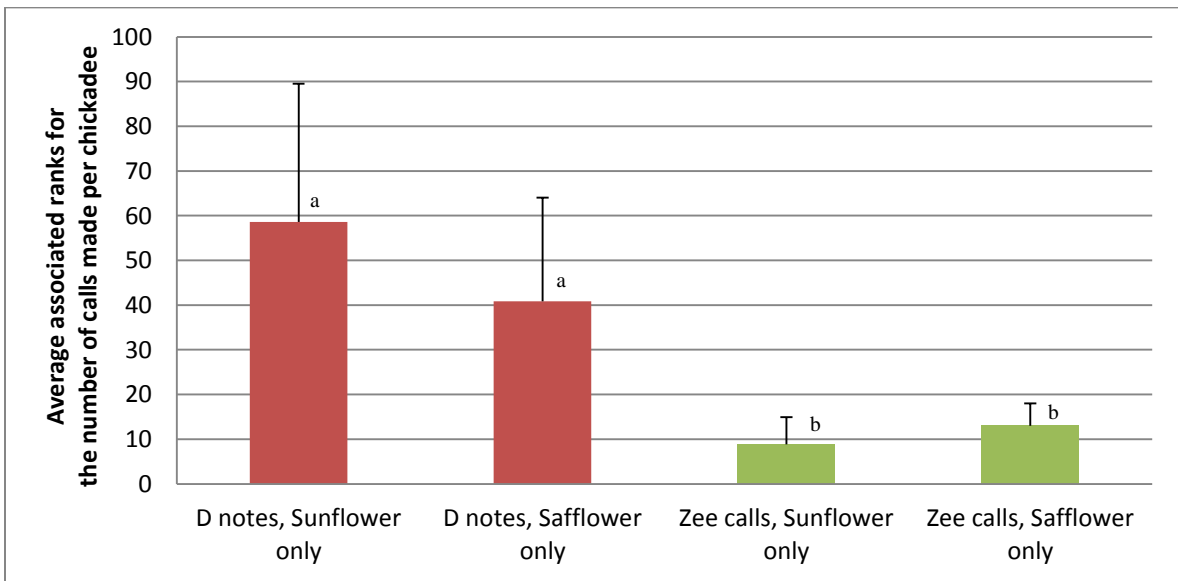


Fig. 9: “D-notes” and “zee” vocalizations used during feeder visits. (a) Comparison between the average number of “D-notes” (left two bars) and “zee” calls (right two bars) made per chickadee across single sunflower and single safflower feeder presentations are shown. (b) Comparison of average associated ranks for the number of the same two calls across single sunflower and single safflower feeder presentations are shown. In both graphs, the error bars indicate the standard deviation from the mean. The same letters indicate which two are significantly different from each other.



a.



b.

Fig. 10: “Tseet” calls and chickadee foraging behavior. Association between the number of sunflower (♦) and safflower (■) seeds taken per chickadee against the number of “tseet” calls per chickadee are shown. The session without “tseet” calls were excluded from this data.

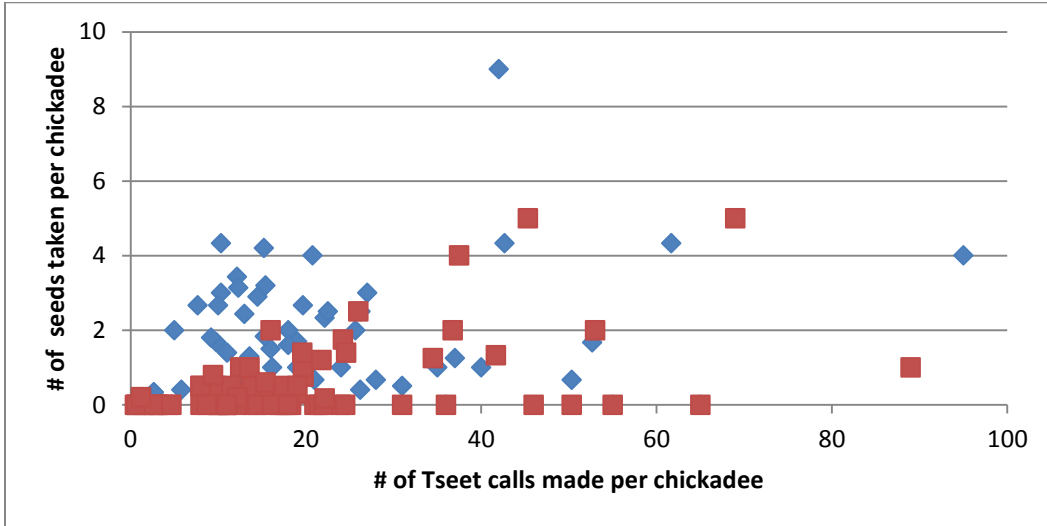


Fig. 11: “Tseet” calls and heterospecific foraging behavior. Association between the numbers of sunflower (♦) and safflower (■) seeds taken per heterospecific against the number of “tseet” calls per chickadee are shown. The session without “tseet” calls were excluded from this data.

