Differential Response to Interspecific and Intraspecific Signals Amongst Chickadees

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Abstract

Black-capped chickadees (*Poecile atricapillus*) and mountain chickadees (*P. gambeli*) have a similar vocal repertoire and share many other life history traits; yet, black-capped chickadees are socially dominant to mountain chickadees where populations overlap. Previous research suggested that in contact zones, both species respond weakly to heterospecific songs during the breeding season, and have suggested minimal interspecific competition. However, both black-capped and mountain chickadees discriminate between conspecific and heterospecific *chick-a-dee* calls, suggesting attention is paid to interspecific signals. We compared the responses of both black-capped and mountain chickadees to conspecific and heterospecific *chick-a-dee* calls during the winter, when both species compete for the same food resources. We conducted an aviary playback experiment exposing both species to playback composed of heterospecific and conspecific *chick-a-dee* calls, which had been recorded in the context of finding food sources. Responses from the tested birds were measured by recording vocalizations and behaviour. Black-capped chickadees responded significantly more to conspecific than to heterospecific stimuli, whereas the subordinate mountain chickadees responded to both mountain and black-capped chickadee calls. Based upon the reactions to playbacks, our results suggest these two closely related species may differ in their perception of the relative threat associated with intra- versus interspecific competitors.

Introduction

Closely related species that live in sympatry often occupy different ecological niches, thus reducing the potential for interspecific competition over limiting resources (Dhondt 1989). In Europe, where it is common to have more than one species within the family Paridae (titmice and chickadees) occurring in sympatry (Dhondt 2007), studies suggest that interspecific competition may be prevalent (Dhondt 2011). Alatalo et al. (1985, 1987) showed that willow tits (*Poecile montanus*), crested tits (*Lophophanes cristatus*) and coal tits (*Periparus ater*) compete over foraging sites in winter. By experimentally removing one of the species, they observed that the other species often shifted to occupy parts of the trees vacated by the removed species. This suggested that the niche segregation among co-occurring species may function to reduce interspecific competition. In the sympatric zone of five *Paridae* species within England, Lister (1980) observed that tits minimize niche overlap and increase aggressive interactions between species when food is scarce. Similarly, in North American members of the family *Sittidae*, white-breasted nuthatches (*Sitta carolinenesis*) and red-breasted nuthatches (*S. canadensis)* forage on different parts of the trees when they co-occur, but white-breasted nuthatches will expand their foraging area into red-breasted nuthatch feeding locations when the latter species is absent (Stallcup 1968).

In North America, the distribution of the *Paridae* species tends to be more allopatric than that in Europe; sympatric zones often occur on the intersection between species' range limits, but often involve only two overlapping species (Dhondt 2007). In these contact zones, interspecific competition between chickadees and titmice is likely to occur. Such is the case

between Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) that form mix-species flocks in the winter, in which the tufted titmouse is socially dominant to the Carolina chickadee (Waite & Grubb 1988). When Cimprich & Grubb (1994) experimentally removed the dominant titmice, Carolina chickadees spent more time foraging on the ground, the microsites typically preferred by the titmice in this region.

Black-capped chickadees (*Poecile atricapillus*) and mountain chickadees (*P. gambeli*) are considered sister-species (Gill et al. 1993, 2005) that diverged approximately 2.5 Mya (Gill et al. 2005) and still share similar social organization and vocal repertoire (McCallum et al.1999; Foote et al. 2010). These two species typically segregate by both habitat and altitude within their geographic range, and populations of either species are often allopatric at the local scale. However, contact zones do occur where ecological and altitudinal ranges intersect. Hill & Lein (1988, 1989) found little evidence that either chickadee species interact directly with heterospecifics during the breeding season. Interactions during the non-breeding season, however, have received less study. In our study site, black-capped and mountain chickadees form mixed-species winter flocks, in which black-capped chickadees are socially dominant to mountain chickadees (Grava et al. 2012) at both temporary winter feeding stations and in aviary trials. During these aggressive interactions at feeders between both individuals and flocks, chickadees often vocalize using *chick-a-dee* calls. This suggests that these calls may be used in interspecific, as well as intraspecific, interactions.

