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Variations in Intra- and Interspecific Response to Mobbing Calls
by the Black-capped Chickadee (*Poecile atricapillus*)

Katerina Faust

Honors Thesis 2014

Colby College, Biology Department

Variations in Intra- and Interspecific Response to Mobbing Calls
by the Black-capped Chickadee (*Poecile atricapillus*)

Honors Thesis

Presented to
The Faculty of The Department of Biology
Colby College

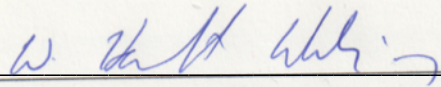
In partial fulfillment of the requirements for the
Degree of Bachelor of Arts in Biology: Neuroscience with Honors

Katerina Faust

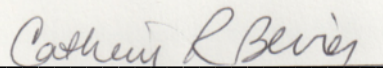
Waterville, ME

May 2014

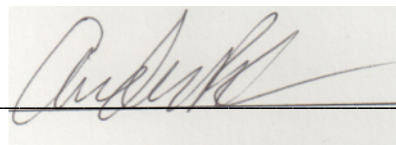
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ABSTRACT

Mobbing calls are produced by a variety of bird species in response to predator sightings. These mobbing calls often function in intraspecific recruitment, but have recently been shown to have an interspecific response component as well. The mobbing calls produced by the Black-capped Chickadee (*Poecile atricapillus*) are distinct and encode information about the threat level of the predator. Conservation biologists often use playbacks of chickadee mobbing calls to detect species of birds and numbers of individuals in an area with higher accuracy than counts conducted without the use of playbacks. In this study, the factors that could potentially influence intra- and interspecific response to chickadee mobbing calls were investigated, including: threat level encoded in the mobbing call (low or high), time of day, season, type and amount of tree cover, and weather conditions. The species and number of birds responding to playbacks of mobbing calls were compared to baseline levels of birds in the area, as well as to the response to territorial chickadee songs, an intraspecific signal. Playbacks took place at sites in the Perkins Arboretum at Colby College, from November 2013 to April 2014. More species and a greater number of total birds responded to low *dee* playbacks in the morning than they did at midday or afternoon. A greater number of total birds responded to low *dee* calls in conditions without wind when compared to windy conditions. More species and a greater number of birds responded to low *dee* calls in the rain when compared to conditions with snow or without precipitation. Chickadees also produced significantly more *dee* notes in response to tapes with mobbing calls, when compared to tapes with songs, though there was no significant difference in calls as a response to high *dee* or low *dee* tapes. These results suggest that the most accurate estimate of bird populations in an area can be assessed via low *dee* playbacks on mornings with no wind.

INTRODUCTION

Many species of birds are found to take part in mobbing, an aggressive behavior that involves surrounding and potentially attacking a predator in order to drive it away (Curio 1978). Mobbing encompasses loud vocalizations and rapid movements, as well as behaviors such as wing flicks or tail flicks (Curio 1978). Mobbing calls can carry a variety of information, alerting others to danger, and advertising the presence of other mobbing birds and the location and movement of the predator (Frankenberg 1981). Mobbing is generally viewed as an adaptive response to the discovery of a predator nearby, though there are a variety of hypotheses purported to explain this behavior.

Some of these hypotheses apply to the benefits accrued by primary mobbers (the birds that are first to discover and attack the predator), including the move on hypothesis and the perception advertisement hypothesis. The move on hypothesis proposes that the risks included in mobbing, such as reprisal attacks from the predator leading to injury or death, are outweighed by the benefits that would result from driving the predator out of the area, a hypothesis supported by various studies (e.g. Pettifor 1990; Flassekamp 1994; Pavey & Smyth 1998). Flassekamp found that mobbing was greatly distressing to predators such as Tawny Owls (*Strix aluco*) and Little Owls (*Athene noctua*). Mobbing can force the predator to leave their roost, and abandon the area in which the mobbing species forage (Pavey & Smyth 1998). Mobbing frequently forces predators to leave the immediate area – Pettifor (1990) found that European Kestrels (*Falco tinnunculus*) flew an average of 2-7 times further to find their next perch if mobbed while stationary, and moved a distance 6-8 times further during flight than the distance moved while not being mobbed. The mobbing birds benefit from this, as the predator will most likely hunt elsewhere for the immediate future.

However, mobbing does incur risks. Pied Flycatchers (*Ficedula hypoleuca*), for example, are more likely to have their nests predated if mobbing calls are heard near their nests (Krama & Krams 2004), possibly because the noise attracts other predators to that site. However, if the predator is driven off quickly, it may not increase the risk of predation, as opposed to situations with prolonged mobbing (Krama & Krams 2004).

The perception advertisement hypothesis also applies to primary mobbers, and models following this theory are difficult to distinguish from those of the move on hypothesis. According to the perception advertisement hypothesis, primary mobbers alert the predator that its intended prey has detected its presence, and thus may discourage the predator from attacking (Frankenberg 1981). Flasskamp (1994) discusses the gradation between the move on hypothesis and the perception advertisement hypothesis based on the behavior of the predator: if a predator immediately leaves the area upon eliciting calls, then the benefits of both hypotheses can be considered. However, if it does not and a mob forms in result, then the move on hypothesis would be considered the major influence, as the predator did not relocate upon its discovery. Another hypothesis related to the perception advertisement hypothesis is the alerting others hypothesis – that the vocalizations and sudden movements of birds who have spotted a predator will alert other birds to the danger (Curio *et al.* 1978). In this case, the birds that perceive the predator incidentally warn other potential prey to the predator's presence.

Secondary mobbers – birds that hear the primary mobbers and move towards that area – will obtain similar benefits as primary mobbers, and also join at reduced risk, due to risk dilution and confusion effects. Risk dilution refers to the fact that when more birds mob the predator, the risk to each individual bird is lowered, as discussed by Flasskamp (1994). Secondary mobbers may be attracted “by contagion” to areas, simply by viewing the mobbing behavior of other

birds, which can lead to large mobbing aggregations (Altmann 1956). Confusion effects refer to the confusion of the predator, and include confusion choruses, which Morse (1970) defines as “a series of call notes given simultaneously by many birds from scattered locations,” given to confuse the predator as to the location of birds based on auditory cues, as all the birds present call at once. Cover-seeking behaviors and what Morse (1977) refers to as the “ensuing scramble” upon perceiving the predator could add to the confusion effects.