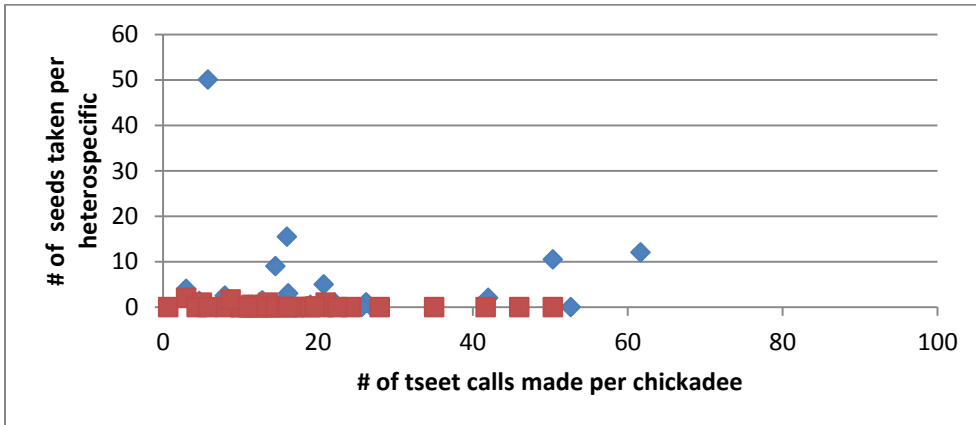


Fig. 12: “Zee” calls in response to predator cue. Comparison between the number of “zee” calls per chickadee when predator was present and absent are shown ($H_{1,I} = 0.170$; $P = 0.192$). The upper error bars indicate the standard deviation from the mean. The sessions without “zee” calls and an outlier were excluded.

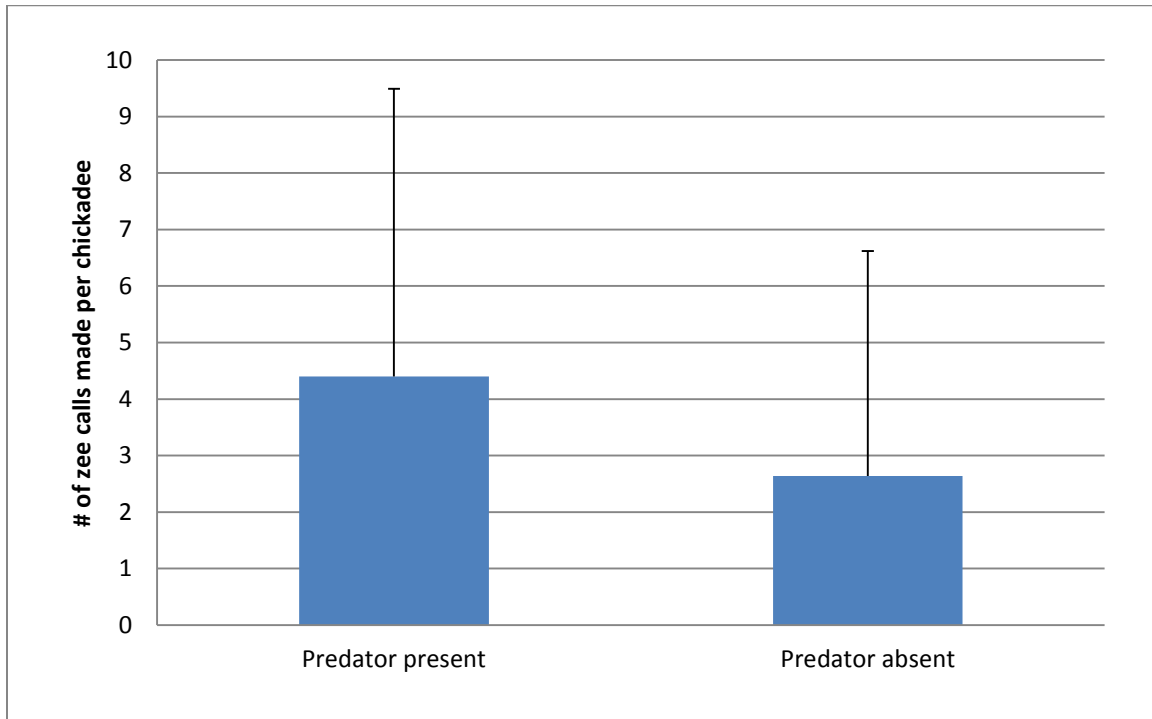
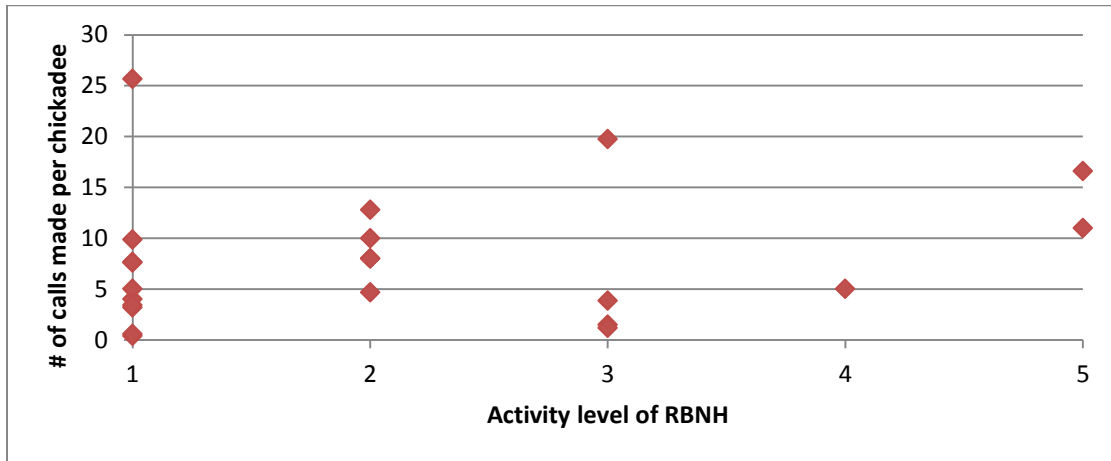


