5-2015

Mixed-species Flock Members' Reactions to Novel and Predator Stimuli

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Recommended Citation

Browning, Sheri Ann, "Mixed-species Flock Members' Reactions to Novel and Predator Stimuli. " PhD diss., University of Tennessee, 2015.
https://trace.tennessee.edu/utk_graddiss/3327

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I am submitting herewith a dissertation written by Sheri Ann Browning entitled "Mixed-species Flock Members' Reactions to Novel and Predator Stimuli." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

Todd M. Freeberg, Major Professor

We have read this dissertation and recommend its acceptance:

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(Original signatures are on file with official student records.)

Mixed-species Flock Members' Reactions to Novel and Predator Stimuli

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Sheri Ann Browning
May 2015

ACKNOWLEDGEMENTS

Thank you to all the bird lovers in my family, including Mom, Dad, Nana, and Grandmother, who taught me at a young age to appreciate birds and their predators. Who could have known that all the time I spent watching the backyard birds and the occasional hawk were preparing me for this 8-year journey? Mom and Dad – I love you both very much, and would not have made it to where I am now without your love and support.

Thank you to my brother, Bobby, and sister, Holly. Both have supported me, even without truly understanding what I was studying or why. That's what I call love!

Of course, many thanks go to my advisor, Dr. Todd Freeberg. I have felt like Sisyphus at times, struggling to push this dissertation boulder up the (Smoky) Mountains, but he has always been there to help, (de)motivate, and provide advice. I can only hope to be as accomplished as he is in the future.

Thanks also to my committee members, Drs. Gordon Burghardt, Matthew Cooper, David Buehler, and Katie Sieving, who have supported me, sparked interesting conversations, and provided constructive criticism throughout my journey. Because of them, I have grown into a better thinker, researcher, and writer.

I am also thankful for my lab mates, David Book, Steven Kyle, and Brittany Coppinger, and NIMBioS colleagues, Arik Kershenbaum, Amiyaal Ilany, and Elizabeth Hobson, who have always been there when I needed help, whether it be catching rogue birds in the aviaries, taking care of the birds, or providing feedback on manuscripts or presentations.

Thanks also go to Suzanne Winters and Carrie Newton-Hodge for their help with data collection and inter-rater reliability during the initial experiment that sparked my interest in mixed-species flock members' reactions to novel stimuli. I am also grateful to Megan Wu and Phylicia Washington for their help with inter-rater reliability for subsequent experiments.

I am appreciative of Rosalee Kashel and Bailey Mulderig, who took care of my birds for me this past Christmas, allowing me a short, but glorious break from fieldwork.

Special thanks to Kevin Hoyt and the staff at the University of Tennessee Forest Resources AgResearch and Education Center. I spent so much time there, that I sometimes felt like it would have been more efficient if I just set up camp next to the aviaries for the winter!

Thanks to the University of Tennessee's Psychology Department for their dissertation grant and also to Connie Ogle, who has been able to help me when I needed it, even when she was being pulled in multiple directions.

Thanks to all of my friends in Tennessee and Virginia who have cheered me on as I trudged through seemingly endless files to code, wished me warm thoughts on especially cold data collection days, provided fun incentives if I was productive, and allowed me to complain to them when I had birdless trapping days.

And last, but not least, thanks go to all the chickadees, titmice, and nuthatches I have observed, trapped, banded, and/or studied. I couldn't have done it without them! They are smarter than I give them credit for (and I give them lots of credit!) They are also stubborn and tested my patience more often than I would have liked, but it was worth it to get a better understanding of what goes on in their world. Dr. Seuss's character, the Lorax, says he speaks for the trees. In my dissertation, I'm speaking for the birds.

ABSTRACT

Novel stimuli are ubiquitous. Few studies have examined mixed-species group reactions to novelty, although the complex social relationships that exist can affect species' behavior. Additionally, studies rarely consider possible changes in communication. However, for social species, changes in communication, including rates, latencies, or note-types within a call, could potentially be correlated with behavioral traits. As such, this research aimed to address whether vocal behavior is correlated with mixed-species' reactions to novel objects. I first tested the effect of various novel stimuli on the foraging and calling behavior of Carolina chickadees, *Poecile carolinensis*, and tufted titmice, *Baeolophus bicolor*. Chickadees and titmice both had longer latencies to forage in the presence of novel stimuli. Chickadees also modified their vocal behavior, having shorter latencies to call and using more 'D' notes in their calls in the presence of novel stimuli compared to titmice. Chickadees and titmice reacted to the novel stimuli similarly to how I would expect them to react to a predator. Therefore, a second experiment was conducted directly comparing chickadee and titmouse reactions to a novel (Mega Bloks®) stimulus and a predator (Cooper's hawk) stimulus. Chickadees and titmice had an intermediate latency to forage in the presence of a novel stimulus compared to control and predator contexts. Again, chickadees had shorter calling latencies across contexts compared to titmice. As a final experiment, using semi-naturalistic aviaries, I tested whether chickadee flock size and the presence or absence of titmice influenced reactions to novel and predator stimuli. Chickadees called more in smaller chickadee flocks compared to larger chickadee flocks, and also when titmice were absent compared to when they were present. These results were stronger in predator contexts compared to novel contexts. This suggests that conspecific flock size influences calling behavior, such that smaller flocks, which may experience higher stress levels and may be required to exhibit more anti-predatory behavior, call more than larger flocks. Taken together, this work has important implications for the complexity of social relationships in mixed-species groups, the social roles species play within the group, and how group size influences vocal behavior and reactions to various degrees of threat.

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CHAPTER I: INTRODUCTION

"All animals feel Wonder, and many exhibit Curiosity" (Darwin, 1874, p.80)

Scope

Novel stimuli are ubiquitous. From birth or hatching, individuals are introduced to new stimuli, and must learn about them and gain experience such that non-adaptive responses to stimuli are minimized. Habituation to the novel stimulus can occur either over time during one experience or after repeated experiences (Leussis & Bolivar, 2006). Often, an individual's reactions to novel stimuli, whether it is attracted to novelty (neophilic), or tries to avoid novelty (neophobic), are repeatable over time. Behavior patterns that are repeatable over time and across contexts are considered behavioral types, or personality traits (Gosling, 2001). The study of personality in animals has increased exponentially in the last two decades, resulting in many new personality-related terminologies and continuums (Gosling, 2001). The neophobia-neophilia continuum is an often described continuum in the personality literature. This introduction thus begins by defining neophobia and neophilia, and then describing them in relation to several other prevalent personality continuums.

Next, I discuss the history of animal personality research. Researchers commented on observed differences in individual reactions to novel stimuli as early as the late 1800s. It is important to acknowledge the roots of this field, because while the breadth of this field has increased, many of the methodologies to study novelty remain the same. Subsequently, I discuss the traditional ways to measure reactions to novelty.

I will follow the historical review with a broad review of the relevant literature regarding differences in reactions to novel stimuli. There are many aspects of an individual's life that can influence its reactions to novel stimuli; these influence individuals on the species-, group-, and/or individual-levels. As such, I will discuss several influences on each level and provide examples from the animal personality literature.

This review of the literature will make it apparent that measuring approach or avoidance behavior is a preferred method for testing novelty reactions, but I will introduce the idea of using vocal communication as an additional measure of neophobia and neophilia. In the human literature, certain personality traits, such as extroversion, are correlated with an increase in vocal rate and amplitude (Mairesse, Walker, Mehl, & Moore, 2007). Therefore, the possibility that vocal behavior is also associated with certain behavioral traits in animals will be discussed.

The introduction will end with an overview of the study system of interest: mixed-species flocks of Carolina chickadees and tufted titmice. These two species are well-studied and much is already known about how they behaviorally and vocally react to threatening predator stimuli (Bartmess-Levasseur et al., 2010; Courter & Ritchison, 2009; Nolen & Lucas, 2009; Sieving, Contreras, & Maute, 2004; Sieving, Hetrick, & Avery, 2010; Soard & Ritchison 2009). Considering this, they are an ideal group to test for behavioral and vocal differences in responses to novelty. The introduction thus concludes with an outline of the three experiments that were conducted to test for vocal and behavioral reactions to both novel and predator stimuli in chickadees and titmice.

Novel Stimuli, Neophobia, and Neophilia

A stimulus is novel, or new, based on an individual's past experience (Corey, 1978), such that stimuli that an individual has little to no experience with are more novel than stimuli that an individual has experienced frequently. In addition, the degree of dissimilarity and discontinuity from objects or situations that an individual has experienced before must be considered (Greenberg & Mettke-Hofmann, 2001). A squirrel, for example, will likely treat the first oddly-shaped acorn similarly to how it treated all previous normally-shaped acorns because it is not so dissimilar from its past acorn experiences. The squirrel may generalize the odd-shaped acorn to acorns it has previously seen. However, if an acorn is an unusual color, such as pink, it may be perceived as discontinuous from the squirrel's previous acorn experiences and be treated as novel (e.g. Kelly & Marples, 2004).

Consequently, novel stimuli come in many forms. These forms include (1) auditory stimuli, such as a cry of a hawk, (2) olfactory stimuli, such as the musk of male deer, (3) potential food objects, such as a moth species, (4) neutral objects, such as pine cones or a piece of litter, (5) other conspecifics, heterospecifics, or predators, and (6) the habitat, such as when a bird migrates to warmer climates or emigrates from one local population to another local population. The size and/or color of the stimulus can also render it novel (Greenberg, 1983; Kelly & Marples, 2004).

Once an individual perceives a stimulus as novel, there are three possible responses: (1) an individual can be curious and attracted to the new stimulus, and therefore approaches and explores it, (2) an individual can be fearful of the new stimulus and avoid it, or (3) an individual can decide not react at all, either due to ambivalence or ignoring the stimulus. While the approach-avoid dichotomy has been used often in the literature, it has been argued that the term 'withdraw' is more appropriate than 'avoid', as the opposite of 'avoid' is 'to seek,' which speaks to greater levels of motivation (Schneirla, 1959). An individual that is attracted to novel stimuli is considered to be neophilic, while an individual that avoids novel stimuli is considered neophobic. An ambivalent individual is conflicted, having two incompatible tendencies (one, to approach, the other, to avoid) that are elicited by the same stimulus (Hinde 1970). This ambivalent response can be characterized as the absence of movement, which can make it difficult to differentiate from an 'ignore' response. However, other physical responses can be indicative of ambivalence. For example, in rats, ambivalent individuals did not move, but had tension in their bodies and 'high intensity stretched attention,' which aided in the differentiation between 'ambivalence' and 'ignore' behaviors (van Der Poel, 1979). A lack of any change in behavior or posture after the introduction of a stimulus more likely indicates that the individual has ignored it (e.g. Glickman & Sroges, 1966).

Neophobia and neophilia are often described as existing on a continuum, such that an individual can exhibit both fear and curiosity towards a stimulus in rapid alternation (Berlyne, 1950), but that one is stronger than the other, and thus is the prevailing reaction observed (Greenberg & Mettke-Hofmann, 2001). Familiarization, or a reduction of the initial response to novelty, can occur when an individual has gained enough experience with the novel stimulus such that exploration or avoidance ceases (Greenberg & Mettke-Hofmann, 2001). Neophobic and neophilic reactions are often quantitative (discussed further below), allowing researchers to directly compare the neophilia or neophobia of species, groups, and individuals. For example, in a comparison of two species of sparrows, song sparrows, *Melospiza melodia*, were considered 'more neophobic' than swamp sparrows, *M. georgiana*, based on latencies to feed near a novel object (Greenberg, 1990b). It would not be appropriate, however, to simply deem song sparrows as a neophobic species. They are merely more neophobic compared to swamp sparrows. This is also true when comparing individual reactions to novel stimuli. Some individuals are more or less neophobic or neophilic than others. For example, individual starlings, *Sturnus vulgaris*, differentially responded to being placed in a novel environment (Boogart, Reader, & Laland, 2006). Those with shorter latencies to feed were more neophilic than those with longer latencies.

Other studies divide reactions to novelty into three nominal categories—neophobic, intermediate, and neophilic—based on quantitative scores, where each category is operationally defined by the researcher. For example, the locomotion of sister rats, *Rattus norvegicus*, was measured after they were placed in a novel environment (Cavigelli, Yee, & McClintock, 2006). The authors then designated the two most active sisters as 'neophilic', the two least active sisters as 'neophobic', and those closest to the family mean as 'intermediate'. At times in the literature, neophobia and neophilia are used interchangeably with shyness and boldness. Pumpkinseed sunfish, *Lepomis gibbosus*, for instance, were described as either shy, intermediate, or bold, after their reactions to a novel threat and novel food source were recorded (Coleman & Wilson, 1998). Sunfish that fled from the novel stimuli every time were labeled ‘shy’, ‘intermediate’ individuals did not flee each time, but on average never got closer than 5 cm from the object, and ‘bold’ individuals on average approached within 5 cm of the object.

Personality Terminology

‘Neophobia’ and ‘neophilia’ and ‘shy’ and ‘bold’ terminology were used in a similar manner in the previous sister rats and sunfish examples. Measuring an individual’s level of neophobia or neophilia is only one of many ways to quantify behavioral types (Sih, Bell, & Johnson, 2004). Behavioral types—also called personality traits (Gosling, 2001), behavioral syndromes (Sih, Bell, & Johnson, 2004), behavioral reactions norms (Dingemanse, Kazem, Réale, & Wright, 2010), coping styles (Koolhaas et al., 1999), or temperaments (Réale, Reader, Sol, McDougall, & Dingemanse, 2007)—are behavior patterns that are consistent across contexts (Sih et al., 2004). There is some variation within these personality terms. For example, while behavioral syndromes are used to describe when the same behavior (e.g. aggression) is correlated across different contexts, it can also be used to describe when one behavior is correlated with another behavior (e.g. aggression and boldness) across different contexts (Dingemanse et al., 2007). Behavioral reaction norms, on the other hand, are consistent reactions in a single (social) context, but not necessarily across contexts (Agrawal, 2001).

In addition to several personality terms, there are multiple described continuums in the animal personality literature, including the neophobia/neophilia, fast/slow explorers, shy/bold, extrovert/introvert, proactive/reactive, approach/avoidance, and impulsive/deliberate continuums (Table 1, located in the Appendix at the end of the chapter). Other measures to describe individual differences in reactions to stimuli include flight initiation distances (e.g. Altmann, 1958), fight/flight, and aggressive/defensive reactions.

As described earlier, the neophilia/neophobia continuum describes individuals that are either attracted to, or repelled by, new or unfamiliar objects. The approach/avoidance continuum is analogous in that individuals who are curious about a stimulus will approach it while individuals who are fearful of the stimulus will avoid it (McDougall, 1908). Similarly, the shy/bold continuum (Wilson, Clark, Coleman, & Dearstyne, 1994) describes bold individuals as those that are attracted to risk and shy individuals as those who avoid risk. Therefore, the difference between the shy/bold and neophobia/neophilia continuums is that for the shy/bold continuum, the stimulus or context is risky—it can be a risky predator encounter or risky habitat location as well. This propensity to take risks is also often measured using presentations of novel stimuli or novel environments (e.g. Wilson et al., 1994).

The reactive/proactive continuum (Koolhaas et al., 1999) is similar to the shy/bold continuum in that reactive individuals can be considered shy and proactive individuals can be considered bold (Sih, Bell, & Johnson, 2004). However, the reactive/proactive continuum is different in that it includes physiological measures. Reactive individuals often have low testosterone, high parasympathetic reactivity, and low sympathetic reactivity in response to threatening stimuli. In contrast, proactive individuals have high testosterone, low parasympathetic reactivity, and high sympathetic reactivity (Koolhaas et al., 1999). Thus, this continuum better addresses the stress levels of individuals in novel or threatening situations.

The fast/slow explorer continuum addresses latencies to approach stimuli, and can sometimes be tested for correlations with other physiological measures. For example, great tits, *Parus major*, were pre-selected for being 'fast' or 'slow' explorers based on their scores in a novel object test and an open arena test (Carere, Groothuis, Mostl, Daan, & Koolhaas, 2003). Individual tits were then placed in a social stress test, where they were introduced to an aggressive male. Corticosteroid metabolites were measured the day before the introductions as well as on the day of and the day after confrontations. The less aggressive and more cautious ‘slow explorers’ had a greater corticosteroid response to the aggressive confrontation of another male tit compared to the more aggressive and bolder ‘fast explorers’.

An individual’s aggressive or non-aggressive (defensive) reactions to novel or threatening stimuli can also be indicative of personality. For example, researchers measured the reactions of domestic cats, *Felis catus*, to several threatening stimuli including a novel room and the recording of a conspecific threat vocalization (Adamec, Stark-Adamec, & Livingston, 1983). The cat’s exploration of the room and defensive posturing to the vocalization were measured. Subsequently, their scores in these tests were compared to how the cats reacted to a prey species, a rat. Cats that exhibited more defensive postures to the conspecific vocalizations and little exploration of the novel room reacted non-aggressively/defensively to the rat compared to cats that had higher exploration levels in the novel room and less defensive posturing (Adamec et al., 1983). In general, individuals who are more aggressive show a more active response to aversive stimuli and try to remove themselves from the source of stress or harm, while non-aggressive (defensive) individuals react more passively with immobility (Benus, Bohus, Koolhaas, & van Oortmerseen, 1991).

Aggressive or defensive reactions are similar to fight or flight reactions. The fight or flight response is an active response to a threatening stimulus, such that ‘fighting’ individuals approach, posture, and/or defend their position, while ‘fleeing’ individuals withdraw and try to avoid the threat (Cannon, 1915). Some describe the fight or flight responses interchangeably as an active coping style to stressors (e.g. Koolhaas, 2008).

Less Frequently Used Descriptors for Individual Differences

Extroversion and introversion are typically discussed in the human personality literature, but correlates are also observed in animals (reviewed in Gosling & John, 1999). Individuals high in extroversion can be more social, assertive, and or active, compared to introverted individuals. For instance, in a survey of personality traits, gorillas, *Gorilla gorilla*, that were scored as being more active, playful, curious, and sociable by their zookeepers were considered more extroverted than less social and non-active gorillas (Gold & Maple, 1994).

Flight initiation distance can also be indicative of species and/or individual differences in responses to stimuli. Flight initiation distances refer to the distance an individual allows a threat to approach without causing it to flee. Originally described by Hediger in 1934, a long flight initiation distance is indicative of a shy individual and a short flight initiation distance is indicative of a bold individual (Altmann, 1959). More recent analyses of flight initiation distances suggest that species differences are more prevalent than individual differences (Runyan & Blumstein, 2004). Nevertheless, there are some exceptions, as is the case for individual burrowing owls, *Athene cunicularia*, who exhibited high individual repeatability in flight initiation distances when human threats approached (Carrete & Tella, 2010).

Additionally, individual differences in speed and accuracy when responding to stimuli has been tested in several species. Individuals can make 'fast-and-sloppy' (Chittka, Skorupski, & Raine, 2009) or 'impulsive' (Davis & Burghardt, 2007) decisions or, in contrast, can make 'meticulous and slow', or 'deliberate' decisions. For example, red-bellied cooters, *Pseudemys nelsoni*, were trained in a novel food acquisition task, where individuals had to choose between, and knock over, bottles to obtain food (Davis & Burghardt, 2007). Over the duration of the experiment, there was variation in the amount of time it took individuals to knock over the bottles. Some turtles were 'impulsive,' swimming to the bottles and knocking them over without regard for which one had food underneath. Others were 'deliberate,' pausing to look at both bottles before knocking one down. Impulsive turtles had lower success rates compared to deliberate turtles. The authors suggested that these differences may be related to the turtle's ability to learn the task or it may be associated with individual differences. Similarly, when presented with a maze, 'hasty' guppies, *Poecilia reticulata*, were more likely to make inaccurate decisions compared to individuals who were careful and slower to make decisions (Burns & Rodd, 2008). Few studies have directly tested the links between such differences in speed and accuracy with other behavioral traits, such as neophobia/neophilia or shyness/boldness. However, in one study of three-spined sticklebacks, *Gasterosteus aculeatus*, bold fish placed in a T-maze with a food reward were quicker to make the correct decision compared to shy fish, but boldness was not related to accuracy over time (Mamuneas, Spence, Manica, & King, 2014). Taken together, these studies raise the question of how cognitive abilities influence individual behavioral traits.

Overall, for the purposes of this dissertation, the behavioral types 'neophobia' and 'neophilia' will be used to describe animals when only presenting novel stimuli and the behavioral types 'shy' and 'bold' will be used to differentiate between behavioral reactions when comparing presentations of novel and predator stimuli. No physiological measures were collected, so the proactive/reactive and slow/fast explorer continuums are not appropriate.

History of Personality and Novelty Research in Animals

Before discussing the current research on novelty, it is important to understand the history of this field of research. The study of individual differences in behavioral reactions is not a new topic. Researchers have been observing how individual animals differentially react to stimuli since at least the late 1800s. Consider this observation by Charles Darwin (1874) regarding how several primate species reacted to a predator model and various novel objects:

> "...I took a stuffed and coiled-up snake into the monkey-house at the Zoological Gardens, and the excitement thus caused was one of the most curious spectacles which I ever beheld. Three species of Cercopithecus were the most alarmed; they dashed about their cages and uttered sharp signal-cries of danger, which were understood by the other monkeys. A few young monkeys and one old Anubis baboon alone took no notice of the snake...These monkeys behaved very differently when a dead fish, a mouse, and

> some other new objects were placed in their cages; for though at first frightened, they soon approached, handled and examined them" (p. 81).

Similar to this example, many of the early descriptions of animal personality were anecdotal. For instance, in L. R. Talbot's descriptions of his experiences as a newly-licensed bird bander, he suggested that the birds he was trapping showed their 'personality' when he observed the different levels of motivation for birds to fly through a small opening to get into a gathering cage (Talbot, 1922). Len Howard, who, like Talbot, enjoyed birding, but kept them as pets instead, wrote a book entitled *Birds as Individuals* (Howard, 1953). Howard spent years feeding and observing many species and began to recognize them by their individual characteristics, including by their plumage, individual mannerisms, facial expressions, and other idiosyncrasies (Howard, 1953).

Other early observations of 'personality' were experimental. For example, in 1935, Ivan Pavlov studied differences in dog temperaments and related it to how individual dogs dealt with stress (reviewed in Strelau, 1997). Rats were also placed into novel arenas, or 'open-field tests' and their reactions or 'emotionality' were measured, based on activity levels and physiological measures, such as urination and defecation (Hall, 1934). There were individual differences in how rats responded to the open field test and the open field became less novel to them the more often they experienced it.

A similar line of research compared the personalities of blackbirds, including brown-headed cowbirds, *Molothrus ater*, starlings, *Sturnus vulgaris*, red-winged blackbirds, *Agelaius phoeniceus*, and common grackles, *Quiscalus versicolor*, and their reactions in an observation cage (Burtt & Giltz, 1969). The authors measured each bird's activity in the cage based on several counts, including the number of location changes, hops, and time spent active on the floor, which resulted in a composite score. A small score indicated that the bird had greater 'complacency' compared to a larger score, which indicated 'agitation'. Because many birds were trapped repeatedly, the authors were able to determine that some individuals were more ‘complacent’ than others. Thus, individuals were considered to exist on a complacency-agitation continuum, a continuum that resembles the neophobia/neophilia and shy/bold continuums in the literature today.

Other researchers were noticing similar continuums in other species. Prior to being described as neophobia, fearful reactions to new objects were called ‘new object reactions’ (Barnett, 1963). These new object reactions were observed by researchers studying pest species, such as creeping voles, *Microtus oregoni*, rats, *Rattus rattus*, common shrews, *Sorex araneus*, common mice, *Mus musculus*, and brown lemmings, *Lemmus trimucronatus*, whose populations fluctuated mysteriously during World War II and were of interest due to their plague-carrying abilities (Barnett, 2001). Many researchers observed that some individuals were easy to trap, while others required several days before they would approach the traps and get caught (e.g. Merry, 1949). This long latency to approach the traps was thought to be due to a fear of the trap itself, because it was an object with which individuals were not familiar. S. A. Barnett, who coined the phrase ‘new object reaction’ later started calling it neophobia, when he noticed that the reactions were not always due to an ‘object’ (Barnett, 1954).

Animals were frequently used by researchers studying human social and personality psychology during the 1930s through 1950s, though for almost 40 years subsequently, the research of non-human animal personality was not as popular of a topic (reviewed in Weinstein, Capitanio, & Gosling, 2008). This was likely due to individual differences in reactions being considered noise around an adaptive mean (Bell, 2007; Wilson, 1998). However, this did not prevent some researchers from measuring consistent individual differences in various species. For example, common garter snakes, *Thamnophis radix*, were found to have consistent individual differences in antipredator displays, and were discussed in terms of personality (Arnold & Bennett, 1984). Similarly, young common garter snakes exhibited consistent preferences for one of two novel prey cues, either minnow extract or redworm extract, and this was attributed to stable individual differences (Burghardt, 1975). In addition, the personality traits of animals in applied fields received some attention. Researchers, for instance, were interested in Holstein cow, *Bos taurus*, temperaments and how they were related to social dominance, as more docile cows were easier to milk (Dickson, Barr, Johnson, & Wieckert, 1970). Similarly, measuring the fearfulness of individual dogs was imperative in determining whether they would make suitable guide dogs (Goddard & Beilharz, 1984). Additionally, some studies discussed individual differences in reactions to stimuli, without directly discussing them in a personality context. Interest in individual differences in animal personalities and their consequences was revived starting in the 1980s and since then, almost 70 different species' personalities have been studied, ranging from ants to gorillas (reviewed in Gosling, 2001).

How to Measure Neophobia and Neophilia

With so many personality-related terms, some overlapping in meaning, it can be difficult to arrive at a methodological consensus (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). Historically, there were two methods for testing an individual animal's reaction to novelty. If a researcher were interested in how an individual reacted in a novel environment, the animal would be introduced to a forced exploration task called an open-field test, which consisted of an open space with walls that prevented the animal from escaping. These tests were first utilized by Calvin Hall to measure the emotionality of rats, *Rattus norvegicus* (1934). There are a range of possible measurements in this task, including locomotion, time spent not moving, field areas visited, counts of species-specific behavior (e.g. sniffing, digging, grooming), as well as physiological reactions, such as defecation, urination, or heart rate (reviewed in Walsh & Cummins, 1976). Latency to habituate to the novel stimulus (e.g. Rodríguez-Prieto, Martín, & Fernández-Juricic, 2010) as well as sensitization or enhancement of neophobia (e.g. Robbins, 1980) could also be measured. Researchers could also place a novel object in an open field test and measure an individual's latency to approach or explore the novel object after being habituated to the open-field (e.g. Heyser &

Chemero, 2012). A caveat of this approach, however, is that some measured behavior, such as an increase in locomotion, may indicate an increase in exploratory behavior, though, it could also be correlated with an individual's attempt to escape from the novel arena (Corey, 1978; Walsh & Cummins, 1976).

A stronger method of measuring reactions to novelty is a free-choice task, such as an apparatus that has several compartments, where a novel stimulus can be placed in one compartment, thus allowing an animal the opportunity to go to another compartment to avoid it, if desired, or remain in the compartment and explore it (e.g. Griebel, Belzung, Misslin, & Vogel, 1993). This method allows for an easier interpretation of the approach to, and avoidance of, novel stimuli compared to the open-field test (Corey, 1978). Several variables can be measured using this method, including latencies to approach and manipulate the object, duration of exploration, and the number of visits to the novel object to explore it (Greenberg & Mettke-Hofmann, 2001).

The free choice tasks described above are employed in laboratory settings. An equivalent method for testing for reactions to novel stimuli in an animal's natural environment is to place the stimulus on or near a location that individuals frequently visit during baseline contexts when no stimulus is present, or by providing an incentive, such as food, and measuring latencies to approach (e.g. Greenberg, 1983; Lendvai, Bókony, & Chastel, 2011; Visalberghi, Janson, & Agostini, 2003). For example, Visalberghi and colleagues (2003) presented novel foods and novel objects to wild tufted capuchins, *Cebus apella*, on platforms near the location where they were accustomed to foraging and approach latencies were measured. Similarly, novel objects were placed on top of the nest boxes of female house sparrows, *Passer domesticus*, and measurements of their latencies to approach the stimulus and enter the nest box to feed their young were taken (Lendvai et al., 2011). In these examples, individuals were given the free-choice to avoid the novel stimuli or approach.

While determining whether to conduct stimulus presentations in natural settings or laboratory settings is important, it is also important to consider the type of stimuli presented when measuring novelty reactions. A stimulus that is neutral and novel is ideal for neophobia and neophilia experiments. For example, Greenberg (1983) presented variously sized leaves to warbler species near a food source and measured their latencies to approach. Leaves were a natural occurrence in their environment, though large leaves were not. In contrast, a stimulus that is novel, but that can be associated with risk, such as a novel predator model, is not necessarily measuring neophobia and neophilia, but rather is measuring an individual's boldness or shyness levels (Wilson et al., 1994). However, the shy/bold continuum can be used to describe reactions to neutral, novel stimuli if these stimuli are presented in a context where there is likely foraging or predation risk (van Oers & Naguib, 2013). For example, if by exploring the novel leaves presented, warblers were required to forage out in the open, where predation threat was greater, their behavior would better be described as shy or bold, depending on their latencies and/or frequencies to approach. Similar comments can be made for sunfish exploring a new trap baited with food; if by exploring the trap, it puts individuals at risk, the shy/bold continuum is more appropriate than neophobia and neophilia (Wilson et al., 1994).

Habituation and Dishabituation

Habituation, or the diminishment of a response to stimuli, can occur with repeated tests (van Oers, Klunder, & Drent, 2005). For example, Tinbergen and Lorenz conducted seminal experiments in 1937, where they presented young birds with cardboard silhouettes of variously shaped birds (reviewed in Schleidt, Shalter, & Moura-Neto, 2011). Some silhouettes had long necks, such that when it 'flew' in one direction, it looked like a goose was overhead, yet when it flew in the opposite direction, it looked like a hawk with a long tail was flying overhead. With repeated trials, young birds slowly failed to react to the stimuli, regardless of the bird silhouette, thus illustrating habituation. Habituation to novel stimuli can also occur. For example, green warblers, *Sylvia borin*, were less exploratory after subsequent presentations of novel stimuli (Mettke-Hofmann, Rowe, Hayden, & Canoine, 2006). Additionally, some researchers have tested whether there were individual differences in habituation rates. Individual habituation rates of Eastern chipmunks, *Tamias striatus*, for example, were tested in a novel environment, though, no individual differences in habituation were observed (Martin & Réale, 2008). On the other hand, male house sparrows habituated to novel stimuli faster than female house sparrows, but after controlling for sex, there were no individual differences in house sparrow habituation rates (Ensminger & Westneat, 2012).