Shedd (1982) broke down mobbing behaviors into four basic classes: silent approach, vocal approach, mobbing (an approach with vocalizations and visual displays such as wing and tail flicks), and attacking (a mobbing bird striking the predator). Silent approach was more common to younger birds. Shedd (1982) determined that silent and vocal approaches were used when the risk of mobbing outweighed the benefits, with the vocal approach falling into the perception advertisement hypothesis category. These two classes of mobbing behavior were seen in breeding robins (*Turdus migratorius*) that were off of their territory and in robins that had abandoned their territories after the end of the breeding season, leading Shedd (1982) to conclude that territoriality is an important influence on the mobbing response. The other two classes, mobbing and attacking, likely support the move on hypothesis, as a more concentrated effort is made to displace the predator. Many birds are known to engage in a wide variety of these types of mobbing, including Black-capped Chickadees (*Poecile atricapillus*)

Black-capped Chickadees

Black-capped Chickadees are small parids found across the northern United States in woodlands and suburbs (Dunn & Alderfer 2011). They produce a *chick-a-dee* call and a *fee-bee* or *fee-bee-ee* whistled song, as well as a *seet* alarm call (Dunn & Alderfer 2011). Predators of Black-capped

Chickadees include relatively small, quick predators such as Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*Accipiter cooperii*), and Eastern Screech-owls (*Megascops asio*) (Morse 1970; Saborse & Renne 1970). Low temperatures can also cause chickadees to alter their foraging behaviors in the early morning to seek out locations exposed to sunlight (Morse 1970). In the winter, chickadees forage more on trunks and small limbs than in the summer, and increase their foraging on the trunks of birches in particular (Morse 1970); thus chickadees are likely found to be foraging in deciduous woods more frequently in the winter. Morse (1970) suggests that more foraging opportunities exist in deciduous forests rather than in mixed forests for flocks containing chickadees, as flocks tended to fly through the mixed forest without stopping to forage.

Black-capped Chickadees can convey a series of complex information with their *chick-a-dee* call, one of the reasons that their vocalizations were selected as playbacks for this experiment. Baker and Becker (2002) found that threat levels were correlated with calling rate, with chickadees quicker to call and producing more calls when a falcon predator mount was a closer distance. Later it was discovered that information on predator size, threat level, and movements were given in the *chick-a-dee* call (Templeton *et al.* 2005). Small predators are more dangerous to chickadees as they are more maneuverable, as are predators with smaller wingspans. Chickadees produced more *dee* notes (the last part of the *chick-a-dee* call) in response to smaller predators (Templeton *et al.* 2005). Additionally, small predators elicited *dee* notes that were longer in duration, a shortened interval between the *chick* and *dee* sections of the call and a shortened interval between the first and second *dee* notes. However, chickadees were not found to distinguish between raptor and mammal predators in their calls, only the threat level posed by the predator. Besides providing information about the threat level of the predator, the

type of call also lets others know whether the predator is stationary or moving. The *chick-a-dee* call indicates a stationary or perched predator, while the *seet* call is used for a quickly moving predator (Templeton *et al.* 2005).

However, the response of chickadees is constrained by knowledge of predators. Saborse and Renne (2012) found a possible predator-specific call structure in chickadees when comparing between chickadees from an area with a historic screech-owl presence and those from an area without screech-owls. When presented with a screech-owl model, chickadees that were from an area with a persistent screech-owl population produced calls with more *dee* notes, a shorter duration of the first *dee* note, and a shorter interval between the first and second *dee* notes, when compared to chickadees from an area lacking screech-owls (Saborse & Renne 2012). The authors concluded that these differences were likely due to a failure to learn specific vocalizations for screech-owls in the chickadees from a region lacking screech-owl presence, rather than a failure to recognize the screech-owl as a threat. Therefore, although there may be small alterations to calls based on knowledge, overall call structure remains the same.

Playbacks of mobbing calls, such as chickadee mobbing calls, are often used in studies and have been shown to produce responses from conspecific and heterospecifics (Zimmerman & Curio 1988; Turcotte & Desrochers 2002; Krama & Krams 2004). Desrochers *et al.* (2002) examined the effect of mobbing call playbacks on winter chickadee foraging and found that risk assessment in mobbing is based on the distance to the cause of mobbing (a potential threat) for birds under cover. This finding is similar to that of Baker and Becker (2002), where calling rate escalated with decreasing distance to a predator model. The chickadees in the Desrochers *et al.* (2002) study did not stop visiting feeders during mobbing call playbacks, but decreased their visits to feeders further from the forest's edge and increased their visits to feeders close to the

forest. During the playback, 60% of the chickadees also produced mobbing calls, but no alarm calls (Desrochers *et al.* 2002). These findings may indicate that hearing mobbing calls does not translate into direct threat for birds assessing the area, unless a predator is sighted. Conspecifics also respond to playbacks of chickadee mobbing calls. Templeton *et al.* (2005) found that chickadees can detect threat level in mobbing call playbacks and respond accordingly. Chickadees generated longer, more intense mobbing behavior in response to calls recorded from flock mates in the presence of a small predator than they did from those produced in response to a larger (and thus less dangerous) predator (Templeton *et al.* 2005).

Interspecific mobbing with Black-capped Chickadees

In Maine, Black-capped Chickadees formed mixed-species flocks with other birds, including Hairy Woodpeckers (*Picoides villosus*), Downy Woodpeckers (*Picoides pubescens*), White-breasted Nuthatches (*Sitta carolinensis*), Red-breasted Nuthatches (*Sitta canadensis*), Brown Creepers (*Certhia americana*), and Golden-crowned Kinglets (*Regulus satrapa*), though chickadees remain the predominant species and make up about $\frac{3}{4}$ of the flock (Morse 1970). Red-breasted Nuthatches are often found with chickadees in mixed forests and in the summer, these flocks can expand to include other birds such as warblers and vireos (Morse 1970). In mixed-species flocks chickadees have been found to play leadership roles, initiating the movements of the flock, and are referred to as nuclear species (Morse 1970). Winter flocks of birds containing parids are larger in Maine than Louisiana or Maryland. This size increase can be attributed to a greater number of “follower” (or satellite) species; satellite species in the mixed-species flock include White- and Red-breasted Nuthatches and Golden-crowned Kinglets (Morse 1970).

In the absence of nuclear species, satellite species have been shown to increase their vigilance, though this might be due to the overall reduction in numbers of the flock (Dolby & Grubb 1998). Additionally, Downy Woodpeckers have been shown to decrease their vigilance when foraging with a mixed species flock including chickadees or titmice (another parid; both nuclear species), but not when foraging near flocks of other (non-nuclear) species such as sparrows (Sullivan 1984a). In another study, Sullivan (1984b) showed that Downy Woodpeckers foraging with a chickadee-titmouse mixed-species flock and those foraging alone while chickadee-titmouse contact calls were playing had similar levels of vigilance, both of which were lower than the vigilance displayed by woodpeckers foraging alone while the contact calls of a sparrow flock were playing. These results demonstrate the ability of heterospecifics that typically flock with chickadees in the winter to distinguish between chickadee flocks and other flocks. The woodpeckers also responded to chickadee-titmouse alarm calls in a similar manner as their response to predator models (Sullivan 1984b), indicating that some level of heterospecific eavesdropping is present in birds that typically flock with parids.