The *chick-a-dee* call has been extensively studied in chickadees (Hailman 1989; Hailman & Ficken 1996; McCallum et al.1999; Foote et al. 2010). All species within the genus *Poecile* use this complex vocal signal that can convey information in a variety of contexts. *Chick-a-dee* calls of both species are composed of four note types (referred to as A, B, C, and D), sung in a fixed order, A → B → C → D. While this syntax is maintained, the number of repetitions of each note type can vary, and not all note types are included in all renditions of the call, resulting in an infinite number of possible combinations of this call type (Hailman 1989; Lucas & Freeberg 2007). Mountain chickadees also produce two additional variants (or hybrids) of these note types (Bloomfield et al. 2004). These consist of an intermediate note between note A and B (denoted A/B) and a variation of the D note referred to as Dh. While Dh notes were also recorded from black-capped chickadees in our study population, no

recordings of *chick-a-dee* calls from black-capped chickadees in our study area contained *A/B* notes. *Chick-a-dee* calls are used in several different contexts, and the syllable structure of the call appears to vary with this context (Lucas & Freeberg 2007; Freedberg 2008). The one apparent commonality in function across contexts in which is it used is that the call rallies other individuals (mates or flockmates) to the signaller (Freedberg 2008; Foote et al. 2010) either in defence of a resource or in mobbing against a perceived threat. *Chick-a-dees* are often given during within- and between-flock interactions (e.g. Ficken et al. 1978). Birds also use *chick-a-dee* calls when encountering a new food sources (Freedberg 2008) and may convey this information as a means of gathering mates or flockmates to the resource (Mahurin & Freeberg 2009). These calls are also commonly given during interflock disputes (Ficken et al. 1978; Nowicki 1983; pers obs) and may rally flockmates to aid in contests with other flocks. *Chick-a-dees* used in the context of mobbing stationary avian predators may contain larger numbers of, and harsher renditions of, D notes than are associated with the use of the call in other contexts (Gaddis 1985; Baker & Becker 2002; Templeton et al. 2005; Soard & Ritchison 2009; Courter & Ritchison 2010), although some studies suggest that flying avian predators can elicit *chick-a-dees* with large numbers of A notes (Freedberg 2008). The structure of the notes themselves may also convey information used by receivers. Dawson et al. (2006) demonstrated that all notes within both black-capped and mountain *chick-a-dee* calls contain species-specific acoustics characteristics, and Charrier & Sturdy (2005) showed that black-capped chickadees are able to recognize their own species' *chick-a-dee* calls. Within species, individuals can identify flock membership (Nowicki 1983) and specific individuals (Charrier et al. 2004) using *chick-a-dee* call features. None of these studies, however, have addressed if and how sympatric black-capped and mountain chickadees respond to their own species' vs. heterospecifics' calls.

Because black-capped and mountain chickadees have overlapping ecological and environmental requirements in our northern study area, they might compete directly with both conspecifics and heterospecifics during the winter when food is scarce. We investigated whether birds differentially respond to conspecific and heterospecific *chick-a-dee* calls. Stimuli used in the study were recorded from single birds upon locating a temporary food source (bird feeder containing sunflower seeds) with few to no other birds in the immediate vicinity. Thus, the stimulus would likely be perceived by subjects as another bird that has

found and is attempting to gather flockmates to a food resource (Mahurin & Freeberg 2009), but the subject's response may reflect a different motivation towards the 'unfamiliar' bird. Stimuli may represent competitors to the subjects, who might in turn respond aggressively and utilize *chick-a-dee* and other calls of their own, but these might be intended to rally their own flockmates against a perceived threat. If birds respond similarly to calls of either species, it might indicate that every individual is viewed as a potential competitor for resources, regardless of species.

Methods

Study Area and Study Species

Mountain chickadees are typically associated with coniferous forests and higher elevations, whereas black-capped chickadees are found at lower elevations and in mixed forest with a higher deciduous component. In British Columbia, Canada overlapping zones in distribution sometimes occur at these transitional elevations where forest management has created a mosaic of habitats. Such is the case in our study area, the John Prince Research Forest (N54°40' – W124° 24') north of Fort St. James, BC. The research forest is a 13 000 hectare forest at approximately 800 m above sea level, which is maintained through active logging. It consists of patches of forests ranging in age from recent clear-cuts to old-growth sub-boreal Spruce (SBS biogeoclimatic zone) and Interior Douglas Fir (IDF biogeoclimatic zone). Birds in this contact population were caught within their flocks' territories (using mist nets or potter trap) and immediately transported to an aviary (Fig. 1) at the centrally located field station within the research forest. All

birds were captured within 6 km of the field station. To reduce any effect of stress associated with capture, we allowed the birds to habituate for an hour in the aviary before we ran the experiment. A total of 12 black-capped and 13 mountain chickadees were tested between 13 and 22 March 2010.