Dishabituation of stimuli, or the return of an original response, can also occur. For example, gorillas were given an olfactory discrimination test, where cotton balls with an almond scent were presented over four trials, with the fifth trial being a cotton ball with vanilla scent (Hepper & Wells, 2012). The gorillas responded by licking and chewing the cotton balls, and this response habituated across trials, with decreasing licking and chewing. However, this behavior dishabituated when presented with a novel vanilla scent, such that gorillas increased their licking and chewing to the new scent. The dishabituation to the new scent demonstrated that individuals could discriminate between the two olfactory stimuli. Taken together, both habituation and dishabituation can influence reactions to stimuli, including novel stimuli, thus influencing neophobic and neophilic reactions. However, there are a number of other influences on neophobia and neophilia, which will be outlined below.

Influences on Neophobia and Neophilia

Researchers have been testing for individual and/or species differences in reactions to novel and/or threatening stimuli for over two centuries, presenting individuals with a variety of stimuli, both in the field and in the laboratory. Consequently, there is mounting evidence that neophilic and neophobic tendencies affect many aspects of an individual's life. A useful way to categorize these influences is at the species-, group-, and individual-levels. On the species level, foraging habits and migration patterns can influence how individuals react to novelty. Within-species, at the population or group level, social context and group composition can influence reactions to stimuli. Similarly, individual differences, including, age and intraspecific dominance positions, can influence individual-level reactions to novel or threatening stimuli. Examples of these influences are discussed below.

Species-level Influences on Novelty Reactions

Foraging Niche-Generalists or Specialist?

An animal's foraging niche has been shown to be correlated with responses to novel objects, such that generalist species tend to be more neophilic compared to specialist species (Greenberg, 1983). For example, two species of Neotropic migrant warblers, bay-breasted warblers, *Dendroica castanea*, and chestnut-sided warblers, *Dendroica pensylanica*, differ in their foraging behavior. Bay-breasted warblers are opportunistic generalist foragers, eating from a greater diversity of plants, foraging from a greater height range, and gleaning food off of a greater diversity of substrates, compared to chestnut-sided warblers who are more specialized in their foraging ecology (Greenberg, 1983). Generalist species, therefore, are likely to have more experience visiting novel microhabitats and eating novel foods and, as such, are predicted to be less neophobic around novel microhabitats and novel stimuli.

Greenberg (1983) conducted a captive experiment testing whether there were differences in foraging behavior between the two species when live mealworms were hidden in novel microhabitats. Both species were found to approach the food with similar frequency, but, the generalist bay-breasted warblers had more success obtaining the mealworms. The specialist chestnut-sided warblers would typically approach and fly away, and showed more hesitation, suggesting a neophobia of the novel microhabitat.

Similar results have been found when comparing other avian generalists versus specialists (Greenberg, 1990b; Webster & Lefebvre, 2000) as well as between a primate generalist and specialist (Bergman & Kitchen, 2009). However, this correlation between generalist species and increased neophilia is not the case for all generalist species. Novel objects were placed near feeding stations and the latencies to feed and number of visits to the feeder were observed for a large assemblage of foraging birds in Argentina (Echeverria, Vassallo, & Isacch, 2006). One of the prevalent generalist species, the house sparrow, *Passer domesticus*, showed a neophobic response to the novel stimuli, contrary to prediction. The authors suggested that other variables, such as age of the bird (and therefore its environmental experience) and the simplicity and predictability of the environment may have influenced species reactions. Another possibility, not addressed by the authors, was that there were size-based interspecific dominance relationships between species participating in the assemblage, which may have influenced how the generalist house sparrows reacted to the novel stimuli.

Migration Patterns

Species that migrate are more likely to encounter a larger variety of microhabitats and novel stimuli compared to resident species that only need to be familiar with their local environment. Even though they may only spend a short amount of time at any one location during migration, migratory animals are still required to explore novel areas to find shelter and food. As such, the migrant-neophobia hypothesis predicts that migrants should be less neophobic than resident birds when introduced to a novel environment (Mettke-Hofmann & Greenberg, 2005). For example, when comparing two closely related warbler species, one residential and one migratory, researchers found that the migratory birds were quicker to enter a novel room and had greater levels of exploration of the room (Mettke-Hofmann, Lorentzen, Schlicht, Schneider, & Werner, 2009). This is observed within species, too, as was the case for resident and migratory blue tits, *Cyanistes caeruleus*, when presented with a novel object. Migrant individuals had shorter latencies to approach, and thus were considered less neophobic than resident individuals (Nilsson, Nilsson, Alerstam, & Bäckman, 2010).

Group-Level Influences on Novelty Reactions

Social Context: Alone or With Conspecifics?

The presence or absence of other individuals can influence how group members respond to novel or threatening stimuli (reviewed in Webster & Ward, 2011). The presence of conspecifics may reduce stress in social species, and thus facilitate the approach to a novel food or stimulus compared to when an individual is tested alone (Greenberg, 1990a). For example, capuchin monkeys, *Cebus apella* were more likely to try a novel food in the presence of conspecifics compared to when they were alone (Visalberghi & Addessi, 2000). However, contrasting results were found in zebra finches, *Taeniopygia guttata*. One experiment found that finches were more likely to forage from a feeding station with a novel object nearby when they were in a group compared to when they were alone (Coleman & Mellgren, 1994). Yet, a later study tested zebra finches' reactions to a novel environment (measured by number of feeders visited) and a novel object (measured by approach) and showed that individuals decreased their exploratory behavior in both contexts in the presence of conspecifics (with three males as well as with three females) compared to when individuals were alone (Mainwaring, Beal, & Hartley, 2011). Similarly, common ravens, *Corvus corax*, were also quicker to approach novel objects when they were alone compared to when they were in pairs or larger groups; however, they spent more time exploring and manipulating the novel object in social contexts (Stöwe, Bugnyar, Heinrich, & Kotschal, 2006). A possible explanation for solitary birds being more neophilic is that in the groups, the focal bird and their flock mates respond to the novel context, and any hesitation or fear may be due to a contagious phenomenon where the reaction of one individual spreads quickly to the rest of the flock (Sirot, 2006; Mainwaring, Beal, & Hartley, 2011). If contagion of a behavioral reaction is at work, it suggests that the composition or ratio of neophobic and neophilic individuals in the group is also important.

Group Composition

Several studies have tested how the composition of behavioral types influences group dynamics (reviewed in Webster & Ward, 2011). For example, young perch, *Perca fluviatilis*, were tested for behavioral differences in feeding behavior (number of prey attacks) and habitat use, first when they were randomly assorted into mixed behavioral type groups and then again after they had been divided into three groups based on their behavioral type: bold, intermediate, or shy (Magnhagen & Staffan, 2005). Shy perch had the greatest behavior change observed after being introduced to their new group: they increased the number of prey they attacked and utilized more of their habitat compared to when they were in the mixed-group. When bold individuals were introduced to their new groups, they modified their habitat use, decreasing the amount of time they spent out in the open. Intermediate individuals did not change their behavior once placed in their new groups. Thus, the mix of behavioral types in the group can influence individual behavior.

While these studies have looked at the influence of group behavioral type compositions on behavior, few studies have tested specifically how group composition affects reactions to novel stimuli. One study, however, manipulated the composition of behavioral types (shy versus bold) in shoaling guppies, *Poecilia reticulata*, and found that composition influenced fishes' latencies to approach a novel feeder (Dyer, Croft, Morrell, and Krause, 2009). Individuals in groups with a mix of both behavioral types were quicker to approach the novel feeder compared to individuals in groups with just shy individuals or just bold individuals. This suggests that a variety of behavioral types may be beneficial in groups or populations, particularly in variable environments where encounters with novel stimuli may be more likely.

Intraspecific Dominance

Dominance hierarchies within a group can influence how individuals react to novel stimuli. Subordinate individuals are more likely to take risks in their environment if dominant individuals are exploiting and defending less risky and beneficial resources (Ficken, Weise, & Pop, 1990; Greenberg, 2003; Wilson et al., 1994). For example, studies of corvids show that subordinate individuals forage in peripheral and sometimes novel areas, compared to dominant individuals (Katzir, 1982). As such, they have more experience with novel stimuli and are predicted to be more neophilic than their dominant conspecifics.

However, not all species exhibit this trend where subordinate individuals are relegated to approach novel stimuli first. For example, female rats, *Rattus norvegicus,* when presented with a novel food in triads, did not exhibit the tendency for subordinates to be more neophilic (Nott & Sibly, 1993). Dominant rats were found to have a shorter latency to feed from novel, highly palatable foods compared subordinate rats. These authors suggested that subordinate individuals may reduce their exploratory behavior in order to reduce possible contact with dominant individuals. Similarly, when breeding pairs of coyotes, *Canis latrans*, were presented with novel stimuli, dominants were the first to approach novel stimuli near a familiar food source compared to subordinates (Mettler & Shivik, 2006). These studies suggest that in some species, dominance and neophilia may be correlated, such that dominant individuals are more likely to take risks than subordinates.

Individual-Level Influences on Novelty Reactions

Age

Young animals are born or hatched into a completely novel environment, and if the animal is young, it has the opportunity to explore prior to becoming self-reliant. Juveniles, who are born with little to no information, are able to gather information about their environment while their parents can provide protection from predators (Greenberg & Mettke-Hofmann, 2001). As such, individuals are predicted to be more neophilic when they are juveniles compared to when they are adults (Kummer & Goodall, 1985). In general, neophilia is expected to be high until an individual becomes familiar with their natal environment, and then a switch to neophobia occurs (Greenberg & Mettke-Hofmann, 2001). For example, eight species of birds were hand-reared and their fear responses to various stimuli, including moving their nests outside, presenting a whistle sound similar to an adult predator call, and handling, did not illicit neophobic responses when birds were around one week old (Barraud, 1961). Birds began exploring around 16-18 days old, during which they would crane their necks, twist their bodies, and scan their environment. This positive correlation between age and neophobia has been observed in many other species, including raptors (Biondi, Bó, & Vassallo, 2010) and some non-human primates (Visalberghi, Janson, & Agostini, 2003; Fu et al., 2013).

When animals are younger, they often exhibit more play behaviors compared to when they are older (Burghardt, 2005). Exploration of stimuli has often been confused with play behavior. However, there are some key distinctions. Individuals who are exploring an object or context typically have stereotyped behavior, are more deliberate in their attention, have a neutral or negative affect associated with the object, and have low heart rate variability (Burghardt, 2005). In contrast, individuals playing with an object, do so with a familiar object, have more variable attention, have positive affect, and have high heart rate variability. Therefore, exploration of an object can lead to play with the object, and this is more frequently observed in juveniles compared to adults.

Nevertheless, there are some instances where a positive correlation between age and neophobia is not observed. For example, seven different species of callitrichid monkeys housed in family groups of various ages were given novel puzzle boxes with food (Kendal, Coe, & Laland, 2005). Latencies to first contact the puzzle box, the researchers' neophobia measure, were not correlated with age. Nevertheless, adults were more likely to be the first to succeed in opening the box compared to younger individuals, which suggested a higher level of exploration and/or innovation. These results suggest that in some species, neophilia does not have age boundaries, and may be related to other factors, including social learning, or social role in the group (not tested). Similarly, in Gouldian finches, *Erythrura gouldiae*, older flock members had shorter latencies to approach novel stimuli compared to younger flock members, perhaps because of their roles as flock leaders (Mettke-Hofmann, 2012).

Age-related influences on responses to novelty apparently may not be as easily defined. Group-level influences may also be in effect, such as social context, or social learning may be occurring (as may be the case for the adult callitrichid monkeys being the first to contact a food puzzle box). Additionally, in the case of the comparative bird study (Barraud, 1961), perhaps simpler motor and perceptual issues were at play, which influenced individual reactions to novel stimuli over time. However, early experiences with novelty are known to impact responses to novelty later in life (e.g. Cavigelli & McClintock, 2003), therefore, age-related influences are important to consider.

Intraspecific Dominance

Intraspecific dominance can also affect neophobia on the individual-level. For example, in black-capped chickadees, *Poecile attricapillus*, subordinate individuals are less neophobic (have shorter approach latencies) in novel contexts compared to their dominant conspecifics (An et al., 2011). Similarly, when tested alone in a novel environment and subsequently paired with another unknown individual, male mountain chickadees, *Poecile gambeli*, were more likely to be become dominant during the encounter if they were low-explorers and visited fewer locations during their test in the novel environment (Fox, Ladage, Roth, & Pravosudov, 2009). This indicates that individual dominance status within a group may be influenced by other factors, including neophobia. It also reiterates the potential influence of social context (alone versus with a conspecific) on neophobic reactions.

Vocal Behavior: Another Possible Novelty Response Measure

Most of the previously conducted novelty experiments have measured latencies to approach a novel object or level of exploration of a novel environment. Another possible, but only recently addressed, measure that could be correlated with behavioral responses to novelty, is vocal behavior. In the human literature, personality traits can be recognized directly from vocal conversations (Mairesse, Walker, Mehl & Moore 2007). For example, high speech rates and longer, more repetitive conversations are often indicative of an extroverted personality (Mairesse et al. 2007). Whereas in the animal literature, there are few studies that directly test whether vocal behavior is correlated with responses to novelty, recent research on several *Parid* species suggests that vocal behavior patterns are maintained across situations (Harvey & Freeberg, 2007) and that they are correlated with behavioral types (e.g. Guillette & Sturdy, 2011). For example, in black-capped chickadees, *Poecile atricapillus,* there was a positive correlation between the production of non-reproductive calls (alarm and *chick-a-dee* calls) and exploratory behavior during a stressful context, suggesting that the more neophilic individuals are more vocal (Guillette & Sturdy, 2011). The opposite was found for songs in great tits, *Parus major*, during the breeding season; there was a negative correlation between the exploratory behavior of an unknown intruder and its singing rates (Amy, Sprau, de Goede, & Naguib, 2010). Another study using great tits found a sex difference in calling behavior, such that singing behavior was correlated to exploratory behavior of a novel environment in males, but not females (Naguib, Kazek, Schaper, van Oers, & Visser, 2010). Overall, these studies suggest that behavioral types are correlated with vocal behavior, and that different vocal strategies may be used in association with various stimulus types and during different contexts (e.g. breeding season versus non-breeding season).

Vocal behavior is an important consideration because it is a ubiquitous behavior and provides information beyond what individual presence and latency measures alone can provide. Therefore, when studying reactions to novelty, including vocal behavior as a measure may give greater power, or may make detection of individual differences more robust. For example, perhaps two animals both have the same latency to approach a novel object, but one produces more calls or has a shorter latency to call compared to the other. In this case, it would be possible for an extrovert/introvert-like dimension to exist, with an individual that calls often and in several contexts being an extrovert and an individual that calls sparsely across contexts being an introvert. This idea differs from common definitions of extroverted and introverted animals, however. In the animal personality literature, extroversion has been linked to sociability and activity-based descriptions, such as 'vivacity', 'lively temperament' and 'energy' (Gosling & John, 1999). Extroversion has not been linked to vocal behavior so commonly in the non-human animal literature (Mairesse et al. 2007). In essence, vocal behavior, categorized using the extroversion/introversion continuum, may be distinct from the neophobia/neophilia continuum that strictly measures reactions to novelty. However, a difference in vocal output, but no significant difference in approach latencies, may be influenced by other factors, including inter- or intraspecific dominance or presence of other conspecifics.

The Study System

Members of the Paridae family (chickadees, titmice, and tits) have often been studied in the personality literature. A majority of the research has focused on great tits, *Parus major*, (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005), though a few have studied other related species, including mountain chickadees, (e.g. Fox et al., 2009), black-capped chickadees, (e.g. Guillette & Sturdy 2009), and Carolina chickadees (e.g. Harvey & Freeberg, 2007).

This dissertation research focuses on mixed-species flocks of Carolina chickadees and tufted titmice. Chickadees and titmice form flocks during the late fall and winter in the eastern United States, along with other follower species such as white-breasted nuthatches, *Sitta carolinensis*, downy woodpeckers, *Picoides pubescens,* and hairy woodpeckers, *Picoides villosus* (Morse, 1970; Smith, 1991). Members of such groups obtain many benefits including increased foraging efficiency and reduced predation risk (Berner & Grubb, 1985; Curio, 1978; Krause & Ruxton, 2002; Lima, 1995). There is an interspecific size-based social dominance hierarchy between these species such that tufted titmice are socially dominant over Carolina chickadees (Morse, 1970; Cimprich & Grubb, 1994). This dominance hierarchy is based on agonistic interactions, including supplants.

The chickadee and titmouse vocal system is ideal to study in order to determine if there are vocal correlates to behavioral types. These species have a complex vocal system in which their most frequent non-reproductive vocalization, the *chick-a-dee* call, is made up of a distinct number of notes that follow strict note-ordering rules allowing for the production of a very large number of unique calls (Krams et al., 2012). This *chick-a-dee* call is used commonly throughout the year by both males and females in a wide range of social contexts (Bloomfield, Phillmore, Weisman, & Sturdy, 2005; Owens & Freeberg, 2007). The vocal system and note-usage of chickadees and titmice has been studied extensively. The harsher, broadband 'D' notes of their *chick-a-dee* call can be used aggressively in predator and mobbing situations (Courter & Ritchison, 2009; Nolen & Lucas, 2009; Sieving, Contreras, & Maute, 2004; Sieving, Hetrick, & Avery, 2010; Soard & Ritchison, 2009), but can also be used to recruit flock mates to food (Mahurin & Freeberg, 2008). According to motivation-structural rules (Morton, 1977), notes that are lower in frequency and broadband, such as 'D' notes, should signal potential aggression. These acoustic characteristics should also make them easy to locate, so the use of 'D' notes in calls may also function to recruit individuals to the location of the signaler for mobbing. Additionally, when presented with live predator models of various sizes, black-capped chickadees varied the note composition of their calls in relation to the size of, or degree of threat related to, predators (Templeton, Greene, and Davis, 2005). Similar results were obtained and similar interpretations were made for Carolina chickadees (Soard & Ritchison, 2009) and tufted titmice (Courter & Ritchison, 2010).

Because chickadees and titmice have a well-studied vocal repertoire, where arousal levels have been suggested to be related to 'D' note production (e.g. Mahurin & Freeberg, 2009), approach or avoidance reactions in the presence of novel stimuli may also be correlated with vocal 'D' note output. Additionally, no study to date has determined if there are species differences in approach latencies to novel stimuli between chickadees and titmice. However, chickadees are more likely to approach risky predator models than are titmice (Nolen & Lucas, 2009), and therefore, by testing their reactions in the presence of novel stimuli, we may be able to better explain why these species differences were observed in a predator context.

Outline of this Dissertation Work

Considering the above, this dissertation aims to address whether there are species differences in chickadee and titmouse reactions to novel stimuli, and if so, determine why this may be the case. Are differences due to species-level influences, such as foraging niche or is group-level composition an influence? In addition to measuring approach latencies and approach rates, as is characteristic for neophobia research, I will be addressing the relatively unstudied possibility of vocal correlates to novel stimulus reactions.

To address these questions, three experiments were conducted. The first two experiments were conducted in the field and tested the foraging and calling behavior of chickadees and titmice first, in the presence of several novel stimuli (Chapter 2) and subsequently in the presence of either novel or predator stimuli (Chapter 3). The final experiment was conducted in semi-naturalistic aviaries, where flock composition was manipulated and individual responses to novel and predator stimuli were measured (Chapter 4). All experiments measured latencies to forage near the presented stimuli and foraging rates. Additionally, because calling behavior was of interest, latencies to vocalize, calling rates, and ‘D’ note usage per call were also quantified. Chapter 5 concludes this work with a discussion of the overarching findings and implications for future research.

It is important to investigate how chickadees and titmice react to novel stimuli, both behaviorally and vocally. With ever encroaching anthropogenic effects on natural habitats (Vitousek, Mooney, Lubchenco, & Melillo, 1997), it can be adaptive to be more neophilic, especially when neophobia may increase the time an individual spends, or completely prevent an individual from, finding a mate (e.g. Sih & Watters, 2005), finding food (e.g. Rabinowitch, 1965 as cited in Coppinger, 1969), or finding shelter (e.g. Mettke-Hofmann et al., 2009). Additionally, because many species that share habitat with chickadees and titmice eavesdrop on their signaling systems, are known to be attracted to the location of their calls, and obtain useful information from their signals, chickadees and titmice are important sources of information for numerous species (Gunn, Desrochers, Villard, Bourque, & Ibarzabal, 2000; Hetrick & Sieving, 2009; Schmidt, Lee, Ostfeld, & Sieving, 2008; Sullivan, 1984; Templeton & Greene, 2007). As such, the behavioral and vocal reactions of chickadees and titmice to novel and threatening stimuli may help to maintain mixed-species flocks. Thus, this dissertation aims to determine whether there are differences in flock member reactions and possible reasons why these differences may exist.

Appendix: Tables

Table 1. Definitions of terminology

	Definition	Authors
Personality	"those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving"	Funder, 2004; p.5
Behavioral Syndrome	"suites of correlated behavior across situations"	Sih, Bell, & Johnson, 2004; p. 372
Temperament	"individual behavioral differences [that] are repeatable over time and across situations"	Reale et al., 2007; p. 291
Behavioral Reaction Norm	"the set of behavioural phenotypes that a single individual produces in a given set of environments"; quick responses by individuals due to variation in the social environment	Dingemanse et al., 2010; p. 51 Agrawal, 2001;
Avoidance	an impulse that leads an animal to flee from a stimulus that elicits fear	McDougall, 1908
Approach	an impulse that leads an animal to examine the stimulus that excites it more closely	McDougall, 1908
Long Flight Initiation Distance	a farther distance to which a person can approach a wild animal and cause it to flee; indicative of shyness	Altmann, 1958
Short Flight Initiation Distance	a shorter distance to which a person can approach a wild animal and cause it to flee; indicative of boldness	Altmann, 1958

Table 1. Continued.

	Definition	Authors
Aggressive	“show an active response to aversive situations…in a social setting, they react with flight or escape when defeated; in non-social situations, they react with active avoidance of [aversive stimuli] and with sustained activity during an uncontrollable task”	Benus et al., 1991; p. 1008
Non-aggressive/ Defensive	“adopt a passive strategy; in social and non-social aversive situations, they react with immobility and withdrawal”	Benus et al., 1991; p. 1008
Fight	active response to a threatening stimulus, resulting in the approach towards the threat and/or defense of an individual’s position	Cannon, 1915
Flight	active response to a threatening stimulus, resulting in fleeing, or withdrawal from the threat	Cannon, 1915
Bold	“thrive on risk and novelty”; “act normally or become actively exploratory in [unfamiliar situations]”	Wilson et al., 1994; p. 442 Wilson et al., 1993; p. 250
Shy	“shrink away from risk and novelty”; “react to unfamiliar situations by retreating or becoming quiet and vigilant”	Wilson et al., 1994; p. 442 Wilson et al., 1993
Coping styles	“a coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals”	Koolhaas et al., 1999; p. 925

Table 1. Continued.

	Definition	Authors
Proactive/ active coping style	"fight-flight response...characterized by territorial control and aggression", "low HPA-axis reactivity...but high sympathetic reactivity"	Koolhaas et al 1999; p. 925
Reactive/ passive coping styles	"conservation-withdrawal response... characterized by immobility and low levels of aggression", "higher HPA axis reactivity and higher parasympathetic reactivity"	Koolhaas et al 1999; p. 925; p. 929
Neophilia	"instances of exploration in which investigation is elicited by an object's novelty"	Greenberg & Mettke-Hofmann 2001; p. 125
Neophobia	"the avoidance of an object or other aspect of the environment solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past"	Greenberg & Mettke-Hofmann 2001; p.125
Extrovert	A personality factor with many correlating behavior types, including increased sociability, assertiveness, and activity	Gosling & John 2010
Introvert	A personality factor with many correlating behavior types, including decreased sociability, assertiveness, and activity	Gosling & John 2010
Slow Explorer	"Approach a novel object slowly, but explore it intensely, spending much time on exploration"; resembles a passive coping style	Verbeek, Boon, & Drent 1996; p. 946
Fast Explorer	"approach a novel object fast, but explore it short and superficially"; resembles an active coping style	Verbeek, Boon, & Drent 1996; p. 946

CHAPTER II

THE DIFFERENTIAL REACTIONS OF CAROLINA CHICKADEES, *POECILE CAROLINENSIS*, AND TUFTED TITMICE, *BAEOLOPHUS BICOLOR*, TO NOVEL STIMULI

A version of this chapter is in preparation to be submitted for review in a scientific, peer-reviewed journal. My contributions to this work include: (a) helping to formulate the research idea and hypothesis (b) training the research assistants (c) designing the experiment (d) collecting data (e) doing the statistical analysis (f) interpreting results and (g) writing the manuscript. Katherine Morrison, Suzanne Winters, and Carrie Newton-Hodge helped me with data collection.

Abstract

Attraction to, or avoidance of, novel objects can impact many aspects of an individual's life, including its success in foraging, mating, and predator avoidance. Often, neophobia and neophilia are studied in single-species groups. However, it is also important to consider neophobia and neophilia in mixed-species groups, as these groups often consist of complex social relationships, such as interspecific dominance hierarchies, that can influence how individuals respond to stimuli. We conducted an experiment to assess the vocal and behavioral reactions of mixed-species flocks of Carolina chickadees and tufted titmice to novel stimuli. At feeding stations used by chickadees and titmice, we presented three stimuli of varying predicted novelty: a dog food bowl placed on a feeding station with bird seed in the bowl, a plastic dove model placed within 0.5 meters of food, or a person standing 5 meters from the feeding station. Seed-taking latencies, call latencies, and vocalizations were recorded for each species. Seed-taking latencies were longer in the presence of novel stimuli compared to pre-stimulus baseline contexts without novel stimuli for both chickadees and titmice. In the presence of novel stimuli, chickadees were quicker to vocalize and used more 'D' notes in their calls, compared to titmice. These results suggest that chickadees may have a sentinel-like status in the flock. This study is one of only a few studies that have tested the vocal reactions of individuals in the presence of novel stimuli. As such, these results provide a foundation for future work exploring the functions of communicative differences in mixed-species flocks.

Introduction

"Every bird is a personality."
(Schjelderup-Ebbe, 1935, p. 947)

Individual birds decide to approach or not to approach objects thousands of times a day (Greenberg & Mettke-Hofmann, 2001). Individuals may either be familiar with stimuli and therefore have habituated to them, or may have had little to no experience with the stimuli and consider them novel. There are many costs and benefits associated with being neophobic or neophilic around novel stimuli. Birds can benefit from neophilia by acquiring new information, however increased neophobia reduces the risk of predation (Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013), risk of wasting time on information that does not immediately bring payoffs, or risk of illness (if a novel object is a poisonous food). Responses to novel objects can influence habitat selection, especially if there is seasonal migration or dispersal (Klopfer & Ganzhorn, 1985). Additionally, neophilia can influence foraging success, especially in areas with high anthropogenic influence (Short & Petren, 2008).

Studies to assess neophobia and neophilia have been conducted on a wide range of taxa including birds (Greenberg & Mettke-Hofmann, 2001), non-human primates (Visalberghi, Janson, & Agostini, 2003), mammals (Dalmau, Fabrega, & Velarde, 2009), fish (Galhardo, Vitorino, & Oliveira, 2012), and invertebrates (Mather & Anderson, 1999). An equally important endeavor, however, is to use the comparative approach and test how mixed-species groups react to novel stimuli. Mixed-species groups obtain many benefits including increased foraging efficiency and decreased predation threat (Krause & Ruxton, 2002). For instance, associating with other ungulate species decreases the chance of Thomson's gazelles, *Gazella thomsoni*, being attacked by cheetahs, *Acinonyx jubatus*, because predator detection is improved in larger groups (Fitzgibbon, 1990). Similarly, tropical herbivorous Acanthurid fish species are preyed upon less and have better feeding efficiencies because they are less vulnerable to attacks from competitors when feeding in mixed-species groups rather than alone (Reinthal & Lewis, 1986). As such, it is possible that groups also benefit from the presence of participating neophilic species. To date, no experiments have tested chickadee and titmice reactions to novelty. However, if there are species differences in reactions to novel stimuli, this may be an additional benefit accrued by members participating in mixed-species flocks of chickadees and titmice during the over-wintering months when food is less abundant.

Most novelty studies are interested in changes in foraging behavior and/or approach behavior and do not address possible changes in communication. But, for social species, changes in communication—including call types, rates, latencies, or note-types per call—could potentially impact flock behavior. No study has addressed whether vocal behavior is correlated with mixed-species' reactions to novel objects, though a small set of studies has addressed the vocal correlates of reactions to novel objects in single-species groups (Amy et al., 2010; Guillette & Sturdy, 2011; Naguib et al., 2010). For instance, Guillette and Sturdy (2011) presented black-capped chickadees with a stressful context (audio of a mobbing call) and found a positive correlation between calling behavior and exploration (neophilia) of a novel environment. This suggests a link between vocal output and reactions to novelty in chickadees.

Our study system, which consists of naturally-occurring mixed-species flocks of chickadees and titmice, was presented with three different novel stimuli: a dog food bowl filled with bird seed, a plastic dove model, and a person standing 5 meters from a feeding station. We wanted the stimuli to be salient, but not threatening. Because larger sized objects can increase neophobic reactions (Greenberg, 1993), we chose to have the person stand 5 m from the feeding station, rather than within 0.5 m. A 10-minute pre-stimulus baseline was recorded prior to presenting each novel object on a feeding station for 10-minutes. Foraging latencies, calling latencies, and number of 'D' notes used per call were measured.

