Chickadee behavioural response to varying threat levels of predator and conspecific calls

by

Jenna V. Congdon

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Abstract

Chickadees produce many vocalizations, including the *chick-a-dee* call that they use as a mobbing call in the presence of predators. Previous research has shown that chickadees produce more D notes in their mobbing calls in response to high-threat predators compared to low-threat predators, and may perceive predator and corresponding mobbing vocalizations as similar. I presented black-capped chickadees with playback of high- and low-threat predator calls and conspecific mobbing calls to examine vocal and movement behaviours. Chickadees produced more *chick-a-dee* calls in response to playback of a high-threat predator than a low-threat predator, and to reversed high-threat mobbing calls than the original high-threat mobbing calls. Chickadees also vocalized more in response to mobbing calls compared to baseline, regardless of threat level. Chickadees did not produce significantly more D notes in response to high-threat mobbing calls compared to low-threat mobbing calls, but D note production showed some similarities to previous findings. The difference in chickadees production of *tseets* across playback approached significance as chickadees increased calling in response to conspecific mobbing calls. Perch hops decreased in response to conspecific-produced vocalizations, but increased in response to heterospecific-produced vocalizations. Non-perch hop movement behaviour, including food and water visits, decreased across the playback of almost all conditions, regardless of threat or producer. These results suggest that chickadees may produce mobbing calls more in response to high-threat predator vocalizations as an attempt to initiate mobbing with conspecifics, while they produce less mobbing calls in response to a low-threat predator that a chickadee could easily outmaneuver, and chickadees may increase perch hopping in response to predator playback in preparation for a “fight or flight” situation.

Preface

This thesis is an original work by Jenna V. Congdon. All procedures followed the Animal Care (CCAC) Guidelines and Policies and were approved by the Animal Care and Use Committee for Biosciences at the University of Alberta (AUP 108). This thesis is currently being revised to be submitted for publication. I was responsible for the concept formation, data collection, data analysis, and manuscript composition. A.H. Hahn and N. McMillan assisted with data analysis and contributed to manuscript edits. M.T. Avey provided the stimuli for this experiment. C.B. Sturdy was the supervisory author and was involved with concept formation and manuscript revision.

Dedication

My thesis is dedicated in loving memory of Bernard J. McComiskey. He was one of my biggest supporters and my family's hero. Although he has passed, I have continued to try to make him proud through my hard work.

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This thesis follows the format prescribed by the APA Style Manual and the University of Alberta’s Department of Psychology.

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Introduction

Communication is when "one organism transmits a signal that another organism is capable of responding to appropriately" (Pearce, 2008, p. 327). Information is transferred from a sender to a receiver through a signal. Signals have been defined as behavioural, physiological, or morphological characteristics created or preserved as a result of natural selection because they convey information to other organisms, which is beneficial (Otte, 1974). Communication signals have also been more simply defined as acts which alter the behaviour of other organisms (Maynard-Smith & Harper, 2003). Animals communicate about identity (flock and individual), mood, intentions (e.g., fighting), and environmental factors such as the location of food, potential mates, and predator threat (Pearce, 2008; Smith, 1991). There are several ways to communicate information: chemical, electrical, tactile/thermal, vibrations, visual, and auditory (Hauser, 1996; Pearce, 2008). Animals, including humans, convey information through these types of communication in either an active or passive form. Examples of active communication are whale echolocation, impala stotting towards a predator, and deer antler fights over territory and mating opportunities; passive communication includes the colouring of poison dart frogs, and stinging bees and wasps, the stripes of a dangerous snake, the dull plumage of a sick bird, or a peacock's mate-attracting bright feathers (Pearce, 2008).

Animals are capable of communication, but what about language? Language is said to have several properties that differentiate it from communication (Hockett, 1960) such as: 1) arbitrariness of units, 2) semanticity, 3) displacement, and 4) productivity. Arbitrariness of units suggests that language must have discrete units (e.g., words) where a single object can be referred to by many different words or languages. Semanticity requires language to have specific meaning (i.e., refer or make mention to something). Displacement is the ability to communicate about events in another time or space, rather than in proximity to the sender and the receiver. Last, productivity is grammar and syntax, the rules of production. With language, an individual needs to be able to create many sentences with a limited vocabulary (as described in Pearce, 2008).

Although controversial, the *chick-a-dee* call produced by chickadees, a group of North American songbirds, may satisfy many of the criteria for language (Hailman & Ficken, 1986; Doupe & Kuhl, 1999). First is the arbitrariness of language, as words do not necessarily resemble the objects to which they are referring. Hockett (1960, p. 6) explained that "the word 'salt' is not salty or granular" and that "'whale' is a small word for a large object; 'microorganism' is the reverse". The *chick-a-dee* call, like most bird vocalizations (e.g., not including mimicry), does not resemble the many things that it appears to contain information about, such as individual and flock identity, or predator location and threat level (see detailed review under "Vocalizations"). A single object can also be referred to by many different words or languages. Chickadees produce many vocalizations, including the *chick-a-dee* call that they use as a mobbing call in the presence of predators; *chick-a-dee* mobbing calls made in response to a particular predator elicits similar levels of brain activity in chickadee auditory regions as the calls of the predator itself (Avey, Hoeschele, Moscicki, Bloomfield, & Sturdy, 2011). This suggests that both vocalizations are perceived and/or encoded similarly, and thus potentially referring to the same thing despite that *chick-a-dee* calls do not resemble owls calls, and neither vocalizations resemble actual owls. In regards to semanticity, referential communication in nonhuman animals has been well-studied since Seyfarth and Cheney (1990). The number of D notes in a *chick-a-dee* mobbing call, used for recruitment of nearby non-predator species, is positively correlated with higher levels of threat. A great horned owl (*Bubo virginianus*) merits approximately two D notes per call, while a

Northern saw-whet owl (*Aegolius acadicus*) merits approximately four (Templeton, Greene, & Davis, 2005). Displacement is the most difficult requirement to address with the chickadee model; however, we do know that honeybees can communicate the location of displaced food sources (Riley, Greggers, Smith, Reynolds, & Menzel, 2005). In regards to the *chick-a-dee* call, Freeberg and Lucas (2002) found that Carolina chickadees (*Poecile carolinensis*) approached a playback speaker and subsequently took from a seed stand following C-rich calls. This suggests that the note composition, specifically C notes, indicates information about the presence of food. Last, the *chick-a-dee* call clearly meets the productivity requirement as chickadees perceive these four-note calls as natural, open-ended categories; chickadees are able to categorize novel exemplars that are acoustically distinct, but share common qualities (Bloomfield, Sturdy, Phillmore, & Weisman, 2003). (For a detailed comparison of birdsong and human speech and language see ten Cate, 2014.)

Vocal learning occurs in species that learn their communication sounds by listening to a model (e.g., parent), and then imitating these vocalizations. Vocal learning demonstrates that a species' repertoire is not entirely innate. Songbirds are part of a small number of animal groups, including (for example) bats, parrots, hummingbirds, cetaceous whales and dolphins, and humans, (Jarvis, 2007; Wilbrecht & Nottebohm, 2003; Smith, 1991) that learn their communication sounds by listening to a model (e.g., parent) and then imitate these vocalizations (Jarvis, 2007).

Chickadees

Chickadees, part of the Paridae family, are a type of non-migratory North American songbird. There are seven species of chickadee: black-capped, mountain, Carolina, Mexican, boreal, chestnut-backed, and grey-headed (Otter, 2007; Smith, 1991). The black-capped chickadee (*P. atricapillus*) is one of the most widely studied species due to its extensive range spreading from coast to coast and their frequent interaction with humans (Burg, 2007). They are most closely related to the mountain chickadee (*P. gambeli*), and can be found throughout Canada and the northern half of the United States.

Chickadees are used as a study species in a wide variety of research, but the bulk of research conducted with chickadees investigates their communication and perceptual abilities. The vocal communication system of chickadees is highly complex, consisting of several vocalizations used in a wide variety of contexts, from mate attraction and territory defense, to flock mobilization and predatory alarm. As a vocal learner with a complex vocal system, chickadees provide a strong comparative model for language and cognition (Wilbrecht & Nottebohm, 2003; Douple & Kuhl, 1999).