Stimuli Description

Both male and female black-capped and mountain chickadees produce *chick-a-dee* calls all year round (Hailman & Ficken 1996). The calls used were recording at different temporary winter feeding station in early winter 2010 (December 2009 and January 2010), using a Marantz PMD671 digital recorder with either a Sennheiser ME67 with a K6 power supply or a Sennheiser MKH70 with an MZA14 power supply. To control for the context, recordings were made in the absence of predators and were produced by a single bird when first arriving at the food source. The birds were spatially isolated from other flockmates when calls were produced, and this period is greater than 1 mo prior to the break-up of winter flocks and separation of pairs onto breeding territories, which occurs in late April to early May in our study area. As a result, we can largely exclude the contexts of predator identification/response, sexual display or even immediate agonistic interactions from the stimuli recordings. Rather, the *chick-a-dee* calls used in the study would be contextually associated with location of a winter food source and attracting mates/flockmates to aid in defence of this resource (Mahurin & Freeberg 2009). As there is no discernable difference between male and female *chick-a-dee* calls (e.g. Bloomfield et al. 2004; Charrier et al. 2004), we did not control for sex of bird recorded for playback stimuli.
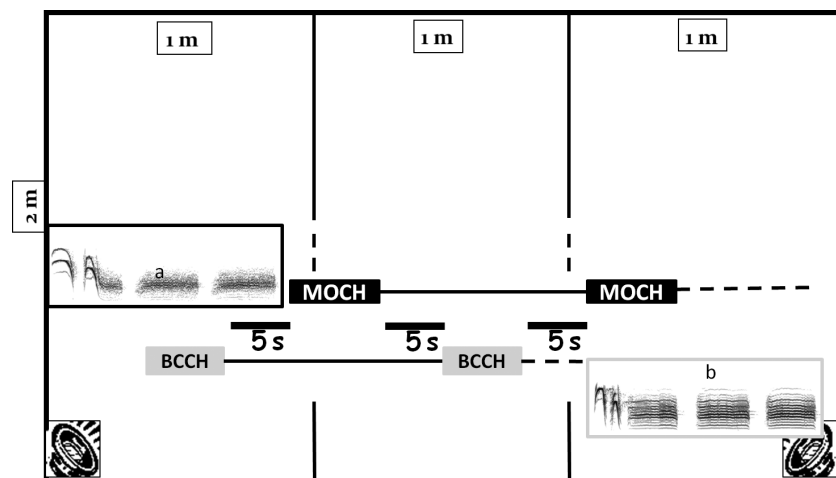

Fig. 1: Aviary design and playback stimuli with (a) the spectrographic representation of a mountain (MOCH) *chick-a-dee* call and (b) the spectrographic representation of a black-capped (BCCH) *chick-a-dee* call.

To avoid any effect of note syntax, we selected calls from both species and paired each mountain *chick-a-dee* call with a black-capped *chick-a-dee* call of similar note composition. We used a single *chick-a-dee* stimulus from 10 individuals of each species and then paired these (one mountain and one black-capped chickadee stimulus) to create 10 different playback dyads. Because A, A/B and B notes represent a continuous gradient of syllables (Bloomfield et al. 2004) in mountain *chick-a-dee* calls, we grouped those three note types into a single category (A–B). To be consistent, we also classified black-capped *chick-a-dee* call note type A and B as one note type: A–B. Note type C was particularly rare (in <1% of the calls) in the calls we recorded at the temporary feeding stations; as a result, we did not include any C notes in our playbacks. All calls used were composed of one, two or four note A–B, one Dh-note and two D note (4–7 notes in total for an average call length of 1.14 s). Using Avisoft SASLab-Pro software (Berlin, Germany), each call was filtered to erase background noise: low-pass filter at 1 kHz and high-pass filter at 10 kHz.