Predictions

We used previous results to predict how chickadees and titmice would react to novel stimuli. Chickadees and titmice are both considered generalist foragers (Lucas, Freeberg, Egbert, & Schwabl, 2006), mainly foraging for insects in the lower canopy and shrubs (DeGraaf, Tilghman, & Anderson, 1985). As such, any observed differences in their reactions to novelty would not likely be related to their foraging ecology. Their interspecific dominance status, however, may influence their foraging and calling latencies.

Dominant individuals are known to restrict access to food for subordinates in numerous species, including bonnet macaques, *Macaca radiata*, (Boccia, Laudenslager, & Reite, 1988), sows (Brouns & Edwards, 1994), and willow tits, *Parus montanus*, (Ekman & Lilliendahl, 1993). While none of these studies measured latencies for dominant individuals to forage compared to subordinates, the dominant's ability to restrict access implies that subordinates are not the first ones to eat, and therefore must have longer latencies than their dominant heterospecifics. Additionally, these examples tested intraspecific dominance hierarchies; however, studies testing interspecific food competition found that dominant species can restrict subordinate species' access to preferred foraging locations (e.g. Nakano, 1995). Therefore, we predicted: *1. During baseline contexts, titmice, being the larger and interspecifically dominant species, would have shorter latencies to forage than chickadees* (Table 2; all tables in this chapter at located in Appendix B at the end of the chapter). Because subordinate species may be relegated to forage in novel and/or less-protected microhabitats (Ficken, Weise, & Popp, 1990; Greenberg, 2003; Wilson et al., 1994), we predicted: *2. During novel stimulus contexts, the subordinate chickadees would exhibit less neophobia, and would therefore have shorter latencies to forage compared to titmice.* Additionally, between species, it was predicted that: *3. Both species would have longer latencies to forage when novel stimuli were present compared to baseline contexts.*

Regarding calling behavior, latencies to call can provide information about the perceived likelihood of a threat, with shorter call latencies indicative of a more immediate threat. For instance, when presented with predator models either 6 m away or 1 m away from a foraging stand, black-capped chickadees had shorter call latencies during the more threatening 1 m predator context compared to 6 m (Baker & Becker, 2002). As such, we expected: *4. Chickadees and titmice would have shorter calling latencies in the presence of novel stimuli, compared to baseline contexts.*

Furthermore, intraspecific dominance rank within the flock can influence call latencies in predator contexts (Zanette & Ratcliffe, 1994). Subordinate black-capped chickadees consistently had significantly shorter call latencies when presented with a hawk model compared to higher-ranking flock members (Zanette & Ratcliffe, 1994). While this has not been directly tested in Carolina chickadees or tufted titmice, if interspecific dominance is influencing calling latencies, we expected that between species: *5a. The interspecifically subordinate chickadees would have shorter calling latencies in the novel contexts compared to titmice.* Conversely, it is also possible for titmice to have a shorter latency to vocalize compared to chickadees, based on their designation as sentinels or 'community informants' in these mixed-species flocks (Hetrick & Sieving, 2012). However, this titmouse designation may be unique to Floridian flocks, where titmice participate in 100% of flocks, but chickadees are found in only 20% (Contreras & Sieving 2011). Other studies (e.g. Templeton, Greene, & Davis, 2007) denote chickadees as the principle sentinels in mixed species flocks. Similarly, while Nolen and Lucas (2009) do not name chickadees as sentinels in their study, chickadees were more likely to call in the presence of an owl model compared to titmice; therefore, the authors suggested that vocal information about predators may flow from chickadees to titmice. Chickadees and titmice tend to participate equally in Tennessean flocks (Bartmess-Levasseur et al., 2010); however, on average, slightly more chickadees participated than titmice in this study. As such, if calling behavior is related to the potential designation of titmice being sentinels, in this flock, an alternate prediction is that: 5b. *The sentinel-like titmice would have shorter calling latencies in the novel contexts compared to chickadees*.

Additionally, we expected birds to have vocally different responses in novel contexts compared to baseline (non-stimulus) contexts, perhaps as recruitment for, or drawing the attention of, other flock members (e.g. Bartmess-Levasseur et al., 2010; Mahurin & Freeberg, 2009). Therefore, we predicted that: *6. Chickadees and titmice would use more 'D' notes in their calls when novel stimuli were on the feeding station.*

Stimuli

Three different novel stimuli were presented: (1) three variations of a plastic model that was approximately the size, shape, and color pattern of a mourning dove, *Zenaida macroura*, (Edge Expedite Dove Clip-On Decoys) that was clipped to the feeding station platform, (2) a red, blue, or gold plastic dog food bowl that contained seed and was placed on the feeding station platform, and (3) a person standing 5 m away from the feeding station looking in the direction of the feeding station (Figure 1; located at the end of this chapter in Appendix A). The person (the same individual for all presentations) dressed differently at each site to add variation within this stimulus type. We chose these three stimuli of varying novelty (or varying predicted experience) to ensure at least one of the stimulus types would result in a neophobic reaction rather than cause the flock to abandon the foraging area. We presumed that the 'person' stimulus would be the least novel. All of the sites we used were in areas with common human presence (including non-researchers). However, this stimulus was still considered novel because humans rarely came within 5 meters of the station and did so only to stock the stations or set up equipment (lasting a minute at the longest). We assumed the 'dove' model would be an intermediate novel stimulus, because doves do live in the environment of chickadees and titmice and will occasionally forage on the feeding station. Doves can compete with flock members for food, but they are infrequently observed with flock members and are rarely observed foraging from our feeding stations. Consequently, some flock members are likely to have seen real doves in nature, however, not in the foraging context we presented. The ‘bowl’ was presumed to be the most novel, because it did not mimic any natural object in their environment, nor would birds have likely encountered it foraging elsewhere. It also required that birds land on and touch the bowl to take a seed.

Methods

We conducted the experiments at three different locations in eastern Tennessee: the University of Tennessee Forest Resources, Research, and Education Center (36° 00’ N, 84° 13’ W: 12 sites), Ijams Nature Center (35° 57’ N, 83° 52’ W: 5 sites), and Norris Dam State Park (36° 14’ N, 84° 06’ W: 6 sites). Feeding stations at these locations were stocked weekly with approximately 100 g of a 1:1 mixture of black oil sunflower seed and safflower seed. Within each location, we sampled behavior of flocks at sites that were separated from one another by at least 400 m to ensure flock independence (Bartmess-LeVasseur et al., 2010).

Data were collected from October 2010 through February 2011 and from November through December of 2011. Each site contained a feeding station made of a flat, wooden platform (25 X 40 X 2 cm) mounted on a steel pole such that the platform sat approximately 1.5 m above the ground. Recordings began when at least two birds were foraging from the feeding station. We presented stimuli and recorded vocalizations at the feeding stations between 08:00 and 14:00 (Eastern Standard Time). When we arrived at a site, we stocked the feeding station with seed and set up the recording equipment. A Sennheiser ME-62 microphone was mounted on a microphone stand that was placed 1 m away from the feeding station. The microphone was aimed toward the feeding station and was connected to a Marantz PMD660 portable digital recorder that recorded sound files onto a compact flash memory card at a sample rate of 44.1 kHz and 16-bit resolution. Observers sat behind a camouflage blind at least 10 m away from the feeding station and waited for birds to approach the feeding station.

Procedure

The three stimuli were presented first with a 10-minute pre-stimulus baseline context followed by a 10-minute stimulus recording. The presentation order of the stimuli was counter-balanced across sites. Once a pre-stimulus recording began, the subsequent stimulus recording was always completed, with only short breaks to walk the bowl, dove, or person to the feeding station. After a stimulus was presented, we allowed at least 10 minutes to lapse before starting the next baseline recording.

Most sites were presented all three stimuli on the same day, however, four of the 23 sites required splitting recordings into two days due to the flock leaving the area. When this occurred, we waited at least two days to return to the site and the remaining stimuli were presented.

Data Analysis

Sound files were saved as .wav files and viewed in Cool Edit Pro (2.0). Before coding calls, we used a Butterworth high pass filter at 750 Hz to remove lower frequency background noise. From sound files, we obtained latencies to take seed, seed-taking rates, latencies to call, and call rates. If a species did not take a seed in a 10-minute recording period, their latency was denoted as 600 seconds. We then coded the calls of chickadees and titmice based on the number of 'D' notes per call.

I coded the 'chick-a-dee' calls of titmice and chickadees for all sound recordings. Two others (CN and SW) then each independently scored ten different 10-minute recordings (twenty 10-minute files total) that were blinded to identifying information (roughly 10% of the total sample). Inter-observer reliability for seed-taking latencies and call latencies for chickadees and titmice was high (Spearman's correlation, r_s median = 0.974, range = 0 .833 – 1.000). CN and SW also coded approximately 400 calls each (roughly 10% of the call set) for number of 'D' notes. The calls spanned all recording contexts. Inter-observer agreement for chickadee and titmouse 'D' notes was 'almost perfect' (Landis & Koch, 1977; median Cohen's kappa statistic = 0.953).

Seed-taking latencies, call latencies, and number of 'D' notes per call for chickadees and titmice were log transformed for normalization. Mixed model analyses of variance were run on the three dependent variables with 'Species', 'Stimulus', and 'Context' within-subjects factors and 'Site' as a random factor.

Results

The data set comprises twenty-three hours of audio recordings (six 10-minute recordings per site) from 23 sites and a total of 1,676 chickadee calls and 1,196 titmouse calls. There was an average of 3.8 chickadees (range: 0 - 8) and an average of 3.1 titmice (range 0 - 5) participating in each mixed-species flock. Seed-taking rates and seed-latencies were significantly correlated for chickadees and titmice (r = -0.754, n = 259, $P < 0.001$; Cohen's d = -1.22, effect size r = -0.521); therefore, we only analyzed seed-taking latencies, because they are an appropriate measure to determine approach latencies to the novel stimuli. Similarly, call latencies and call rates were significantly correlated for chickadees and titmice (r=-0.233, n = 260, $P < 0.001$; Cohen's d = -0.90, effect size r = -0.413); therefore, we only analyzed calling latencies, because they are better indicators of threat immediacy (e.g. Zanette & Radcliffe, 1994). The mean seed-latencies, seed rates, call latencies, and call rates are listed in Table 3.

Seed-taking Latency

There was a significant three-way interaction between species, stimulus, and context (Figure 2). See Table 4 for mixed-model statistical results. Chickadees and titmice reacted similarly in both the pre-stimulus and stimulus contexts for the bowl and dove contexts; however, there were differences in their reactions to the person stimulus. Chickadees did not significantly increase their latencies to forage when a person was standing 5 m from the feeding station, but, titmice did. This suggests that titmice were more neophobic to the person stimulus compared to chickadees. Additionally, because chickadee and titmouse seed-taking behavior was not as strongly affected by the person standing 5 m away from the feeding stand as the other two stimuli, there was also an interaction between stimulus and context.

There was also context effect, such that seed-taking latencies were shorter during pre-stimulus baseline contexts (μ = 62.1 secs) compared to stimulus contexts (μ = 397.8 secs). Similarly, there was a stimulus effect; seed-taking latencies for the dove (μ = 267.8 secs) and bowl stimuli (μ = 323.5 secs) were significantly longer than the seed-taking latencies for the person stimulus (μ= 89.1 secs).

From the 23 total sites, chickadees took seeds from the stand at 7 of the 23 sites (μ = 418.7 sec latency) when the bowl was present compared to titmice, who took seeds from the stand at 10 of the 23 sites (μ = 249.3 sec latency) when the bowl was present. There was only one site where a chickadee took a seed from the stand when the dove was present (201.0 sec latency) while no titmice took a seed when the dove was present.

Call Latency

Chickadees had shorter call latencies than titmice across contexts with a mean latency of 81.1 seconds for chickadees and 188.2 seconds for titmice (Figure 3). See Table 5 for mixed-model statistical results. There was also a species by context interaction, such that chickadees had significantly shorter call latencies than titmice during stimulus presentations (μ= 49.1 sec) compared to baseline (μ= 113.2 sec) while titmice had call latencies during stimulus presentations (μ= 192.6 sec) that were not significantly different from pre-stimulus contexts (μ= 183.7 sec). In other words, chickadees and titmice did not have significantly different calling latencies in baseline contexts ($F_{1, 34} = 0.868$, $P = 0.358$), but chickadees had significantly shorter calling latencies in the novel stimulus contexts ($F_{1, 28} = 27.369$, $P < 0.001$).

'D' Note Usage

Chickadees and titmice used more 'D' notes during stimulus contexts compared to pre-stimulus contexts (Figure 4). See Table 6 for mixed-model statistical results. There was an effect of context, such that chickadees used significantly more ‘D’ notes ($\mu = 3.6$ per call) than titmice ($\mu = 2.3$ per call), with chickadees increasing the number of ‘D’ notes significantly more during stimulus presentations (although there was no significant species by context effect). There was a stimulus by context effect, such that chickadees and titmice had more ‘D’ notes in their calls in the presence of the bowl and dove stimuli compared to the person stimulus.

Discussion

This experiment was one of only a few studies that have compared how mixed-species groups react to novelty, and it addressed the possibility of a vocal component of reactions to novel stimuli. Our goal was to determine if there were species differences in foraging rates, calling rates, and ‘D’ note usage in the presence and absence of novel stimuli. We found that chickadees and titmice do react differently to novel stimuli: both species shorten their foraging latencies, and increase the number of ‘D’ notes per call, but only chickadees decrease their calling latency in the presence of novel stimuli.

Our first and second predictions (Table 2)—that chickadees and titmice would have different foraging latencies depending on the presence or absence of novel stimuli and that this would be influenced by their interspecific dominance relationships—were not supported. We found that there were no differences in foraging latencies for chickadees and titmice across contexts. Our third and fourth predictions, that between species, the presence of novel stimuli would increase foraging latencies and decrease calling latencies compared to baseline, no stimulus contexts, were supported as well.

Why might this be? One possibility is that intraspecific dominance interactions occur more frequently than interspecific dominance interactions (Morse, 1970). Intraspecific dominance hierarchies in Carolina chickadees and tufted titmice are linear, where adult males are the most dominant, followed by juvenile males, adult females, and then juvenile females (Grubb & Pravosudov, 1994; Pravosudov, Grubb, Doherty, & Bronson, 1999). We did not quantify dominance interactions at the feedings stations, because individuals were not individually color banded, although interspecific and intraspecific supplants did occur. Previous research has suggested a cost to chickadees foraging in the presence of socially dominant titmice. For example, when titmice were removed from woodlots, chickadees began foraging in ‘titmouse-like’ locations (on the ground, higher in the canopy, and on dead limbs), which suggested that titmice prevented chickadees from foraging in those preferred locations (Cimprich & Grubb, 1994).

Another reason why we might not have observed differences in chickadee and titmice seed-taking latencies is that our birds were taking seeds from a non-natural foraging location and a location that prevented successful seed caching. Because titmice typically forage on the ground and higher in the canopy on branches (Cimprich & Grubb, 1994), these are their likely caching areas. Our birds would take a seed from the feeding station and then fly away, presumably to cache it, thus supporting this idea. Therefore, rather than defending the area where they found the cacheable item (the feeding station), it is possible that titmice defend their caching locations more strenuously (Daily, Clayton, & Emory, 2006). Thus, we would not see significant interspecific influences at the feeding station, but would see them in the more natural titmouse foraging areas. This may also explain why Cimprich and Grubb (1994) observed chickadees foraging in more ‘titmouse-like’ locations—with the titmice absent, the chickadees could search for, and pilfer, titmouse caches. Perhaps if we had placed seeds in more ‘titmouse-like’ locations, we would have observed differences in seed taking latencies between species.

Because titmice are interspecifically dominant and have the ability to monopolize highly preferred foraging locations (Cimprich & Grubb, 1994), why do they allow chickadees to participate in the flocks? As a whole, flock members benefit from decreased predation, due to the ‘many eyes effect’ and ‘safety in numbers,’ where larger numbers of vigilant individuals provide protection from predators more successfully than smaller groups with less vigilant individuals

(Krause & Ruxton, 2002; Morse, 1977). Species that are vulnerable to predation benefit by joining other species and exploiting their vigilance (Sridhar, Beauchamp, & Shanker, 2009). In this experiment, prediction 5a was supported: chickadees were the first species to call in the presence of novel objects compared to titmice. This suggests that chickadees were more vigilant and were quicker to observe and respond to the novel stimuli, and this goes against the alternative prediction that titmice may be sentinel-like in these flocks. These results provide further evidence that chickadees are sentinels, or community informants in these flocks (Templeton, Greene, & Davis, 2007). In another well-studied mixed-species flocking system in Sri Lanka, the orange-billed babbler, *Turdoides rufescens*, is typically the first species to call, though they are less reliable than the proposed flock sentinels, the greater racket-tailed drongos, *Dicrurus paradiseus*, which characteristically calls secondarily but more accurately (Goodale & Kotagama, 2005). Regardless, other members of these Sri Lankan flocks react to the two species' vocalizations equivalently. Considering this, perhaps chickadees in our flocks are key sentinels, such that accurate information flows from chickadees to titmice (Nolen & Lucas, 2009). Conversely, Floridian titmice are more abundant than chickadees in mixed-species flocks, and information has been shown to flow from titmice to chickadees in those populations (Sieving, Hetrick, & Avery, 2010). This suggests that the difference in species' calling latencies, including sentinel status, may also be related to their majority status in the flock. Chickadees are slightly more abundant in our Tennessee flocks than titmice (this study: average of 3.8 chickadees and 3.1 titmice). It may also be the case that as subordinate members of the flock, chickadees are forced to act more riskily, including calling first during potential threats, which increases the chance of alerting a predator to their location (Zanette & Ratcliffe, 1994). However, calling first in a risky situation can also be beneficial to chickadees because it may allow them to either elicit an alarm call and flee to cover, or elicit mobbing calls, which attract flock mates and many other species to their location (Gunn et al., 2000).

There were no significant species effects for 'D' note usage, although chickadees did increase the number of 'D' notes used across stimulus contexts compared to titmice. Between-species, prediction 6 was supported, with chickadees and titmice increasing their 'D' notes in stimulus contexts compared to pre-stimulus contexts. 'D' notes are used in a variety of contexts, including in predator and mobbing contexts (Courter & Ritchison, 2009; Nolen & Lucas, 2009; Sieving, Contreras, & Maute, 2004; Sieving, Hetrick, & Avery, 2010; Soard & Ritchison 2009), as well as to recruit flock mates to food sources (Mahurin & Freeberg, 2008). Because they are broadband notes and easy to localize, 'D' notes are an ideal note to use to attract the attention of other flock mates to a stimulus. As first callers, chickadees likely brought the novel stimuli to the attention of titmice, which initiated their 'D'-rich calls.

Chickadees and titmice also reacted to the novel stimuli much like they would react to a predator: they increased the average number of 'D' notes per call and increased their foraging latencies (Bartmess-LeVasseur et al., 2010). This is not surprising, as reactions to novelty can either involve fear, in the form of neophobia, or curiosity, in the form of neophilia. Further experiments should test whether chickadees and titmice react to these novel stimuli in a graded manner, as they do for varying levels of perceived threat (Courter & Ritchison, 2009; Soard & Ritchison 2009) or if they treat novel stimuli and predator stimuli similarly. Additionally, while there was no direct comparison of calling behavior during novel and predator stimuli, previous measures of 'D' notes used in a predator context (Cooper's hawk model at 1 m) show an average of approximately six 'D' notes per call for chickadees and titmice (Bartmess-Levasseur et al., 2010). This experiment finds that chickadees and titmice use, on average, 3.4 'D' notes per call, suggesting that chickadees and titmice do respond to novel stimuli in a graded manner compared to predators.

Conclusions

The significant differences observed in the vocal behavior of chickadees and titmice lend themselves to future studies to further address communicative reactions in the presence of novel stimuli. Compared to titmice, chickadees were typically the first to call during the novel stimulus contexts. In total, the results here show that the presence of novel objects on or near the feeding stations resulted in a neophobic response, significantly increasing foraging latencies for both species. If chickadees are sentinels in these flocks, they should also be the first to vocalize in other threating contexts, such as when predators are present. This experiment provides the foundation for future studies of comparative reactions to novelty and predators in mixed-species groups.

Appendix A: Figures

Figure 1. Experiment One: the three varieties of plastic dove model and plastic dog bowl.

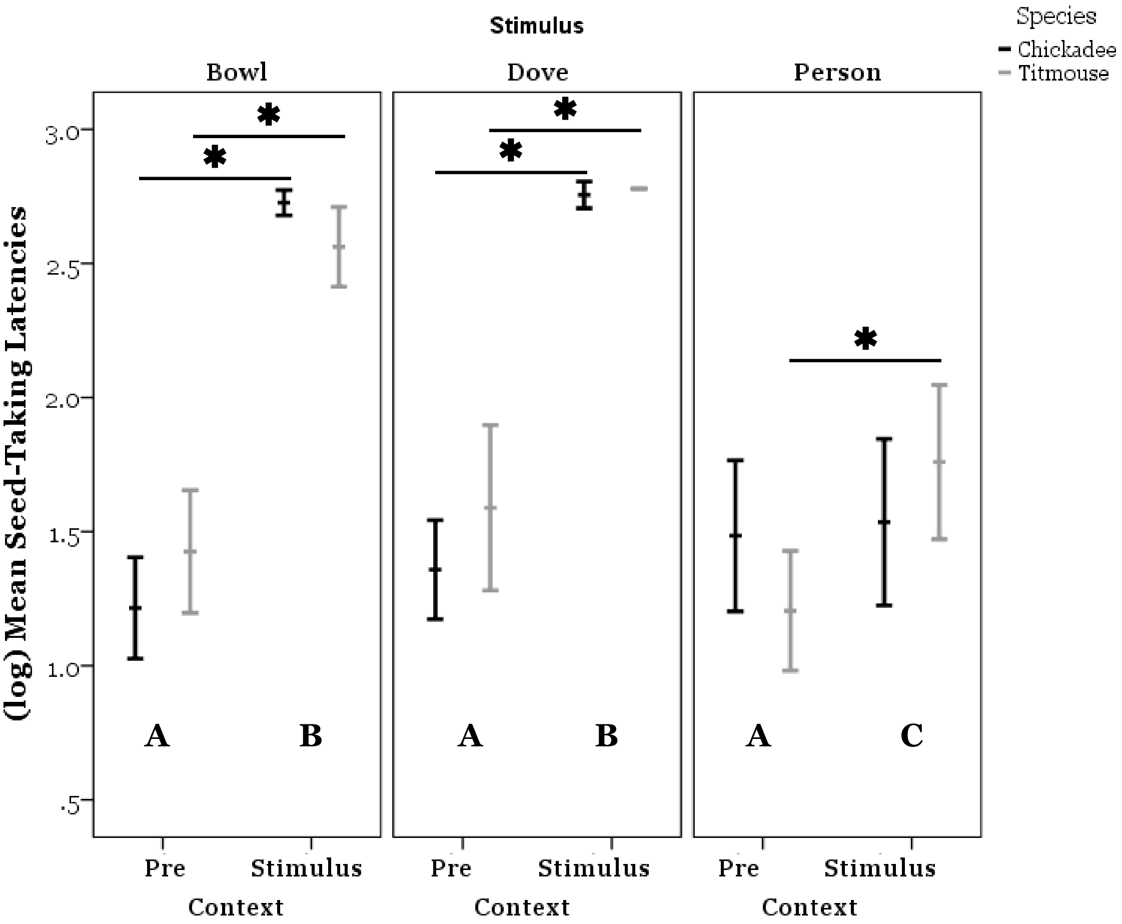

Figure 2. Experiment One: mean seed-taking latencies (log-transformed) across stimuli and contexts. Birds were given 10 minutes to respond in both pre-stimulus and stimulus contexts. Error bars represent means with 95% confidence intervals. Lines with stars denote significant differences within-species. All significant differences between contexts (pre- versus stimulus) are noted with different letters. Overall, there was a significant three-way interaction between context, species, and stimulus. This was mainly attributed to the fact that chickadees and titmice were similarly affected by the presence of the bowl and dove stimuli, but titmice were more strongly affected by the person stimulus, than chickadees. Titmice had significantly longer seed-taking latencies in the person context.

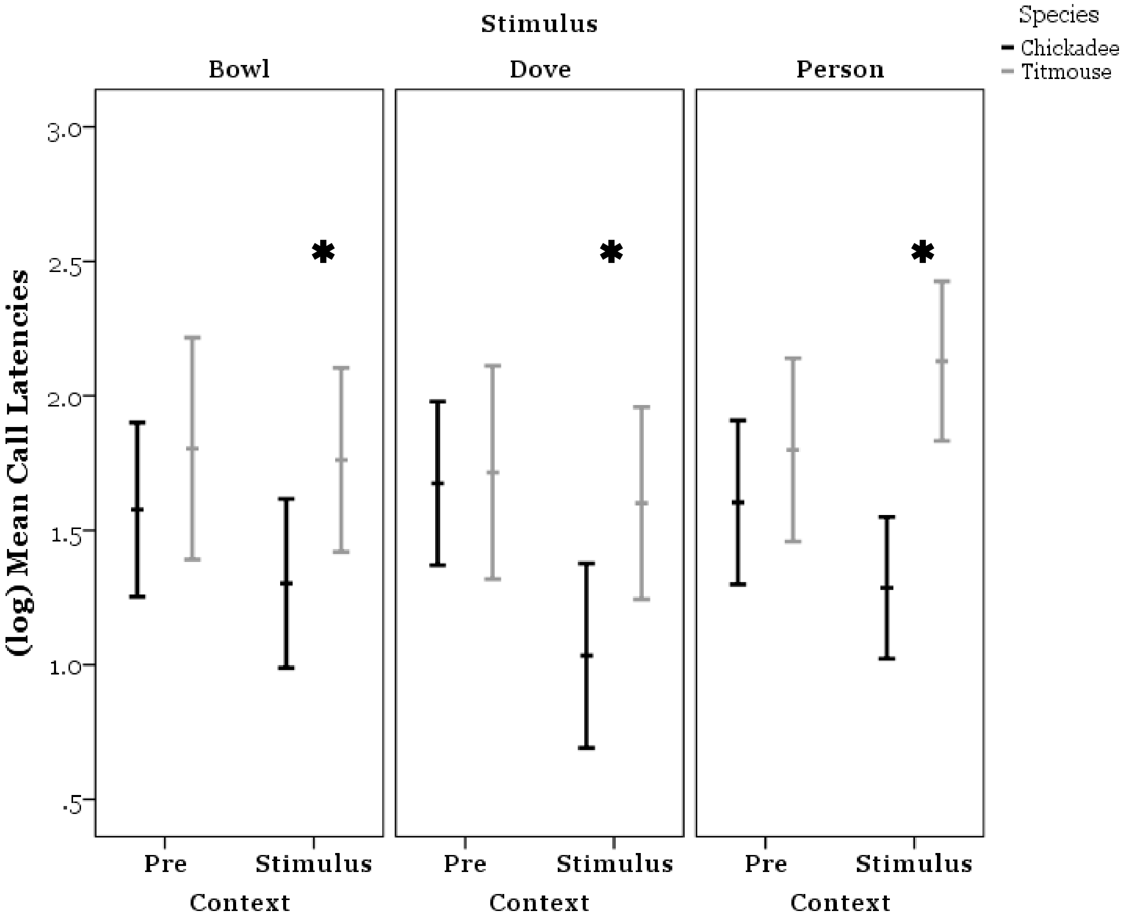

Figure 3. Experiment One: mean call latencies (log-transformed) across stimuli and contexts. Error bars represent means with 95% confidence intervals. There were no significant differences in call latencies between contexts; however, chickadees had significantly shorter calling latencies than titmice in stimulus contexts compared to baseline pre-stimulus periods (noted by stars).

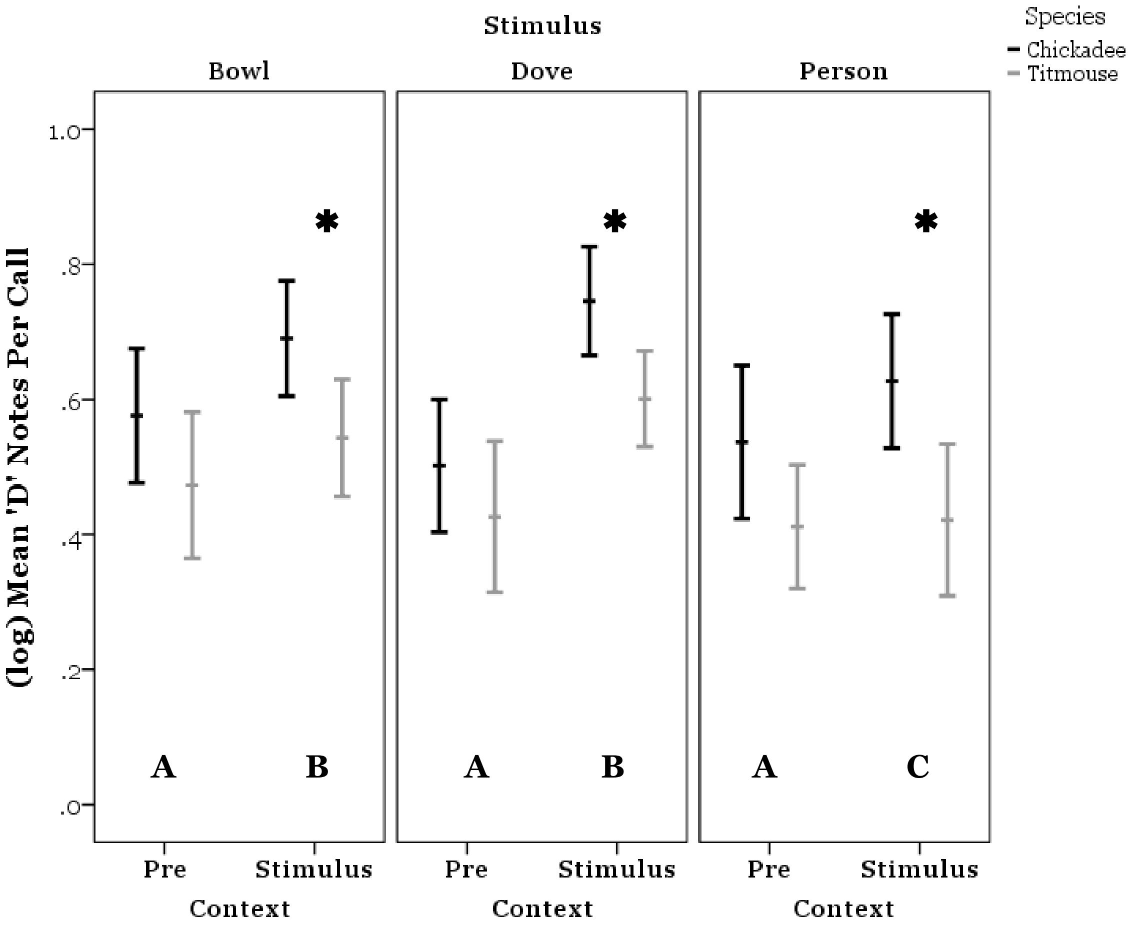

Figure 4. Experiment One: mean 'D' notes per call (log-transformed) across stimuli and contexts. Error bars represent means with 95% confidence intervals. All significant differences between contexts (pre- versus stimulus) are noted with different letters. Stars denote significant differences between-species. Chickadees used more ‘D’ notes in their calls than titmice, with more ‘D’ notes being used in stimulus contexts compared to pre-stimulus contexts. Chickadees and titmice also used more ‘D’ notes in the bowl and dove contexts compared to the person context.