Vocalizations. Chickadees produce several vocalizations that are critical to many aspects of their survival. Of these vocalizations, the most recognizable and studied is the *chick-a-dee* call. This call is produced year-round by both sexes (e.g., Odum, 1942). The *chick-a-dee* call is separated into a '*chick*' portion regularly followed by a '*dee*' portion. It is comprised of four note types: A, B, C, and D. The notes follow a syntax in which they are produced alphabetically, where A notes always precede B notes and so on. Also, these notes appear as a graded continuum, where A notes gradually become B notes as they decrease in frequency (Hailman, Ficken, & Ficken, 1985; Hailman & Ficken, 1986; Hailman, Ficken, & Ficken, 1987). Chickadees also omit and repeat note types (e.g., AAAABBDDDD); this allows for a seemingly endless combination of note types. Therefore, the *chick-a-dee* call is one of the most intricate non-human animal vocalizations that has been studied (Sturdy, Bloomfield, Carrier, & Lee, 2007).

To date, research has uncovered many details about the information encoded in the note types of the *chick-a-dee* call. Baker and Becker (2002) presented taxidermic mounts of predators at 1 m and 6 m distances. They found that black-capped chickadees vocalized more quickly and produced more *chick-a-dee* mobbing calls in the 1-m condition than the 6-m condition, and more A notes per call were produced in the 6-m condition while more B notes per call were produced in the 1-m condition. These results indicate that the proximity of a predator, or the immediacy of threat, may be signaled by the rate of calling as well as the note composition of the mobbing calls, specifically with respect to A and B notes. Freeberg and Lucas (2002) observed differential responding in Carolina chickadees to the playback of calls with or without C notes; Carolina chickadees approached the speaker and took seeds from a novel site more following *chick-a-dee* calls that contained C notes than calls that did not. Later, Charrier, Bloomfield, and Sturdy (2004) conducted bioacoustic analyses of black-capped chickadee calls and noted that C notes contained the most amount of information and had the greatest potential for individual recognition. The latter '*dee*' section is aptly named as it is composed of D notes; studies have also demonstrated that the *chick-a-dee* call is used as a signal to coordinate flock movements and that chickadees can recognize the identity of flock-mates through D note acoustics (Mammen & Nowicki, 1981). Further work examining D notes in Carolina chickadees (Mahurin & Freeberg, 2009) found that calls produced by the first chickadee to take a seed from a feeding station contained more D notes than did calls produced by subsequent chickadees. Moreover, chickadees approached the feeding site quicker following the playback of *chick-a-dee* calls containing many D notes than to calls with less D notes. Therefore, recruitment appears to be initiated through calls containing a large number of D notes.

In the presence of predators, chickadees use their *chick-a-dee* mobbing call to mobilize and coordinate chickadees (conspecifics) and other avian species (heterospecifics) to attack and harass a nearby predator (Hailman, Ficken, & Ficken, 1987). Chickadees are prey to many avian species such as owls and hawks, as well as terrestrial animals, including cats and weasels. A small owl would be more likely to catch a chickadee than a larger owl because it can maneuver through the trees with ease; therefore, smaller predators are of higher threat to a birds' survival. Large owls may also simply not demonstrate an interest in pursuing small prey, such as chickadees, likely because a small bird would represent a small gain for a relatively large predator and significant energy expenditure. Research has shown that the numbers of D notes produced in black-capped chickadees' *chick-a-dee* mobbing calls are positively correlated with the degree of predator threat (Templeton et al., 2005). Specifically, more D notes are repeated in response to smaller, higher-threat predators, creating a direct negative correlation between body length and D note production. Last, Soard and Ritchison (2009) used Carolina chickadees to look at the '*chick*' note versus the '*dee*' note production to mounts of raptors. More '*chick*' notes and fewer '*dee*' notes were produced to larger, lower-threat predators, and few or no '*chick*' notes and significantly more '*dee*' notes were produced to smaller, higher-threat predators. Carolina chickadees also increased calling rates and made closer approaches in response to the playback of *chick-a-dee* calls that were produced in response to a small predator mount than a large one. The *chick-a-dee* call, used as a mobbing call, appears to inform flock members about the presence of a predator and the level of threat that it presents.

The *chick-a-dee* call is only one of the many types of major vocal signals produced by chickadees; *gargles* are a learned vocalization commonly produced by black-capped chickadees, and can be considered similarly important to the *chick-a-dee* call or *fee-bee* song (Odum, 1942;

Baker & Gammon, 2007). *Gargles* have a noisy complexity, are produced primarily by males, and are made up of several distinct syllables (Ficken, Weise, & Reinartz, 1987). Titled the “dominance note” by Odum (1942), this vocalization is often observed during interactions at food sources, can be elicited with a mirror, and it must be socially learned and established in early life (Ficken et al., 1987). For young birds, the *gargle* call can allow them to access a flock, compete more effectively for food, and increase their attractiveness to females and mating potential (Baker & Gammon, 2007; Ficken et al., 1987).

Songs (versus calls) produced by most songbirds species are highly complex (Catchpole & Slater, 2003), but black-capped chickadees produce a simple two-note *fee-bee* song (Sturdy et al., 2007). Male songbirds are known to use song when defending their territory or attracting females. Due to this notion, it was originally thought that only males sing. More recent research on song production has investigated sex differences in the acoustic properties of the *fee-bee* song that indicate that the sex of the caller can be identified by the frequency decrease in the *fee* note (i.e, the *fee* glissando) (Hahn, Krysler, & Sturdy, 2013). It is also not uncommon for black-capped chickadees to produce a three-note song or a single *fee* note (Odum, 1942).

Tseets are the most frequently produced chickadee vocalization, but are minimally understood; this vocalization is a contact call when chickadees are separated, common to both black-capped and mountain chickadees (Odum, 1942). Guillette, Bloomfield, Batty, Dawson, and Sturdy (2010) examined the bioacoustics of the single-note *tseet*, and found that there were several acoustic features contained in *tseets* that correctly identified individuals or members of a particular flock.

Movement behaviours. Chickadees consume food and water, groom, and move between locations. Chickadees housed in laboratory cages have distinct, typical behaviours that are often scored for behavioural analyses. The most common movement behaviours are perch hops (e.g., Hoeschele et al., 2010). It is unknown whether chickadees increase or decrease this basic movement behaviour when presented with high versus low threat vocalizations, or predator- versus chickadee-produced calls.

Healthy laboratory chickadees visit their food cups and water bottles several times in a day. These behaviours are important to satisfy physiological needs for survival, but should be the first to decrease in the presence of danger. When in the presence of a predator, it would be logical to decrease food and water visits to stay vigilant or decrease exposure to a predator (i.e., stay inconspicuous). Nowicki (1983) suggested that chickadees could identify their flocks based on acoustic features of calls, and designed a field playback study to examine responses of birds to playback of resident and foreign flocks' calls when the resident chickadees were foraging. Chickadees continued to forage and did not produce additional calls in comparison to baseline when they heard resident calls; chickadees significantly decreased foraging behaviour and increased calling in comparison to baseline when they heard foreign flocks' calls.

Pecking bouts are a behaviour unique to animals with beaks. The chickadee diet typically consists of seeds and small insects. Sunflower seeds, high in fat, are a favourite, especially in the long winter months (Smith, 1991). Chickadees will conduct several pecking bouts in order to break the coat and access the seeds inside.

Another movement behaviour, which is also demonstrated by chickadees, is the beak wipe. The criterion for this behaviour is that the bird "swipes wing across beak" (Hoeschele et al., 2010). This behaviour in chickadees is rarer than the aforementioned behaviours, but is likely similar to preening. Chickadees produce many other movements, such as preening (i.e., grooming) and rubbing their beaks on perches.

Hoechele and colleagues (2010) also recorded ruffles and defined this movement behaviour as “shakes feathers”. Smith (1991) originally described black-capped chickadees ruffled crown (specific to the head) and body ruffling, both visual displays that are common in aggressive encounters. Body ruffles, noted most often in autumn, involve fluffing the back feathers as well as drooping the wings and spreading the tail feathers. Body ruffles are also often followed by gargles, the vocalization used in predominantly in situations involving dominance interactions. Simply by producing this visual display, it appears that the producer gains access to food sources in aggressive intra- and interflock interactions. Establishing dominance is likely why this movement behaviour is most often witnessed in juvenile birds (Piaskowski, Weise, & Ficken, 1991).