The stimuli broadcast to individual birds were recorded at least 5 km from the subject bird's territory to avoid previous contact between subjects and source of stimuli. We used a two-speaker playback design with speakers mounted on either side of the aviary (Fig. 1). We broadcasted playback in the aviary using a stereo file composed of one species' call type on the right channel alternating with the other species' call type on the left channel. This resulted in *chick-a-dees* of one stimulus type (mountain vs. black-capped chickadee) being broadcast from one speaker, with the calls of the other stimulus type broadcast from the opposing speaker. This inter-speaker distance would not be atypical for the spacing of individuals of different flocks having found a common food source. Stimuli were presented in alternating fashion; one stimulus (e.g. mountain chickadee call) was broadcast from one speaker, followed by 5 s of silence, and then followed by a broadcast of the other stimulus (e.g. black-capped chickadee) from the other speaker, followed by 5 s silence. This sequence was repeated 8 times for a total of nine identical mountain *chick-a-dee* calls alternating with nine identical black-capped *chick-a-dee* calls (Fig. 1). This playback design was chosen so as to 'force' a choice from the subject birds as to which of the two concurrent stimuli it was more important to mount a response (which was perceived to pose a greater 'threat' – for example, Illes et al. 2006). If both stimuli convey similar threat, then the bird is expected to divide its attention between them. We block-randomized the species of the first broadcast

stimulus (black-capped versus mountain), and from which channel each species' call was broadcasted, to create an equal number of all combinations. The volume of each playback was between 74 and 78 dB measured at 1.5 m (Goldline SPL 120 sound pressure level metre). We used 10 different stimuli pairs to test 13 mountain chickadees and 12 black-capped chickadees. Each playback was used a maximum of two times with conspecific birds and maximum three times in total (either to test two black-capped and one mountain chickadee or one black-capped and two mountain chickadees).

Playback Experiment

Birds were placed into the central compartment of the aviary, and sliding doors were used to isolate the bird from the outer two compartments containing the playback speakers. We allowed 1 h for habituation to the aviary prior to starting the experiment. At the start of the experiment, the two doors isolating the outer compartments were opened, allowing the bird access into these areas that contained feeders and the broadcast speakers. The feeder in the central compartment was removed. Once the compartments were opened, we began 2 min of pre-playback observations. We then began the broadcasts and conducted observations during the playback and then continued observations for 2 min following the end of the broadcast. We recorded the birds' behaviour, spatial location within the aviary and vocalizations during these three periods – pre-playback, during playback, post-playback – using a Marantz PMD671 digital recorder with a Sennheiser MKH70 with an MZA14 power supply. Spatial position of the bird was dictated onto these tapes by an observer at a blind 5 m from the aviary.

Birds' Movement, Acoustic and Statistical Analysis

We split response during trials into response towards heterospecific call and toward conspecific calls. Approaches were defined as entering the outer sides of the partitioned aviary in which the stimuli were being broadcast. Vocal responses directed towards a particular stimulus were defined as the bird orienting its body towards and vocalizing in the direction of one or the other speaker. Responses measured were the following: response latency (s) during the 5 s following each stimulus for a bird to respond with either vocalizations or movement directed towards the speaker (response latency was measured between '0' - when the bird react while the call was still playing- to '5' -if the bird did not respond-); time spent within

the same outer compartment of the aviary as either stimulus; and number of vocalizations given in the 5-s silence period that followed each stimulus. The response of subjects to heterospecific and conspecific stimuli was measured as the cumulative number of vocalizations or movements directed towards these stimuli types across the trial.

Recordings were analysed using Avisoft SASLab-Pro software. We counted not only the number of vocalizations (e.g.: *chick-a-dee* calls, contact calls) from the tested bird during the four experimental periods, but also the note composition (A–B, C, Dh and D) of each *chick-a-dee* call. Statistical analysis was conducted on STATISTICA 8 software (Tulsa, OK, USA). We used only non-parametric tests because of small sample size. We compared measures of response within-subjects across the pre-playback, playback and post-playback periods using Friedman ANOVAs, and then Wilcoxon Signed-Rank Tests for post hoc comparisons. We compared response measures within each period of the trials, and cumulative behaviour across trials, between subjects (mountain chickadees vs. black-capped chickadees) using Mann–Whitney U tests.