Appendix B: Tables

Table 2. Experiment One: predictions.

	Prediction	***Supported?***
Seed-taking Latencies	1. During baseline contexts, titmice, being the larger and interspecifically dominant species, would have shorter latencies to forage than chickadees.	No, there were no species differences in seed-taking latencies across contexts.
	2. During novel stimulus contexts, the subordinate chickadees would exhibit less neophobia and would therefore have shorter latencies to forage compared to dominant titmice.	
	3. Both species would have longer latencies to forage when novel stimuli were present compared to baseline contexts	Yes
Calling Latencies	4. Chickadees and titmice would have shorter calling latencies in the presence of novel stimuli, compared to baseline contexts.	Yes
	5a. The interspecifically subordinate chickadees would have shorter calling latencies in the novel contexts compared to titmice.	Chickadees had shorter latencies to call in novel contexts compared to titmice.
	OR	
	5b. The sentinel-like titmice would have shorter calling latencies in the novel contexts compared to chickadees.	
‘D’ Note Usage	6. Chickadees and titmice would use more ‘D’ notes in their calls when novel stimuli were on the feeding station.	Yes

Table 3. Experiment One: means for seed- and call latencies (in sec) and seed- and call rates (per 10 minutes) for chickadees and titmice for each novel stimulus in baseline pre-stimulus contexts (Pre) and stimulus contexts (Stim).

	Chickadee						***Titmouse***					
	Bowl		**Dove**		**Person**		**Bowl**		**Dove**		**Person**	
	Pre	**Stim**	**Pre**	**Stim**	**Pre**	**Stim**	**Pre**	**Stim**	**Pre**	**Stim**	**Pre**	**Stim**
Seed Latency	25.2	544.8	36.2	580.0	81.8	88.6	68.4	440.6	130.6	600.0	33.3	147.2
Seed Rate	9.0	0.2	8.1	0.1	8.6	6.4	7.1	1.1	6.7	0	8.2	5.1
Call Latency	119.9	60.3	115.0	45.7	104.8	41.6	238.5	147.7	186.7	120.0	153.0	283.5
Call Rate	7.8	15.9	7.6	15.6	4.7	10.6	5.8	12.1	6.0	30.1	7.9	5.9

Table 4. Experiment One: mixed-model results for seed-taking latencies. Bold values are statistically significant.

	Num. df	***Denom. df***	***F***	***Sig.***
Intercept	1	93.4	2,979.6	**<0.001**
Species	1	147.8	0.5	0.487
Stimulus	2	89.3	31.1	**<0.001**
Context	1	103.2	243.2	**<0.001**
Species * Stimulus	2	89.2	0.66	0.521
Species * Context	1	147.8	0.1	0.804
Stimulus * Context	2	89.3	24.2	**<0.001**
Species*Stimulus*Context	2	89.2	4.0	**0.022**

Table 5. Experiment One: mixed-model results for calling latencies. Bold values are statistically significant.

	Num. df	*Denom. df*	*F*	*Sig.*
Intercept	1	36.3	635.7	**<0.001**
Species	1	150.7	20.8	**<0.001**
Stimulus	2	40.7	1.5	0.242
Context	1	30.3	1.9	0.174
Species * Stimulus	2	107.7	.6	0.546
Species * Context	1	149.0	7.8	**0.006**
Stimulus * Context	2	109.4	1.6	0.199
Species*Stimulus*Context	2	106.6	.5	0.603

Table 6. Experiment One: mixed-model results for 'D' note usage. Bold values are statistically significant.

	Num. df	*Denom. df*	*F*	*Sig.*
Intercept	1	21.0	717.6	**<0.001**
Species	1	153.0	27.9	**<0.001**
Stimulus	2	44.2	2.5	0.093
Context	1	17.5	17.8	**<0.001**
Species * Stimulus	2	100.7	0.3	0.735
Species * Context	1	150.6	1.9	0.174
Stimulus * Context	2	101.6	3.9	**0.023**
Species*Stimulus*Context	2	100.1	0.02	0.974

CHAPTER III: CHICKADEES AND TITMICE RESPOND TO NOVEL STIMULI DIFFERENTLY THAN THEY DO TO PREDATOR STIMULI

A version of this chapter is in preparation to be submitted for review in a peer-reviewed journal. The manuscript combines the experiment discussed in this chapter with the experiment in Chapter 2. My contributions to this work include: (a) formulating the research idea and hypothesis (b) training the research assistants (c) designing the experiment (d) collecting data (e) doing the statistical analysis (f) interpreting results and (g) writing the manuscript.

Abstract

Many studies have tested vocal and behavioral reactions of mixed species avian flocks to predators, and increasingly more studies are testing for reactions to novel stimuli. Few studies, however, have directly compared behavioral reactions to predator stimuli with those to novel stimuli. This experiment measured the vocal and behavioral responses of mixed-species flocks of Carolina chickadees and tufted titmice to four different contexts at feeding stands in their natural environment. A novel (Mega Bloks® object), predator (plastic Cooper's Hawk), neutral (piece of wood), and control (no stimulus) context were presented on feeding stations stocked with bird seed. Vocalizations were recorded and foraging behavior at the feeding stands was videotaped. For both species, foraging latencies in the novel context were intermediate to the predator context and to the control and baseline contexts. Chickadees had shorter calling latencies than titmice across stimulus contexts and had significantly shorter calling latencies than titmice in the hawk context. Chickadees also used more 'D' notes in their calls than titmice across contexts. Thus, chickadees and titmice do react differently to predators and novel stimuli, with the main difference being a graded response in their foraging latencies. Chickadee calling behavior observed in this experiment supports previous research, suggesting that chickadees may be sentinels in these flocks. Overall, these results can help us better understand antipredator behavior and the possible functions of mixed species flocks.

Introduction

"The normal thing is for birds, especially titmice, to
act intelligently in unusual circumstances
unless they get flustered through fear"
(Len Howard, as cited in Holliday, 1953)

Personality traits are suites of correlated behavior patterns that occur across time and contexts (Sih et al., 2004). The neophobia-neophilia and shy-bold continuums are axes of behavioral variation that are studied frequently in the animal personality literature. Neophobic individuals typically avoid novel, or new stimuli, while neophilic individuals typically are attracted to novel stimuli. The neophobia-neophilia continuum is similar to the shy-bold continuum in that both address reactions to novel stimuli, however the shy-bold continuum also includes reactions to risky situations. Therefore, 'shy' individuals avoid risky or novel stimuli and react to such situations by retreating or becoming quiet (Wilson et al., 1993; Wilson et al., 1994). In contrast, 'bold' individuals are attracted to risky and novel stimuli and react by either acting normally or increasing their activity (Wilson et al., 1993; Wilson et al., 1994). The shy-bold continuum can be misleading, however, because sometimes 'shy' and 'bold' behavioral types are tested in contexts when only novel stimuli or novel contexts are presented (e.g. Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003). More often, 'shy and 'bold' behavioral types are tested only in a risky context (e.g. Sinn, Apiolaza, & Moltschaniwskyj, 2006).

To test for shyness or boldness across contexts, both a predator and a novel stimulus should be presented. However, few studies have tested for reactions to both novel and predator stimuli when accessing individuals for shyness or boldness. Nevertheless, in one study, chaffinches, *Fringella coelebs*, were tested in several contexts, including a stressful context (novel environment), a low-risk predator context (when a hawk flew 2m to the side of chaffinches), and a high-risk predator context (when a hawk flew directly above chaffinches)

(Quinn & Cresswell, 2005). The researchers found that birds with high activity levels in the stressful context were less likely to freeze during, and were faster to resume activity after, the predator contexts. In other words, bold ('hyperactive', their terminology) birds were more active in both contexts than shy birds.

Interestingly, there is not always a positive correlation between behavior in novel and predator contexts. For example, in a study of convict cichlids, *Amatitlania nigrofasciata*, researchers presented fish with a standardized predator attack while the cichlids were foraging and later tested the fish with a novel object and a novel environment (Jones & Godin, 2009). The authors found that fish with higher exploration scores in the novel contexts had longer latencies to respond to the predator. The authors posited two possible explanations for their results. First, they suggested that the bolder, more exploratory fish allotted more time to foraging rather than predator avoidance, and thus, delayed their response to a predator in order to prevent a possible lost opportunity for foraging. As a second explanation, the authors suggested that bold individuals may have different perceptual abilities compared to shy individuals, such that their ability to perceive predators is not as sharp. Overall, this study highlights the importance of presenting novel and predator stimuli together to ascertain the correlates of boldness and shyness.

Why is it important to determine whether an individual is bold or shy? The characteristics associated with shyness and boldness can affect many aspects of an individual's life. For instance, shyness and boldness levels can influence how far an individual disperses from its natal site (Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Dingemanse, et al., 2003). Great tits, *Parus major*, who had high exploration scores, and thus were more bold, dispersed farther from their natal sites compared to individuals who had low exploration scores (Dingemanse et al., 2003). Additionally, an individual's level of shyness or boldness can influence fitness (Both, Dingemanse, Drent, & Tinbergen, 2005). Nest success, fledgling size, and condition are correlated with behavioral traits in great tits. Slow-exploring, or shy females, tended to have better nest success and have larger fledglings, especially if the females mated with high-exploring (bold) males. The authors posited that the bolder males were likely more able to obtain and defend higher quality territories.

Perhaps most importantly, an individual's shyness or boldness can influence its risk of predation and foraging efficiency (Lima, Valone, & Caraco, 1985; Sih, 1982). Often, there is a trade-off between predator avoidance and foraging; high quality foraging sites are desirable, however, foraging reduces an individual's ability to remain vigilant, thus putting them at increased risk for predation (Gilliam & Fraser, 1987; Godin & Smith, 1988). Animals can assess, and in some ways, control, their risk by deciding when, where, what, and how to eat (reviewed in Lima & Dill, 1990). They can also decide to coalesce into groups, thus reducing individual vigilance rates.

Typically, the shy-bold continuum is used to describe behavioral differences on the individual level. However, like the neophobic-neophilic continuum, the shy-bold continuum can also describe behavioral differences on the species level. For example, some species of seabirds are bolder, and can be baited to forage near boats for capture using cast nets, compared to shy species, which rarely approach the boats (Bugoni, Neves, Peppes, & Furness, 2008). Considering this, my study tested the behavioral and vocal reactions of two Parid species, Carolina chickadees and tufted titmice, in the presence of novel and predator stimuli. These species form mixed-species flocks in the over-wintering months and obtain many benefits from such flocking, including increased foraging efficacy and reduced predation risk (Curio, 1978; Berner & Grubb, 1985; Lima, 1995; Krause & Ruxton, 2002). To my knowledge, no study has addressed whether these species differentially react to novel and predator stimuli (although many studies have tested them in a novel or predator context (Chapter 2; Bartmess-Levasseur et al., 2010; Courter & Ritchison, 2010; Nolen & Lucas,2009; Soard & Ritchison, 2009). Previous research (described in Chapter 2) showed that chickadees and titmice differentially reacted to novel stimuli. Both species increased their foraging latencies in the presence of novel stimuli near a preferred food source. Additionally, both species increased the mean number of 'D' notes per call in the presence of the novel objects, which was typical of these species when they were presented with predator stimuli (Bartmess-Levasseur et al., 2010; Courter & Ritchison, 2010; Soard & Ritchison, 2009; Templeton & Greene, 2007). The average number of 'D' notes produced during the novel stimulus presentations was higher than what flock members in this population have been known to produce in the presence of predator stimuli (e.g. Bartmess-Levasseur et al., 2010). However, I could not be certain if flock members used significantly more 'D' notes in predator contexts compared to novel contexts unless both types of stimuli were presented to the same flocks. Therefore, in this experiment, naturally-occurring flocks of Carolina chickadees and tufted titmice were presented with 4 contexts: a plastic Cooper's hawk model (predator), a Mega Bloks® object (novel), a piece of wood (control), and no-stimulus (baseline). Each context was presented for 10 minutes, in a counterbalanced order by site. Seed-taking latencies, calling latencies, and number of 'D' notes produced were measured at each site.

Predictions

Regarding seed-taking latencies, I had several predictions: 1. *There would be no species differences in seed-taking latencies,* based on the results from Chapter 2. Because the wood stimulus was a control to test whether my walking up to the stand to place a stimulus on the feeding station affected flock behavior, I predicted that 2. *There would be no differences in seed-taking latencies in the no-stimulus baseline context compared to the wood control context*. Additionally, I predicted that 3. *Chickadees and titmice would significantly increase their latencies to forage in the presence of the novel stimuli compared to the baseline and control stimulus presentations,* and that 4. *The predator stimulus would result in the longest seed-taking latencies compared to the remaining contexts (baseline, wood control, and novel)* (Table 7). The novel stimulus, while new, was not associated with any immediate certain risk, therefore, the bolder members of the flock were likely to approach it and/or forage near the novel object much quicker than they would approach and forage near a predator model, which was associated with immediate and certain risk. Here, boldness is being quantified as a foraging response latency.

Regarding call-latencies, previous research shows that chickadees have significantly shorter calling latencies than titmice in novel stimulus contexts (Chapter 2). As such, it is likely that chickadees are more vigilant than titmice and are able to inform flock mates of the presence of unusual or threating stimuli by vocally alerting the flock. Considering this, I predicted: 5. *Chickadees would have shorter calling latencies than titmice across contexts*. Similarly, because I do not expect the no-stimulus baseline and wood stimulus contexts from being different, I predicted that: 6. *There would be no differences in calling latencies in the no-stimulus baseline context compared to the wood control context,* and 7. *Chickadees and titmice would have intermediate latencies to call in the novel context compared to baseline and predator contexts, based on degree of threat*.

Lastly, much research has been conducted on the vocal systems of chickadees and titmice, and specifically on both species' use of 'D' notes in predator contexts. Many studies of Carolina chickadees, tufted titmice, and related species reveal that they use 'D' notes in a graded manner, based on perceived threat level, where an increase in 'D' notes is associated with an increased perceived threat level (Courter & Ritchison, 2009; Soard & Ritchison 2009; Templeton et al., 2005). Consequently, I predicted that: 8. *If chickadees and titmice perceive the novel Mega Bloks® object as less threatening than a Cooper's hawk model, that they would have a graded response, using an intermediate number of 'D' notes in the novel context compared to baseline and predator contexts*. Similar results were found in herring gulls, *Larus smithsonianus*, when presented with a neutral bird vocalization, novel auditory cues, and predator vocalizations (MacLean & Bonter, 2013). The herring gulls used a graded response for the novel auditory stimulus, such that it was intermediate to the neutral and predator auditory cues. As such, in the current experiment, birds were predicted to produce more ‘D’ notes in a graded manner, such that baseline and control contexts < novel < predator.

Methods

Data were collected from January 2013 through March 2013 at the same main locations mentioned in Chapter 2. I modified the feeding station in this experiment compared to the first experiment, using a 28.5 x 112 x 2 cm flat, wooden platform that had a small built-in trough to place seed. The trough helped prevent birds from pushing too many seeds off the station. Stimuli were placed on the side opposite of the feeding trough, such that stimuli were consistently less than 1 m away from the seed during stimulus presentations.

Stimuli

There were four different stimulus conditions: control (no stimulus), a control object (a piece of wood), a novel object (shape built from Mega Bloks®), and a predator model (plastic Cooper’s hawk) (Figure 5). The wood was used as a control for the process of walking up to the station and placing an object on it. Several variations of each stimulus, including the Mega Bloks® and hawk predator model (e.g. different colors or markings) were used to minimize pseudoreplication. Additionally, all stimuli were similar in size, because larger objects can increase neophobia compared to smaller objects (e.g. Greenberg, 1983).

Procedure

The recording equipment, observer distance, and blind were used as described in Chapter 2. A Canon GL2 video camera was also set up five meters from the feeding station to capture foraging behavior. A video camera was added to this study because it was previously noticed (Chapter 2) that some birds approached the feeding station, or took a seed from the feeding station, almost immediately after a trial was started. Therefore, by video recording each site, I was able to determine if birds took a seed when my back was turned after placing a stimulus on the feeding station and walking back to the blind.

Once birds were continuously foraging from the feeding station, the observer turned on the audio equipment, walked up to, and turned on, the video camera, named the identifying information for the trial and placed the stimulus on the stand opposite of the feeding trough. Once the stimulus was on the feeding station and the observer began walking away, the first recording session began. The order of presentation for the four stimuli (baseline, wood, Mega Bloks® novel object, predator hawk model) was semi-randomly assigned at each site, with the aim of having a counter-balanced order of stimuli at the end of the study. I had four 10-minute stimulus periods with at least 10 minutes between successive stimulus presentations. Birds at each site were presented each stimulus only once.

Inter-rater Reliability

Twelve separate video files spanning all recording contexts (roughly 10% of the total sample) were independently scored for chickadee and titmouse seed-taking latencies and call latencies. Inter-observer reliability for both species was high (Spearman's correlation, r_s median = 0.971, range = 0.950 - 0.984). Inter-observer agreement for 'D' notes was 'almost perfect' (Landis & Koch, 1977; Cohen's kappa statistic = 0.818 for chickadees and 0.906 for titmice).

Statistical Analysis

Seed-taking latency, call latency, and number of 'D' notes per call for chickadees and titmice were log transformed for normalization. Seed-taking latencies are a good measure of approach latencies to the various stimuli (Chapter 2) and call latencies are good indicators of threat immediacy (Zanette & Radcliffe, 1994). Subsequently, mixed models analyses of variance were run on the three dependent variables, 'Species' and 'Stimulus,' as within subjects-factors and 'Site' as a random factor.

Results

Approximately 17 hours of sound recordings were recorded from 26 sites and a total of 3,356 chickadee calls and 3,710 titmouse calls were coded. An average of 3.4 chickadees (range: 2 – 6) and 3.1 titmice (range 1 – 5) participated in each flock.

Seed-taking Latency

The mean seed-taking latencies between chickadees (μ = 247.9 sec) and titmice (μ = 217.9 sec) were not significantly different (Figure 6). See Table 8 for average latencies and rates and Table 9 for mixed model statistical results for seed-taking latencies. There was a significant stimulus effect, such that seed-taking latencies were significantly different across stimulus contexts. Seed-taking responses to all stimuli were significantly different from one another with a $P < 0.001$, except the control versus wood context ($P = 0.269$), which had similar seed-taking latencies.

In the hawk context, chickadees only took a seed from the stand at 2 of the 26 sites (μ latency = 203.6 sec). Similarly, there were only 2 sites where titmice took a seed from the stand while the hawk model was present (μ latency = 76.8 sec). Often, this was the first and only time a bird took a seed during the hawk context.

There was no main effect of stimulus presentation order ($F_{3, 115} = 1.8$; $P = 0.150$), suggesting that birds did not habituate to the stimuli over the course of data collection at a single site. There was also no stimulus by order interaction ($F_{9, 99} = 1.4$; $P = 0.179$), indicating that the previously presented stimuli did not affect flock members' seed-taking latencies during the subsequent stimuli presentations.

Call Latency

Chickadees had shorter mean call latencies (110.6 sec) across contexts compared to titmice (159.2 sec) (Figure 7). See Table 10 for statistical results for call latencies. Chickadees had significantly shorter calling latencies than titmice in the hawk context ($P = 0.002$) and in the wood context ($P = 0.050$). There was a context effect, such that mean call latencies for the control (139.6 sec), wood (188.1 sec), novel (153.3 sec), and hawk (58.7 sec) stimuli were significantly different ($F_{3,98} = 12.396$, $P < 0.001$). The control context had a shorter latency than the wood context ($P = 0.014$) and novel context ($P = 0.046$). In addition, the hawk context had shorter call latencies than the wood ($P < 0.001$) and novel contexts ($P < 0.001$). Lastly, there was no difference in call latencies when comparing the control context to the hawk ($P = 0.303$) or the novel context to the wood ($P = 0.445$).

There was no main effect of order on calling latencies ($F_{3,114} = 1.0$; $P = 0.414$); birds did not habituate their calling behavior across stimulus presentations. Additionally, there was no stimulus by order interaction ($F_{9,78} = 1.3$; $P = 0.248$), indicating that previously presented stimuli had no effect on subsequent measures of flock member's call latencies.

'D' Note Usage

Chickadees used more 'D' notes than titmice across the four stimuli with chickadees using a mean of 4.9 'D' notes per call compared to 2.7 'D' notes per call for titmice (Table 8). See Table 11 for mixed-model statistical results for 'D' note usage. Chickadees and titmice used 'D' notes significantly differently across the four stimuli, with both species using more 'D' notes to the hawk stimuli ($\mu = 4.3$) compared to the novel ($\mu = 3.7$), control ($\mu = 3.5$), and wood ($\mu = 3.6$) stimuli (Figure 8). There was no significant difference in 'D' note usage to the novel, wood, and control stimuli.

There was no main effect of stimulus presentation order ($F_{3,41} = 0.3$; $P = 0.846$), indicating that flock members did not habituate to the stimuli over the course of data collection at one site. There also was no stimulus by order effect ($F_{9,24} = 1.3$; $P = 0.267$), indicating that previously presented stimuli did not affect flock members' 'D' note usage in subsequent stimulus presentations.

Discussion

The results in this experiment corroborate findings from my previous study (Chapter 2). My first prediction, that there were no differences in seed-taking latencies for chickadees and titmice across all four stimuli, was supported. On the population level, chickadees and titmice are equally bold, having similar seed-latencies to novel and predator stimuli. Additionally, chickadees and titmice had similar seed-taking latencies and 'D' note usage to the control and the wood stimuli, indicating that my walking up to and placing a stimulus on the feeding station did not significantly affect their behavior. Thus, my second and sixth predictions were also supported. Additionally, foraging latencies for both species were the longest to the predator stimulus, supporting prediction 4. This was not surprising, because only two chickadees and two titmice foraged at the feeding station when the hawk was present. Anecdotally, it seemed as if these birds were unaware of the hawk's presence, so it is difficult to ascertain if these forays were due to extreme boldness or poor individual vigilance.

Furthermore, chickadees and titmice had intermediate seed-taking latencies to the novel stimulus, thus supporting prediction 3. These intermediate seed-taking latencies suggest that the birds were aware of the stimuli and were hesitant to forage near it. It is likely that the bolder individuals, or individuals who were not deterred by the novel stimulus and thus had shorter latencies to take a seed, were the ones that foraged during this context, although individuals were not color-banded, therefore I cannot be certain.

Regarding calling behavior, chickadees had shorter call latencies than titmice across contexts, a result that supports my fifth prediction as well as previous findings in Chapter 2. In fact, they reacted most strongly to the predator stimulus, calling significantly sooner than titmice. Therefore, prediction 7, which postulated that chickadees and titmice would have graded latencies to respond to novel stimuli compared to baseline contexts and predator stimuli, was not supported. Chickadees seem to play a sentinel-like role in these flocks (Browning et al., in prep.; Soard & Ritchison, 2009; Templeton & Greene, 2007).

In a mixed-species group of tamarins, Avila-Pires saddle-back tamarins, Sagu*inus fuscicollis avilapiresi*, and red-cap moustached tamarins, *S. mystax pileatus*, differentially react to predators (Peres, 1993). For example, saddle-back tamarins are better at detecting terrestrial predators, whereas the moustached tamarins are better at detecting aerial and arboreal predators. As such, their mixed-species grouping is suggested to be related to the collective protection both species provide. In the future, it would be interesting to test mixed-species flocks of chickadees and titmice with several other predator types, such as a terrestrial cat, arboreal snake, or predator in flight, to determine if chickadees are also the first to vocally react and detect these predator types. Similarly, novel objects could be placed on the ground (as a terrestrial threat) or rigged on a zipline as a possible aerial threat (e.g. Zachau & Freeberg, 2012). Perhaps chickadees are better at detecting perched predators or threats in the upper canopy, where they typically forage. Titmice prefer foraging on the ground and lower in the canopy (Cimprich & Grubb, 1994) and may be better suited for detecting terrestrial and aerial predators.

Interestingly, studies show that there are differences in visual acuity of chickadees and titmice, which can influence anti-predator behavior. Chickadees have lower visual acuity than titmice, and therefore have higher head movement rates to scan than titmice (Moore, Doppler, Young, & Fernández-Juricic, 2013). White-breasted nuthatches, frequent flock followers, have better visual acuity than both chickadees and titmice. These differences in visual acuity may explain why previous studies have noted that chickadees and nuthatches are typically the first to mob a predator. With chickadees' need for higher scanning rates to overcome their visual shortcomings and the better visual acuity of nuthatches, it is likely these species are able to detect predators well. In instances where nuthatches are not participating in the flock, or when nuthatches are foraging on tree trucks, thus blocking much of their vision, chickadees may be the most vigilant species in the flock.

Lastly, regarding ‘D’ note usage, chickadees were found to use more ‘D’ notes across stimuli and contexts compared to titmice. This mirrors the results from Chapter 2. One interesting difference between the two studies, though, is that chickadees and titmice increased their ‘D’ notes in the presence of the three novel stimuli in Chapter 2, but did not increase their ‘D’ note production above baseline for the novel Mega Bloks® objects in this study. In fact, they only increased their ‘D’ notes for the predator stimulus, which supported previous research (Courter & Ritchison, 2009; Soard & Ritchison 2009; Templeton et al., 2005), but did not support my eighth prediction that they would have a graded threat response. Why might this be? In the experiment described in Chapter 2, the person stimulus did not affect birds as strongly as the bowl and dove. One could argue that the bowl stimulus was more salient, because it required the birds to touch it to obtain food, compared to the other stimuli. Similarly, it is possible that flock members were treating the dove stimulus as a food competitor, which may explain an increase in ‘D’ notes – they could have been scolding it in an attempt to get it to leave the feeding station (e.g. Haythorpe, Sulikowski, & Burke, 2012). In the current experiment, the Mega Bloks® object was placed far enough away from the food, such that individuals did not have to touch it (although some titmice did land on it).

In view of the results of Chapter 2 and this chapter, a possible association between boldness (measured by latency to take a seed near a novel or threatening stimulus) and vocal behavior in chickadees and titmice was not observed. In fact, the only indication that there may be a difference in boldness and shyness between chickadees and titmice is that chickadees have shorter calling latencies than titmice. This finding, however, may be related to other behavioral characteristics of chickadees, such as their ability to detect threats. In addition, because chickadees and titmice had similar foraging latencies in the presence of both novel and predator stimuli, I cannot say that one species is more bold or neophilic than the other.

In conclusion, chickadees and titmice do treat novel stimuli differently from predator stimuli, and this is observed by a graded increase in their foraging latencies. Vocally, chickadees consistently have shorter latencies to vocalize compared to titmice, and this may be related to their perceptual abilities or to something more global, such as their flock size or composition. For example, perhaps the ratio of 'fast responding' chickadees and titmice influences foraging and calling behavior. Future studies are needed to better understand these differences in vocal behavior between chickadees and titmice in novel and threatening contexts.

Appendix A: Figures

Figure 5. Experiment Two: the four stimulus contexts. Top (left to right): baseline no-stimulus, wood context. Bottom (left to right): Mega Bloks® novel object, plastic Cooper's hawk model.