If the increase in vigilance demonstrated by Dolby and Grubb (1998) was due to the absence of nuclear species, rather than overall reductions in numbers, it is possible that nuclear species spend more of their time on vigilance and lead to the initiation of predator-associated behaviors, such as mobbing. Nolen and Lucas (2009) conclude that nuclear species that also play a role in heterospecific mobbing may share several features, such as “loud and harsh mobbing calls, have high rates of calling, or [making] close physical approaches towards the predator,” all features that Black-capped Chickadees possess. Previous studies have shown that heterospecific birds respond to playbacks of chickadee mobbing calls, and can be recruited to join in the mobbing (Betts *et al.* 2005; Templeton & Greene 2007; Nolen & Lucas 2009).

Some species are even able to discern semantic content (meaning) from the alarm calls or mobbing calls of other species. For example, heterospecific alarm calls were equally as effective as conspecific alarm calls in inducing a response in Campbell's (*Cercopithecus campbelli*) and Diana monkeys (*Cercopithecus diana*) (Zuberbühler 2000). Additionally, Diana monkeys could determine the type of predator based on the specific call given by Campbell's monkeys (Zuberbühler 2000). Similar results have been found among avian species as well. Templeton and Greene (2007) discovered that Red-breasted Nuthatches distinguish between playbacks of chickadee mobbing calls based on threat level, similar to the Templeton *et al.* (2005) findings that chickadees can determine threat level from chickadee mobbing call playbacks. Small predator chickadee calls resulted in the nuthatches moving closer to the speaker and performing more wing flicks (a mobbing behavior), overall producing a stronger mobbing response (Templeton & Greene 2007). The authors suggested this heterospecific eavesdropping may be adaptive, as it would allow the nuthatches to conserve energy by only mobbing the most dangerous predators. Chickadees and nuthatches are of a similar size, thus small predators pose a threat to both species.

Nolen and Lucas (2009) studied the mobbing response to Eastern Screech-owl models in groups of Carolina Chickadees (*Poecile carolinensis*), Tufted Titmice (*Baeolophus bicolor*), and White-breasted Nuthatches. Carolina Chickadees are very similar to Black-capped Chickadees in appearance and vocalizations, but their ranges rarely overlap, with Carolina Chickadees found in the south and Black-capped Chickadees further north (Dunn & Alderfer 2011). The species of the first mobbing individual did not affect the mobbing onset time of the group, and all species (chickadees, titmice, and nuthatches) were equally likely to join the mob once it started (Nolen & Lucas 2009). Nolen and Lucas (2009) also found interspecific interactions were present during

the mobbing, both in minimal approach distance and calling rate. For example, the chickadee calling rate increased as nuthatch calling rate increased, and vice versa.

Factors influencing interspecific mobbing response

Many different environmental factors have been shown to modulate the mobbing response of birds, and studies frequently have conflicting findings. These factors include size of the mobbing birds, territoriality (and, in a related manner, breeding season), whether the predator is changing location, and time of day.

Heterospecific mobbing recruitment is dependent on the size of the bird producing mobbing calls (Forsman & Mönkönen 2001). Large birds (≥ 20 g) are unlikely to respond to the mobbing calls of small birds (< 20 g), whereas small birds respond to mobbing calls of both large and small birds. Forsman and Mönkönen (2001) suggest that the reason for this difference might be that larger birds are more likely to be preyed upon, and thus would face greater risk in responding to mobbing calls. The authors speculate that smaller birds would benefit from responding to the mobbing calls of larger birds, as the larger birds devote more time to vigilance, allowing small birds to conserve their energy. Interspecific mobbing response is also influenced by predation risk (Forsman & Mönkönen 2001). More species of birds responded to mobbing call playbacks from Willow Tits (*Parus montanus*) and Redwings (*Turdus iliacus*) if the predation risk was low – in this case, further from the nest of a Sparrowhawk (a predator; *Accipiter nisus*). According to Forsman and Mönkönen (2001), the stronger mobbing response with lowered predation risk might benefit birds, especially naïve or young individuals, as they have the chance to examine a potential threat with a low risk of predation. The risk of predation might also play into the findings mentioned earlier, as large birds are not at risk from predators

of small birds, and thus would not benefit from mobbing them. The authors also found, as expected, that mobbing call playbacks attracted more birds than the playback of territorial songs, which is typically an intraspecific signal only (Forsman & Mönkönen 2001).

Territoriality is highly important in predicting the mobbing response and intensity, as mentioned previously when discussing Shedd's (1982) study on robins. The heterospecific mobbing response of birds is contingent on territory boundaries, as shown by two species of warbler (Black-throated Green Warblers, *Dendroica virens*, and Black-throated Blue Warblers, *Dendroica caerulescens*) responding to every chickadee mobbing playback within their territory, and only 8.1% responding to the same playback outside their territory (Betts *et al.* 2005). The authors concluded that these responses corresponded to the move on hypothesis, with benefits associated with displacing the predator from their own territory, and potential downfalls associated with mobbing the predator in a neighboring territory – such as forcing it to relocate to their own territory. However, the birds stopped responding to the playbacks at all once the breeding season ended. This finding parallels Shedd's (1982) finding that robins reduced their mobbing response at the end of the season, which is logical as all three species are migratory and abandon their territories at the conclusion of the breeding period. Without a defined territory to maintain, the birds may conserve energy by simply avoiding predators until it is time to migrate. Zimmerman and Curio (1988) found season-related changes to mobbing behavior as well. Great Tits (*Parus major*) approached and called significantly earlier in response to danger near their nest hole, which at that point in the season contained nestlings, than they did in trials further from the nest hole or during the non-breeding season (Zimmerman & Curio 1988).

Black-capped Chickadees also display a seasonal variation in mobbing responses (Shedd 1983). Mobbing intensity is lowest in December and January and highest in July and August, the

two months that fledglings would be present in chickadee territories. Interestingly, Shedd found that mobbing intensity is also low during April and May, when territories were already established by pairs, but before nesting had occurred. Shedd speculates that this could be due to large territory sizes, and the withdrawal of females towards the end of May for incubating the eggs. As Black-capped Chickadees are non-migratory (Dunn & Alderfer 2011), they might be expected to produce a mobbing response, even at low intensities, year round.

Time of day is also important when considering mobbing responses. Rollfinke and Yahner (1990) conducted winter bird counts and found that more Black-capped Chickadees and White-breasted Nuthatches were recorded in the morning, and more Golden-crowned Kinglets detected in the morning or at midday than in late afternoon. Hairy Woodpecker and Downy Woodpecker detection did not depend on time of day. These findings contrast those of Turcotte and Desrochers (2002), where time of day did not affect the number of species or individuals detected while using playbacks of chickadee mobbing calls. Rollfinke and Yahner (1990) also found that more Black-capped Chickadees, White-breasted Nuthatches, and Golden-crowned Kinglets could be detected in early winter (before January 18) than in midwinter or late winter, though the presence or absence of the two woodpeckers was not related to the winter period. Winter bird counts at midday (11:00-13:59) resulted in the same number of total bird species as counting during the morning, and Rollfinke and Yahner (1990) speculated that the presence or absence of all winter bird species could be detected at any time of day, given enough transects. Time of day and winter period may influence the response of birds to mobbing calls, especially heterospecific mobbing calls.