Fig. 13: The “D-notes” and red-breasted nuthatch activity. Association between the number of “D-notes” per chickadee against the activity levels of RBNU are shown ($n=27$; $r_s=0.408$; $P=0.035$). The sessions without “D-notes” and RBNU activity were excluded.



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CHAPTER THREE: CONCLUSIONS

This study examined how birds forage in an anthropogenic environment. Humans have a large influence on the surrounding environment, and the effects of human activity on wildlife activities are of conservation concern. My study did not find human provided food source or the presence of a domestic cat model to dramatically changed chickadee foraging activities. However, I found minor changes in the social behaviors of foraging backyard chickadees based on the type of bird seed available.

My research found the number of seeds taken was significantly higher for the sunflower seeds, and most agonistic vocalization behaviors were displayed around the sunflower feeder. There were more recordings of the contact and mild alarm calls while taking the less desired safflower seeds, while more aggressive alarm calls were associated with the sunflower feeder and seeds. Chickadees' foraging activities may not have been directly affected, but the different use of these vocalizations showed some change in foraging tactics between seed presentations.

Another major influence on foraging behavior was the naturally occurring interspecific social interactions. The artificial feeders gathered chickadee flocks with familiar heterospecific individuals. Heterospecific individuals also showed preference towards sunflower seeds, which may have influenced their behavior around specific seeds.

Unlike the seed type and social influences, I found no major changes in foraging behaviors of chickadees based on the presence of a domestic cat model. The predator presentation was marginally associated with high pitch alarm calls. With the lack of experience, the high alarm "zee" calls may have been uttered by younger chickadees that

were unaware of the potentially non-threatening decoy. However, the age or ranking of each bird was unknown. Most chickadees were either able to identify the artificial predator or did not change feeding behavior in presence of a domestic cat. It is possible that a simple presence of a ground predator was not a great enough threat for the chickadees to switch their attention from foraging to active anti-predator behaviors.

FUTURE INVESTIGATIONS

The results of my study developed more questions that have not been previously investigated. Future studies should focus on why the chickadees, and possibly other bird species, prefer the sunflower seed over the safflower seeds. Nutritionally, the sunflower seeds provide slightly higher metabolic energy (1,543 kcal/kg) than the safflower seeds (1,193 kcal/kg; National Research Council 1994). The significant preference for the sunflower seed may be due to physical attributes rather than nutritional content. The sunflower seeds are more flat and longer than the safflower seeds; the shape may play a role in how the seeds are unshelled, or even how the seeds store over winter.

Seed choice also influenced different vocalizations. Different alarm calls may be influenced by seed type and social environment, as I saw in the different uses of “D-notes” and “zee” calls. Dominance rankings of each bird should be studied when assessing the context in which the alarm calls are used. I also found “tseet” calls to be associated with the number of safflower seeds taken and not with the preferred sunflower seeds. Future studies should also examine the use of chickadee contact calls and their flock movement in the presence of particular seeds.

Another discovery was the lack of anti-predator behaviors during predator presentations. The habituation to domestic cats should be closely investigated using sites with varying cat activities. There may be changes in the foraging tactics of chickadees and their heterospecific flock mates by using realistic predator models, such as those used in Templeton et al. (2005). Changing the presentation of feeders may affect anti-predator behavior in foraging birds. The feeders could be placed on the ground during the ground predator presentation, and use the feeder posts during the aerial predator presentation. The location of the food source and predator types may also affect social interactions. Furthermore, presentation of a control (i.e. non-predator) decoy may also help evaluate the predator cue used by foraging birds. Closer evaluation of food choice across species in the presence of different predators may reveal behavioral adjustments made by chickadees and other backyard wildlife to accommodate variations in foraging situations.

APPENDIX A



Continuing Education
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MEMORANDUM

February 1, 2011

TO: Dr. Alec R. Lindsay
Department of Biology

FROM: Terrance Seethoff, Ph.D. *TS*
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**
Application's # IACUC 171
Approval Period: 02/01/2011-01/31/2014

The Institutional Animal Care and Use Committee, has approved your application by designated member review to use vertebrate animals in research entitled "Field studies of Chickadees and Jays".

If you have any questions, please contact me.

kjm