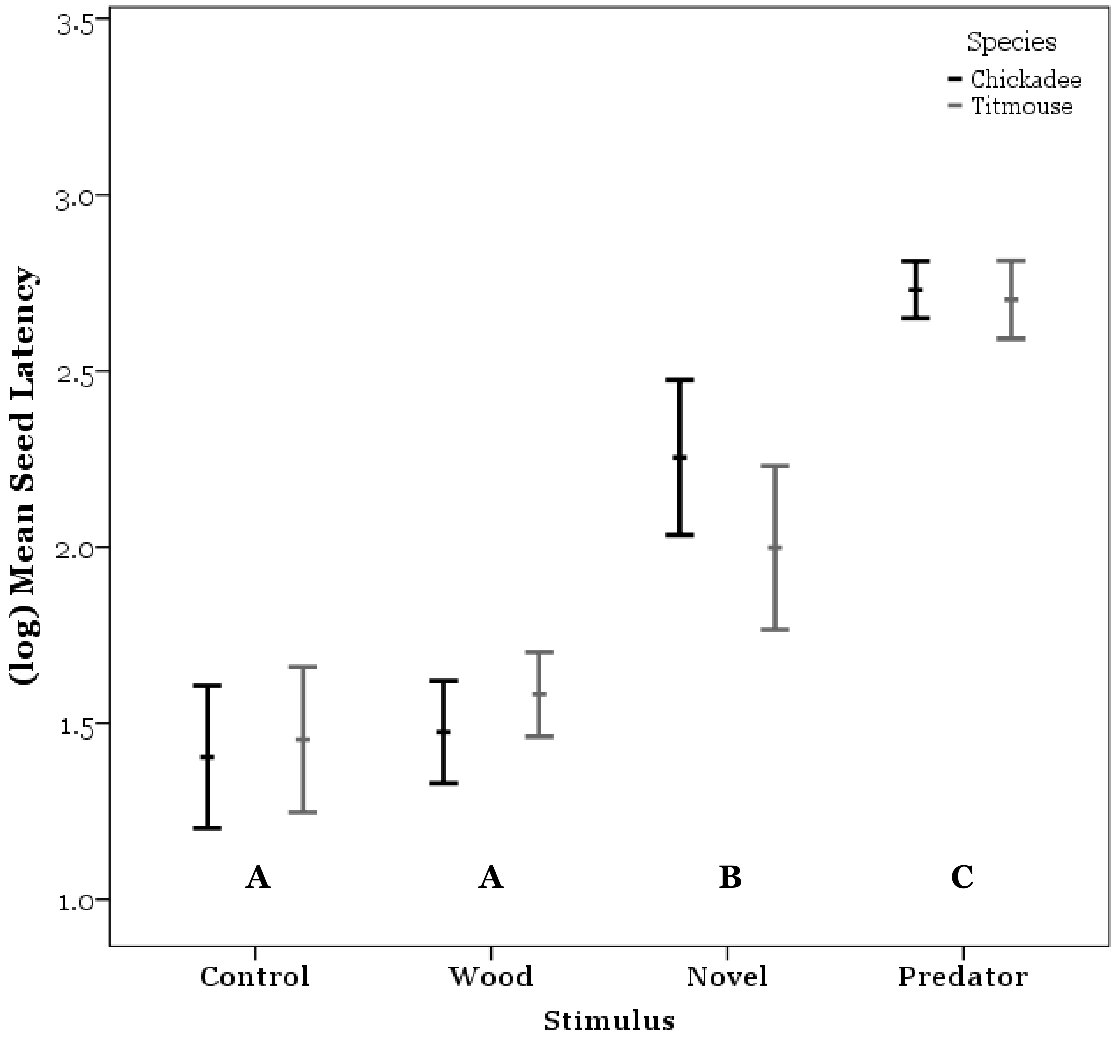

Figure 6. Experiment Two: the (log) mean seed-taking latencies for each stimulus. Error bars represent means with 95% confidence intervals. Letters represent significant differences between stimuli. There were no species differences in mean seed-taking latencies.

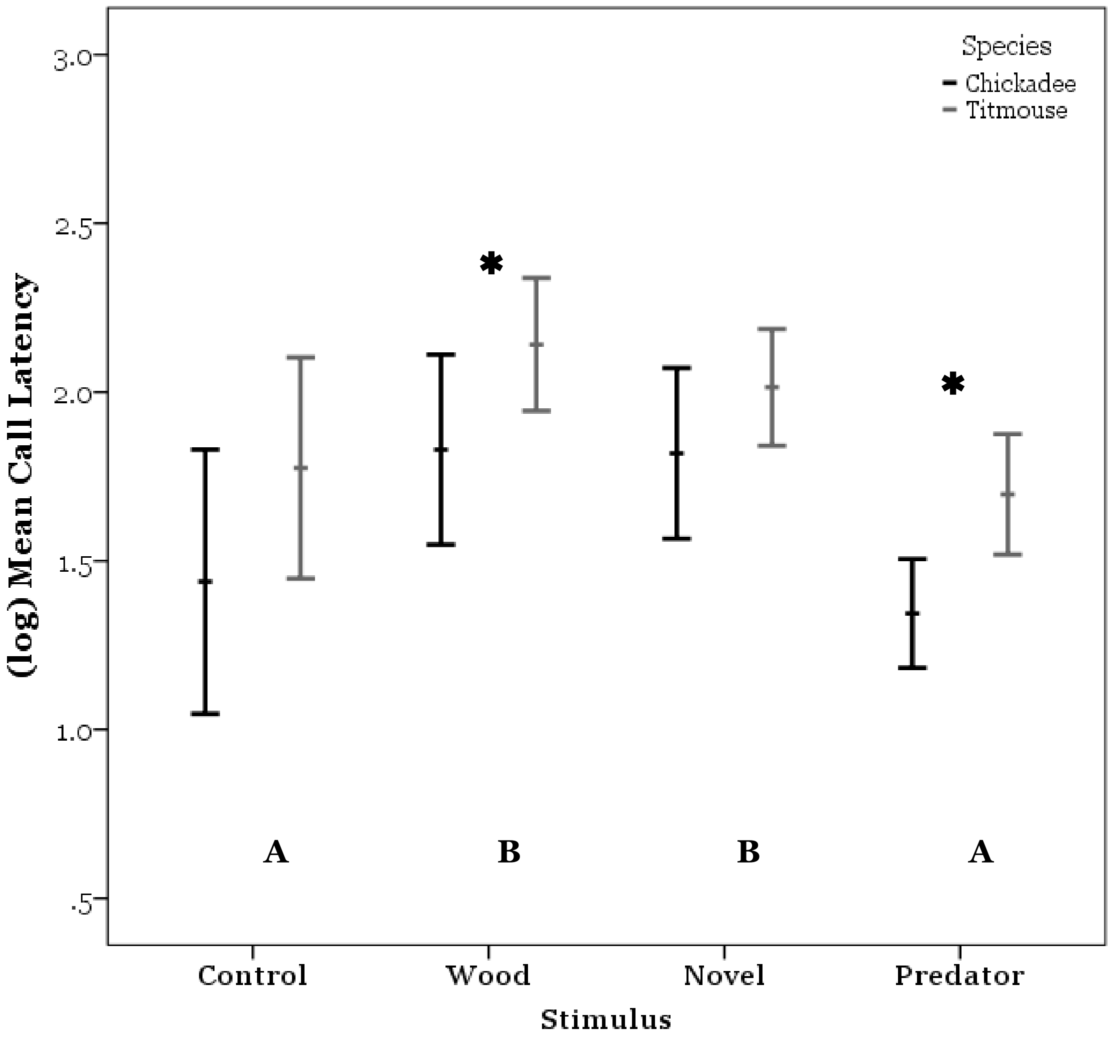

Figure 7. Experiment Two: the (log) mean call latencies for each stimulus. Error bars represent means with 95% confidence intervals. Letters represent significant differences between stimuli. Chickadees had significantly shorter calling latencies than titmice to the wood and predator stimuli (denoted by stars).

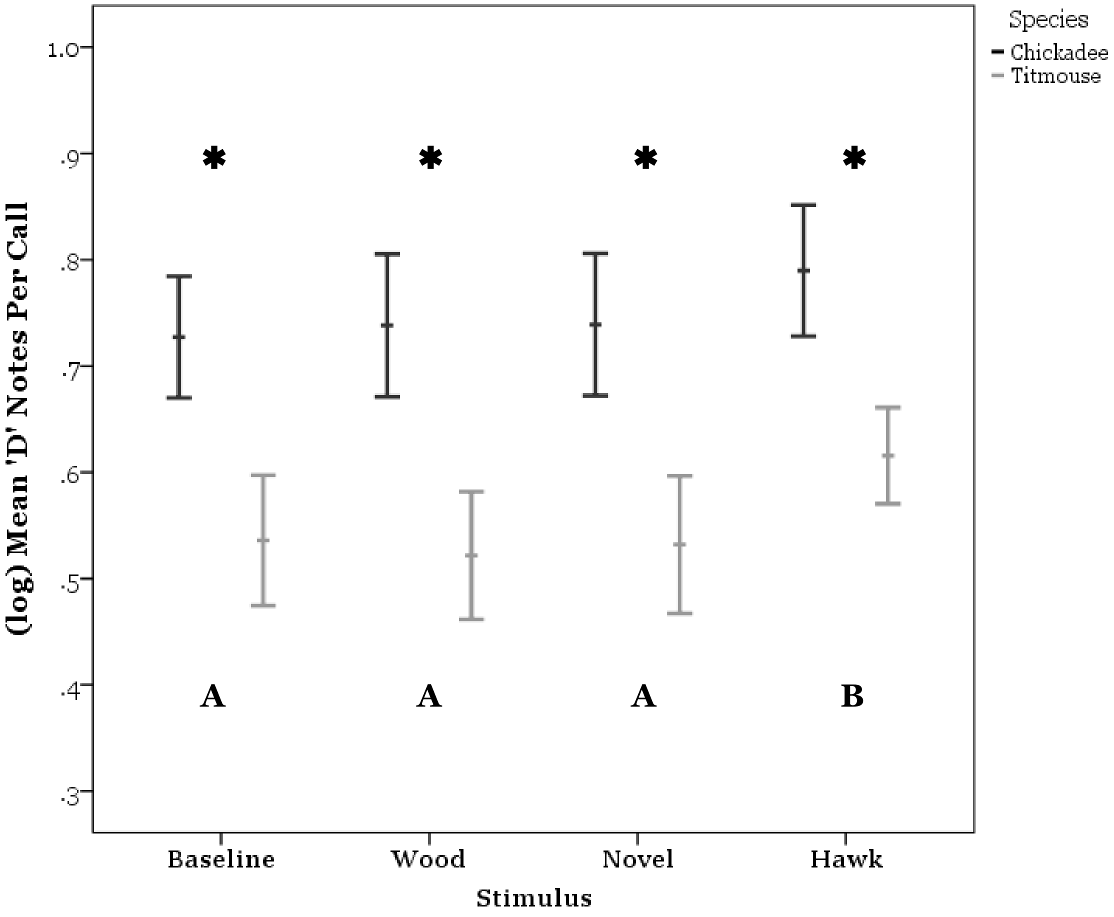

Figure 8. Experiment Two: the (log) mean 'D' notes per call for each stimulus. Error bars represent means with 95% confidence intervals. All significant between-species comparisons are noted with stars. Chickadees used significantly more 'D' notes in each call than titmice across stimulus presentations (denoted by stars). Differences in mean 'D' notes used for each stimulus are noted with letters. Both species only significantly increased the number of 'D' notes per call when the hawk stimulus was presented.

Appendix B: Tables

Table 7. Experiment Two: predictions

	Prediction	*Supported?*
Seed-taking Latencies	1. There would be no species differences in seed-taking latencies.	Yes
	2. There would be no differences in seed-taking latencies in the no-stimulus baseline context compared to the wood control context.	Yes
	3. Chickadees and titmice would significantly increase their latencies to forage in the presence of the novel stimuli compared to the baseline and control stimulus presentations.	Yes
	4. The predator stimulus would result in the longest seed-taking latencies compared to the remaining contexts (baseline, wood control, and novel).	Yes
Calling Latencies	5. Chickadees would have shorter calling latencies than titmice across contexts.	Yes
	6. There would be no differences in calling latencies in the no-stimulus baseline context compared to the wood control context.	Yes
	7. Chickadees and titmice would have graded latencies to call in the novel context compared to baseline and predator contexts, based on degree of threat.	No, chickadees and titmice only decreased their latencies in the predator context.
‘D’ Note Usage	8. If chickadees and titmice perceive the novel Mega Bloks® object as less threatening than a Cooper’s hawk model, that they would have a graded response, using an intermediate number of ‘D’ notes in the novel context compared to baseline and predator contexts.	No, chickadees and titmice only increased their ‘D’ notes significantly in the predator context.

Table 8. Experiment Two: mean latencies (in sec) and rates (per/10 minutes) for foraging and calling behavior.

	Chickadee				Titmouse			
	Control	**Wood**	**Novel**	**Hawk**	**Control**	**Wood**	**Novel**	**Hawk**
Seed-taking Latency	56.0	47.4	319.1	569.5	51.9	48.3	213.8	557.9
Seed Takes	9.87	8.93	2.39	0.06	9.00	8.87	3.90	0.09
Call Latency	108.2	157.5	144.2	33.2	171.2	218.7	162.5	84.6
Call Rate	6.45	4.37	9.63	23.53	4.06	3.12	7.50	37.86

Table 9. Experiment Two: mixed-model results for seed-taking latencies. Bold values are statistically significant.

	Numerator df	*Denominator df*	*F*	*Sig.*
Intercept	1	41.0	3,214.1	**< 0.001**
Species	1	133.3	0.3	0.569
Stimulus	3	88.8	224.8	**< 0.001**
Species * Stimulus	3	88.8	1.6	0.195

Table 10. Experiment Two: mixed-model results for call latencies. Bold values are statistically significant.

	Numerator df	*Denominator df*	*F*	*Sig.*
Intercept	1	31.4	1,115.8	**< 0.001**
Species	1	133.6	13.0	**< 0.001**
Stimulus	3	97.3	12.4	**< 0.001**
Species * Stimulus	3	97.3	0.3	0.838

Table 11. Experiment Two: mixed-model results for 'D' note usage. Bold values are statistically significant.

	Numerator df	*Denominator df*	*F*	*Sig.*
Intercept	1	24.3	2,797.9	**<0.001**
Species	1	144.4	96.0	**<0.001**
Stimulus	3	76.9	3.7	**0.015**
Species * Stimulus	3	76.6	0.2	0.884

CHAPTER IV:

MIXED-SPECIES FLOCK SIZE INFLUENCES CHICKADEE REACTIONS TO NOVEL AND PREDATOR STIMULI: AN AVIARY STUDY

My contributions to this work include: (a) formulating the research idea and hypothesis (b) designing the experiment (c) trapping and banding all birds (d) collecting all data (e) doing the statistical analysis (f) interpreting results and (g) writing the manuscript.

Abstract

Mixed-species flocks of Carolina chickadees, *Poecile carolinensis*, and tufted titmice, *Baeolophus bicolor*, form during the overwintering months, and together, obtain many benefits, including increased foraging efficiency and decreased predation risk. Previous studies have shown that chickadees have significantly shorter calling latencies than titmice across several contexts, including in the presence of novel and predator stimuli. This difference may be related to the relative number of sentinel-like chickadees participating in the flock. Therefore, using aviaries, I tested the influence of chickadee flock size (two or four conspecifics) and the presence or absence of four titmice on chickadee calling behavior in two threatening contexts: low-threat novel object contexts and high-threat predator stimulus contexts. Sixteen aviaries total were presented 6 predator stimuli and 6 novel stimuli, one per day, and calling and foraging behavior was audio recorded. Using principal components analysis, call latencies and call rates loaded onto one factor (Calling Behavior), such that higher Calling Behavior scores indicated higher calling rates and shorter latencies to call. Foraging rates and foraging latencies load onto another factor (Feeder Avoidance) such that higher Feeder Avoidance scores indicated longer latencies to forage and lower foraging rates. Chickadees had lower Calling Behavior and Feeder Avoidance scores in novel object contexts compared to the predator contexts. They also produced fewer 'D' notes in their calls during the novel contexts compared to the predator contexts. Regarding flock size, chickadees had lower Calling Behavior scores when four chickadees were present compared to only two chickadees. Additionally, chickadee Calling Behavior scores were lower in the presence of titmice compared to when they were absent. Taken together,

these results suggest that group size influences anti-predator behavior, such that chickadees react less strongly to threatening stimuli in larger groups compared to when they are in smaller groups.

Introduction

We learned to be patient observers like the owl.
We learned cleverness from the crow,
and courage from the jay, who will attack an owl
ten times its size to drive it off its territory.
But above all of them ranked the chickadee
because of its indomitable spirit.
(Jones, 1978, p. 103)

Mixed-species groups occur across several taxa, including primates (e.g. Heymann & Buchanan-Smith, 2000), fish (Ward, Axford, & Krause, 2002), ungulates (Fitzgibbon, 1990), and birds (Moynihan 1962; Morse, 1970). Members in these groups obtain many benefits, including decreased predation risk and increased foraging efficiency (Lima & Dill, 1990). Some postulate that it is the ability for heterospecifics to exploit information from one another, especially high-quality information (Bell, Radford, Rose, Wade, & Ridley, 2009), that is a driving force in the formation of mixed-species groups (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010). For example, groups members can use signals to determine predator type (Rainey, Zuberbühler, & Slater, 2004), or degree of threat (Bell, Hankison, Laskowski, 2009; Fallow & Magrath, 2010; Templeton & Greene, 2007). In addition, some participants may be better able to find important resources, including food. Turkey vultures, *Cathartes aura*, and black vultures, *Coragyps atratus*, for example, are communal roosters and benefit from such group living by gleaning information from their roost mates (Buckley, 1996). Turkey vultures have a more acute sense of smell, and thus are able to find food more quickly than black vultures, which mainly use visual cues (Buckley, 1996). Therefore, black vultures usually use cues from turkey vultures to find food. Overall, it is important to assess the costs and benefits associated with species participating in mixed-species groups.

Mixed-species flocks of Carolina chickadees and tufted titmice and other follower species, including white-breasted nuthatches and downy woodpeckers, have been studied in an attempt to determine the costs and benefits of mixed-species avian flocks. Many of these studies have focused on how flocking influences anti-predatory behavior, including vigilance and alarm calling. According to the 'many eyes' hypothesis, vigilance per individual should decrease as the number of participating members increases (Lima & Dill, 1990). This is evident for downy woodpeckers and white-breasted nuthatches, as they spend less time being vigilant when participating in the flock and, as a result, are able to spend more time foraging (Sullivan, 1985b, Dolby and Grubb, 1998). Similarly, downy woodpeckers gave alarm calls less often in response to predators when other members of the mixed flock were present (Sullivan 1985a). However, when titmice were removed from woodlots, chickadee vigilance behavior did not increase (Cimprich & Grubb, 1994). In addition to benefiting from the presence of 'many eyes' and reducing alarm calling behavior when other individuals are present, some individuals benefit from other flock members' speed of detection and defense against predators. For example, chickadees and nuthatches are typically the first to approach and start mobbing threatening predators compared to titmice (Nolen & Lucas, 2009).

Furthermore, chickadees and titmice in these flocks are known to use graded vocal signals to identify the degree of predation threat (Courter & Ritchison, 2010; Soard & Ritchison, 2009). Chickadees also obtain information from titmouse calls regarding degree of predator threat (Hetrick and Sieving, 2012). Other flock members obtain information from chickadee and titmouse vocalizations. For example, chickadees and titmice frequently call to each other to maintain contact within mixed-species flocks (Hailman, 1989). Downy woodpeckers use these contact calls to assess the presence of heterospecific flock members (Sullivan, 1984). Downy woodpeckers also respond to heterospecific alarm calls, but rarely produce alarm calls themselves. They use the calls of chickadees and titmice as an 'all clear' signal after the danger of predation has passed (Sullivan, 1984).

In order to better understand the intricacies of the relationships between species participating in these mixed-species flocks, previous research tested whether species-level behavioral traits, such as neophobia and neophilia or shyness and boldness could help explain the differential reactions to novel and predator stimuli observed (Chapters 2 and 3). For example, why might chickadees be more likely to mob a predator compared to titmice? Is it related to their subordinate status in relation to titmice? What about species-level behavioral traits? In a mixed-species group, having a species that is bolder or more neophilic can be advantageous, especially if individuals with these traits tend to inspect threats more often (e.g. Pellegrini, Wisenden, & Sorensen, 2010) and explore novel microhabitats where food or safe shelter may be found (e.g. Wilson et al., 1993). Previous research, however, showed there was no evidence that either species was more neophilic or bold than the other, based on latencies to forage near novel or threatening stimuli (Chapters 2 & 3). Interspecific dominance hierarchies did not seem to be influential, either. However, because those studies also measured the vocal behavior of flock participants, interesting results revealed that chickadees consistently had shorter *chick-a-dee* calling latencies compared to titmice, and called significantly faster in predator contexts. In addition, although chickadees had shorter calling latencies, they did not have higher calling rates than titmice across contexts (Browning, unpublished data).

A decrease in *chick-a-dee* call latency in the presence of threatening stimuli is important, as it can serve to alert other participating flock members of potential threat (Baker & Becker, 2002). Latencies to call can also indicate the urgency of the threat, as was observed when black-capped chickadees were presented hawk models at two distances, 1 m (higher threat) and 6 m (lower threat) (Baker & Becker, 2002). Chickadees had a shorter latency to call when the hawk was at the more threatening distance of 1 m.

The ‘many eyes’ hypothesis postulates that an increase in the number of members in a group decreases the level of vigilance each individual participating in the group needs (Krause & Ruxton, 2002). Previous studies testing the ‘many eyes’ hypothesis in mixed-species flocks of chickadees and titmice have found that removal of titmice modified the foraging habits of chickadees, but did not increase their overall vigilance (Cimprich & Grubb, 1994). In contrast, titmice who foraged alone had higher vigilance rates compared to when they were foraging with chickadees (Pravosudov & Grubb, 1999). While the previous experiments in Chapters 2 & 3 did not overtly measure vigilance (by means of head turns or 'look ups'), there was an assumed trade-off between vigilance and foraging, such that the more vigilant an individual was, the less foraging it was able to do (Dolby & Grubb, 1998). Additionally, individuals who are less vigilant because they are participating in heterospecific groups are less likely to vocalize during threat (Sullivan 1985a). Previous results (Chapters 2 & 3) did not observe species differences in foraging behavior in threatening contexts, but did observe species differences in calling behavior in threatening contexts. More specifically, chickadees had significantly shorter calling latencies than titmice in both novel and predator contexts. This may have been due to normal flock variations in the number of species participating.

In light of this, in the current experiment, I wanted to further explore why chickadees had shorter latencies to call compared to titmice. Considering the previous research on the costs of interspecific interactions to chickadees (e.g. Pravosudov & Grubb, 1999), and how the absence of titmice improved chickadee foraging behavior (Cimprich & Grubb, 1994), I wanted to determine how flock composition influenced chickadee behavioral and vocal reactions to novel and predator stimuli. Using semi-naturalistic aviaries, I manipulated the presence or absence of titmice, and also manipulated chickadee flock size (2 or 4 individuals). In East Tennessee populations, the average number of chickadees and titmice per flock is 3.4 ± 1.2 SD and 3.1 ± 1.1 SD, respectively (Chapters 2 & 3). Therefore, I aimed to capture flocks of 4 individuals for each species, but due to difficulties trapping 4 chickadees at certain locations, half of the chickadee flocks only had 2 individuals. Thus, chickadee flock sizes mimicked natural fluctuations in chickadee flock size, with half of the flocks being 'average-sized' with 4 chickadees and half being 'small-sized' with 2 chickadees. Each aviary flock was tested with a total of 6 novel and 6 predator stimuli and foraging rates and latencies as well as calling rates and latencies were recorded. Additionally, because previous research consistently showed significant differences between baseline contexts and novel and predator contexts, I focused on the behaviors observed in the novel and predator contexts in this study.

Stimuli

Many experiments testing for chickadee and titmouse reactions to predator stimuli use either real hawks and owls or models of these species (Baker & Becker, 2002; Bartmess-Levasseur et al., 2010; Courter & Ritchison, 2010; Templeton, Greene, & Davis, 2005). There is a negative correlation between the number of 'D' notes used per call and the wingspan of avian predators (Courter & Ritchison, 2010; Soard & Ritchison, 2009). This would lead one to believe that avian predators with smaller wingspans, such as eastern screech owls, *Megascops asio*, and sharp-shinned hawks, *Accipiter striatus*, would be more threatening than larger owls and hawks, such as great horned owls, *Bubo virginianus*, and Cooper's hawks, *Accipiter cooperii*. In fact, avian predators such as the sharp-shinned and Cooper's hawks have been listed as the main avian predators of chickadees (Mostrom, Curry, & Lohr, 2002) and titmice (Grubb & Pravasudov, 1994). Snakes are also listed as nest predators for both species (Grubb & Pravasudov, 1994; Mostrom, Curry, & Lohr, 2002). As such, in order to present a variety of predator stimuli, I included stimuli of differing perceived threat, including a plastic great horned owl and a plastic snake, as well as stuffed study skins of eastern screech owls, a Cooper's hawk, and a sharp-shinned hawk (Figure 9).

A variety of novel stimuli were also presented. Stimulus size and color can influence reactions to novelty (Berlyne, 1950; Greenberg, 1993). For example, various species of warblers had longer latencies to approach large leaves compared to small leaves (Greenberg, 1983). The color pink is also consider novel, because pink is not a color frequently seen in their environment, and therefore individuals are not likely to associate it with any prior stimuli (Kluen, Kuhn, Kempenaers, & Brommer, 2012). For that reason, I chose to use colorful objects, including two pink objects (a baby rattle and a ball), a trio of plush bowling pins, a wooden bird model, a Bristle Block Stackadoo ® object, and a paper 3D star.

Predictions

Foraging Behavior

Based on previous research, I expected that 1. *Foraging rates and foraging latencies would be negatively correlated.* Because chickadees have been known to forage in more preferred areas when titmice were removed (Cimprich & Grubb, 1994), I predicted that 2. *Chickadees would have significantly shorter foraging latencies and higher foraging rates when titmice were absent compared to when they were present*. Because vigilance rates should decrease with increasing number of individuals present (Krause & Ruxton, 2004), 3. *Chickadees in flocks of four individuals were predicted to have higher foraging rates and shorter foraging latencies than flocks with two chickadees*. Additionally, across flock compositions, 4. *Chickadees were predicted to have higher foraging rates and shorter foraging latencies in the novel contexts compared to predator contexts* based on similar results (Chapters 2 & 3).

Calling behavior

It was predicted that 5. *There would be a negative relationship between calling rates and calling latencies*. Additionally, 6. *Higher calling rates and lower latencies to call were predicted in the predator contexts compared to novel contexts*.

There are two possible effects that group size and/or composition can have on chickadee calling behavior. One, call rates in social groups have been shown to increase as a function of group size (e.g. Payne, Thompson, & Kramer, 2003). Furthermore, number of alarm callers can be indicative of threat urgency, as is the care in Richardson's ground squirrels, *Spermophilus richardsonii* (Sloan & Hare, 2008). Squirrels increased the time spent being vigilant when two squirrels were alarm calling compared to only one. Because the 'many eyes' hypothesis postulates that larger groups should be better equipped to recognize threats (Lima & Dill, 1990), one could assume that these groups vocalize about the threat with a faster latency and also have higher calling rates. Therefore, I predicted that 7a. *An increase in flock size, whether it be intraspecific (only 2 chickadees to only 4 chickadees) or interspecific (4 chickadees only to 4 chickadees and 4 titmice) would decrease calling latencies and increase calling rates*. Flocks with four chickadees are therefore predicted to have shorter calling latencies than flocks with 2 chickadees, because more 'sentinel-like' individuals would be present to react to the stimuli.

However, another postulate of the 'many eyes' hypothesis is that, in larger groups, individual vigilance levels are reduced, thus reducing stress and providing more time for foraging. Birds with higher energetic stress levels, or increased stress due to lack of proper nutrition, are known to have higher calling rates (Lucas, Schraeder, & Jackson, 1999). Therefore one could predict that 7b. *A decrease in flock size, whether it be intraspecific or interspecific, will require higher vigilance levels, causing birds to forage less often, and therefore result in higher individual stress levels*. Subsequently, this stress can manifest as higher calling rates and shorter calling latencies.

'D' Note Usage

Broadband 'D' notes are used often in mobbing contexts (Courter & Ritchison, 2009; Nolen & Lucas, 2009; Sieving, Contreras, & Maute, 2004; Sieving, Hetrick, & Avery, 2010; Soard & Ritchison 2009; Templeton, Greene, & Davis, 2005). Previous studies show that they are used more often in predator contexts compared to novel contexts, during which chickadees treat the novel stimulus much like baseline contexts (Chapter 3). Considering this, I predicted this study would repeat these findings, such that 8. *More 'D' notes would be used in calls for predator contexts compared to novel contexts*. Additionally, because mobbing calls are used to attract more species to the location (Gunn et al., 2000), I predicted that 9. *Individuals in smaller flock sizes would use more 'D' notes in* *their calls than individuals in larger flock sizes, regardless of mixed-species flock composition*. Furthermore, if chickadees do play a more ‘sentinel-like’ role in these flocks, then 10. *Flocks with more chickadees were predicted to use more ‘D’ notes than flocks with fewer chickadees*.

Methods

Data were collected from October 2013 through February 2014 and October 2014 through January 2015 with two rounds of data collected during the first winter and two additional rounds collected during the second winter. Chickadees and titmice were captured from independent flocks separated by at least 400m (Bartmess-LeVasseur et al., 2010) at the University of Tennessee Forest Resources AgResearch and Education Center (UTFRREC) in Oak Ridge, Tennessee (35°59’37.40”N, 84°12’58.08”W, elevation 309 m) using walk-in treadle traps. These traps were placed on a wooden board (24cm X 40cm X 2cm) atop a steel pole (1.8 m in height) and baited with a 1:1 mixture of sunflower and safflower seeds. I tried to capture all birds using walk-in treadle traps because there is evidence that trapping experience has long term behavioral consequences (Linhart, Fuchs, Poláková, & Slabbekoorn, 2012). However, if the required number of birds had not been captured after at least five treadle trapping days at a single site, mist nets were used to capture the remaining birds. I only had to use mist nets to capture 3 of the total 48 birds used in this study. After being captured, all chickadees were fitted with unique colored leg bands. They were then weighed, had their wing-chords measured in order to ascertain sex (based on Harvey & Freeberg, 2008) and released into an aviary. Captured titmice were fitted with unique colored leg bands and were released into an aviary. No additional measurements were made for titmice.

Aviaries

There were four semi-naturalistic outdoor aviaries (6m X 9m X 3.5m) that had at least two young trees (maximum of 3 m in height), multiple perches hanging from the ceiling, and branches resting in the aviary corners. There was also a building attached to one side of the aviary that provided shelter from the elements. A feeding station was placed in the center of each aviary, on a metal pole (height varied between 127-140 cm) fixed with a wooden board on top (71cm long X 24 cm wide). This is where all stimuli were placed during data collection. A long perch was placed about half a meter above the feeding station. Food and water were provided ad libitum in variously sized plastic bowls and ceramic ramekins and were placed on the central feeding stand and in the building. Ad libitum foods included safflower seeds, sunflower seeds, peanut suet pellets, a fruit and nut mixture, and shelled sunflower seeds. Their most preferred foods, dried mealworms and live mealworms, were only provided on acclimation and data collection days.