Movements of the predator can also alter the mobbing response (Shalter 1978), not just environmental factors. Shalter presented Pied Flycatcher pairs with an owl model in a specific

location until they became habituated and their mobbing reaction to the sight of it decreased, then shifted the owl model to a new position. The Pied Flycatcher mobbing response was renewed by the change in position of the predator, which Shalter proposes may imply the input of spatial context to predator recognition.

Proposed experiment

Playbacks of chickadee mobbing calls are useful for detecting and estimating numbers of wild bird species. Turcotte and Desrochers (2002) found that chickadee mobbing playbacks allowed for detection of more species and more individuals than counts without the use of playbacks. The authors also stated that playbacks might be useful for the detection of particularly rare or secretive species throughout the year. Templeton and Greene (2007) have similar views, and also indicate that the threat level during the recording of the chickadee mobbing calls is important for future studies. Further research into the heterospecific response to chickadee mobbing call playbacks, and the factors that affect that response, would be useful for conservation purposes.

I propose a study to further investigate factors such as: type of chickadee mobbing call (i.e. the threat level during the recording of the calls), time of day, season, weather, amount of cover, and type of cover. Wild birds that typically form winter flocks with chickadees, such as Hairy and Downy Woodpeckers, Red- and White-breasted Nuthatches, and Golden-crowned Kinglets (Morse 1970) are expected to form the majority of the response to chickadee mobbing calls, as they would recognize chickadee mobbing calls and possibly benefit from responding. More heterospecifics are expected to respond to high-threat level (high *dee*) calls, which indicate more dangerous predators, as well as more birds responding during the morning rather than later in the day, when there is less bird activity. Additionally, an increased response (higher numbers

of birds present, and more species) is expected in late winter when compared to fall or early winter, as breeding season approaches and migrants return to set up territories, as well as the increased territoriality of overwintering birds. An increased response is also predicted in areas with increased cover, and in deciduous woods, as winter flocks might find more foraging material there (Morse 1970). Cloud cover and temperature are not expected to play a large role in mobbing response variation, but precipitation and high winds may limit mobbing response.

MATERIALS AND METHODS

All experiments were conducted within the Perkins Arboretum and Bird Sanctuary or in other areas around campus at Colby College in Waterville, ME where chickadees are typically encountered, in order to ensure that the response of other bird species was due to the mobbing calls and not the novel stimulus of a previously unheard bird call. Experiments were spaced out so that there was at least seven days between experiments conducted at the same location, to avoid habituation (Shedd 1983, Hurd 1996). Shalter (1978) found that reaction to predators incorporates a spatial component, such that habituation does not occur with a shifting predator location. This could conceivably apply to mobbing calls as well, where shifting the location of the mobbing incident prevents habituation by the local birds. Fourteen different locations were selected for this study, with varying amounts of cover (low, medium, or high) and varying types of cover (deciduous, coniferous, or mixed).

Playback tapes

Chickadee recordings were obtained from Macaulay Library, an online database maintained by the Cornell Lab of Ornithology, as well as from manual recordings of local chickadees.

Recordings from areas whose chickadees have regional differences in call or song structure from Maine chickadees were not included. These recordings were composed into three different playback tapes via Raven Pro 1.4: a “high *dee*” tape containing the recordings of chickadees responding to a high threat predator (≥ 6 D notes in each call; Figure 1a), a “low *dee*” tape containing the recordings of chickadees responding to a low threat (≤ 4 D notes in each call; Figure 1b), and a “song” tape containing chickadee territorial songs (Figure 1c) with no mobbing calls, and thus no potential predation threat. The song tape was used as a control to account for birds that were responding to the sounds of chickadees and not to a potential mobbing situation. As chickadee songs are used to indicate territoriality, it was expected that only chickadees would respond to this playback tape. Each playback tape was five minutes long.

Variables

Several different variables were taken into account with this experiment as well, besides type and amount of cover and playback tape type (Table 1). Experiments were carried out between 07:00 and 16:00 hours during the day. Experiments between 07:00 and 10:00 were considered to be in the morning, experiments between 10:00 and 13:00 were considered to be at midday, and experiments between 13:00 and 16:00 were considered to take place in the afternoon. Several different weather variables were also measured and recorded at the start of the experiment, including temperature, amount of wind, cloud cover, and precipitation. Temperature was recorded as the current temperature in Waterville, ME via Yahoo! Weather, and was later

divided into three categories: 0-14° F, 15-29° F, and 30-45° F for the purposes of analysis.

Amount of wind was measured using the Beaufort scale for wind on land, and was recorded as no wind (Beaufort scale 0-1), light wind (Beaufort scale 2-3), or windy (Beaufort scale 4-5) for the highest amount of wind for the duration of the experiment. Cloud cover was recorded as sunny, partly cloudy (cloud cover 50-75%), or cloudy (>75% cloud cover). The categories of precipitation included rain (including freezing rain), snow, or no precipitation. Experiments were broken down by season as well, including late fall (November), early winter (January), and late winter (mid-February to mid-March).

Procedure

Experiments were conducted following the methods of Hurd (1996), with five periods to each experiment. A Bluetooth speaker was set up in the middle of the experimental area, on top of a log or on a branch near the ground, such that there was space available for birds to perch and approach the speaker. The speaker was set to broadcast all chickadee sounds at a volume to simulate the normal volume that a chickadee would produce. After set up, the observer withdrew 3 m from the speaker, and a five-minute acclimation period was allowed, followed by a five-minute baseline recording of birds in the area (radius of 10-15 m) using binoculars. Birds that flew above the forest were not counted as part of the experiment, only birds that landed in the trees or flew between the trees in the experimental area were counted. Data recorded included species of bird, time of arrival, the maximum number of individuals of that species seen at one time, the maximum number of individuals that approached within 3 m of the speaker at one time, and any mobbing behavior seen (calls, tail flicks, etc.). Counting only the numbers of birds seen at one time helped to prevent counting any bird twice. After the baseline recording, one of the

playback tapes was played, followed by a ten-minute period of silence to allow any responding birds to disperse, and then another of the playback tapes, in such a manner that one mobbing tape and the song tape were played during each experiment. Fifty of these experiments were carried out at the various locations between mid-November 2013 and mid-March 2014.

Additionally, five experiments were carried out at the end of the data collection period using a chickadee model (a life-size chickadee ornament with feathers and proper coloration, see Figure 2) attached to a branch above the speaker (within 2 ft). This modification added a visual cue component to the auditory cues of the chickadee calls and songs, to determine whether the response of birds was altered when both visual and auditory cues were present.

Analysis

Results were analyzed using Stata 12, mainly via t-tests and one-way ANOVAs. Experiments with a visual cue were compared via paired t-tests to experiments conducted with the same type and amount of cover and tape type, along with similar weather conditions and time of day.