Finally, in addition to Templeton and colleagues’ (2011) finding that chickadees produced more D notes to smaller predators, they found that chickadees approached within 3 m of the speaker more often to the mobbing calls produced to a small predator versus a larger predator or control vocalizations.

Referential Communication

As discussed in brief earlier, referential communication is the exchange of information about an external referent, and is commonly observed in humans and non-human primates (Seyfarth & Cheney, 1990; Call & Tomasello, 1994). Animals require the ability to communicate about predators to ensure that they survive, have the opportunity to reproduce, and pass on their genes. Some of the best evidence for non-human referential communication has been provided by vervet monkeys that live in troops, which produce unique alarm calls to three different types of predators. In the presence of an avian predator, they produced a “chuckle”. Other monkeys in the troop responded by looking up to the sky or taking cover in a nearby bush. In the presence of a leopard, they produced a “loud bark” that resulted in troop members fleeing up trees to safety. Last, in a presence of a snake, they produced a “high-pitched chuttering” that resulted in members of the troop looking around. This last alarm signal and troop response is likely to co-ordinate and initiate mobbing behaviour (Struhsaker, 1967). Birds also appear to vocalize referential signals to flock members; for example, male chickens produce calls that signal the presence of food to conspecifics (Evans & Evans, 1999). However, little evidence has been provided to support similar abilities in songbirds for communicating about predator presence.

Stemming from Templeton’s work, Avey et al. (2011) determined whether neural responses of black-capped chickadees varied with the threat level conveyed by mobbing calls, and whether neural response to mobbing calls was the same neural response evoked by the actual predators’ calls. This was accomplished by measuring the amount of neural expression of the immediate early gene (IEG) ZENK following the playback of various acoustic stimuli to wild-caught and hand-reared chickadees. Avey et al. presented low- and high-threat stimuli, including predator-elicited mobbing calls and the corresponding predator calls, and then compared levels of gene expression among the playback groups. Results confirmed that higher levels of ZENK were observed in the high-threat condition and that, within the same threat level, there was no difference between the amount of IEG expression in response to predator-elicited mobbing calls compared to the actual predator calls. With hand-reared chickadees, however, mobbing calls resulted in higher IEG expression than corresponding predator calls. This difference was thought to be due to hand-reared birds lacking experience with predators, or their calls, which indicates that assessment of the degree of threat appears to have a learned component.

Previous experiments (e.g., Templeton et al., 2005) have examined vocal production in the presence of a live or mounted (i.e., stuffed) predator, and to audio recordings of predator-elicited mobbing calls, but not in response to audio recordings of actual predator calls. Also, no previous research has examined how chickadees physically respond (i.e., movement behaviours) to predator calls versus mobbing calls. My research examined how chickadees communicate about predator threat: specifically, I investigated chickadee vocal and movement behavioural responses to varying threat levels evoked by the auditory stimuli offered by predator and conspecific calls. My playback experiment included six conditions: 1) low-threat predator calls, 2) low-threat predator-elicited conspecific mobbing calls, 3) high-threat predator calls, 4) high-threat predator-elicited conspecific mobbing calls, 5) control non-chickadee calls, and 6) control reversed conspecific mobbing calls.

Based on previous research (e.g., Templeton 2005, Hoeschele et al. 2010), I predicted that: 1) chickadees would emit a greater increase of *chick-a-dee* calls following playback of *chick-a-dee* mobbing calls compared to predator vocalizations, to help initiate mobbing; 2) under high-threat conditions, chickadees would produce more *chick-a-dee* calls compared to other vocalizations; 3) chickadees would emit less non-mobbing call vocalizations (e.g., *tseets*) in all playback conditions compared to baseline; and 4) chickadees would produce more D notes in response to high-threat vocalizations compared to low-threat vocalizations, for both predator calls and the corresponding mobbing calls (i.e., stimuli of the same threat level); 5) chickadees would suppress movement more in the presence of high-threat stimuli than low-threat; and 6) movement would be suppressed more in response to predator calls (i.e., hiding) than to chickadee-produced mobbing calls, as mobbing calls should elicit mobbing behaviour.

Methods

Subjects

I used six adult black-capped chickadees (three male, three female) in this experiment. Subjects were captured from two regions in Edmonton, Alberta, Canada (North Saskatchewan River Valley, 53.53N, 113.53W; Mill Creek Ravine, 53.52N, 113.47) between January 2010 and February 2012. At time of capture, birds were identified as adults by examining the colour and shape of the rectrices (Meigs, Smith, & Van Buskirk, 1983; Pyle, 1997). Sex was determined by DNA analysis (Griffiths, Double, Orr & Dawson, 1998). Before the experiment, birds were housed in individual cages (30 × 40 × 40 cm, Rolf C. Hagen, Inc., Montreal, Quebec, Canada) allowing both visual and auditory contact with conspecifics. Home cages had nesting boxes based on availability. Birds were held under the natural light cycle for Edmonton, Alberta. Birds had *ad libitum* access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St Louis, MO, USA), water (vitamin supplemented three times a week; Prime vitamin supplement; Hagen, Inc.), grit (Rolf C. Hagen Inc., Montreal, Quebec, Canada), and cuttlebone. Birds were also provided three to five sunflower seeds daily, one superworm (*Zophobas morio*) three times a week, and a mixture of eggs and greens (spinach or parsley) twice a week.

Apparatus

During the experiment, subjects were housed in sound-attenuating chambers (inner dimensions 58 × 168 × 83 cm; Industrial Acoustics Corporation, Bronx, New York, USA). Prior to being housed in a chamber, home cages were modified to only contain the following: two water bottles, two food cups, three equally-spaced plastic perches, and a small cardboard rodent house. Every attempt was made to ensure the cage was geometrically symmetrical. The acoustic isolation chamber door was opened once daily to top up food and water and provide a supplemental worm to each bird following playback. To prevent excessive noise disturbances, the birds that were not being recorded had husbandry provided following the entirety of the playback trials. The additional water bottles and food cups ensured that the sound chamber doors did not have to be opened more than once every 24 hours. All subjects were also monitored twice daily (1000 and 1700) via video camera accessed externally.

Playback Stimuli

Avey et al. (2011) obtained mobbing calls by presenting black-capped chickadees with mounts of a northern saw-whet owl (high threat predator) and a great horned owl (low threat predator). These mobbing calls, along with the individual northern saw-whet, great-horned owl, and red-breasted nuthatch calls, and computer-manipulated reversed northern saw-whet induced mobbing calls, also generated and used in Avey and colleagues, were used in the current study (see Avey et al., 2011 for full details on obtaining the playback stimuli). In total, I used: great horned owl calls (GHOW), black-capped chickadee mobbing calls made in response to the presentation of a great horned owl (MOB GHOW) mount, northern saw-whet owl calls (NSWO), black-capped chickadee mobbing calls made in response to a northern saw-whet owl (MOB NSWO) mount, red-breasted nuthatch (*Sitta canadensis*) calls (RBNU), and reversed black-capped chickadee mobbing calls made to a northern saw-whet owl (REV MOB NSWO) mount. Two different sets were generated for each stimulus category (e.g., two sets of northern saw-whet owl calls) to ensure that a difference in responding across conditions was due to the threat level of the stimulus, and not the length of the stimulus or individuals' vocalizations used to generate the stimulus. Stimuli files from Avey et al. (2011) were 30 minutes in duration. These original playback files were edited to a final duration of to 15 minutes each. Each file consisted of 15 60-s cycles made up of of 15 s of playback and 45 s of silence. The number of calls presented within each 15-s window varied across conditions, but were as natural as possible for the species selected (see Table 2).