Flock Compositions

The number of chickadees (two or four) and the presence or absence of titmice (zero or four) was manipulated (Figure 10). Two chickadees were placed in two aviaries and four chickadees were placed in the other two aviaries, resulting in 12 total chickadees per aviary round. Chickadees placed in the same aviaries were mostly trapped from the same site, and therefore were participating in the same flock, although six chickadees had to be captured from neighboring flocks due to difficulties trapping the necessary number of birds from the same flock. Once all twelve chickadees had been captured for an aviary round, four titmice were captured from two sites and placed into each of two aviaries. One of the eight titmice groups had three titmice rather than four. I was only able to capture three titmice at one site, and because titmice react aggressively to non-flock members in the aviaries (Freeberg, personal communication), I did not attempt to capture another bird from a neighboring site.

Acclimation

Once all chickadees and titmice had been captured, flocks were given at least one week to acclimate to the aviaries and to my presence. Each day during the acclimation period, I sat in the aviaries in the same location I would sit during real data collection for forty-five minutes to one hour per day. I observed the birds, calling out their behavior to acclimate them to my voice as well. Birds were also introduced to live mealworms during this time. Aviaries were prepared for data collection once all birds were acclimated to my presence and readily fed from the central feeding station.

Procedure

In a given aviary, a microphone was placed within 1 m and facing the central feeding station. It was connected to a Marantz PMD660 portable digital recorder that recorded sound files onto a compact flash memory card at a sampling rate of 44.1 kHz and 16-bit resolution. Access to the inner aviary building was blocked. The highly preferred dried and live mealworms were placed on the central feeding stand, but other food options (e.g. sunflower seeds) were left on the feeding stand, and a 10-minute baseline audio recording was started. Calling behavior, foraging behavior, and dominance interactions (chases and supplants) were noted for each chickadee. After the 10-minute baseline audio recording, I quickly placed the stimulus on the central feeding stand, opposite the food, and began the stimulus audio recording. Stimulus audio recordings lasted 30-minutes at most, though calling behavior of each chickadee was only noted for the first 10-minutes. An extra 20 minutes was provided to allow time for the more shy birds to approach and/or feed near presented stimuli. If all chickadees in a flock foraged at the central stand prior to the 30-minute cap, the audio recording was ended.

Stimuli

During each round, an aviary was presented with a total of six predator and six novel stimuli (Figure 9, located at the end of this chapter in Appendix A). Predator models included study skins of a sharp-shinned hawk, *Accipiter stiatus*, red morph of an eastern screech owl, *Megascops asio*, grey morph of an Eastern screech owl, Cooper's hawk, *Accipiter cooperii*, plastic coiled rattlesnake, and plastic great horned owl, *Bubo viginianus*. The rattlesnake was not a predator to these species, but resembled the general shape of an eastern rat snake, *Pantherophis alleghaniensis*, a natural nest predator of chickadees and titmice. In order to maintain the study skins in an upright position on the feeding station, wire was shaped around a bamboo rod, such that a pocket was formed where the tail and feet of the study skins could be placed, thus keeping the model in a stable upright position. The bamboo rod was then fastened to the feeding station with a c-clamp.

Novel stimuli consisted of a Bristle-block Stackadoo ® object, Hello Kitty Ball, 3D paper star, wooden bird model, a trio of stuffed bowling pins (Fun Years Soft Starts©), and a plastic geometric pink baby rattle. Each aviary round was presented with all twelve stimuli in the same order, with one stimulus being presented to each aviary per day.

Titmouse-Switching

After the first three predator stimuli and three novel stimuli had been presented to each aviary, the two sets of four titmice that were in two aviaries were captured using baited walk-in treadle traps placed on the central feeding station in the aviaries and moved to the two aviaries that previously did not have titmice (Figure 10). Once all titmice had been switched to their new aviaries, birds were given at least four days to acclimate to their new flock compositions. Afterwards, the remaining three predator stimuli and three novel stimuli were presented to the flocks.

Statistical Analyses

All audio recordings were saved as .wav files and viewed in Cool Edit Pro (2.0). From these recordings, latencies to forage from the central stand, foraging rates, latencies to call, and calling rates were obtained for each chickadee. Calls from each chickadee were coded based on the number of 'D' notes per call.

SPSS (Version 22) was used to run the statistical analysis. Factor analysis was done on the four main dependent variables (call latency, call number, foraging latency, foraging visits) for each individual chickadee, using principle components analysis (PCA) with a Varimax rotation. Mixed models analyses were run on each resulting Factor, with individual 'Chickadee' as a random factor and 'Titmice Present' and 'Stimulus' as repeated factors. Given the significant effects of novel and predator stimuli found in the two previous experiments, this study focused only on the differences observed in the Novel and Predator contexts and removed the Baseline contexts from analysis. If significant 3-way or 2-way interactions were found, further mixed models analyses were run to determine the relationship between the interacting factors. Similar analyses and data exploration were done for 'D' notes.

Results

One hundred and twenty eight hours of sound recordings were obtained from 48 chickadees housed in 16 semi-naturalistic aviary flocks, resulting in 15,065 coded chickadee calls. Of those coded calls, approximately 92% were from identified flock members and approximately 8% were from unidentified flock members.

Factor analysis reduced the four independent variables to two factors, accounting for 75.9% of the variance. Foraging latency (0.897) and foraging rates (-0.892) loaded onto PC1 (Feeder Avoidance) such higher PC1 scores were associated with longer latencies for an individual to forage at the central stand and fewer foraging visits at the central feeding stand in a 10-minute period. Similarly, call latency (-0.845) and call rates (0.811) loaded onto PC2 (Calling Behavior) such that higher PC2 scores were associated with shorter latencies for an individual to call and a higher individual calling rate during a 10-minute period.

PC1 (Feeder Avoidance)

There was a main effect of stimulus type, such that chickadees had shorter latencies to forage and had higher foraging rates (lower Feeder Avoidance scores) in novel contexts compared to predator contexts (Figure 11; Table 13). See Table 14 for average seed and call latencies and rates. There was also a significant three-way interaction between 'chickadees present', 'titmice present', and stimulus ‘type’ (novel, predator) (Figure 12). Flocks of four chickadees had faster latencies to forage and higher foraging rates in the presence of novel stimuli, when titmice were also present. When no titmice were present, flocks of four chickadees have significantly lower Feeder Avoidance scores than flock of two chickadees when a predator was presented.

PC2 (Calling Behavior)

There was a significant main effect for stimulus type, such that chickadees had significantly higher Calling Behavior scores (shorter latencies and higher calling rates) in the predator contexts compared to the novel contexts (Figure 13; Table 15). There was also a significant main effect for number of chickadees present, such that flocks with 4 chickadees had shorter calling latencies and higher calling rates than flocks with 2 chickadees. Similarly, there was a significant main effect for presence of titmice, where flocks with titmice had significantly longer calling latencies and lower calling rates than flocks without titmice.

‘D’ Note Usage

There was a significant effect of stimulus type, such that chickadees used significantly more ‘D’ notes in the Predator context compared to the Novel context (Figure 14; Table 16). There were no other significant main effects or interactions.

Discussion

The results in this experiment suggest that group size influences chickadee behavior in the presence of novel and predator stimuli. As was predicted from previous research, chickadee foraging rates and foraging latencies were associated and were combined into a single principal component, named ‘Feeder Avoidance’ (prediction 1). A low ‘Feeder Avoidance’ score indicated that chickadees had higher foraging rates and shorter foraging latencies. Similarly, calling latency and calling rate were negatively associated as predicted (prediction 5) and were combined into another principal component, named

'Calling Behavior'. Together, these variables and 'D' note usage depended on the stimulus type presented, chickadee flock size, and presence or absence of titmice.

Novel versus Predator Stimuli

As expected, chickadees differentially reacted to novel and predator stimuli. Regardless of conspecific flock sizes or the presence or absence of titmice, chickadees exhibited less Feeder Avoidance in novel stimulus contexts compared to predator stimulus contexts (prediction 4). Chickadees also had longer latencies to call and lower calling rates in novel contexts compared to predator contexts, thus supporting prediction 6. Finally, chickadees used more 'D' notes in their calls in predator contexts compared to novel stimulus contexts, supporting prediction 8. Together, these results suggest that novel stimuli affect chickadee calling and foraging behavior, but not as strongly as predator stimuli.

Effect of Chickadee Flock Size

Half of the flocks tested in this experiment had two chickadees participating and the other half had four chickadees participating. The prediction that chickadees would have significantly less Feeder Avoidance when four chickadees were in the flock compared to only two (prediction 3), was not supported. Even if chickadees in the smaller flocks were required to be more vigilant than chickadees in flocks of four, this did not significantly affect their foraging rates in the presence of novel and predator stimuli.

Nevertheless, chickadee group size did affect Feeder Avoidance in predator contexts (but not in novel context) when titmice were not present. Chickadees in flocks of four avoided the feeder significantly less than chickadees in flocks of two. This suggests that chickadees are faster to approach predators when more conspecifics are present. Chickadees have been known to be one of the primary responders to predators, approaching and mobbing perched predator stimuli quicker than titmice (Nolen & Lucas, 2009). This may be related to the greater probability that a chickadee will detect and respond to a predator when four are present versus two, assuming the ‘many eyes’ hypothesis (Krause & Ruxton, 2002).

Additionally, chickadee flock size affected Calling Behavior. Flocks with only two chickadees had shorter calling latencies and higher calling rates than flocks of four chickadees. These results support prediction 7b, suggesting that possible stressors to chickadees participating in smaller flocks (e.g. increased individual vigilance levels; Lima, 1995) increased their calling behavior (e.g. Lucas, Schraeder, & Jackson, 1999). Flocks with four chickadees had lower Calling Behavior scores across contexts. This was likely due to a dilution of vigilance which reduced individual stress levels and resulted in lower calling rates and longer calling latencies. Future studies should include vigilance measures, such as rate of ‘look ups’ per individual, to gauge if calling rates and vigilance are negatively associated.

While chickadees in flocks of four called significantly less than chickadees with only two conspecifics in the flock, there was no effect of chickadee flock size on the number of ‘D’ notes used per call across contexts. Thus, prediction 10 was not supported. This suggests that even though chickadees in flocks of two increased their calling rates compared to chickadees in groups of four, they did not necessarily perceive their situation as more threatening.

Effect of Presence or Absence of Titmice

In general, the absence of the socially dominant titmice did not significantly decrease chickadee Feeder Avoidance, thus not supporting prediction 2. However, there was an effect of the presence or absence of titmice on Feeder Avoidance in novel stimulus contexts when four chickadees were in the flock. Chickadees in flocks of four had significantly lower Feeder Avoidance when titmice were present compared to when they were absent. Thus, chickadees were bolder in their reactions to novelty when titmice were also present. This may either be an effect of flock composition or group size, as when titmice were present, there were 8 total birds participating as opposed to 4 birds when only chickadees were present. Further research needs to address whether it is the mix of chickadees and titmice in the flocks of eight participants that influenced Feeder Avoidance scores, or if it is an effect of 'safety in numbers', where any additional four bird species paired with four chickadees (e.g. an additional four chickadees or nuthatches) also results in a decrease in Feeder Avoidance.

Regarding Calling Behavior scores, the presence of titmice significantly decreased chickadee Calling Behavior across contexts compared to when titmice were absent. In other words, when titmice were participating in the flock, chickadees had longer latencies to call and lower calling rates compared to when titmice were absent. Again, this suggests 'safety in numbers' or a dilution of perceived risk when titmice are also participating in the flock. The number of 'D' notes per chickadee call, however, was not influenced by the presence or absence of titmice, thus providing no support for prediction 9. Because an increase in 'D' notes is associated with an increase in perceived risk (Bartmess-Levasseur et al., 2010; Courter & Ritchison, 2010; Soard & Ritchison, 2009; Templeton & Greene, 2007), it is likely that the increased calling rates by chickadees when titmice were not present was related more to individual stress levels, possibly due to the perceived need for increased vigilance levels. Because chickadees are suggested to be sentinels in these flocks, it would be interesting to test how flock size and composition influences their vigilance rates, measured by 'look ups' (Pravosudov & Grubb, 1999) or by inter-scan intervals (e.g. Roberts, 1995). If chickadees truly are less stressed in larger groups, and it is a function of diluted vigilance and anti-predator behavior, I would expect to see decreased vigilance in larger groups.

Conclusions

Taken together, these results suggest that group size and the presence or absence of participating heterospecifics might be a factor influencing how mixed-species flocks react to various stimuli, including low-threat novel and high-threat predator stimuli. Further research is needed to determine whether the presumed increase in stress in smaller flocks is due to an increase in the level of vigilance required per individual. This experiment provides the foundation for future studies of the influences of flock composition, and how other factors, such as vigilance rates, kin selection, or ratio of other participating members, influences anti-predator behavior in mixed-species groups.

Appendix A: Figures

Figure 9. Experiment Three: the predator stimuli and novel stimuli presented. Predators in top image from left to right: plastic Great horned owl model, study skins of a female Cooper’s hawk, a sharp-shinned hawk, a screech owl (red morph), a screech owl (grey morph), and a plastic rattlesnake. Novel stimuli in bottom image: (top row) Bristle Block Stackadoo® object, paper star, Hello Kitty© ball (bottom row) baby rattle, wooden bird, and stuffed bowling pins.

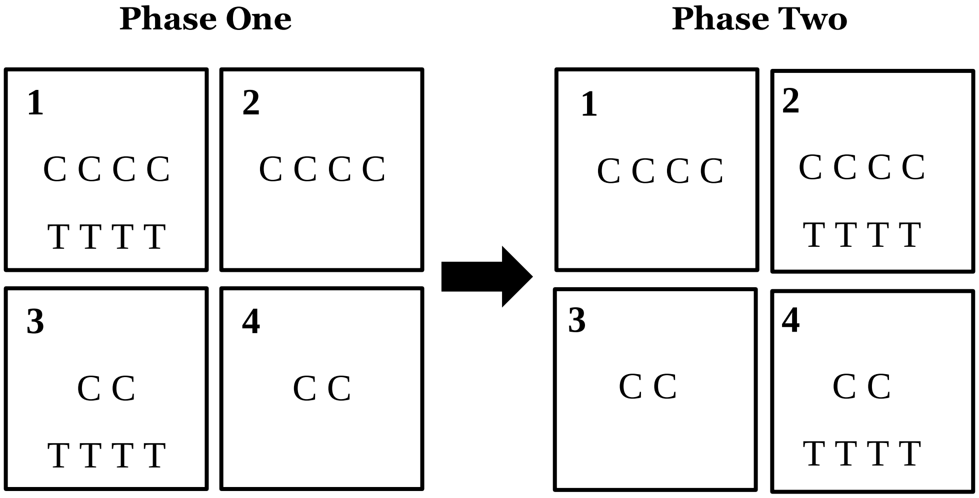

Figure 10. Experiment Three: flock compositions during Phase One and Phase Two. Each square represents one aviary; C = Chickadee; T = Titmouse

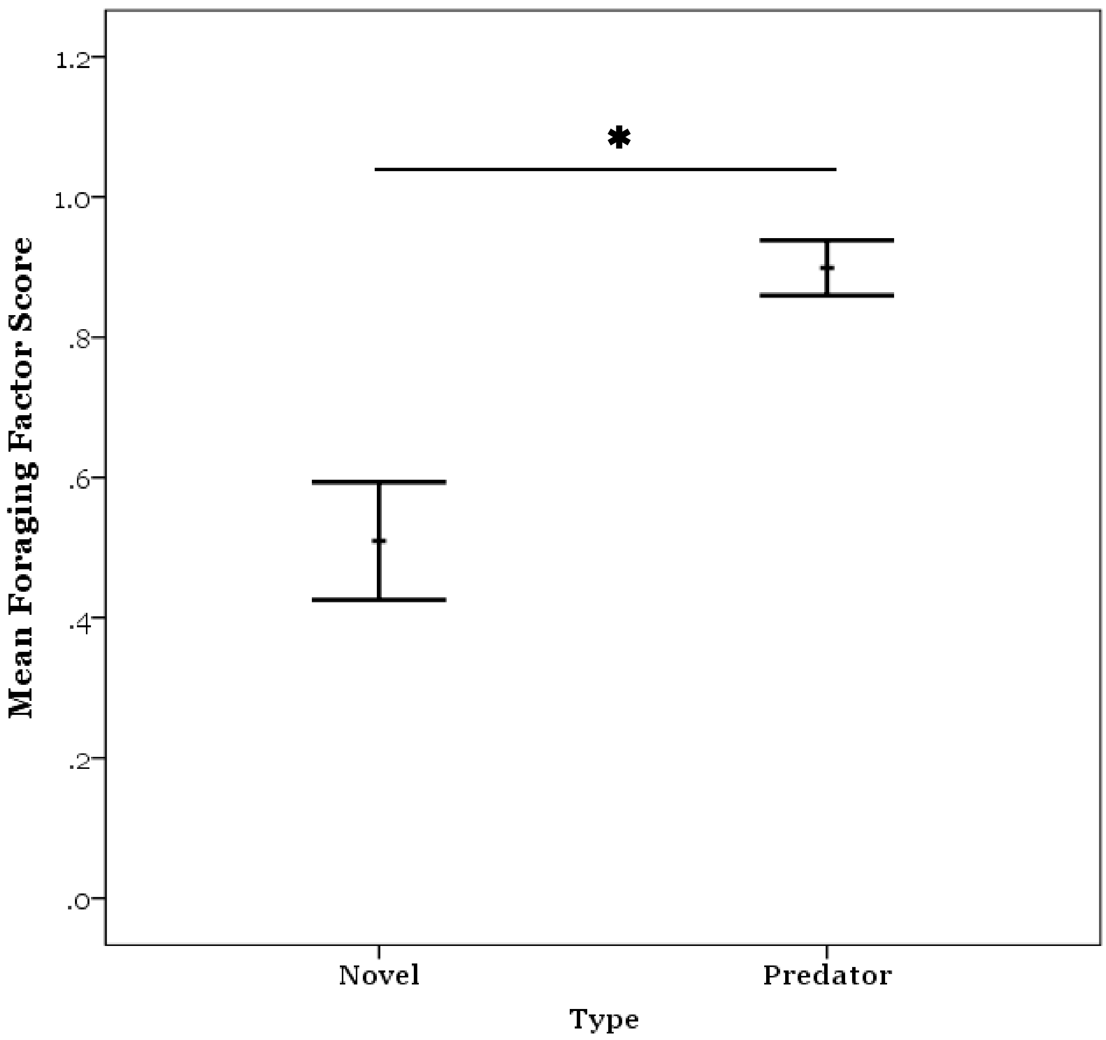

Figure 11. Experiment Three: the main effect of stimulus type for Feeder Avoidance scores. Error bars represent means with 95% confidence intervals. A bar with a star indicates a significant difference. Chickadees had significantly higher foraging latencies and lower foraging rates in the presence of predator stimuli compared to novel stimuli.

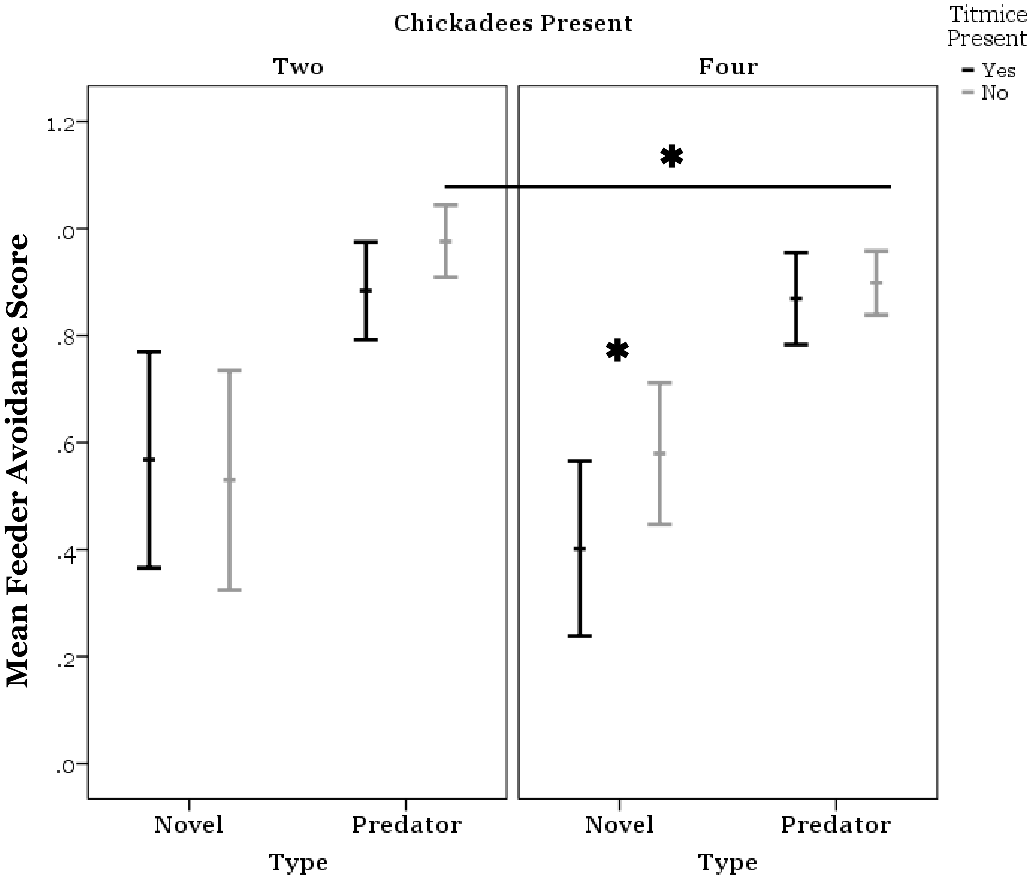

Figure 12. Experiment Three: mean Feeder Avoidance scores. Error bars represent means with 95% confidence intervals. A bar with a star represents significant differences in mean Feeder Avoidance between chickadees flock sizes. Lower Feeder Avoidance scores indicate a shorter foraging latencies and a higher foraging rate. A star without a bar indicates significant differences between the presence and absence of titmice. When four chickadees are present, chickadees have lower Feeder Avoidance when titmice are also present compared to when they are absent. In predator contexts, when titmice are absent, chickadees have lower Feeder Avoidance when four chickadees are present compared to only two. Regardless of flock size or composition, chickadees have lower Feeder Avoidance in novel contexts compared to predator contexts.

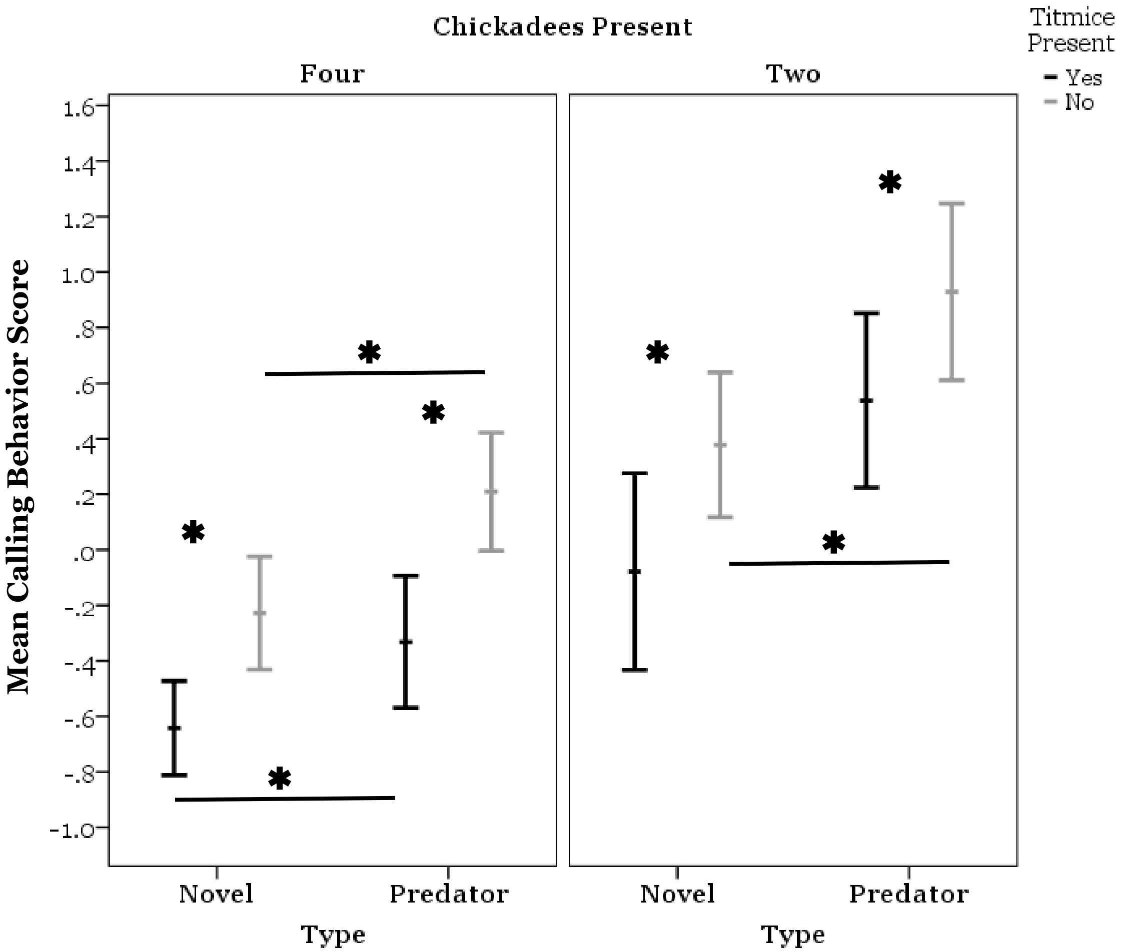

Figure 13. Experiment Three: mean Calling Behavior scores. Error bars represent means with 95% confidence intervals. A bar with a star represents significant differences in mean Calling Behavior scores between chickadees flock sizes. Lower Calling Behavior scores indicate longer calling latencies and lower calling rates. A star without a bar indicates significant differences between the presence and absence of titmice.

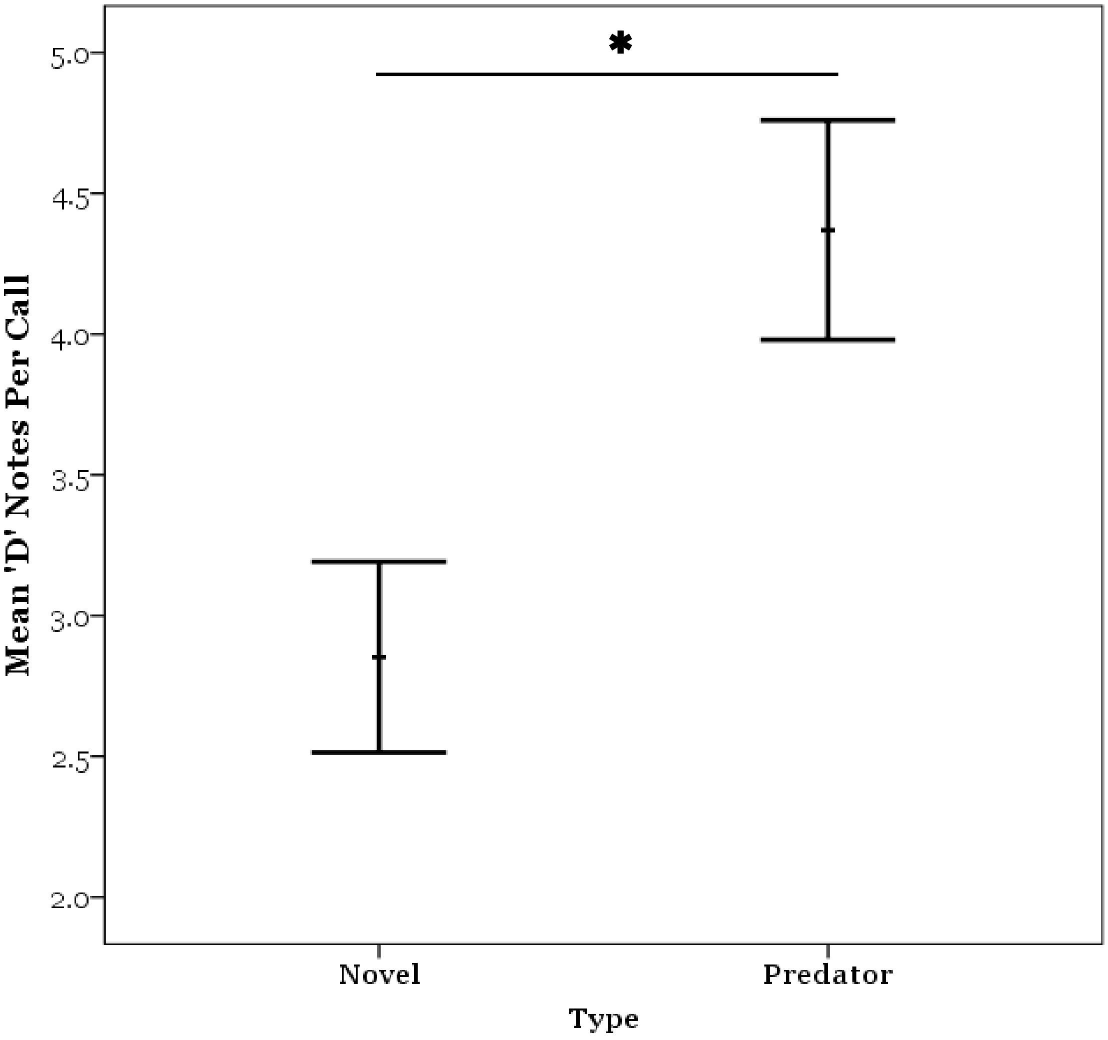

Figure 14. Experiment Three: the main effect of Type for mean ‘D’ notes per call. Error bars represent means with 95% confidence intervals. Chickadees used more ‘D’ notes in predator contexts compared to novel contexts.

Appendix B: Tables

Table 12. Experiment Three: predictions.