Results

Spatial Movement

Movement latency of response
We did not find any differences between tested species (black-capped vs. mountain chickadees) in their latency to approach the first broadcast stimulus (regardless of stimulus class) (Mann–Whitney U-test, $p = 0.13$, $N = 25$). Also, neither subject species showed a difference in latency to respond to either conspecific versus heterospecific stimuli (black-capped chickadees: Wilcoxon test, $p = 0.81$, $N = 12$; mountain chickadees: Wilcoxon test, $p = 0.88$, $N = 13$).

Spatial location response

We did not find significant differences in the time spend in the conspecific compartment of the aviary during the PRE, playback and POST periods for either mountain chickadees (Friedman ANOVA, $N = 13$, $df = 2$, $p = 0.25$) or black-capped chickadees (Friedman ANOVA, $N = 12$, $df = 2$, $p = 0.92$). We further did not find significant differences for the time spend in the heterospecific compartment during the three experimental period for either black-capped (Friedman ANOVA, $N = 12$, $df = 2$, $p > 0.9$)

or mountain chickadees (Friedman ANOVA, $N = 13$, $df = 2$, $p > 0.1$).

When considering only the playback period, there was no significant difference in the time that the subject birds spent in each compartment (conspecific, central, vs. heterospecific) among either the tested black-capped chickadees (Friedman ANOVA, $N = 12$, $df = 2$, $p = 0.66$) or mountain chickadees (Friedman ANOVA, $N = 13$, $df = 2$, $p = 0.24$).

Finally, the time each test species spent in the conspecific compartment during the playback period does not differ significantly when comparing the responses of tested black-capped vs. mountain chickadees (Mann–Whitney U-test, $N = 25$, $p = 0.76$). Similarly, we found no significant differences for the time each test species spent in the heterospecific compartment during the playback (Mann–Whitney U test, $N = 25$, $p = 0.85$).

Vocal Response

Vocal response latency
There was no difference in the latency to the first vocal response to the first stimulus presented (regardless of the stimulus type) between the tested black-capped and mountain chickadees (Mann–Whitney U-test, $p = 0.13$, $N = 25$). Further, we found no difference in how rapidly mountain chickadees responded with vocalizations to either conspecific or heterospecific stimuli (Wilcoxon test on the average response latency to each presented stimulus throughout the playback, $p = 0.28$, $N = 13$). However, black-capped chickadees had a lower latency when responding to conspecific stimuli compared to heterospecific stimuli (Wilcoxon test, $p = 0.03$, $N = 12$, Fig. 2).

Vocalization rates and composition

Tested birds of either species had higher vocalization rates during the playback period than during the pre- and post-playback periods (Friedman ANOVA: black-capped chickadees – $N = 12$, $df = 3$ $p = 0.02$; mountain chickadees – $N = 13$, $df = 3$, $p < 0.001$). We also compared vocal activity between the two study species during the different phases of the experiment (Fig. 3). We found that the black-capped chickadees had higher overall vocal activity than did the mountain chickadees during the non-playback periods, but it was significant only between species for the pre-playback phase (Mann–Whitney U-test, $p = 0.04$, $N = 25$, Fig. 3). While the playbacks were broadcasted, we found that mountain chickadees were more vocal than black-capped chickadees, especially
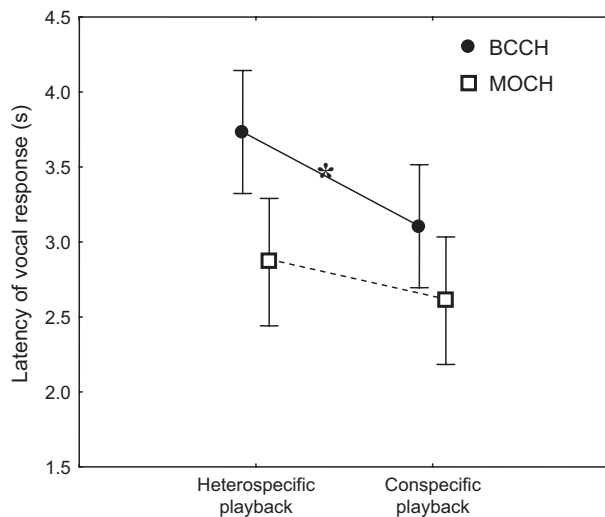
Fig. 2: Vocal response latency (s) for both black-capped chickadees (BCCH, N = 12) and mountain chickadees (MOCH, N = 13) to hetero-specific stimuli and conspecific stimuli. Values are means ± SE. *indicates significant differences.