Playback Procedure

Prior to and during playback, each subject was housed in their home cage located within one of six randomly-assigned sound-attenuating chambers. Each bird was given 24 hr to acclimatize to the chamber before hearing one of the playback conditions. Subjects were exposed to a randomly-assigned playback condition every other day (i.e., three subjects per day, alternating days), with an average of 47.5 hr between playbacks. Start times were constant for each bird (i.e., 12:45 p.m., 1:15 p.m., or 1:45 p.m.). The order that the subjects were run was randomly assigned on day one of playback and remained the same throughout the experiment. I randomly assigned the order that each subject would hear playback stimuli using a 6 × 6 Latin square; all six subjects heard all six playback conditions. Each subject was recorded for a total of 30 minutes a day (15 minutes of silence, 15 of playback). Playback sessions were carried out sequentially, to one individual at a time, to ensure that a subject could not hear other potentially-conflicting stimuli at the time of their own playback and recording session.

Audio recordings of the playbacks were obtained using six AKG C 1000S condenser microphones (frequency response: 50–20,000 Hz; AKG Acoustics, Vienna, Austria), and six solid-state recorders (Marantz PMD670, D&M Professional, Itasca, IL, USA). Video recordings of the playbacks were obtained using six video cameras (four Sony Handycam DCR-SX45, Sony Electronics Asia Pacific Pte Ltd., Tokyo, Japan; two Canon VIXIA HF R500, Canon Canada Inc., Mississauga, Ontario, Canada) and video capture software (EZ Grabber, Geniatech, Beijing, China) installed on a personal computer. In each chamber, stimuli were played back through a speaker (Fostex FE108 Σ or Fostex FE108E Σ full-range speaker; Fostex Corp., Japan; frequency response range 80-18,000 Hz) and amplifier (Cambridge Audio, azur 640A Integrated Amplifier; London, UK) with an mp3 player (Creative ZEN; Singapore). The amplitude was measured at the level of the perches from the centre position of the cage and playback amplitude was set to approximately 75 db with a Brüel & Kjær Type 2239 sound level meter (Brüel & Kjær Sound & Vibration Measurement A/S, Nærum, Denmark; A weighting, slow response). I conducted the experiment August 15-21, 2014, before the fall equinox in mid-August, when both *chick-a-dee* calling and *fee-bee* song production is low (Avey, Quince & Sturdy, 2008).

Re-recordings

During building construction, loud background noise caused an observable difference when recording the playback of subject S-3591 and baseline of subject 3637 on August 19, 2014. These subjects were re-run 48 hours later, on August 21st, to obtain uninterrupted recordings. Re-running the playback condition appeared to produce no observable difference in vocal or movement behaviour.

Tape Coding

Audio and video files were scored separately for chickadee vocal and movement responses, respectively. Coders used SIGNAL sound analysis software (Engineering Design, Version 5.10.24, RTS, Berkeley, California, USA) to identify chickadee vocalizations, and VLC Media Player (VideoLAN, 2.1.3 Rincewind, Paris, France) to score movement behaviour. I, and two undergraduate volunteer coders that were blind to the playback conditions and predictions, scored the files. I then verified the scoring completed by the coders; this coding was used for analysis. Coding of audio files was initiated 15 minutes (or 900ms) prior to the beginning of the first playback stimulus' waveform in the spectrogram displayed in the SIGNAL window; coding of video files was initiated 15 minutes prior to hearing the first playback stimulus (e.g., If MOB

GHOW started at 15:02, baseline scoring would start at 00:02). We scored five classes of vocal behaviours: *chick-a-dee* calls (organized by the number of D notes), *gargles*, *fee-bee* songs (including *fee*-only songs), *tseets*, and other/unidentified vocalizations. We scored eight classes of movement behaviours: perch hops, food visits, water visits, ruffles, pecking bouts, beak wipes, “approaches” (see Table 1 for definition), and other/unidentified movements. See Table 1 for a description of the scored behaviours.

Statistical Analyses

Behavioural data from six experimental conditions were separated into two phases: baseline and playback. Tallies were summed for each bird’s vocal and movement behaviours, in 15s blocks, for the two phases of each condition. I subtracted baseline sums from playback to obtain a difference from baseline measure for each behaviour in every condition. The vocalization scores were then used in a repeated measures ANOVA for vocal behaviours. A separate repeated measures ANOVA was conducted for the movement behaviours. Further repeated measures ANOVAs and paired-samples t-tests were conducted for each behaviour across the six playback conditions. The Huynh-Feldt correction was used on all repeated measures tests to correct for any possible violations in sphericity. Alpha levels were set at 0.05. Graphs were produced to display differences in behaviour across the six playback conditions. All graphs were plotted as an average sum of the birds' behaviours calculated as playback minus baseline. Therefore, each graph demonstrates the positive or negative effect of playback on behaviour in relation to baseline.

Results

Overall Vocal Output

Figure 1 illustrates the difference from baseline in vocal responses of: *chick-a-dee* calls (broken down by D note composition), *gargles*, *fee-bee* and *fee* only songs, and “other” vocalizations made to each stimulus set. This graph shows that chickadees produced fewer *chick-a-dee* calls and overall vocalizations during playback of GHOW from baseline. Chickadees also decreased production of *chick-a-dee* calls and overall vocalizations during playback of NSWO from baseline, but there was a slight increase in production of *chick-a-dee* calls containing one to six or more D notes. A one-way repeated measures ANOVA indicated that there were no significant differences among playback conditions ($F_{2,9} = 1.99$, $p = 0.194$, $\eta_p^2 = 0.28$). However, there was a significant difference in the *chick-a-dee* call production between GHOW (M = -15.67, SD = 24.04) and NSWO (M = 9.50, SD = 11.20) conditions, $t(5) = -2.61$, $p = .048$, d = 1.34, with chickadees producing more calls in response to the high-threat owl calls than the low-threat ones. There was also a significant difference in the *chick-a-dee* call production between MOB NSWO (M = 23.00, SD = 50.93) and REV MOB NSWO (M = 55.83, SD = 52.044) conditions, $t(5) = -3.51$, $p = .017$, d = 0.64, with chickadees producing fewer calls in response to the high-threat owl-related mobbing calls than the control condition. No other comparisons were significant (all values ps ≥ .58).

In addition, in comparison to heterospecific-produced playback conditions, chickadees produced more *chick-a-dee* calls in response to all conspecific-produced playback conditions (Fig. 1). It appears that overall birds also produced more vocalizations of any type in response to these stimuli. However, birds produced fewer *chick-a-dee* calls containing many D notes in response to the MOB GHOW condition, and fewer *gargles* in the MOB NSWO condition.

Figure 1 shows that chickadees produce slightly more *chick-a-dee* calls, over other vocalizations, in the NSWO condition in comparison to the GHOW playback condition. However, a 4 × 6 repeated measures ANOVA indicated no significant difference in the production of *chick-a-dee* calls in comparison to other vocalizations ($F_{1,5} = 3.53$, $p = .12$, $\eta_p^2 = 0.41$).

Non-*chick-a-dee* call vocalizations are of interest as well, as the production of most other vocalizations have not been studied in a playback experiment utilizing predator and conspecific mobbing calls. Figure 2 shows that chickadees increased their production of *tseets* in response to chickadee-produced vocalizations, regardless of threat. The difference in *tseet* production across playback conditions approached significance (one-way repeated measures ANOVA; $F_{2,11} = 3.46$, $p = .06$, $\eta_p^2 = 0.41$). *Gargles* (one-way repeated measures ANOVA; $F_{2,12} = 1.20$, $p = .34$, $\eta_p^2 = 0.19$); songs, including *fee-bee* and *fee*-only vocalizations (one-way repeated measures ANOVA; $F_{5,25} = 1.45$, $p = .24$, $\eta_p^2 = 0.23$); and other vocalizations were shown not to differ across conditions (one-way repeated measures ANOVA; $F_{1,7} = 1.92$, $p = .22$, $\eta_p^2 = 0.28$).

As discussed above, chickadees produced fewer *chick-a-dee* calls and overall vocalizations during playback of GHOW, and chickadees produced slightly more *chick-a-dee* calls containing one to six or more D notes in the NSWO condition in comparison to baseline. However, the difference in D note composition across playback conditions was not significant (7 × 6 repeated measures ANOVA; $F_{2,12} = 1.27$, $p = .32$, $\eta_p^2 = 0.20$). Despite this, there are evident differences in the D note composition of mobbing calls for GHOW versus NSWO (Fig. 1). When interpreting within threat-level, chickadees produced fewer *chick-a-dee* calls relative to baseline in GHOW, but produced more in response to MOB GHOW in comparison to baseline. The increased *chick-a-dee* mobbing calls in response to MOB GHOW typically contained one to three D notes per call.