RESULTS

Twelve species of birds other than Black-capped Chickadees were seen in response to playbacks of chickadee vocalizations (Table 2). Black-capped Chickadees showed the greatest response and were sighted at all experimental sites; they were also the only species observed approaching the speaker. Heterospecifics sighted most often were White-breasted Nuthatches, Hairy Woodpeckers, and Downy Woodpeckers, all members of the mixed-species flock. No significant

species-specific responses were seen, but White-breasted Nuthatches had a trend towards appearing more frequently during call playbacks ($p < 0.08$, Fisher's exact test).

There were no significant differences between the response of birds to the tape and the order in which the tape was played, either song followed by call or call followed by song. There were also no significant interactions between the type of mobbing call on the tape (high *dee* or low *dee*) and bird response, except for the song condition. There were significantly higher numbers of birds present during the song playback in experiments that included low *dee* playbacks than there were in experiments that included high *dee* playbacks ($p < 0.05$, $t = 1.7$, $df = 48$) (Figure 3).

Time of year and time of day

There was a non-significant trend towards increased numbers of birds responding to chickadee songs in late fall, when compared to experiments conducted in the winter ($p = 0.0668$, $F = 2.87$, $df = 2$) (Figure 4). However, this trend may be due to a smaller sample size in the fall ($n = 6$) when compared to early winter ($n = 27$) and late winter ($n = 17$). There were significant interactions between time of day and bird recruitment, both in terms of numbers of species and total numbers of birds ($p = 0.0040$, $F = 7.15$, $df = 2$; $p = 0.0084$, $F = 5.98$, $df = 2$) (Figure 5a).

Significantly more species responded to low *dee* calls in the morning when compared to experiments conducted in the afternoon ($p < 0.01$). Additionally, significantly greater numbers of birds responded to low *dee* calls in the morning when compared to midday or afternoon ($p < 0.05$). There was a non-significant trend towards interactions between time of day and numbers of birds present during the baseline data collection ($p = 0.0667$, $F = 2.87$, $df = 2$) (Figure 5b).

Type of cover

There was a significant interaction between type of cover and species richness ($p = 0.0189$, $F = 4.78$, $df = 2$) (Figure 6a). Significantly more species showed up in response to high *dee* calls in coniferous forest when compared to deciduous or mixed forest ($p < 0.01$). All other interactions between type of cover and bird response were not significant, though there was a non-significant trend towards interactions between type of cover and species richness in the song condition ($p = 0.0764$, $F = 2.72$, $df = 2$) (Figure 6b). There were no significant interactions between amount of cover (low, medium, or high) and bird response.

Weather conditions

No significant interactions were found between cloud cover and bird response, or between temperature and bird response.

There were significant interactions between wind condition and number of birds present at baseline levels ($p = 0.0380$, $F = 3.51$, $df = 2$) (Figure 7a). Significantly higher numbers of birds were present during baseline data collection when there was no wind, compared to windy conditions ($p < 0.05$). Additionally, there was a non-significant trend towards interactions between species richness and wind condition at baseline ($p = 0.0600$, $F = 2.99$, $df = 2$). Another significant interaction occurred between number of birds and wind condition during low *dee* playbacks ($p = 0.0058$, $F = 6.57$, $df = 2$) (Figure 7b). Significantly higher numbers of birds responded to low *dee* calls on days without wind, compared to windy days ($p < 0.01$).

There were significant interactions between precipitation and bird response during low *dee* playbacks, both in species richness ($p = 0.0169$, $F = 4.94$, $df = 2$) and total number of birds ($p = 0.0006$, $F = 10.51$, $df = 2$) (Figure 8a). Significantly more species responded to low *dee*

playbacks in the rain compared to playbacks in the snow ($p < 0.01$), and significantly higher numbers of birds responded to playbacks in the rain than in the snow ($p < 0.01$) or in conditions without precipitation ($p < 0.01$). There were also significant interactions between precipitation and bird response during song playbacks, both in species richness ($p = 0.0072$, $F = 5.48$, $df = 2$) and numbers of birds ($p = 0.0040$, $F = 6.21$, $df = 2$) (Figure 8b). Significantly more birds responded to song playbacks with no precipitation when compared to snow ($p < 0.05$), and more birds responded to song playbacks in the rain than in the snow ($p < 0.01$). However, the sample sizes were small for precipitation conditions, with only four experiments performed in the rain and three in the snow, when compared to forty-three conducted without precipitation.

Chickadee response

The intraspecific response of chickadees to chickadee mobbing call playbacks was also examined. There were significant interactions between tape type (song, low *dee*, or high *dee*) and the number of *dee* notes that the chickadees produced in response ($p < 0.0001$, $F = 13.5$, $df = 2$). Significantly fewer *dee* notes were produced during playbacks of chickadee song when compared to playbacks of tapes with low *dee* ($p < 0.05$) or high *dee* ($p < 0.01$) calls (Figure 9).

Chickadee model

The presence of a visual cue did not alter the response of birds to chickadee playbacks. Changes in the number of species or changes in the number of birds present from baseline were not significant when comparing between experiments with or without the visual cue.

DISCUSSION

General observations

The birds responding to chickadee mobbing calls were small, as might have been expected from the research of Forsman & Mönkönen (2001). Several larger species were spotted (e.g. American crows) but only on the periphery of the area, and generally did not remain for the duration of the playbacks. The most common respondents (other than chickadees) were Hairy Woodpeckers, Downy Woodpeckers, White-breasted Nuthatches, and Golden-crowned Kinglets, birds that are often found in mixed-species flocks with chickadees in the winter (Morse 1970). However, no significant species-specific response to the playbacks was detected, which makes it harder to determine whether heterospecific eavesdropping was taking place.

The finding that higher total numbers of birds responded to song playbacks in experiments that included low *dee* playbacks, when compared to experiments including high *dee* playbacks is interesting, especially in the light of findings that the order in which the tapes were played was not significant (low *dee* and then song, or song and then low *dee*). There was no significant difference in the species richness during song playbacks, which indicates that possibly more birds of one species were responding. It is possible that on the days when experiments including low *dee* playbacks were conducted, weather conditions were more favorable for increased bird response during the song playback, but were changed when the low *dee* playback was conducted, such as an increase in the amount of wind.

Time of year and time of day

The intensity of the response to mobbing playbacks was overall very low. Heterospecifics responded either with a silent approach or a vocal approach, which Shedd (1982) theorized might

mean that the risk of mobbing outweighed the benefits. The vocal approach would most likely support the perception advertisement or alerting others hypotheses, rather than the move on hypothesis, as no greater attempts (such as increasing call intensity or approaching the speaker) were made to dislodge the supposed predator. This result may be due to the fact that experiments were conducted in the non-breeding season. Many studies have shown that there is reduced mobbing response once the breeding season ends (e.g. Shedd 1982; Zimmerman & Curio 1988; Betts *et al.* 2005). Some of the results were dramatic, with Black-throated Blue and Black-throated Green Warblers mobbing 100% of the time within their own territory during the breeding season and ceasing to respond to the playbacks at all once breeding season had ended (Betts *et al.* 2005). The benefits of mobbing are most likely reduced in the non-breeding season. The territories held by the mixed-species flock in the winter are much larger than the territories maintained by pairs during the breeding season (e.g. Stefanski 1967), and thus birds could potentially relocate to avoid a predator without being displaced from their territory, saving energy that would otherwise be expended upon mobbing. Additionally, there would be no offspring who would be threatened by predation, so the move on hypothesis probably holds less weight during this period. Birds might shift their response from concentrating on displacing the predator to observance of the predator, while alerting each other and the predator of its presence: the alerting others and perception advertisement hypotheses.