Fig. 3: Vocalisation rate (per minute) during the four experimental phases of the experiment (PRE-Playback: 2 min period before the play-back was broadcasted, Conspecific Playback: response during broad-cast of conspecific playback, Heterospecific Playback: response during broadcast of heterospecific playback was broadcasted, POST- Playback: 2 min after the playback was broadcasted) for both black-capped chickadees (BCCH, N = 12) and mountain chickadees (MOCH, N = 13). Values are Means ± SE. *over a double arrow indicates significant differences during a broadcast period between species (Mann–Whitney U test, p < 0.05). *over a line indicates significant differences between comparison stimuli within species (Wilcoxon test, p < 0.05)

during the heterospecific playback period (Mann–Whitney U-test, p = 0.05, N = 25, Fig. 3).

During the playback period, we compared vocalization rates given in response to either stimulus class. This was defined as the total vocalizations given during the broadcast of a stimulus and the silence period following it until the opposing stimulus was broadcast from the opposing speaker. We combined the total number of vocalizations in these periods for either stimulus type (heterospecific vs. conspecific) across the trial. Black-capped chickadees had a higher vocalization rates per minute in response to conspecific playback than to the heterospecific playback (Wilcoxon test, p = 0.005, N = 12, Fig. 3). However, there was no difference in the response of mountain chickadee subjects to either conspecific or heterospecific stimuli (Wilcoxon test, p = 0.28, N = 13, Fig. 3).

We found a parallel effect when we separate the response measures by call types (contact calls vs. *chick-a-dee* calls) given in response to stimuli. Black-capped chickadee produced more contact calls (Wilcoxon test, p = 0.03, N = 12) and more *chick-a-dee* calls (Wilcoxon test, p = 0.01, N = 12) to conspecific stimuli than to heterospecific stimuli during the playback period. Conversely, there was no difference in contact calls (Wilcoxon test, p = 0.13, N = 13) nor in *chick-a-dee* calls (Wilcoxon test, p = 0.87, N = 13) given in response to heterospecific vs. conspecific stimuli by tested mountain chickadees. Mountain chickadees do, however, produced significantly more contact calls than *chick-a-dee* calls in their response to both conspe-
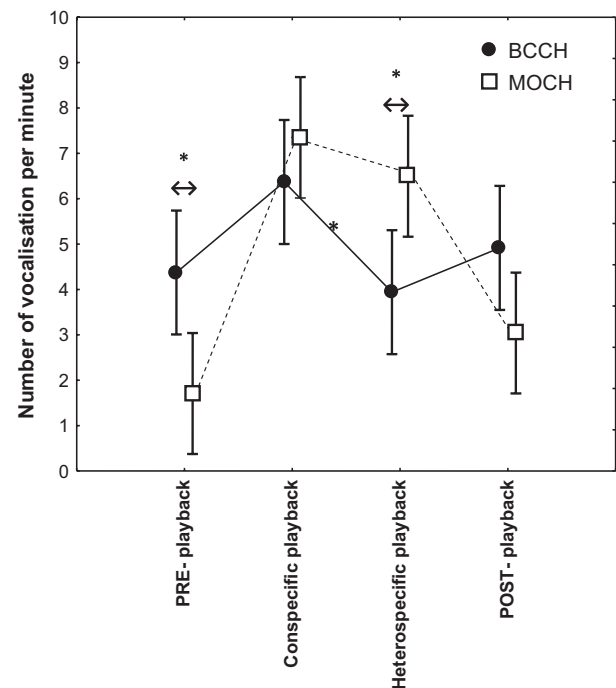
cific stimuli (Wilcoxon test, p = 0.001, N = 13) and heterospecific stimuli (Wilcoxon test, p = 0.002, N = 13). There was no such difference in the black-capped chickadees' response to conspecific playback (Wilcoxon test, p = 0.07, N = 12) or heterospecific playback (Wilcoxon test, p = 0.16, N = 12).