Overall Movement Output

From Figure 3, it is evident that chickadees produced fewer perch hops relative to baseline in response to chickadee-produced calls (i.e., MOB GHOW, MOB NSWO, and REV MOB NSWO) regardless of threat. In contrast, chickadees produced more perch hops relative to baseline in response to non-chickadee produced calls (i.e., GHOW, NSWO, and RBNU). When analyzing the frequency of this movement across playback conditions, there was a significant effect of playback type on frequency of perch hops (one-way repeated measures ANOVA; $F_{5,25} = 3.45$, $p = .02$, $\eta_p^2 = 0.41$).

Figure 4 illustrates the difference from baseline of non-perch hop movement behaviour across the six playback conditions. Almost all non-perch hop movements decreased during playback across all six conditions, however these were not significantly different, relative to baseline (several one-way repeated measures ANOVAs; food visits: $F_{5,24} = 1.25$, $p = .32$, $\eta_p^2 = 0.20$; water visits: $F_{2,9} = 2.20$, $p = .17$, $\eta_p^2 = 0.31$; pecking bouts: $F_{2,11} = 0.80$, $p = .49$, $\eta_p^2 = 0.14$; beak wipes: $F_{3,14} = 1.04$, $p = .40$, $\eta_p^2 = 0.17$; and “other” movements: $F_{4,21} = 1.52$, $p = .23$, $\eta_p^2 = 0.23$).

Ruffles and approaches are plotted together in Figure 5, because they were both specifically predicted to be agonistic behaviours. From this, it appears that chickadees ruffled more in response to low-threat playback in comparison to high-threat. Approaches instead appear to have increased most in response to the high-threat mobbing condition (i.e., MOB NSWO). A one-way repeated measures ANOVA indicated no significant difference in the production of ruffles across playback conditions ($F_{3,13} = 1.79$, $p = .20$, $\eta_p^2 = 0.26$). A one-way repeated measures

ANOVA, indicated that approaches did not differ significantly across playback ($F_{3,17} = 1.21$, $p = .34$, $\eta_p^2 = 0.20$).

Discussion

Black-capped chickadees were presented with playback of high- and low-threat predator calls and conspecific mobbing calls. The main findings of this study, examining vocal and movement responses, indicated that *chick-a-dee* mobbing call production and frequency of perch hops varied depending on threat-level and producer. Once a predator is detected, anti-predatory behaviours can assist prey in defending themselves; *chick-a-dee* calling helps recruit conspecifics to mob a nearby predator whereas increased perch hopping could prepare a bird for a “fight or “flight” scenario. Therefore, these two behaviours appear to be more connected with effective anti-predatory responses than all other measured behaviours.

Vocal Behaviour

The *chick-a-dee* call is a complex vocalization that conveys food and predator-related information to nearby conspecifics and heterospecifics (e.g., Nowicki 1983; Templeton, 2005). Despite being a well-studied vocalization common among Parid species, exactly how this call communicates specific information is unclear (Wilson & Mennill, 2011). Previously, it was found that chickadees continued to forage and did not produce additional calls in comparison to baseline when they heard resident calls, but reduced foraging behaviour and increased calling in comparison to baseline when they heard foreign flocks’ calls (Nowicki, 1983). Wilson and Mennill (2011) manipulated the signaling rate (i.e., duty cycle) and structural variation of the *chick-a-dee* call and found that signaling sequences with a high duty cycle attracted more conspecific and heterospecific receivers, that approached the speaker more quickly, closely, and remained near for longer.

I predicted that chickadees would increase their rate of *chick-a-dee* calls following playback of *chick-a-dee* mobbing calls compared to predator vocalizations. Significant differences were found in the *chick-a-dee* call production between GHOW and NSWO conditions, with chickadees producing more calls to the high-threat owl-produced calls than the low-threat ones, and between MOB NSWO and REV MOB NSWO conditions, with chickadees producing more calls to the chickadee-produced control condition than the high-threat owl-related chickadee mobbing calls. The higher production of *chick-a-dee* calls in the NSWO condition in comparison to the GHOW condition may be a result of chickadees calling for 'help' in response to a quick, high-threat owl, whereas they can easily outmaneuver a slower, low-threat owl and opt not to recruit conspecifics. It is unclear why chickadees would call more to reversed chickadee calls than the identical 'normal' calls. Previous studies have found that syntax matters in the production of the *chick-a-dee* calls, and responding is reduced when the syntax is altered (i.e., note types produced alphabetically; Hailman, Ficken, & Ficken, 1985; Hailman & Ficken, 1986; Hailman, Ficken, & Ficken, 1987; Charrier & Sturdy, 2005), thus reversal could essentially create a foreign vocalization. The reversal of the call could also result in the alarm call being even more threatening to a chickadee as if a conspecific is in some sort of unknown danger. However, Avey et al. (2011) found that playback of this control stimulus resulted in the least amount of IEG expression in birds, even lower than the control, non-chickadee vocalizations of the red-breasted nuthatch. No other playback conditions were found to result in significantly different *chick-a-dee* call production. Although my prediction was not supported, these results are in line with Avey's findings that, within threat level, chickadees produced similar neural expression regardless of whether the playback was chickadee- or predator-produced. Therefore, IEG expression was found to increase in response to both high-threat playback conditions, and chickadees' vocal behaviour was affected similarly. It seems that there may be a connection between auditory input, vocal output, and neural expression.

Second, I predicted that chickadees would produce more *chick-a-dee* calls compared to other vocalizations in high-threat conditions (i.e., NSWO and MOB NSWO). This prediction was not supported as chickadees did not produce more *chick-a-dee* calls compared to other vocalizations in high-threat conditions.

Third, I predicted that chickadees would emit less non-mobbing call vocalizations in all playback conditions compared to baseline. I expected that chickadees would likely vocalize less to mobbing playback because they would be emitting their own mobbing calls, and that they would also vocalize less to predator playback because they would emit less overall. This prediction was not supported as chickadees increased their production of *tseets* in response to chickadee-produced vocalizations, regardless of threat (Fig. 2), and this increase approached statistical significance. *Tseets* are typically a contact call for chickadees; chickadees may produce this vocalization when they hear other chickadees, as indicated by these playback conditions, rather than a predator. When investigating vocal differences across playback conditions, no significant results were found for *gargles*, songs, and 'other' vocalizations. *Gargles* are typically produced by juveniles to establish themselves and gain access to food. It is unlikely that this vocalization would be useful in the presence of a predator. Chickadees use their *fee-bee* song to attract mates and maintain territory; Figure 1 indicates that song production only decreased, relative to baseline, in response to high- and low-threat owl calls. Again, it would be appropriate to sing in the presence of a conspecific and abstain when a predator is nearby.

Fourth, I predicted that chickadees would produce more D notes in response to high-threat vocalizations related to high-threat compared to low-threat, for both predator calls and the corresponding mobbing calls (i.e., stimuli of the same threat level). Templeton et al. (2005) found that chickadees produced more D notes when detecting a high-threat saw-whet owl (approximately four per call) than to a low-threat great horned owl. Avey et al. (2011) found that chickadees expressed more IEG in auditory brain regions in response to high threat predator- and chickadee-produced calls than low threat predator- and chickadee-produced calls, despite the acoustic differences of the predator and conspecific stimuli. Due to these neurological findings, I predicted that I would observe a similar pattern in a behavioural task. Specifically, I predicted that chickadees would produce more D notes in response to high-threat vocalizations compared to low-threat vocalizations, for both predator calls and the corresponding mobbing calls (i.e., stimuli of the same threat level). The increased *chick-a-dee* mobbing calls in response to MOB GHOW typically contained one to three D notes per call, and calls in response to MOB NSWO typically contained more three to six D notes (Fig. 1). An increase from baseline in calls containing three to six or more D notes is also evident in the NSWO playback condition. These trends support this prediction, and demonstrate some similarities with the typical production of two to three D notes per call to live great horned owls and approximately four D notes per call to live northern saw-whet owls, as reported by Templeton et al. (2005).