Black-capped Chickadees had an increased intensity of response when compared to heterospecifics, but their response was still low in comparison to the response of chickadees in the breeding season. Shedd (1983) found that chickadee mobbing intensity was lowest in January, and low overall during the non-breeding season; these results support his findings.

Time of day is an important variable to consider during mobbing call playbacks. During playbacks of low *dee* calls, significantly more species and significantly greater numbers of birds responded in the morning, when compared to other times of day. There was an overall trend towards greater numbers of birds observed at baseline in the morning, but this would not alter findings with mobbing call playbacks, as bird response was always measured as a change from baseline. The baseline results fall in line with the findings of Rollfinke and Yahner (1990), who found that certain species could be seen more commonly in the morning than at other times of the day. The low *dee* results contrast the findings of Turcotte and Desrochers (2002) that time of day does not matter.

Turcotte and Desrochers (2002) used chickadee mobbing call playbacks in order to count the number of birds in the area. If high *dee* mobbing calls were used in these playbacks, then their results would align with the current findings, for experiments with high *dee* calls did not have any interactions between time of day and bird response. Only low *dee* calls were found to have this interaction, with increased numbers of birds responding to low *dee* calls in the morning. As birds are commonly more active in the morning, they may be more willing to expend the energy to investigate the low *dee* calls (and thus a low threat predator), assuming that heterospecifics are capable of detecting the threat level encoded in chickadee calls. As Red-breasted Nuthatches are capable of this heterospecific eavesdropping, it follows that other species in these mixed-species flocks would have similar capabilities. The fact that response to high *dee* calls (and thus high threat predators) was not linked to time of day may indicate that mobbing a predator and displacing it from that location is a high priority for birds that are in the area and capable of responding to a threat.

Type and amount of cover

There were no interactions between mobbing response and amount of cover. There were interactions between mobbing response and type of cover, however. More species responded to high *dee* calls in coniferous forest than in mixed or deciduous forest. However, there was a non-significant trend towards fewer species responding to chickadee songs in coniferous forest.

These results might indicate that there are more species overwintering in Maine that prefer coniferous habitats. The birds might be present but not readily visible during song playbacks, as coniferous forest has inherently more cover than the other types of forest, and songs are an intraspecific signal, so heterospecifics might not respond. During high *dee* calls, the birds might become agitated and begin to move around more and call, becoming conspicuous, so that they were included in the species count. As this result was not found with the low *dee* calls, it may indicate that heterospecific eavesdropping is taking place.

Weather conditions

Wind and precipitation were the only weather conditions that influenced bird response. Cloud cover and temperature were not factors in mobbing response. A greater number of birds were present at baseline in conditions without wind, and a greater number of birds responded (as a change from baseline) to low *dee* playbacks in conditions with no wind, when compared to windy conditions. The drop in baseline levels of birds in conditions with lots of wind is most likely due to a decline in activity, as wind adds to the difficulty of flying. The altered response during the playbacks may have been due to the difficulty of hearing in the wind, with leaves and branches rustling, as tapes were only played at a volume that approximated the volume of a normal chickadee. However, significant interactions between wind condition and bird response

were only found for one of the playback types (low *dee* calls) and not for the others. It is possible that low *dee* calls do not carry as far, but unlikely. If heterospecifics are capable of detecting threat level in chickadee mobbing calls, they might reduce their response to low-threat calls at times when flying is difficult, in order to conserve energy for the high-threat predators.

Precipitation produced varying levels of response. In the rain, there were more species and more individuals present at baseline, as well as during low *dee* playbacks, while in the snow, there were fewer species and fewer individuals during playbacks, in a change from baseline. There was admittedly a small sample size, but the trends were consistent and opposite for rain and snow. It is possible that sound also played a role, as sound is muffled while snow is falling. Rain may have kept the birds from flying above the canopy, in order to seek shelter from the weather, and thus more birds were in range to respond to playbacks of all kinds.

Chickadee response

There were significant interactions between tape type (song, low *dee*, or high *dee*) and the intraspecific response of chickadees, but not as many as expected. Chickadees produced more *dee* notes in their calls in response to playbacks of call tapes compared to song. However, there was no significant difference in the number of *dee* notes produced at low *dee* and high *dee* playbacks. This is unexpected, given the findings of Templeton *et al.* (2005), that chickadees produced the appropriate number of *dee* notes in response to a tape recorded in the presence of a high threat or low threat predator. There are a couple of ideas that might explain this reaction – first, that the chickadees had somehow habituated to the playbacks, and did not regard the playbacks and the speaker as a real threat (unlikely, given that there was a difference in response between song playbacks and call playbacks, indicating that chickadees did perceive a threat).

Second, the set-up of the experiment may have altered their response. The call tapes were each an amalgam of a variety of recordings of a suitable number of *dee* notes, but it is uncertain under what conditions (e.g. what predator presence) some of them were recorded in. The chickadees might be able to detect something about the calls in the high *dee* playbacks that conveyed a lower threat level. It might also be useful to create more of a polarity between low *dee* and high *dee* calls in order to separate out a response, with high *dee* calls considered to be ≥ 8 *dee* notes and low *dee* calls considered to be ≤ 2 *dee* notes. Third, the season might have played a role, with chickadees reducing the intensity of their mobbing in the non-breeding season, and thus not responding as greatly to high *dee* playbacks. This explanation seems the most likely, as chickadee mobbing intensity was very low overall, relative to mobbing intensity during the breeding season.

A fourth explanation concerns the specific findings of Templeton *et al.* (2005), that chickadees increase mobbing intensity in response to playbacks recorded from flock mates in the presence of a high threat predator. The high *dee* call playbacks in this study were not recorded from the flock mates of chickadees in the area, and thus might not have been considered an honest signal of predators in the area, as the birds producing the calls were unknown.

Chickadee model

The presence of a visual cue (a chickadee model placed on a branch within two feet above the speaker) did not appear to alter the response of birds to playbacks of chickadee vocalizations. This result is not greatly surprising, given the alerting others hypothesis that vocalizations and rapid movements alert other birds to the presence of mobbing birds, and thus a predator. The visual cue was not moving and most likely did not draw any additional attention of birds to the

area. Any birds that were close enough to see the model were also close enough to hear the chickadee vocalization playbacks. Auditory cues appear to be the primary stimulus for mobbing.