Six mountain chickadees (of 13) and 10 black-capped chickadees (of 12) responded to the conspecific playback by producing their own *chick-a-dee* calls. Six mountain chickadees and 4 black-capped chickadees also produced *chick-a-dee* calls in response to the heterospecific playback (Table 1). *Chick-a-dee* calls given in response to the stimuli had significantly fewer notes than the playback stimuli for both mountain chickadee stimuli (Wilcoxon test, N = 8, p = 0.001) and black-capped chickadee stimuli (Wilcoxon test, N = 10, p = 0.02). Among the bird that use *chick-a-dee* calls in response to the stimuli, all mountain chickadees test subjects (n = 6) and all but one black-capped chickadee test subjects (n = 9) used

Table 1: Average number of each note type (A, B, C and D) per *chick-a-dee* call given in response to conspecific and heterospecific stimuli by black-capped and mountain chickadees. Numbers in brackets indicate the number of test subjects that responded to stimuli with *chick-a-dee* calls out of the total number of birds tested (12 black-capped chickadees and 13 mountain chickadees)

Number of note type/ number of *chick-a-dee* call	Black-capped chickadee		Mountain chickadee	
	Response to conspecific playback (n = 10)	Response to heterospecific playback (n = 4)	Response to conspecific playback (n = 6)	Response to heterospecific playback (n = 6)
Note A/B	3.13	2.40	1.23	1.21
Note C	0.44	0.14	0.037	0
Note Dh	0.019	0.19	0.98	0.83
Note D	1.71	1.40	0.39	0.61
All note	4.66	3.95	2.44	2.85

D notes in their *chick-a-dee* call in response to conspecific playback (Table 1). Further, all but one mountain chickadee (n = 5) and all but one black-capped chickadee test subject (n = 3) used D notes in their *chick-a-dee* calls given in response to heterospecific playback (Table 1). Calls given by mountain chickadee test subjects in response to both conspecifc and heterospecific stimuli had significantly fewer D notes than the playback call (Wilcoxon test, N = 6, p = 0.02). Tested black-capped chickadees also gave response calls with fewer D notes than the stimulus, but this is only significant in response to the conspecific playback (Wilcoxon test, N = 10, p = 0.01).

Discussion

Tested birds showed higher vocal activity during the stimulus phase of playback than before or after the stimuli were broadcasted, indicating that both black-capped and mountain chickadees reacted to the stimuli to which they were exposed. However, the increased vocal response of black-capped chickadees was confined to conspecific stimuli. Mountain chickadees, on the other hand, showed an increased vocal response to both heterospecific and conspecific stimuli, but did not appear to differentiate between these stimuli classes. This suggests that black-capped chickadees show lower responsiveness to heterospecific than conspecific calls, but that mountain chickadee responded both strongly, and similarly, to both heterospecific and conspecific stimuli.

One possible explanation for this result is a failure of mountain chickadees to discriminate species-specific cues in calls and thus misdirected intended intraspecific signals, as has been suggested by different authors, especially among closely related species (e.g. Murray 1981). This is unlikely, however, as both black-capped and mountain chickadees are capable of learning and discriminating between either species' calls (Bloomfield & Sturdy 2008). Further, the differences between mountain and black-capped *chick-a-dee* calls are audible to humans, so it is unlikely the birds would fail to learn these differences in sympatric zones. Thus, it is more parsimonious to suggest that mountain chickadees may view conspecific and heterospecific signals as requiring similar levels of response.