Movement Behaviour

I predicted that chickadees would suppress movement more in the presence of high-threat stimuli than low-threat, and that movement would be suppressed more in response to predator calls (i.e., hiding) than to chickadee-produced mobbing calls designed to elicit mobbing behaviour (Prediction 5 & 6, respectively). Perch hops are the most common movement of chickadees in laboratory environments (e.g., Hoeschele et al., 2010) and it was unknown whether chickadees would produce more or less of this basic movement behaviour when presented with high- versus low-threat, or predator- versus chickadee-produced vocalizations. It is clear that chickadees produced fewer perch hops relative to baseline in response to chickadee-produced calls (i.e., MOB GHOW, MOB NSWO, and REV MOB NSWO) regardless of threat. In contrast, chickadees produced more perch hops relative to baseline in response to non-chickadee produced calls (i.e., GHOW, NSWO, and RBNU). There was a trend toward low-threat playback resulting in larger increases and decreases in perch hops from baseline in comparison to high-threat playback (Fig. 3; Prediction 5). With regard to heterospecific versus conspecific calls, including control conditions, chickadees produced more perch hops in response to heterospecific calls while decreasing perch hop frequency in response to conspecific calls (Fig. 3; Prediction 6). There was a negative relationship between vocal responses and perch hops. This result may simply indicate that chickadees typically vocalize when stationary, and vocal production frequency is affected by the context of their environment. Chickadees may also increase perch hopping in response to predator playback in preparation for a "fight or flight" situation. Subsequent studies could equip cages with nest boxes to determine if the reduction of perch hops is actually chickadees' way of hiding in the absence of cover when warned by conspecifics. Overall, results indicate that birds responded opposite to both predictions, as chickadees altered their perch hop behaviour less from baseline in the high-threat conditions, and chickadee movement actually increased in response to predator calls compared to baseline while it decreased in response to mobbing calls.

Non-perch hop movements did not differ significantly across playback conditions. Food and water visits, pecking bouts, and "other" movements generally did decrease from baseline during most playback conditions (Fig. 4). Chickadees would decrease food and water visits in the presence of threat, regardless whether stimuli came from a predator or conspecifics. Previously, Nowicki (1983) found that chickadees significantly reduced foraging behaviour when they heard foreign flocks' calls; a foreign flock would conceivably pose a threat to resources (e.g., territory security or foraging access) the same way that a predator would to survival. Pecking bouts, conducted to break open seeds, and "other" movements, such as preening and rubbing beaks on perches, also leave birds more vulnerable to predation. It would be logical to decrease pecking bouts and other movements to stay vigilant or inconspicuous.

Tied to aggression, chickadees produce ruffles to conspecifics to establish dominance and gain access to food. However, chickadees did not appear to produce ruffles in response to high-threat predator- or chickadee-produced calls for mobbing purposes. This finding could be a result of chickadees not ruffling in high-threat conditions to avoid being noticed by predators; ruffles and *gargles* are typically produced consecutively and could result in higher risk to an individual (Smith, 1991).

Templeton and colleagues (2005) found that chickadees approached within 3 m of the speaker more often to vocalization of small predators than larger predators or control vocalizations. In my experiment, approaches were defined as landing on the wall closest to the speaker; I had predicted that chickadees would perch on the front wall more frequently in response to high-threat playback conditions. Although non-significant, approaches appear to have been increased most in response to the high threat mobbing condition (i.e., MOB NSWO). Templeton found that chickadee approaches were highest in response to the actual vocalization of a high-threat predator, while I found that chickadee approaches were highest in response to high-threat mobbing calls. The original result might not have been found as the speaker does not directly resemble the predators used in Templeton's experiment. However, approaches are most likely connected with mobbing behaviour, which is initiated by conspecific mobbing calls in the presence of predator threat.

Future Directions

To extend the current experiment, I plan to conduct further trials that will include more vocalizations from chickadee and other predator species, as I and Avey et al. (2011) only used a subset of avian species and no mammalian predators (e.g., cats or ferrets; Templeton et al., 2005). For example, I will include mountain and Carolina chickadee mobbing calls, and other avian (e.g., hawks) and mammalian predator calls (e.g., cats or weasels). This will expand our understanding of how animals identify and respond to various predator threats through vocal and movement behaviour. By extending the proposed research in this way, I will increase the generality of my findings to be more broadly applicable.

In addition, I will test whether chickadees perceive mobbing calls and matched predator calls as similar, despite their acoustic differences. I will train birds in an operant discrimination task in which chickadees are trained to respond (‘go’) to one class of mobbing call and withhold responding (‘no-go’) to another class of mobbing call. Following this training, birds will be tested with novel calls from both high- and low-threat predators. I predict that birds will show transfer of training (e.g., birds trained to respond to high-threat mobbing calls will respond to novel high-threat predator calls). If chickadees demonstrate that they treat chickadee mobbing calls produced in response to a specific owl species and the actual owls’ call as similar, this would provide complimentary evidence of referential communication abilities in a songbird, abilities commonly observed in humans and other non-human primates (Seyfarth & Cheney, 1990; Hauser, 1996; Doupe & Kuhl, 1999; Baldwin, 1993; Call & Tomasello, 1994).

Conclusion

In summary, I found that chickadees increased *chick-a-dee* mobbing call production in response to high-threat owl calls versus low-threat owl calls, and to reversed high-threat mobbing calls versus the original high-threat mobbing calls. *Tseet* production across playback conditions approached significance, but differed between conspecific versus heterospecific stimuli rather than high- versus low-threat; all other non-*chick-a-dee* vocalizations did not differ significantly across conditions. The variation of D note production was non-significant as well, but trends are similar to Templeton's findings. Within threat level, vocal production was similar, in line with previous findings of inducing similar neural expression, which indicates a connection between auditory input, vocal output, and neural expression. For movement behaviour, chickadees perch hopped more when hearing calls produced to heterospecifics rather than conspecific-produced calls. In comparison with call production trends, chickadees appeared to call more in response to the playback of heterospecific calls but move less. No differences in perch hopping behaviour were found for high- versus low-threat playback. Non-perch hop movements (i.e., food and water visits, pecking bouts, and other movements) mostly decreased across playback, but this finding was non-significant. Last, despite being tied to aggression, both ruffles and approaches were not significantly different across threat levels.

Table 1. Vocal and movement behaviours of male and female black-capped chickadees that were scored from audio and video files, respectively, and used in the analysis of chickadee behavioural responses to varying threat levels of predator threat. Adapted from Hoeschele et al. (2010).

Behaviour type	Behaviour scored	Behavioural Description
Vocal	*Chick-a-dee* call	Audible (nonstimulus) *chick-a* or *chick-a-dee* call detected
	Gargle call	Audible *gargle* call detected
	Fee-bee song	Audible song detected
	Tseet call	Audible *tseet* call detected
	"Other" vocalizations	Audible unidentified vocalization detected
Movement	Perch hop	Lands on new perch/moves to a new location
	Food visit	Pecks at food in cup
	Water visit	Pecks at water in bottle
	Ruffle	Shakes feathers
	Pecking bout	Performs four or more pecks in succession
	Beak wipe	Swipes wing across beak
	Approach	Lands on the wall closest to the speaker (Note: This movement is often recorded twice as it is usually also defined as a perch hop.)

Table 2. Playback stimuli from Avey et al. (2011) were used. Vocalizations were recorded and collected to comprise two sets of stimuli. Each set contains three chickadee-produced stimuli and three non-chickadee produced stimuli.