Conclusions

Several factors were found to influence the intra- and interspecific response of birds to chickadee mobbing calls, including time of day and wind condition, as well as precipitation and type of cover, though the results of the latter two were somewhat ambiguous. Low *dee* call playbacks on mornings with no wind will most likely result in the greatest bird response. Future work is needed to determine the influence of precipitation, as well as similar studies conducted in the breeding season, to see whether season interacts with environmental variables to alter the response of birds to chickadee mobbing calls. Temperature, cloud cover, and amount of tree cover were not found to influence bird response.

These results have implications for conservation, as accurate assessments of bird populations, especially for endangered or secretive species, are highly important. Knowledge of the factors that influence the mobbing response of birds to playbacks of Black-capped Chickadee calls can lead to greater accuracy in counting the species and numbers of birds in a given area.

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WORKS CITED

- Altmann, S.A. 1956. Avian mobbing behavior and predator recognition. *The Condor* 58(4): 241-253.
- Baker, M.C. and Becker, A.M. 2002. Mobbing calls of Black-capped Chickadees: effects of urgency on call production. *The Wilson Bulletin* 114(4): 510-516.
- Betts, M.G.; Hadley, A.S. and Doran, P.J. 2005. Avian mobbing response is restricted by territory boundaries: experimental evidence from two species of warblers. *Ethology* 111: 821-835.
- Curio, E. 1978. The adaptive significance of avian mobbing I: teleonomic hypotheses and predictions. *Zeitschrift Fur Tierpsychologie* 48: 175-183.
- Curio, E.; Ernst, U. and Vieth, W. 1978. The adaptive significance of avian mobbing II: cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. *Zeitschrift Fur Tierpsychologie* 48: 184-202.
- Desrochers, A.; Belisle, M. and Bourque, J. 2002. Do mobbing calls affect the perception of predation risk by forest birds? *Animal Behavior* 64: 709-714.
- Dolby, A.S. and Grub, T.C. Jr. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behavior* 56: 501-509.
- Dunn, J.L. and Alderfer, J. 2011. National Geographic field guide to the birds of North America. 6th ed. Washington D.C.: National Geographic Society. 574 p.
- Flaskamp, A. 1994. The adaptive significance of avian mobbing V: an experimental test of the move on hypothesis. *Ethology* 96: 322-333.
- Forsman, J.T. and Mönkönnen, M. 2001. Responses by breeding birds to heterospecific song and mobbing call playbacks under varying predation risk. *Animal Behavior* 62: 1067-1073.

- Frankenberg, E. 1981. The adaptive significance of avian mobbing IV: alerting others and perception advertisement in blackbirds facing an owl. *Zietschrift Fur Tierpsychologie* 55: 97-118.
- Hurd, C.R. 1996. Interspecific attraction to the mobbing calls of Black-capped Chickadees (*Parus atricapillus*). *Behavioral Ecology and Sociobiology* 38(4): 287-292.
- Krama, T. and Krams, I. 2004. Cost of mobbing call to breeding pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology* 16(1): 37-40.
- Morse, D.H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs* 40(1): 119-168.
- Nolen, M.T. and Lucas, J.R. 2009. Asymmetries in mobbing behavior and correlated intensity during predator mobbing by nuthatches, chickadees, and titmice. *Animal Behavior* 77: 1137-1146.
- Pavey, C.R. and Smyth, A.K. 1998. Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Animal Behavior* 55: 313-318.
- Pettifor, R.A. 1990. The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. *Animal Behavior* 39: 821-827.
- Rollfinke, B.F. and Yahner, R.H. 1990. Effects of time of day and season on winter bird counts. *The Condor* 92(1): 215-219.
- Saborse, J.A. and Renne, I.J. 2012. Historic presence and absence of predator affects call structure of Black-capped Chickadees. *The Wilson Journal of Ornithology* 124(4): 750-757.
- Shalter, M.D. 1978 Effect of spatial context on the mobbing reaction of pied flycatchers to a predator model. *Animal Behavior* 26: 1219-1221.

- Shedd, D.H. 1982. Seasonal variation and function of mobbing and related antipredator behaviors of the American robin (*Turdus migratorius*). *The Auk* 99(2): 342-346.
- Shedd, D.H. 1983. Seasonal variation in mobbing intensity in the Black-capped Chickadee. *The Wilson Bulletin* 95(3): 343-348.
- Stefanski, R.A. 1967. Utilization of breeding territory in the Black-capped Chickadee. *The Condor* 69(3): 259-267.
- Sullivan, K.A. 1984a. The advantages of social foraging in Downy Woodpeckers. *Animal Behavior* 32: 16-22.
- Sullivan, K.A. 1984b. Information exploitation by Downy Woodpeckers in mixed-species flocks. *Behavior* 91(4): 294-311.
- Templeton, C.N.; Greene, E. and Davis, K. 2005. Allometry of alarm calls: Black-capped Chickadees encode information about predator size. *Science* 308: 1934-1937.
- Templeton, C.N. and Greene, E. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *PNAS* 104(13): 5479-5482.
- Turcotte, Y. and Desrochers, A. 2002. Playbacks of mobbing calls of Black-capped Chickadees help estimate the abundance of forest birds in the winter. *Journal of Field Ornithology* 73(3): 303-307.
- Zimmerman, U. and Curio, E. 1988. Two conflicting needs affecting predator mobbing by great tits, *Parus major*. *Animal Behavior* 36: 926-932.
- Zuberbühler, K. 2000. Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London B* 267: 713-718.