	Prediction	***Supported?***
Foraging Behavior	1. Foraging rates and foraging latencies would be negatively correlated	Yes
	2. Chickadees would have significantly shorter foraging latencies and higher foraging rates when titmice were absent compared to when they were present.	Mainly no, but did have less Feeder Avoidance in novel contexts when titmice were present.
	3. Chickadees in flocks of four individuals would have higher foraging rates and shorter foraging latencies than flocks with two chickadees.	No, there was no effect of chickadees present on foraging behavior
	4. Chickadees were predicted to have higher foraging rates and shorter foraging latencies in the novel contexts compared to predator contexts	Yes
Calling Behavior	5. There would be a negative relationship between calling rates and calling latencies	Yes
	6. Higher calling rates and lower latencies to call were predicted in the predator contexts compared to novel contexts.	Yes
	7a. An increase in flock size, whether it be intraspecific (only 2 chickadees to only 4 chickadees) or interspecific (4 chickadees only to 4 chickadees and 4 titmice) would decrease calling latencies and increase calling rates.	No, increased flock sizes decrease calling behavior across contexts
	OR	
	7b. A decrease in flock size, whether it be intraspecific or interspecific, will require higher vigilance levels, causing birds to forage less often, and therefore result in higher individual stress levels. Subsequently, this stress can manifest as higher calling rates and shorter calling latencies.	There was an effect of titmice present and number of chickadees present. Calling latencies increased and calling rates decreased when titmice were present as well as when 4 chickadees were in the flock.

Table 12. Continued.

	Prediction	*Supported?*
'D' Note Usage	8. More 'D' notes would be used in calls for predator contexts compared to novel contexts	Yes
	9. Individuals in smaller flock sizes would use more 'D' notes in their calls than individuals in larger flock sizes, regardless mixed-species flock composition	No, there was no effect of flock size or composition.
	10. Flocks with more chickadees would use more 'D' notes than flocks with fewer chickadees.	No, there was no effect of chickadees present.

Table 13. Experiment Three: mixed-model results for Feeder Avoidance. Bold values are statistically significant.

	Num. df	***Denom. df***	***F***	***Sig.***
Intercept	1	33.1	427.5	**<0.001**
Titmice Present	1	127.0	1.9	0.168
Chickadees Present	1	33.1	0.5	0.485
Type	1	34.7	30.4	**<0.001**
Titmice Present*Chickadees Present	1	127.0	1.9	0.166
Type*Titmice Present	1	127.0	0.4	0.506
Type*Chickadees Present	1	34.7	0.04	0.833
Type*Titmice Present*Chickadees Present	1	127.0	9.7	**0.002**

Table 14. Experiment Three: mean latencies (in sec) and rates (per 10 minutes) per individual for foraging and calling behavior.

Variable	**Type**			
	Before Novel	**Novel**	**Before Predator**	**Predator**
Foraging Latency	320.2	1,346.6	323.0	1,711.1
Foraging Rate	1.6	0.4	1.5	0.1
Call Latency	186.6	273.3	179.9	184.5
Call Rate	10.0	9.0	11.2	16.0

Table 15. Experiment Three: mixed-model results for Calling Behavior. Bold values are statistically significant.

	Num. df	***Denom. df***	***F***	***Sig.***
Intercept	1	44.1	0.8	0.390
Titmice Present	1	38.9	22.0	**<0.001**
Chickadees Present	1	44.1	15.0	**<0.001**
Type	1	40.8	22.0	**<0.001**
Titmice Present*Chickadees Present	1	38.9	0.001	0.979
Type*Titmice Present	1	223.4	0.002	0.968
Type*Chickadees Present	1	40.8	0.5	0.505
Type*Titmice Present*Chickadees Present	1	223.4	0.3	0.568

Table 16. Experiment Three: mixed-model results for 'D' Note Usage. Bold values are statistically significant.

	Num. df	***Denom. df***	***F***	***Sig.***
Intercept	1	47.1	395.4	**<0.001**
Titmice Present	1	126.8	0.1	0.743
Chickadees Present	1	47.1	0.5	0.496
Type	1	128.5	39.1	**<0.001**
Titmice Present*Chickadees Present	1	126.8	0.02	0.882
Type*Titmice Present	1	126.3	0.2	0.650
Type*Chickadees Present	1	128.5	0.1	0.774
Type*Titmice Present*Chickadees Present	1	126.3	1.2	0.272

CHAPTER V: CONCLUSIONS

"The chickadee and nuthatch are more inspiring
society than statesmen and philosophers…"
(Thoreau, 1906, p. 171)

The approach to, or avoidance of, stimuli is one of the basic decisions animals must make (Schneirla, 1959). Typically, animals approach beneficial stimuli and avoid harmful stimuli (reviewed in Elliot, 2006). However, when a stimulus is novel, individuals cannot be certain the stimulus is beneficial or harmful until they experience it. Some individuals are more likely to approach novel stimuli, regardless of its unknown benefit or harm, while others are more likely to avoid novel stimuli. These differences in individual reactions to novelty can be indicative of different 'behavioral types,' 'personality,' or 'temperaments'. As such, the experiments conducted in this dissertation first aimed to determine if there were species-level differences in how Carolina chickadees and tufted titmice, two species that form mixed-species flocks during overwintering months, responded to novel stimuli (Chapter 2) and then compared those novel reactions to those of predator stimuli (Chapter 3). The final experiment manipulated chickadee flock size and the presence or absence of titmice (Chapter 4) in order to determine if flock size or group composition influenced individual reactions to novel and predator stimuli. Because the final experiment built upon the findings from the first and second experiments, this chapter will focus mainly on conclusions that can be drawn from the final experiment.

Species-level Reactions to Novel and Predator Stimuli

Chickadees and titmice modified their foraging behavior across baseline and stimulus contexts in the experiments described in Chapters 2 and 3, with both species having shorter foraging latencies when novel or predator stimuli were on or near the feeding station compared to baseline contexts. There were no species differences in seed-taking latencies, suggesting that one species was not more neophobic than the other. Additionally, both chickadees and titmice had intermediate latencies to take a seed in novel contexts compared to predator contexts, suggesting either a species-level graded response to varying threat, or individual-level differences in plasticity.

Regarding calling behavior, chickadees had shorter calling latencies than titmice in the presence of both novel and predator stimuli (Chapters 2 and 3). This suggests that chickadees may be sentinels in the group, or are at least more vigilant and/or reactive than titmice in these flocks. This may be due to their perceptual abilities, as chickadee visual acuity is inferior to that of titmice (Moore et al., 2013), thus requiring chickadees to increase their vigilance. It may also be related to a chickadee's subordinate status, because subordinates are often relegated to forage in riskier, less desirable locations, which can increase the need for higher vigilance levels (Katzir, 1982; Pravosudov & Grubb, 1999). As such, it would be beneficial for future studies to test for changes in individual vigilance rates in the presence of novel and predator stimuli and in the presence or absence of more dominant heterospecifics.

Chickadees and titmice also increased the number of 'D' notes used in their 'chick-a-dee' calls in the presence of novel stimuli (Chapter 2), but not significantly differently than they did in the presence of predator stimuli (Chapter 3). It is likely that these species do not consider novel stimuli to be as threatening as a predator. However, because the presence of novel stimuli lengthened their latencies to forage, novel stimuli did impact the behavior of chickadee and titmice participating in mixed-species flocks.

These species differences in vocal behavior observed in Chapter 2 and 3 suggested that other factors, such as flock composition, may influence reactions to novel and predator stimuli. The presence of heterospecifics has been shown to decrease chickadee and titmouse vigilance rates (Pravosudov & Grubb, 1999). This decrease is likely due to the 'many eyes' hypothesis, where vigilance levels per individual are predicted to decrease as group size increases (Lima, 1995). Increased vigilance levels can, in turn, decrease the amount of time individuals are able to forage, resulting in increased stress levels (Lucas, Shraeder, &

Jackson, 1999). Increased stress levels can be associated with an increase in vocal behavior (Lucas, Shraeder, & Jackson, 1999). Consequently, chickadee vocal behavior may be more sensitive to conspecific or heterospecific flock sizes and/or compositions.

Considering this, the final experiment (Chapter 4) manipulated the social context of chickadees, forming flocks of either two or four chickadees, and testing their individual reactions both in the presence and absence of titmice. This allowed me to determine if individuals had consistent reactions across contexts (novel versus predator) and also allowed me to determine if they exhibited behavioral plasticity, changing their reactions depending on flock composition.

Behavioral Consistency versus Behavioral Plasticity

Behavioral consistency or high behavioral repeatability contrasts with behavioral plasticity or behavioral flexibility, where individuals differ in their responses to various contexts (Biro & Adriaenssens, 2013). Behavioral flexibility is beneficial as it can reduce possible fitness costs, particularly in changing environments (Duckworth, 2010). A meta-analysis of experiments that addressed individual repeatability for a variety of behavioral patterns, including mating, migration, habitat selection, and aggression found that approximately 37% of behavioral variation is attributed to between-individual differences in behavior (Bell, Hankison, & Laskowski, 2009). Because repeatability is a function of both between- and within-individual variation, it follows that a majority of behavioral variation (63%) is attributed to within-individual variation, or plasticity (Bell, Hankison, & Laskowski, 2009; Biro & Adriaenssens, 2013). This plasticity can be similar among individuals in a population or vary among individuals (Dingemanse, Kazem, Réale, & Wright, 2010). Individuals can exhibit differences in plasticity for one context, but show no differences in plasticity in other context (Dingemanse et al., 2010). For example, individual wild-caught lemon damselfish, *Pomacentrus bankanensis*, a type of coral reef fish, were tested for differences in activity, boldness, and aggressiveness in different water temperatures (Biro, Beckmann, & Stamps, 2009). Individual scores on these traits increased significantly when the temperature was increased 3 degrees, with aggression increasing, and latencies to emerge from a shelter after a threat (boldness measure), decreasing in warmer temperatures. This was indicative of plasticity. However, not all individuals modified their behavior when the temperature changed. Some individuals had consistent activity, boldness, and aggression across temperature gradients, suggesting that repeatability of behavior may also be indicative of a behavioral or personality trait.

Several studies have tested for the behavioral consistency and plasticity on the species level. As an example, the startle responses of individual hermit crabs, *Pagurus bernhardus*, were measured several times in multiple contexts, including in situ, in the laboratory, and in the presence or absence of various predator cues (Briffa, Rundle, & Fryer, 2008). The researchers found variation in individual responses to the predator contexts across testing periods, indicating behavioral plasticity. The researchers also found that there were consistent differences when individuals were ranked by their individual startle durations (latency to emerge from their shells after being startled) across contexts, suggesting that there was individual consistency in behavior, as well. This study supports the idea that under varying environmental contexts, individuals can change their behavior while remaining consistently different from one another (Mathot & Dingemanse, 2014). Overall, this illustrates the basic premise of personality: in context 1, individuals may be ranked A, B, C, D for a certain behavior (e.g. latency to approach a stimulus, from shortest latency to longest), and in context 2, even with an increase or decrease in latencies, it is often the case that individuals still are ranked A, B, C, D. Individual A, for example, shows behavioral consistency, because it always has the shortest latency. Similarly, Individual A shows behavioral flexibility, because its latency is modified in a second context.

Plasticity of Feeder Avoidance

Chickadees in larger conspecific groups (4 versus 2) showed behavioral plasticity in feeder avoidance by significantly decreasing their latencies to forage and increasing their foraging rates in the presence of titmice compared to the absence of titmice. This flexibility in feeder avoidance was also observed in predator contexts: chickadees exhibited less feeder avoidance when four chickadees were in the flock compared to only two chickadees in the absence of titmice. There are a few possible explanations for these findings, including differences in group size or differences in the composition of individual behavioral types.

Differences in Group Size

Chickadees in flocks of eight birds (4 chickadees, 4 titmice) showed significantly less feeder avoidance in the presence of novel stimuli than chickadees in flocks of only four chickadees and no titmice. This decrease in neophobia or shyness in the larger mixed-species flock may have been due to 'safety in numbers' (Krause & Ruxton, 2002) which can encourage individuals to be more neophilic or bold compared to when they are in smaller groups or when they are alone. For instance, small shoals of minnows, *Phoxinus phoxinus*, and goldfish, *Carassius auratus*, exhibited more shy or 'timid' behavior (hiding in the weeds, rapid darting, and turning) compared to larger shoals of minnows and goldfish, which were less timid, making both longer, and more frequent, visits to open foraging patches (Magurran & Pitcher, 1983). As such, perhaps an increased perception of 'safety' prompted chickadees to approach and forage near novel stimuli when more birds were participating in the flock compared to when fewer birds were participating. These results suggest behavioral plasticity in chickadees, based on mixed-species group size.

An increase in mixed-species group size also increases the likelihood of having a 'keystone' individual influence group behavior (reviewed in Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014). A keystone individual is 'an individual that has a disproportionally large, irreplaceable effect on other group members, and/or the overall group dynamics relative to its abundance' (Sih & Watters, 2005; pp. 1427-1428). For example, the boldest mosquitofish are considered keystone individuals because their boldness allows them to disperse the farthest, where new populations rely upon disperser behavior (Cote, Fogarty, Brodin, Weinersmith, & Sih, 2011). Thus, it is possible that an extremely neophilic and influential individual can influence groups, perhaps by leading them to areas with better protection from predators or with better food availability. Keystone individuals are more often described as influencing single-species groups, although it is possible for keystone individuals to influence other species in their environment, particularly if they participate in mixed-species groups. Further analysis of individual behavioral types in each of the aviary flocks is needed in order to address whether the presence of certain prominent individuals may have influenced flock behavior in the presence of novel and predator stimuli.

Differences in Composition of Individuals

Varying environmental contexts, especially social contexts, are known to affect how individuals react to stimuli. When groups form, individual behavioral differences can be reduced (Krause & Ruxton, 2002). As such, some behavioral types may be less prevalent within the group, allowing the more prevalent types to affect group performance. For example, after forming dyads composed of one bold and one shy stickleback fish, researchers found that shy fish were more likely to leave cover if their bold partner was in an open area (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009). Bold fish, on the other hand, were less responsive to their shy partners. Thus, the presence of the bold individual influenced the behavior of the shy individual. Additionally, in male-female dyads of zebra finches, the more exploratory a bird's partner was, the more exploratory the focal bird was when compared to baseline exploratory measurements when tested alone (Schuett & Dall, 2009). As a final example, observing the behavioral consequences of other group mates can influence an individual's subsequent behavior. Bold rainbow trout, *Onchorhyncus mykiss*, who lost fights, or watched a shy trout approach a novel object, became more shy and subsequently increased their latencies to approach a novel object (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007). In contrast, shy trout that watched bold trout approach a novel stimulus, did not change their approach latencies; however, if these shy trout won a fight, they became bolder and decreased their approach latency to a novel object. The researchers suggested that social experience can influence behavioral types, where shyness or boldness may be more plastic, being related to an individual's self-assessment of their relative competitive ability.

Social conflict—both within- and between-species and whether it is competition for food, mates, or other resources—can select for stable differences between behavioral types (Smith, 1982). There is a positive feedback system that promotes diversity and consistency in behavioral types, both on the individual- and group-level (Bergmüller & Taborsky, 2010). For example, individuals in a group may try to adopt a certain social role depending on their behavioral type, but conflict for resources can lead to character displacement, and the need for behavioral plasticity, in order to adopt a new role in the group. For instance, aggressive fast exploring great tits are only socially dominant in populations when their behavioral type is rare; therefore, only the most dominant fast exploring great tits maintain a high rank, while the lower ranked fast explorers are relegated to a social position even lower than intermediate slow explorers (Réale & Dingemanse, 2010). Subsequently, if this social conflict persists, it can have an enduring influence on an individual's behavioral type, with diversity in behavioral types being selected for across generations, particularly if it results in a reduction of social conflict (reviewed in Bergmüller & Taborsky, 2010)

Taken together, it is possible that the mixture of neophobic and neophilic or shy and bold individuals in each aviary group influenced how chickadees responded to the novel and predator stimuli. Groups with four chickadees had a greater chance of having more dominant behavioral types compared to groups with only two chickadees, and as such, those groups would be expected to approach novel stimuli faster, and thus obtain food faster, compared to smaller, less variable groups. When titmice are also present, their presence adds to the collective mix of personality types (although titmice behavior was not measured), such that bolder titmice may influence chickadee approach latencies. Overall, the feeder avoidance results suggest that chickadee responses to novel and predator stimuli are plastic, or flexible, and can be influenced by social context. Further investigation is needed in order to determine whether this plasticity is influenced by group size or the composition of individual behavioral types.

Plasticity of Vocal Behavior

Furthermore, while research on animal personalities or behavioral traits has boomed in recent years (reviewed in Gosling, 2001), few animal personality studies have addressed whether vocal behavior is correlated with individual behavioral types. The few studies that have measured vocal behavior have found positive correlations between calling behavior and exploration. For example, in black-capped chickadees, an increase in an individual's calling rate was positively correlated with their exploration in a novel environment (Guillette & Sturdy, 2011). Similarly, preferred location for singing can reflect one's personality. Male collared flycatchers, *Ficedula albicollis*, for example, who sang on lower singing posts in the presence of a human observer (which is riskier than singing at a higher, more protected post) were more explorative and acted more riskily in other contexts than those individuals who sang on higher singing posts (Garamszegi, Eens, & Török, 2008).

Additionally, individual vocal behavior, and especially note type or call type, can be related to aggression. For example, aggressive Carolina chickadees are known to use more 'D' notes in their calls compared to less aggressive individuals (Williams, 2009). Similarly, dominant gorillas, *Gorilla gorilla*, call more often and 'sing' less often than subordinate gorillas (Schaefer, 2009). Singing is a submissive expression in gorillas.

The results of this dissertation also show that individuals can exhibit flexibility in their vocal behavior in varying social contexts when presented with novel and predator stimuli. Specifically, chickadee group size and presence or absence of heterospecific titmice influenced chickadee calling latencies and calling rates. Chickadees had lower calling rates and longer calling latencies in larger flocks of chickadees compared to smaller flocks. Additionally, chickadee flocks decreased their calling behavior in the presence of titmice and increased their calling behavior in the absence of titmice. Possible explanations for these findings will be elucidated below.

The Effect of Group Size

Group size is known to affect vocalization rates in many social groups. For example, individual bottle-nosed dolphins, *Tursiops truncatus*, produced more whistles when in larger groups of dolphins compared to smaller groups of dolphins (Jones & Sayigh, 2002). In dolphins, whistle vocalizations are often produced in social contexts, and therefore, an increase in whistles may be due to an increase in social behavior in larger groups. Likewise, elephants are known to produce more vocalizations as natural group size increases (Payne et al., 2003). In addition, squirrel monkeys, *Saimiri sciureus*, produced fewer 'chuck' vocalizations when participating in smaller groups, or 'alliances,' compared to when participating in larger groups (Boinski & Mitchell, 1992). 'Chuck' calls are described as contact calls and it is hypothesized that these calls, including their rates of production, may be related to individual activity (whether the individual is moving), success in foraging (because individuals cannot call as often when they are eating), and distance to the nearest neighbor. As a final example, when Carolina chickadee flock size was manipulated, larger groups produced chick-a-dee calls with greater structural diversity, compared to the chick-a-dee calls of smaller groups (Freeberg, 2006). While not measured in this dissertation, Freeberg's (2006) study suggests that group size can affect several aspects of vocal behavior, including rate and complexity, and thus, group size should be considered as a potential mediating factor when measuring individual vocal responses to stimuli.

Individual stress levels can also influence calling behavior, and in turn, be influenced by the number of individuals participating in the group. For example, Carolina chickadees increased their calling rates in environments where food availability was low (Lucas, Schraeder, & Jackson, 1999). The authors suggested that the energetic stress caused by low food availability may have increased the need for sociality. This increased need for sociality may have led birds to increase their calling to attract other flock mates, which would decrease individual vigilance levels, and possibly help in finding new food sources. Stress levels are predicted to be higher in smaller groups, due to fewer vigilant individuals being present (Elgar, 1989).

The Effect of Group Composition

Although little tested, group composition can also affect the calling behavior of individuals participating in mixed-species groups. For example, Diana monkeys, *Cercopithecus diana*, had higher calling rates of 'clear' calls, a type of close-range social vocalization, when participating in single-species groups compared to mixed-species groups (Uster & Züberbuhler, 2001). The authors suggested that this was due to a reduction of vigilance, because other participating species foraged in varying strata, thus providing more sentinels in a variety of locations. This is a possible explanation for why the presence of titmice in the final experiment of this dissertation significantly decreased chickadee calling behavior across contexts—there were 'more eyes' available.

Future Directions

There are many potential experiments that could be conducted to further our understanding of the influences of reactions to novel and predator stimuli in mixed-species groups. For example, the experiment in Chapter 4 manipulated chickadee flock size and the presence or absence of titmice and focused only on the foraging and calling behaviors of chickadees. It would be interesting to test whether similar findings are obtained when manipulating titmouse flock size and the presence or absence of chickadees. Titmice would be predicted to have less stress when participating in flocks with chickadees, because in a previous study, titmice significantly reduced their vigilance when foraging with chickadees compared to foraging alone (Pravosudov & Grubb, 1999). It remains to be seen whether titmice have higher calling rates and lower calling latencies in smaller flocks, compared to larger flocks, as was the case for chickadees.

Future studies could also further test for species differences in chickadee and titmouse reactions to novel and predator stimuli. Many comparative experiments have shown that titmice are interspecifically dominant over chickadees (Morse, 1970; Pravosudov & Grubb, 1999); however, the results of this dissertation research did not reveal that interspecific dominance influenced foraging latencies. In fact, supplants by titmice directed at chickadees foraging on the feeding station were minimal. If titmice were dominant over chickadees, they would have been expected to have shorter foraging latencies than chickadees, yet no species differences in foraging latencies were observed. I suggested previously that if food had been placed in more titmouse-like locations, such as on the ground, or more chickadee-like locations, such as higher in the canopy, more interspecific dominance interactions may have been observed when testing mixed-species flock reactions to novel or threatening stimuli (Cimprich & Grubb, 1994). As such, titmice may have shorter latencies to forage near a novel stimulus when it is placed on the ground compared to chickadees, because they are more familiar with foraging in that location.

Furthermore, it may be beneficial for future studies to measure the amount of time species or individuals spend on the feeders, as this could be a measure of boldness. For example, in a study of song sparrows, *Melospriza melodia*, and swamp sparrows, *M. georgiana*, swamp sparrows had more ‘short visits’ to the feeding stations compared to song sparrows (Greenberg, 1989) during novel stimulus presentations compared to control trials without the presence of a novel stimulus. The author posits that this may have been related to interspecific dominance hierarchies within the flock, though it may have also been related to the neophobia levels of swamp sparrows in relation to song sparrows.

Additionally, I only analyzed one note type (‘D’ notes) in chickadees and titmice, as these note types are often used in varying degrees of threat (Krams, Krama, Freeberg, Kullberg, & Lucas, 2012). However, other note types may be correlated with responses to novel stimuli and/or predator stimuli. Additionally, there are other aspects of chickadee and titmouse calling behavior that can be tested in the future, including note entropy (e.g. Bartmess-Levasseur et al., 2010), call duty cycle (e.g. Wilson & Mennill, 2011), inter-note interval (e.g. Blumstein, 1995) and inter-call interval (e.g. Ellis, 2008). Variation of any of these elements may communicate to the flock about the stimulus. Furthermore, measuring the harmonics of certain notes or the noisiness of certain notes in the call (e.g. 'D' notes) may reveal information about the urgency of the call, as has been found in the different alarm call types of mongooses, *Suricata suricatta* (Manser, 2001).

Lastly, though not discussed in this dissertation, several measures were collected for each chickadee prior to releasing them into the aviaries and again, after all novel and predator stimuli been presented in the aviaries. First, individual chickadees were videotaped for 10 minutes in a novel cage with a central perch. I measured their latencies to move from their initial position, number of sides of the cage visited, number of movements (perches, flights and hops), as well as calling behavior. After the aviary data collection concluded, individual chickadees were re-tested in the cage, first with a 2-minute baseline and then with a 2-minute presentation of a small novel pink toy, with the same behaviors being measured as in the first cage test. These cage tests were modeled after a similar experiment on great tits, which revealed that this was a good assay to measure individual levels of neophobia (Kluen et al., 2012). Data coding for these video files is incomplete; however, if reactions to novel stimuli are consistent across stimulus contexts (novel versus predator) as well as social contexts (alone versus in a flock), I expect that chickadee reactions to novel stimuli in the aviary context will correlate with their reactions in the cage tests. In contrast, if their reactions to novel stimuli are more plastic, being influenced by social context, their behaviors in the aviary and in the cage test should be unrelated to one another.

Final Remarks

My dissertation research investigated the behavioral and vocal reactions of Carolina chickadees and tufted titmice to the presence of novel and predator stimuli. The results show that there were no species differences in neophobia or neophilia and that both species had a graded foraging response to novelty compared to predators. Because chickadees had shorter calling latencies than titmice in the presence of novel and predator stimuli, it is possible that chickadees play a sentinel role in these mixed-species flocks, at least in the eastern Tennessee population of this study. In the final experiment, chickadees exhibited behavioral flexibility in their foraging and calling behavior in the presence of novel and predator stimuli, depending on the number of conspecifics participating in the flock and/or the presence or absence of heterospecifics. This comparative work contributes to a growing body of literature regarding behavioral traits in animals and also addresses a little studied, but potentially very informative measure of personality: vocal behavior. Future personality studies should include vocal behavior as a measure, as changes in vocal behavior can be indicative of perceived threat. Overall, this work has important implications for the complexity of social relationships in mixed-species groups, the social roles species play within the group, and how group size influences vocal behavior and reactions to various degrees of threat.

REFERENCES

Adamec, R. E., Stark-Adamec, C., & Livingston, K. E. (1983). The expression of an early developmentally emergent defensive bias in the adult domestic cat (*Felis catus*) in non-predatory situations. *Applied Animal Ethology*, *10*(1), 89-108.

Agrawal, A. A. (2001). Phenotypic plasticity in the interactions and evolution of species. *Science*, *294*(5541), 321-326.

Altmann, M. (1958). The flight distance in free-ranging big game. *The Journal of Wildlife Management*, 207-209.

Amy, M., Sprau, P., de Goede, P., & Naguib, M. (2010). Effects of personality on territory defence in communication networks: a playback experiment with radio-tagged great tits. *Proceedings of the Royal Society B*, *277*, 3685-3692.

An, Y. S., Kriengwatana, B., Newman, A. E., MacDougall-Shackleton, E. A., & MacDougall-Shackleton, S. A. (2011). Social rank, neophobia and observational learning in black-capped chickadees. *Behaviour*, *148*, 55-69.

Arnold, S. J., & Bennett, A. F. (1984). Behavioural variation in natural populations. III: Antipredator displays in the garter snake *Thamnophis radix*. *Animal Behaviour*, *32*(4), 1108-1118.

Baker, M. C. & Becker, A. M. (2002). Mobbing calls of black-capped chickadees: Effects of urgency on call production. *Wilson Bulletin*, *114*, 510-516.

Barnett, S. A. (1954). Experiments on “neophobia” in wild and laboratory rats. *British Journal of Psychology*, *49*(3), 195-201.

Barnett, S. A. (1963). *The rat: A study in behaviour*. Chicago, Illinois: Aldine Publishing Company.

Barnett, S. A. (2001). *The story of rats: Their impact on us, and our impact on them*. Australia: Griffin Press.

Barraud, E. M. (1961). The development of behaviour in some young Passerines. *Bird Study*, *8*(3), 111-118.

Bartmess-LeVasseur, J., Branch, C.L., Browning, S.A., Owens, J.L. & Freeberg, T.M. (2010). Predator stimuli and calling behavior of Carolina chickadees

(*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology and Sociobiology*, *64*, 1187-1198.

Bell, A. M. (2007). Future directions in behavioral syndromes research. *Proceeding of the Royal Society B*, *274*(1611), 755-761.

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), 771-783.

Bell, M. B., Radford, A. N., Rose, R., Wade, H. M., & Ridley, A. R. (2009). The value of constant surveillance in a risky environment. *Proceedings of the Royal Society B: Biological Sciences*, rspb20090276.

Benus, R. F., Bohus, B., Koolhaas, J. M., & Van Oortmerssen, G. A. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, *47*(10), 1008-1019.

Bergman, T. J. & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropothecus gelada*). *Animal Cognition*, *12*(1), 63-73.

Bergmüller, R. & Taborsky, M. (2010). Animal personality due to social niche specialization. *Trends in Ecology and Evolution*, *25*(9), 504-511.

Berlyne, D. (1950). Novelty and curiosity as determinants of exploratory behaviour1. *British Journal of Psychology. General Section*, *41*(1-2), 68-80.

Berlyne. D. E. (1960). *Conflict, arousal, and curiosity*. New York: McGraw-Hill.

Berner, T. O. & Grubb, Jr. T. C. (1985). An experimental analysis of mixed-species flocking in birds of deciduous woodland. *Ecology*, *66*, 1229-1236.

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor. *Animal Cognition*, *13*, 701-710.

Biro, P. A., & Adriaenssens, B. (2013). Predictability as a personality trait: consistent differences in intraindividual behavioral variation. *The American Naturalist*, *182*(5), 621-629.

Biro, P. A., Beckmann, C., & Stamps, J. A. (2009). Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, rspb20091346.

Bloomfield, L.L., Phillmore, L.S., Weisman, R.G. & Sturdy, C.B. (2005). Note types and coding in parid vocalizations. III: The chickadee call of the Carolina chickadee (*Poecile carolinensis*). *Canadian Journal of Zoology*, *83*, 820-833.

Blumstein, D. T. (1995). Golden marmot alarm calls: I. The production of situationally—specific vocalizations. *Ethology*, *100*, 113-125.

Boccia, M. L., Laudenslager, M., & Reite, M. (1988). Food distribution, dominance, and aggressive behavior in bonnet macaques. *American Journal of Primatology*, *16*(2), 123-130.

Boinski, S., & Mitchell, C. L. (1992). Ecological and social factors affecting the vocal behavior of adult female squirrel monkeys. *Ethology*, *92*(4), 316-330.

Boogart, N. J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, *72*, 1229-1239.

Both, C., Dingemanse, N. J., Drent, P. J., &Tinbergen, J. M. (2005). Pairs of extreme avian personalities have the highest reproductive success. *Journal of Animal Ecology, 74*, 667-674.

Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1640), 1305-1311.

Brouns, F. & Edwards, S. A. (1994). Social rank and feeding behaviour of group-housed sows fed competitively or ad libitum. *Applied Animal Behaviour Science*, *39*, 225-235.

Brown, G. E., Ferrari, M. C. O., Elvidge, C. K., Ramnarine, I., & Chivers, D. P. (2013). Phenotypically plastic neophobia: A response to variable predation risk. *Proceedings of the Royal Society B*, *280*, 20122712.

Buckley, N.J. (1996) Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. *Auk*, *113*, 473-488.

Bugoni, L., Neves, T. S., Peppes, F. V., & Furness, R. W. (2008). An effective method for trapping scavenging seabirds at sea. *Journal of Field Ornithology*, *79*(3), 308-313.

Burghardt, G. M. (1975). Chemical prey preference polymorphism in newborn garter snakes *Thamnophis sirtalis*. Behaviour, 52(3), 202-224.

Burghardt, G. M. (2005). *The genesis of animal play*. Cambridge, Massachusetts: MIT Press.

Burns, J. G., & Rodd, F. H. (2008). Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. *Animal Behaviour*, *76*(3), 911-922.

Burtt, H. E. & Giltz, M. L. (1969). Measurement of complacency in blackbirds. *The Ohio Journal of Science*, *69*(2), 109-114.

Cannon, W. B. (1915). *Bodily changes in pain, hunger, fear and rage*. New York: D. Appleton & Company.

Carere, C. Drent, P. J., Privitera, L., Koolhaas, J. M., Groothuis, T. G. G. (2005). Personalities in great tits, *Parus major*: stability and consistency. *Animal Behavior* 70, 795-805.

Carere, C., Groothuis, T. G. G., Möstl, E., Daan, S., & Koolhaas, J. M. (2003). Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Hormones and Behavior*, *43*(5), 540-548.

Carrete, M., & Tella, J. L. (2010). Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters*, *6*(2), 167-170.

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, *88*, 465-475.

Cavigelli, S. A. & McClintock, M. K. (2003). Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. *Proceedings of the National Academy of Science*, *100*(26) 16131-16136.

Cavigelli, S. A., Yee, J. R., & McClintock, M. K. (2006). Infant temperament predicts life span in female rats that develop spontaneous tumors. *Hormones and Behaviour*, *50*, 454-462.

Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed–accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution*, *24*(7), 400-407.

Chitty, D. & Kempson, D. A. (1949). Prebaiting small mammals and a new design of live trap. *Ecology*, *30*(4), 536-542.

Cimprich, D. A. & Grubb, Jr. T. C. (1994). Consequences for Carolina chickadees of foraging with tufted titmice in winter. *Ecology*, *75*, 1615-1625.

Coleman, K. & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, *56*, 927-936.

Coleman, S. L. & Mellgren, R. L. (1994). Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *48*(4), 903-907.

Contreras, T.A. & Sieving, K.E. (2011). Leadership of winter mixed-species flocks by tufted titmice (*Baeolophus bicolor*): Are titmice passive nuclear species? *International Journal of Zoology*, Article ID: 670548.

Coppinger, R. P. (1969). The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies part I: reactions of wild-caught adult blue jays to novel insects. *Behaviour*, *35*(1), 45-59.

Corey, D.T. (1978). The determinants of exploration and neophobia. *Neuroscience & Biobehavioral Reviews*, *2*, 235-253.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B*, *365*, 4065–4076.

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K., & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: group composition matters. *Proceedings of the Royal Society B*, *278*, 1670-1678.

Courter, J. R. & Ritchison, G. (2010). Alarm calls of tufted titmice convey information about predator size and threat. *Behavioral Ecology*, *21*, 936-942.

Curio, E. (1978). The adaptive significance of avian mobbing: I. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie*, *48*, 175-183.

Daily, J. M., Clayton, N. S., & Emery, N. J. (2006). The behavior and evolution of cache protection and pilferage. *Animal Behaviour*, *72*(1), 13-23.

Dalmau, A., Fabrega, E. & Velarde, A. (2009). Fear assessment in pigs exposed to a novel object test. *Applied Animal Behavior Science*, *117*, 173-180.

Darwin, C. (1874). *The descent of man*. New York: H. M. Caldwell.

Davis, K. M., & Burghardt, G. M. (2007). Training and long-term memory of a novel food acquisition task in a turtle (*Pseudemys nelsoni*). *Behavioural processes*, *75*(2), 225-230.

DeGraaf, R. M., Tilghman, N. G., & Anderson, S. H. (1985). Foraging guilds of North American birds. *Environmental Management*, *9*(6), 493-536.

Dickson, D. P., Barr, G. R., Johnson, L. P., & Wieckert, D. A. (1970). Social dominance and temperament of Holstein cows. *Journal of Dairy Science*, *53*(7), 904-907.

Dingemanse, N. J., Both, Cristiaan, van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (Parus major). Proceedings of the Royal Society B, 270(1516), 741-747.

Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in*

Ecology & Evolution, *25*(2), 81-89.

Dingemanse, N. J., Wright, J., Kazem, A. J., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, *76*(6), 1128-1138.

Dolby, A. S., & Grubb Jr, T. C. (1998). Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behaviour*, *56*(2), 501-509.

Duckworth, R. A. (2010). Evolution of personality: developmental constraints on behavioral flexibility. *The Auk*, *127*(4), 752-758.

Dyer, J. R., Croft, D. P., Morrell, L. J., & Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, *20*(1), 165-171.

Echeverria, A. I., Vassallo, A. I., & Isacch, J. P. (2006). Experimental analysis of novelty responses in a bird assemblage inhabiting a suburban marsh. *Canadian Journal of Zoology*, *84*, 874-980.

Ekman, J. B. & Lilliendahl, K. (1993). Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. *Behavioral Ecology*, *4*(3), 232-238.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, *64*(1), 13-33.

Elliot, A. J. (2006). The hierarchical model of approach-avoidance motivation. *Motivation and emotion*, *30*(2), 111-116.

Ellis, J. (2008). Which Call Parameters Signal Threat to Conspecifics in White-Throated Magpie-Jay Mobbing Calls?. *Ethology*, *114*(2), 154-163.

Ensminger, A. L., & Westneat, D. F. (2012). Individual and sex differences in habituation and neophobia in house sparrows (*Passer domesticus*). *Ethology*, *118*(11), 1085-1095.

Fallow, P. M., & Magrath, R. D. (2010). Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Animal Behaviour*, *79*(2), 411-417.

Ficken, S. M., Weise, C. M. & Popp, J. W. (1990). Dominance rank and resource access in winter flocks of black-capped chickadees. *Wilson Bulletin*, *102*, 623-633.

Figueroa, J., Solà-Oriol, D., Manteca, X., & Pérez, J. F. (2013). Social learning of feeding behaviour in pigs: Effects of neophobia and familiarity with the demonstrator conspecific. *Applied Animal Behaviour Science*, *148*(1), 120-127.

Fitzgibbon, C. D. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour*, *39*(6), 116-1126.

Fox, R. A., Ladage, L. D., Roth II, T. C., & Pravosudov, V. V. (2009). Behavioral profile predicts dominance status in mountain chickadees. *Animal Behaviour*, *77*(6), 1441-1448.

Freeberg, T. M. (2006). Social complexity can drive vocal complexity group size influences vocal information in Carolina chickadees. *Psychological Science*, *17*(7), 557-561.

Frost, A. J., Winrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 333-339.

Fu, W., Zhao, D., Qi, X., Guo, S., Wei, W., & Li, B. (2013). Free-ranging Sichuan snub-nosed monkeys *Rhinopithecus roxellana*: Neophobia, neophilia, or both? *Current Zoology*, *59*(3), 311-316.

Funder, D. C. (2004). *The personality puzzle* (3rd ed). New York: W. W. Norton.

Galhardo, L., Vitorino, A., & Oliveira, R. F. (2012). Social familiarity modulates personality trait in a cichlid fish. *Biology Letters*, *8*(6), 936-938.

Garamszegi, L. Z., Eens, M., & Török, J. (2008). Birds reveal their personality when singing. *PLoS One*, *3*(7), e2647.

Garamszegi, L. Z., Eens,M. & Török, J. (2009). Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Animal Behaviour*, *77*, 803-812.

Gilliam, J. F., & Fraser, D. F. (1987). Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, 1856-1862.

Glickman, S. E., & Sroges, R. W. (1966). Curiosity in zoo animals. *Behaviour*, *26*(1), 151-187.

Goddard, M. E., & Beilharz, R. G. (1984). A factor analysis of fearfulness in potential guide dogs. *Applied Animal Behaviour Science*, *12*(3), 253-265.

Godin, J. J. & Smith, S. A. (1988). A fitness cost of foraging in the guppy. *Nature*, *333*, 69-71.

Gold, K. C. & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology*, *13*, 509-522.

Goodale, E. & Kotagama, S. W. (2005). Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology*, *21*, 669-676.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354-361.

Gosling, S. D. & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8, 69-75.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*(1), 45-86.

Greenberg, R. & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. *Current Ornithology*, *16*, 119-178.

Greenberg, R. (1983). The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *The American Naturalist*, *122*(4), 444-453.

Greenberg, R. (1989). Neophobia, aversion to open space, and ecological plasticity in song and swamp sparrows. *Canadian Journal of Zoology*, *67*(5), 1194-1199.

Greenberg, R. (1990a). Ecological plasticity, neophobia and resource use in birds. *Studies in Avian Biology*, *13*, 431-437.

Greenberg, R. (1990b). Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. *Animal Behaviour*, *39*(2), 375-379.

Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In S. M. Reader & K. N. Laland (Eds.), *Animal Innovation* (p. 175-196). New York: Oxford University Press.

Griebel, G., Belzung, C., Misslin, R., & Vogel, E. (1993). The free-exploratory paradigm: an effective method for measuring neophobic behavior in mice and testing potential neophobia-reducing drugs. *Behavioural Pharmacology*, *4*, 637-644.

Grubb Jr., T. C. & Pravasudov, V. V. (1994). Tufted titmouse (*Baeolophus bicolor*). In A. Poole (Ed.) *The Birds of North America Online*. Ithaca, New York. Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/086

Guillette, L. M. & Sturdy, C. B. (2011). Individual differences and repeatability in vocal production: stress-induced calling exposes a songbird's personality. *Naturwissenschaften*, *98*, 977-981.

Gunn, J. S., Descorchers, A., Villard, M., Borque, J., & Ibarzabal, J. (2000). Playbacks of mobbing calls of black-capped chickadees as a method to estimate reproductive activity of forest birds. *Journal of Field Ornithology*, *71*(3), 742-483.

Hailman, J. P. (1989). The organization of major vocalizations in the Paridae. *The Wilson Bulletin*, 305-343.

Hall, C. S. (1934). Emotional behavior in the rat. I. Defecation and urination as measures of individual differences in emotionality. *Journal of Comparative Psychology*, *18*(3), 385-403.

Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., & Manica, A. (2009). Social feedback and the emergence of leaders and followers. *Current Biology*, *19*, 248-252.

Hardie, S. M. & Buchanan-Smith, H. M. (2000). Responses of captive single- and mixed-species groups of *Saguinus* to novel nonthreatening objects. *International Journal of Primatology*, *21*(4), 629-648.

Hardie, S. M. (1997). Exhibiting mixed-species groups of sympatric tamarins Saguinus spp at Belfast Zoo. *International Zoo Yearbook*, *35*(1), 261-266.

Harvey, E. M. & Freeberg, T. M. (2007). Behavioral consistency in a changed social context in Carolina chickadees. *Journal of General Psychology*, *134*, 229-245.

Haythorpe, K. M., Sulikowski, D., & Burke, D. (2012). Relative levels of food aggression displayed by Common Mynas when foraging with other bird species in suburbia. *Emu*, *112*, 129-136.

Hepper, P. G., & Wells, D. L. (2012). Olfactory discrimination in the western lowland gorilla, *Gorilla gorilla gorilla*. *Primates*, *53*(2), 121-126.

Hetrick, S.A. & Sieving, K.E. (2012). Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behavioral Ecology*, *23*, 83-92.

Heymann, E. W. & Buchanan-Smith, H. M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews*, *75*, 169-190.

Heyser, C. J. & Chemero, A. (2012). Novel object exploration in mice: Not all objects are created equal. *Behavioural Processes*, *89*(3), 232-238.

Hinde R. A. (1970). *Behaviour on conflict situations*. In R. A. Hinde (ed), Animal behaviour, a synthesis of ethology and comparative psychology (p. 270-290), New York: McGraw-Hill.

Holliday, E. (1953, October 18). Original book studies birds as individuals. *The Chicago Tribune*, p. 9.

Howard, L. (1953). *Birds as individuals*. New York: Doubleday & Company, Inc.

Jones, G. J., & Sayigh, L. S. (2002). Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science*, *18*(2), 374-393.

Jones, K. A., & Godin, J. G. J. (2009). Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proceedings of the Royal Society B: Biological Sciences*, rspb20091607.

Jones, Tom. (1978). *The Tracker*. New York: Berkley Books.

Katzir, G. (1982). Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula L*. I. Response to novel space. *Behaviour*, *81*, 231-263.

Kelly, D. J. & Marples, N. M. (2004). The effects of novel odour and colour cues on food acceptance by the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, *68*(5), 1049-1054.

Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of Callitrichid monkeys. *American Journal of Primatology*, *66*, 167-188.

Klopfer, P. H. (1985). Habitat selection: Behavioral aspects. In M. L. Cody (Ed.), *Habitat selection in birds* (436-454). Orlando, Florida: Academic Press.

Kluen, E., Kuhn, S., Kempenaers, B., & Brommer, J. E. (2012). A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. *Animal Behaviour*, *84*, 279-287.

Kluen, E., Kuhn, S., Kempenaers, B., & Brommer, J. E. (2012). A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. *Animal Behaviour*, *84*(1), 279-287.

Koolhaas, J. M. (2008). Coping style and immunity in animals: making sense of individual variation. *Brain, behavior, and immunity*, *22*(5), 662-667.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J. ... H. J. Blokhuis. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews,* 23, 925-935.

Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: a parid perspective. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1597), 1879-1891.

Krause, J. & Ruxton, G. D. (2002). *Living in groups*. New York: Oxford University Press.

Kummer, H. & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *308*, 203-214.

Landis, J.R. & Koch, G.G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, *33*, 159-174.

Lendvai, Á. Z., Bókony, V., & Chastel, O. (2011). Coping with novelty and stress in free-living house sparrows. *The Journal of Experimental Biology*, *214*(5), 821-828.

Leussis, M. P. & Bolivar, V. J. (2006). Habituation in rodents: A review of behavior, neurobiology, and genetics. *Neuroscience & Biobehavioral Reviews*, *30*(7), 1045-1064.

Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619-640.

Lima, S. L. (1995). On the personal benefits of anti-predatory vigilance. *Animal Behaviour*, *48*, 734-736.

Lima, S. L., Valone, T. J., & Caraco, T. (1985). Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Animal Behaviour, 33,* 155-165.

Linhart, P., Fuchs, R., Polakova, S., & Slabbekoorn, H. (2012). Once bitten twice shy: long-term behavioral changes caused by trapping experience in willow warblers *Phylloscopus trochilus*. *Journal of Avian Biology*, *43*(2), 186-192.

Lucas, J. R., Freeberg, T. M., Egbert, J. & Schwabl, H. (2006). Fecal corticosterone, body mass, and caching rates of Carolina chickadees

(*Poecile carolinensis*) from disturbed and undisturbed sites. *Hormones and Behavior*, *49*(5), 634-643.

Lucas, J. R., Schraeder, A., & Jackson, C. (1999). Carolina chickadee (Aves, Paridae, *Poecile carolinensis*) vocalization rates: effects of body mass and food availability under aviary conditions. *Ethology*, *105*(6), 503-520.

MacLean, S. A. & Bonter, D. N. (2013). The sound of danger: Threat sensitivity to predator vocalizations, alarm calls, and novelty in gulls. *PLOS One*, *8*(12), e82384.

Magnhagen, C. & Staffan, F. (2005). Is boldness affected by group composition in young-of-the-year perch (Perca fluviatilis)? *Behavioral Ecology and Sociobiology*, *57*(3), 295-303.

Magnhagen, C. (2012). Personalities in a crowd: What shapes the behavior of Eurasian perch and other shoaling fishes? *Current Zoology*, *58*(1), 35-44.

Magurran, A. E. & Pitcher, T. J. (1983). Foraging, timidity and shoal size in minnows and goldfish. *Behavioral Ecology and Sociobiology*, *12*(2), 147-152.

Mahurin, E.J. & Freeberg, T.M. (2009). Chick-a-dee call variation in Carolina chickadees and recruiting flockmates to food. *Behavioral Ecology*, *20*, 111-116.

Mainwaring, M.C., Beal, J. L., & Hartley, I. R. (2011). Zebra finches are bolder in an asocial, rather than social, context. *Behavioral Processes*, *87*, 171-175.

Mairesse, F., Walker, M. A., Mehl, M. R., & Moore, R. K. (2007). Using linguistic cues for the automatic recognition of personality in conversation and text. *Journal of Artificial Intelligence Research*, *30*, 457-500.

Mamuneas, D., Spence, A. J., Manica, A., & King, A. J. (2014). Bolder stickleback fish make faster decisions, but they are not less accurate. *Behavioral Ecology*, *26*(1), 91-96.

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1483), 2315-2324.

Martin, J. G., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, *75*(1), 309-318.

Mather, J. A. & Anderson, R. C. (1999). Exploration, play, and habituation in octopuses (*Octopus dofleini*). *Journal of Comparative Psychology*, *113*, 333-338.

Mathot, K. J. & Dingemanse, N. J. (2014). Plasticity and personality. In L. B. Martin, C. K. Ghalambor, & H. A. Woods (Eds.) *Integrative Organismal Biology* (55-70). Hoboken, New Jersey: John Wiley & Sons, Inc.

McDougall, W. (1908). *An introduction to social psychology*. London: Methuen.

Merry, M. G. (1949). Life history of the creeping vole, *Mictrotus oregoni serpens merriam*. Unpublished master's thesis, The University of British Columbia.

Mettke-Hofmann, C. (2012). Head colour and age relate to personality traits in Gouldian finches. *Ethology*, *118*, 906-916.

Mettke-Hofmann, C., & Greenberg, R. (2005). Behavioral and cognitive adaptations to long-distance migration. In R. Greenberg & P. P. Marra, *Birds of two worlds: the ecology and evolution of migration* (p. 114-126). Baltimore: Johns Hopkins University Press.

Mettke-Hofmann, C., Lorentzen, S., Schlicht, E., Schneider, J., & Werner, F. (2009). Spatial neophilia and spatial neophobia in resident and migratory warblers (*Sylvia*). *Ethology*, *115*, 482-492.

Mettke-Hofmann, C., Rowe, K. C., Hayden, T. J., & Canoine, V. (2006). Effects of experience and object complexity on exploration in garden warblers (*Sylvia borin*). *Journal of Zoology*, *268*, 405-413.

Mettler, A. E., & Shivik, J. A. (2007). Dominance and neophobia in coyote (*Canis latrans*) breeding pairs. *Applied Animal Behaviour Science*, *102*(1), 85-94.

Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A., & Pruitt, J. N. (2014). The keystone individual concept: an ecological and evolutionary overview. *Animal Behaviour*, *89*, 53-62.

Moore, B. A., Doppler, M., Young, J. E., & Fernández-Juricic, E. (2013). Interspecific differences in the visual system and scanning behavior of three forest passerines that form heterospecific flocks. *Journal of Comparative Physiology A*, *199*(4), 263-277.

Morse, D. H. (1977). Feeding behavior and predatory avoidance in heterospecific groups. *BioScience*, *27*, 332-339.

Morse, D.H. (1970). Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monograph*, *40*, 119-168.

Morton, E.S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, *111,* 855-869.

Mostrom, A. M., Curry, R. L., & Lohr, B. (2002). Carolina chickadee (*Poecile carolinensis*). In A. Poole (Ed.) *The Birds of North America Online*. Ithaca, New York. Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/636

Moynihan, M. (1962). *The organization and probable evolution of some mixed species flocks of neotropical birds* (Vol. 143, No. 1-7). Smithsonian Institution.

Naguib, M., Kazek, A., Schaper, S. V., van Oers, K., & Visser, M. E. (2010). Singing activity reveals personality traits in great tits. *Ethology*, *116*, 763 – 769.

Nakano, S. (1995). Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. *Canadian Journal of Zoology*, *73*(10), 1845-1854.

Nilsson, A. L. K., Nilsson, J., Alerstam, T., & Bäckman, J. (2010). Migratory and resident blue tits *Cyanistes caeruleus* differ in their reaction to a novel object. *Naturwissenschaften*, *97*(11), 981-985.

Nolen, M.T. & Lucas, J.R. (2009). Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. *Animal Behavior*, *77*, 1137-1146.

Nott, H. M. R. & Sibly, R. M. (1993). Responses to novel food by rats: the effect of social rank. *Crop Protection*, *12*(2), 89-94.

Owens, J.L. & Freeberg, T.M. (2007). Variation in chick-a-dee calls of tufted titmice, *Baeolophus bicolor*: Note type and individual distinctiveness. *Journal of the Acoustical Society of America*, *122*, 1216-1226.

Payne, K. B., Thompson, M., & Kramer, L. (2003). Elephant calling patterns as indicators of group size and composition: the basis for an acoustic monitoring system. *African Journal of Ecology*, *41*(1), 99-107.

Pellegrini, A. F., Wisenden, B. D., & Sorensen, P. W. (2010). Bold minnows consistently approach danger in the field and lab in response to either chemical or visual indicators of predation risk. *Behavioral Ecology and Sociobiology*, *64*(3), 381-387.

Peres, C. A. (1993). Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica*, *61*(2), 61-76.

Pravosudov, V. V. & Grubb Jr., T. C. (1999). Effects of dominance on vigilance in avian social groups. *The Auk*, *116*(1), 241-246.

Pravosudov, V. V., Grubb Jr, T. C., Doherty Jr, P. F., Bronson, C. L., Pravosudova, E. V., & Dolby, A. S. (1999). Social dominance and energy reserves in wintering woodland birds. *Condor*, 880-884.

Pride, R. E. (2005). Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology*, *16*(3), 550-560.

Quinn, J. L. & Cresswell, W. (2005). Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringella coelebs*. *Behaviour*, *142*, 1377-1402.

Rainey, H. J., Zuberbühler, K., & Slater, P. J. B. (2004). Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society B*, *271*, 755-759.

Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. *Social behaviour: genes, ecology and evolution*, 562.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews,* 82, 291-318.

Reinthal, P. N. & Lewis, S. M. (1986). Social behavior, foraging efficiency and habitat utilization in a group of tropical herbivorous fish. *Animal Behaviour*, *34*(6), 1687-1693.

Robbins, R. J. (1980). Learning and nonlearned neophobia enhancement both contribute to the formation of illness-induced taste aversions by deer mice (*Peromyscus maniculatus bairdi*). *Animal Learning & Behavior*, *8*(4), 534-542.

Roberts, G. (1995). A real-time response of vigilance behaviour to changes in group size. *Animal Behaviour*, *50*(5), 1371-1374.

Rodríguez-Prieto, I., Martín, J., & Fernández-Juricic, E. (2010). Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B: Biological Sciences*, rspb20101194.

Runyan, A. M., & Blumstein, D. T. (2004). Do individual differences influence flight initiation distance? *Journal of Wildlife Management*, *68*(4), 1124-1129.

Schaefer, S. A. (2011). Personality, subjective well-being, and vocal communication in captive male western lowland gorillas. (Doctoral Dissertation). Retrieved from rutgers.edu

Schjelderup-Ebbe, T. (1935). *Social behavior of birds*. In C. Murchison (Ed.), A handbook of social psychology (pp. 947–972). Worcester, MA: Clark University Press.

Schleidt, W., Shalter, M. D., & Moura-Neto, H. (2011). The hawk/goose story: the classical ethological experiments of Lorenz and Tinbergen, revisited. *Journal of Comparative Psychology*, *125*(2), 121.

Schmidt, K. A., Lee, E., Ostfeld, R. S., & Sieving, K. (2008). Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. *Behavioral Ecology*, *19*(4), 759-763.

Schneirla, T. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In Nebraska Symposium on Motivation (pp. 1–42). Lincoln: University of Nebraska Press.

Schuett, W. & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *77*(5), 1041-1050.

Short, K. H. & Petren, K. (2008). Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. *Animal Behaviour*, *76*, 429-437.

Sieving, K. E., Contreras, T. A., & Maute, K. L. (2004). Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. *The Auk*, *121*(3), 738-751.

Sieving, K., Hetrick, S. A., & Avery, M. L. (2010). The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: Exploring a mixed framework for threat communication. *Oikos*, *119*, 264-276.

Sih, A. & Watters, J. V. (2005). The mix matters: behavioral types and group dynamics in water striders. *Behaviour*, *142*, 1417-1431.

Sih, A. (1982). Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology*, *63*(3), 786-796.

Sih, A., Bell, A, & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19, 372-378.

Sinn, D. L., Apiolaza, L. A., & Moltschaniwshkj, N. A. (2006). Heritability and fitness-related consequences of squid personality traits. *Journal of Evolutionary Biology*, *19*(5), 1437-1447.

Sirot, E. (2006). Social information, antipredatory vigilance, and flight in bird flocks. *Animal Behaviour*, *72*, 373-382.

Sloan, J. L. & Hare, J. F. (2008). The more the scarier: Adult Richardson's ground squirrels (*Spermophilus richardonii*) assess response urgency via the number of alarm signalers. *Ethology*, *114*(5), 436-443.

Smith, J. M. (1982). *Evolution and the Theory of Games*. Massachusetts: Cambridge University Press.

Soard, C. M. & Ritchison, G. (2009). 'Chick-a-dee' calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Animal Behaviour*, *78*, 1447-1453.

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, *78*(2), 337-347.

Stöwe, M., Bugnyar, T., Heinrich, B., & Kotrschal, K. (2006). Effects of group size on approach to novel objects in ravens (*Corvus corax*). *Ethology*, *112*, 1079-1088.

Strelau, J. (1997). The contribution of Pavlov's typology of CNS properties to personality research. *European Psychology*, *2*(2) 125.

Sullivan, K. A. (1984). Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, *91*(4), 294-311.

Sullivan, K. A. (1985a). Selective alarm calling by downy woodpeckers in mixed-species flocks. *The Auk*, 184-187.

Sullivan, K. A. (1985b). Vigilance patterns in downy woodpeckers. *Animal behaviour*, *33*(1), 328-330.

Talbot, L. R. (1922). Bird-banding at Thomasville, Georgia, in 1922. *Auk*, *39*, 334-350.

Templeton, C. N., & Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Science*, *104*(13), 5479-5482.

Templeton, C.N., Greene, E. & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, *308*, 1934-1937.

Thoreau, H. D. (1906). *The Writings of Henry David Thoreau (Volume 5)*: Houghton Mifflin.

Uster, D., & Zuberbühler, K. (2001). The functional significance of Diana monkey 'clear' calls. *Behaviour*, *138*(6), 741-756.

van der Poel, A. M. (1979). A note on ‘stretched attention’, a behavioural element indicative of an approach-avoidance conflict in rats. *Animal Behaviour*, *27*, 446-450.

van Oers, K. & Naguib, M. (2013). Avian personality. In C. Carere & D. Maestripieri (Eds.), *Animal Personalities* (66-95). Chicago: University of Chicago Press.

van Oers, K., Klunder, M. & Drent, P. J. 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, *16*, 716e723.

Verbeek, M. E., Boon, A. & Drent, P. J. (1996). Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour,* 133, 945-963.

Visalberghi, E. & Addessi, E. (2000). Seeing group members eat a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour*, *60*(1), 69-76.

Visalberghi, E., Janson, C. H., & Agostini, I. (2003). Response toward novel foods and novel objects in wild Cebus apella. *International Journal of. Primatology*, *24*, 653-675.

Vitousek, P. M., Mooney, H. A., Lubchencho, J., & Melillo, J. M. (1997). Human domination of Earth’s ecosystems. *Science*, *277*, 494-499.

Waite, T. A. (1987). Dominance-specific vigilance in the tufted titmouse: Effects of social context. *The Condor*, *89*, 932-935.

Walsh, R. N. & Cummins, R. A. (1976). The open-field test: A critical review. *Psychological Bulletin*, *83*(3), 482-504.

Ward, A. J. W., Axford, S., & Krause, J. (2002). Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice. *Behavioral Ecology and Sociobiology*, *52*, 182-187.

Webster, M. M. & Ward, A. J. W. (2011). Personality and social context. *Biological reviews*, *86*, 759-773.

Webster, S. J. & Lefebvre, L. (2000). Neophobia by the Lesser-Antillean bullfinch, a foraging generalist, and the bannaquit, a nectar specialist. *Wilson Bulletin*, *112*(3), 424-427.

Webster, S. J. & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. *Animal Behaviour*, *62*, 23-32.

Weinstein, T. A. R., Capitanio, J. P., & Gosling, S. D. (2008). Personality in animals. In O.P. John, R. W. Robins, & L. A. Pervin (Eds.) *Handbook of personality: Theory and research* (328-248). New York: Guilford Press.

Williams, E. H. (2009). Associations of behavioral profiles with social and vocal behavior in the Carolina chickadee (*Poecile carolinensis*) (Doctoral dissertation). Retrieved from Trace: Tennessee Research and Creative Exchange.

Wilson, D. R., & Mennill, D. J. (2011). Duty cycle, not signal structure, explains conspecific and heterospecific responses to the calls of black-capped chickadees (*Poecile atricapillus*). *Behavioral Ecology*, arr051.

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B*, *353*, 199-205.

Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, *9*, 442-446.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*(3), 250-260.

Zachau, C. E. & Freeberg, T. M. (2012). Chick-a-dee call variation in the context of flying avian predator stimuli: a field study of Carolina chickadees (Poecile carolinensis). *Behavioral Ecology and Sociobiology*, *66*, 683-690.

Zanette, L. & Ratcliffe, L. M. (1994). Social rank influences conspicuous behavior of black-capped chickadees, *Parus atricapillus*. *Animal Behaviour*, *48*, 119-127.

VITA

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