Stimulus set	Vocalization type (abbreviated)	Number of calls per 15s of playback
Set A	GHOW	3 hooting bouts
	MOB GHOW	2 *chick-a-dee* calls (2 D notes), 3 *chick-a*s
	NSWO	31 whistled toots
	MOB NSWO	6 *chick-a-dee* calls (1-4 D notes), 2 *chick-a*s
	RBNU	12 *yank* notes
	REV MOB NSWO	reversed MOB NSWO A
Set B	GHOW	3 hooting bouts
	MOB GHOW	4 *chick-a-dee* calls (3-4 D notes)
	NSWO	25 whistled toots
	MOB NSWO	5 *chick-a-dee* calls (3-7 D notes)
	RBNU	13 *yank* notes
	REV MOB NSWO	reversed MOB NSWO B

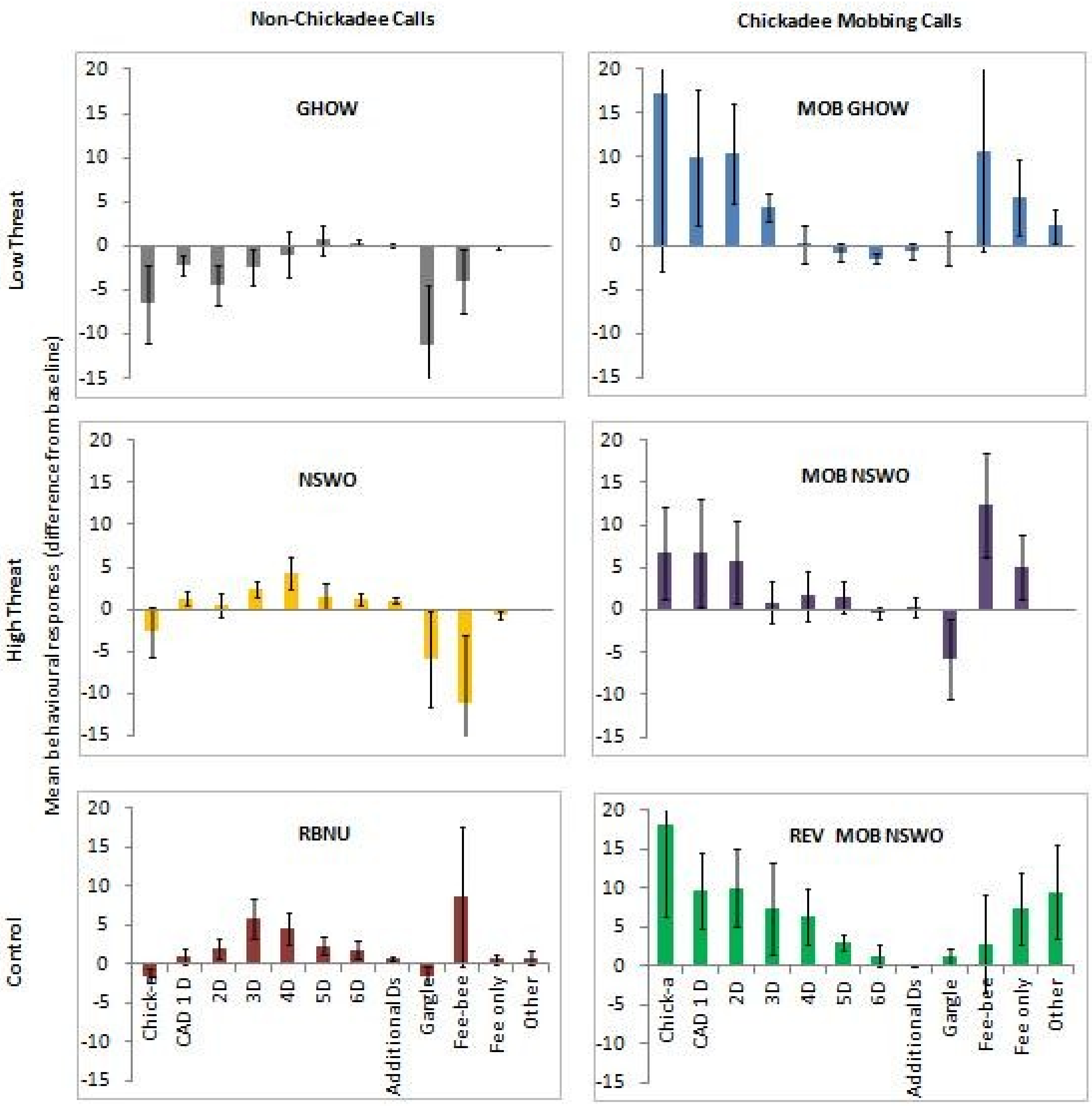

Figure 1. Mean ± SE difference from baseline in vocal responses (*chick-a*s, *chick-a-dee* (“CAD”) calls with 1 D note, 2 D notes, 3 Ds, 4 Ds, 5 Ds, 6 Ds, additional D notes (i.e., 7+ D notes), *gargles*, *fee-bee* songs, *fee* only songs, and “other” vocalizations) of black-capped chickadees after hearing six playback conditions. (GHOW = great horned owl calls; MOB GHOW = black-capped chickadee mobbing calls made in response to the presentation of a great horned owl mount; NSWO = northern saw-whet owl calls; MOB NSWO = black-capped chickadee mobbing calls made in response to a northern saw-whet owl mount; RBNU = red-breasted nuthatch calls; and REV MOB NSWO = reversed black-capped chickadee mobbing calls made to a northern saw-whet owl mount.)

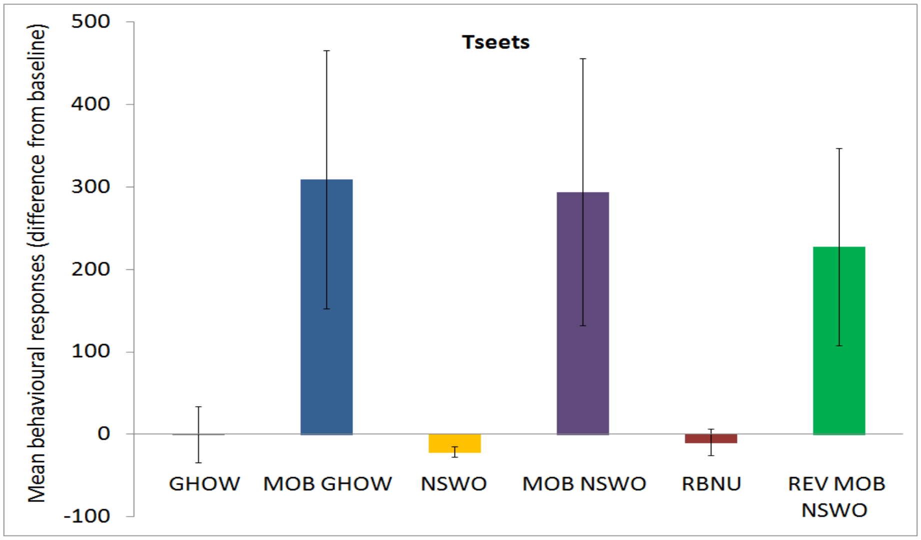

Figure 2. Mean ± SE difference from baseline in *tseet* calls produced by black-capped chickadees following playback of great horned owl calls (GHOW), black-capped chickadee mobbing calls made in response to the presentation of a great horned owl mount (MOB GHOW), northern saw-whet owl calls (NSWO), black-capped chickadee mobbing calls made in response to a northern saw-whet owl mount (MOB NSWO), red-breasted nuthatch calls (RBNU), and reversed black-capped chickadee mobbing calls made to a northern saw-whet owl mount (REV MOB NSWO).