The playbacks used in this experiment were recordings from unfamiliar birds during winter months when birds are foraging in flocks. Consequently, tested birds may perceive these stimuli as constituting a non-flockmate that has located the same food sources as being used by the subject bird. Nowicki (1983) found that chickadees do not typically respond to calls of flockmates by increasing their own vocal rates; in contrast, *chick-a-dee* stimuli from non-flockmates resulted in increased calling rates from subjects, similar to the findings of our study. Non-flockmates constitute direct competitors for resources, and these competitive interactions can escalate to direct physical aggression in chickadees. Thus, competition can involve both loss of resources and the potential for physical threat. As flocks routinely dispute access to experimental feeders, the response calls of the subject birds in our trials may represent attempts to rally their own flockmates to aide in interactions with a perceived competitor/threat. Our previous research in this area found that black-capped chickadees dominate mountain chickadees in these winter flocks (Grava et al. 2012). As such, the subordinate mountain chickadee may not represent a threat to the dominant black-capped chickadee, as even female and juvenile black-capped chickadees can displace adult, male mountain chickadees from resources (Grava et al. 2012). For this reason, we might expect lower responsiveness of tested black-capped chickadees towards heterospecific vs. conspecific stimuli, as seen in this study. Conversely, black-capped chickadees might well constitute a perceived threat to contested resources to a mountain chickadee.

Thus, we might expect that responsiveness of tested mountain chickadees towards heterospecific stimuli might be similar to that given to conspecific stimuli – it may benefit a subject mountain chickadee to rally flockmates to interactions involving both mountain chickadee and black-capped chickadee competitors.

An alternate interpretation of our data is vocal parasitism, whereby the subordinate mountain chickadee uses information from the black-capped chickadee to locate their food. As calls used for the playbacks were recorded at a temporary feeding station, stimuli were composed of calls used in a food-finding context. Black-capped chickadees are a generalist species that occur in a wide variety of habitats, whereas mountain chickadees tend to be more affiliated with coniferous forest (McCallum et al. 1999; Foote et al. 2010). In our study area, forest practices have created a mosaic of habitat types and ages within the research forest (S. Grainger, unpublished report). This mixed habitat might be more challenging for the mountain chickadees than it is for the black-capped chickadees, and mountain chickadees might learn to parasitize black-capped chickadee vocalizations in this contact zone. However, we think this interpretation is unlikely, as such parasitism would predict that the response to stimuli would be associated with an approach without vocalizations ('stealth') to locate the advertised food. Vocalizing in response to playback would presumably alert the more dominant black-capped chickadee to the intruder and could elicit unwanted aggression. In our study, we observed a vocal response to heterospecific stimuli from mountain chickadees, but not a taxis response. Many of these calls were contact calls used to alert others of the signallers location (Odum 1942; Gaddis 1985). Thus, it would not appear that the mountain chickadee subjects were intending to remain undetected. Further, the note types of the *chick-a-dees* given in response to stimuli were A–B and D notes. Such *chick-a-dee* calls are often given during interflock contests (Lucas & Freeberg 2007, pers obs), and, as such, it is likely that the vocalizations were intended for agonistic interactions.

Interestingly, while the response calls contained D notes, the number of D notes in the response calls of either species was consistently lower than the number that had been in the stimuli calls. If the vocal responsiveness of our tested subjects resulted from these birds perceiving the broadcast stimuli as advertising the presence of an avian predator (e.g. Templeton et al. 2005; Soard & Ritchison 2009; Courter & Ritchison 2010), we would have predicted both a taxis response to approach the playback (mobbing) and increase in the number of D notes in the response

calls used by the subject birds. Neither of these responses were seen among our test birds. Further, we would not necessarily have expected subject birds of either species to respond differentially to conspecific/heterospecific stimuli if they perceived that the stimuli were advertising the presence of a predator, as this information conveys an equal threat to small birds regardless of species. *Chick-a-dee* calls recorded from black-capped chickadees in the context of predator mobbing attract both black-capped and mountain chickadees (pers obs), but are also interpreted by other heterospecifics who respond by approaching and mobbing the broadcast speaker (e.g. Templeton & Greene 2007; Hetrick & Sieving 2012). This suggests that the increased calling of subjects elicited during playback studies was unlikely to be associated with perceived predation threat, further supporting our alternate interpretation that responses to the playback are likely to reflect a perceived competitive context. Thus, we conclude that the difference in response to heterospecific vs. conspecific stimuli that we observed between black-capped and mountain chickadees is most likely the result of differences among these species on the perceived risk of interspecific vs. intraspecific interactions. Future work in this area may wish to focus on spectrographic analysis of calls themselves to discern whether the birds encode perceptions of relative threat-level within their *chick-a-dees* (e.g. Sieving et al. 2010).

Acknowledgements

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