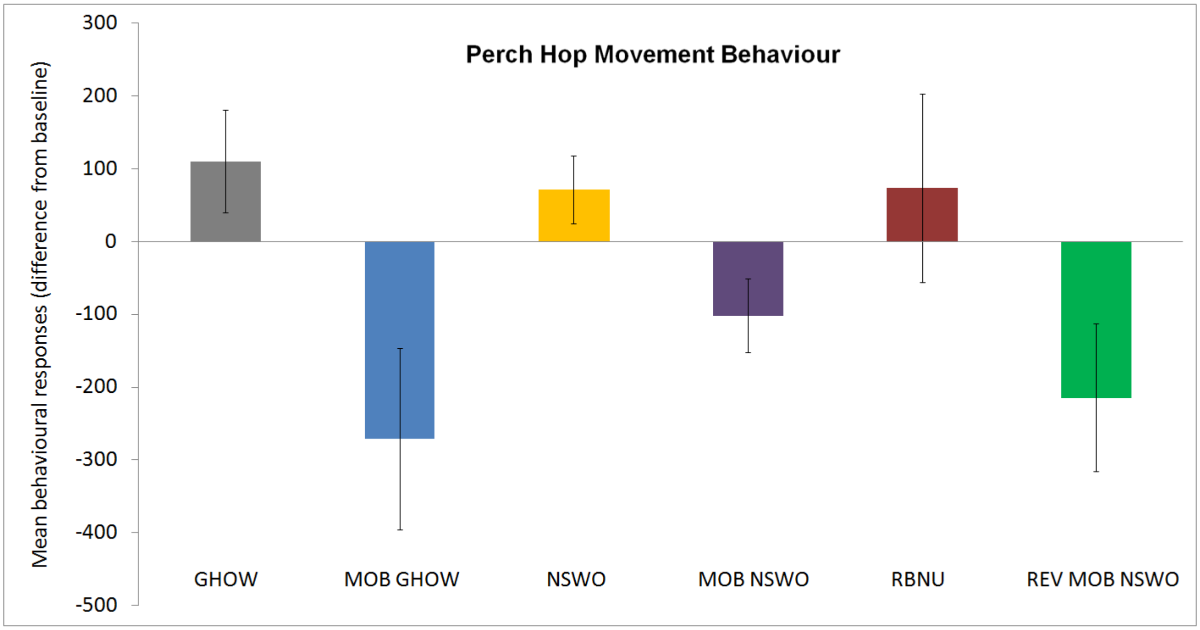

Figure 3. Mean ± SE difference from baseline in perch hops produced by black-capped chickadees following playback of great horned owl calls (GHOW), black-capped chickadee mobbing calls made in response to the presentation of a great horned owl mount (MOB GHOW), northern saw-whet owl calls (NSWO), black-capped chickadee mobbing calls made in response to a northern saw-whet owl mount (MOB NSWO), red-breasted nuthatch calls (RBNU), and reversed black-capped chickadee mobbing calls made to a northern saw-whet owl mount (REV MOB NSWO).

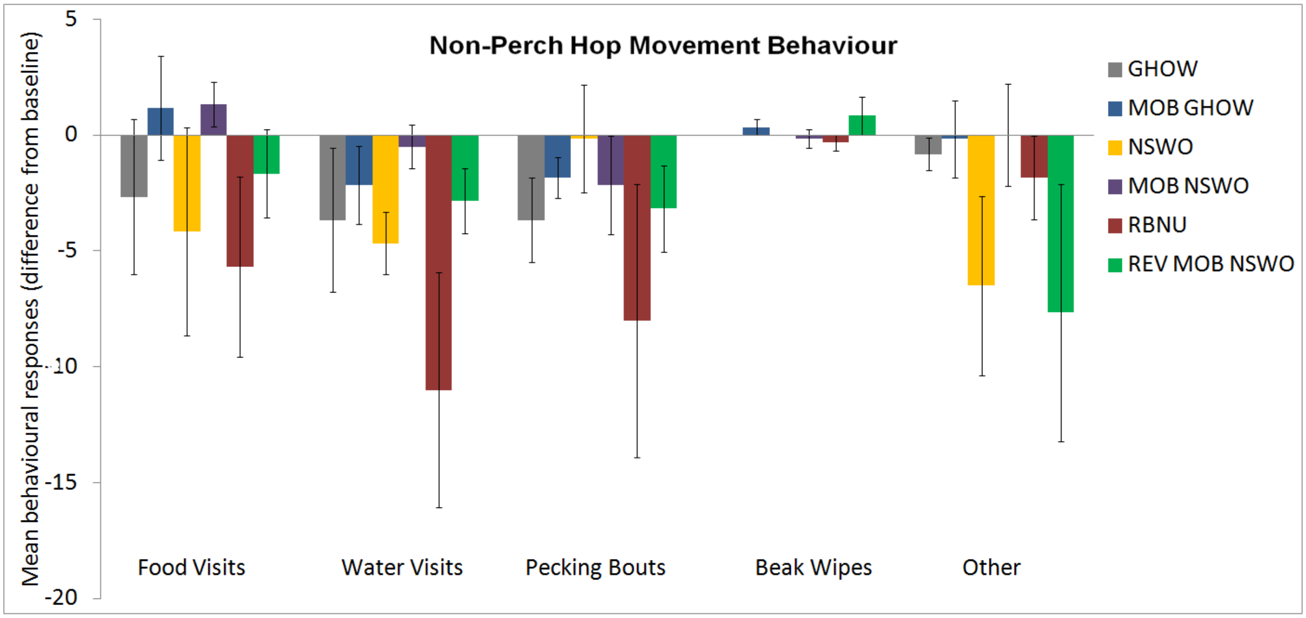

Figure 4. Mean ± SE difference from baseline in movement responses (food visits, water visits, pecking bouts, beak wipes, and other) produced by black-capped chickadees following playback of great horned owl calls (GHOW), black-capped chickadee mobbing calls made in response to the presentation of a great horned owl mount (MOB GHOW), northern saw-whet owl calls (NSWO), black-capped chickadee mobbing calls made in response to a northern saw-whet owl mount (MOB NSWO), red-breasted nuthatch calls (RBNU), and reversed black-capped chickadee mobbing calls made to a northern saw-whet owl mount (REV MOB NSWO).

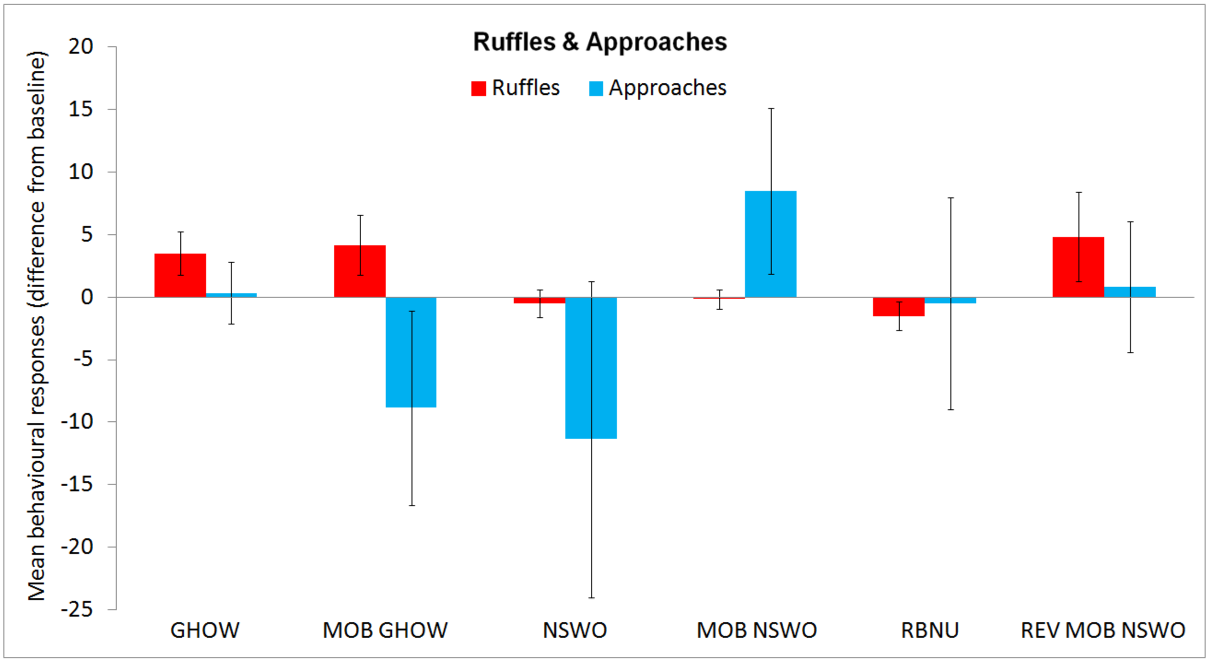

Figure 5. Mean ± SE difference from baseline in movement responses (ruffles and approaches) produced by black-capped chickadees following playback of great horned owl calls (GHOW), black-capped chickadee mobbing calls made in response to the presentation of a great horned owl mount (MOB GHOW), northern saw-whet owl calls (NSWO), black-capped chickadee mobbing calls made in response to a northern saw-whet owl mount (MOB NSWO), red-breasted nuthatch calls (RBNU), and reversed black-capped chickadee mobbing calls made to a northern saw-whet owl mount (REV MOB NSWO).

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