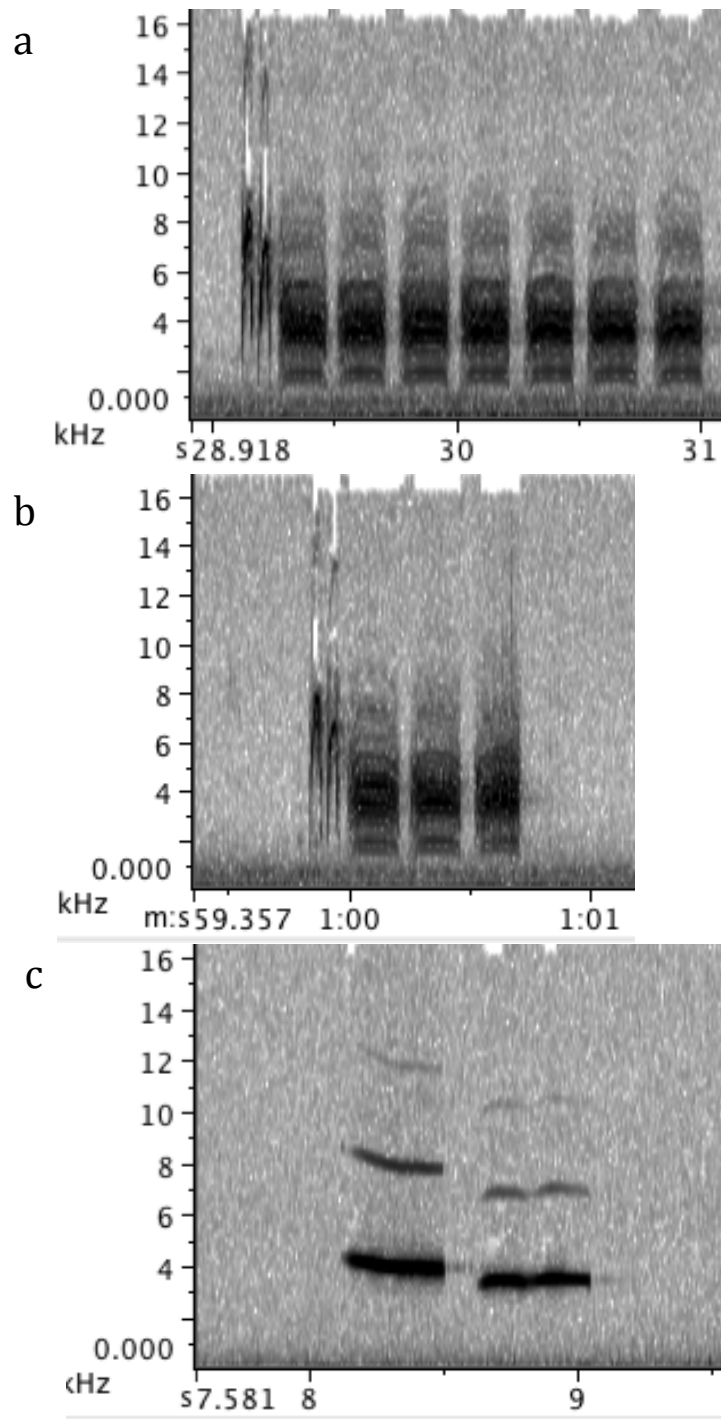


Figure 1. Sonograms of Black-capped Chickadee vocalizations from Raven Pro 1.4. (a) High *dee* mobbing calls and (b) low *dee* mobbing calls recorded in Michigan by Robert Stein in 1963. (c) Songs recorded in Maine by Arthur Allen in 1953.

Variable	Conditions		
Date	Late fall	Early winter	Late winter
Time of day	Morning	Midday	Afternoon
Temperature	0-14° F	15-29° F	30-45° F
Amount of wind	No wind	Light wind	Windy
Cloud cover	Sunny	Partly cloudy	Cloudy
Precipitation	No precipitation	Rain	Snow
Type of cover	Deciduous	Mixed	Coniferous
Amount of cover	Low	Medium	High

Table 1. The environmental variables and each of their various conditions measured during the chickadee observations.



Figure 2. Picture of the experimental set-up with visual and auditory cues. The chickadee model was life-size, with proper coloration, and placed on a branch within 2 ft above the speaker. Chickadee vocalizations were broadcast from the speaker at the volume within the range a chickadee would normally produce.

Species	Max seen	Number of sites	Max approach	Mobbing behavior	Forest
Black-capped Chickadee	10	14	5	Calls, approached speaker	Coniferous Deciduous Mixed
White-breasted Nuthatch	2	4	0	Calls	Coniferous Deciduous Mixed
Hairy Woodpecker	2	3	0	Calls	Deciduous
Downy Woodpecker	2	3	0	Calls	Coniferous Deciduous
American crow	3	3	0		Deciduous
American robin	7	2	0		Deciduous
Golden-crowned Kinglet	2	2	0	Calls	Coniferous Mixed
Blue jay	1	2	0		Deciduous Mixed
Northern cardinal	1	2	0		Coniferous Deciduous
Cedar waxwing	10	1	0		Deciduous
Brown creeper	1	1	0		Deciduous
Hermit thrush	1	1	0		Coniferous
Tufted titmouse	1	1	0	Calls	Mixed

Table 2. A summary of all the species that approached within 10-15 m of the speaker while it was playing chickadee vocalizations. Max seen and max approach refer to the maximum number of that species seen at one time, and the maximum number of that species seen to approach within 3 m of the speaker at one time.

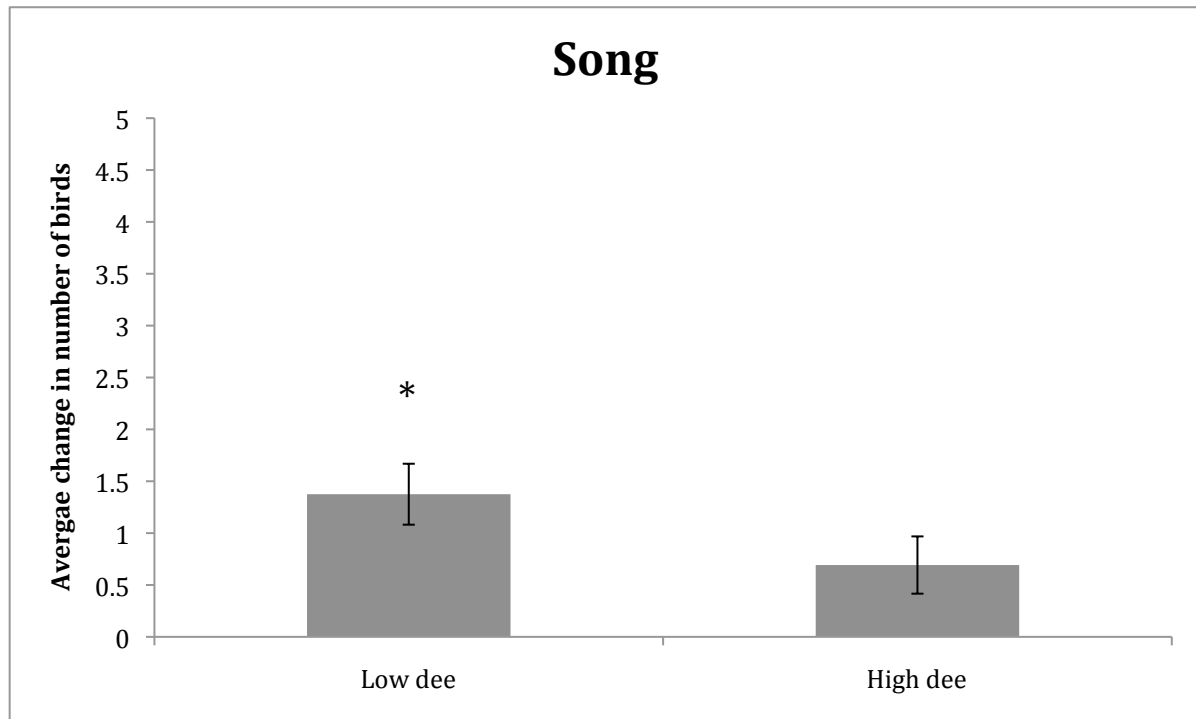


Figure 3. Average (\pm SE) total numbers of birds responding to song playbacks for the various tape types (experiments including low *dee* playbacks and experiments including high *dee* playbacks), as a change from baseline. Stars represent significance ($p < 0.05$, one-way t-test).

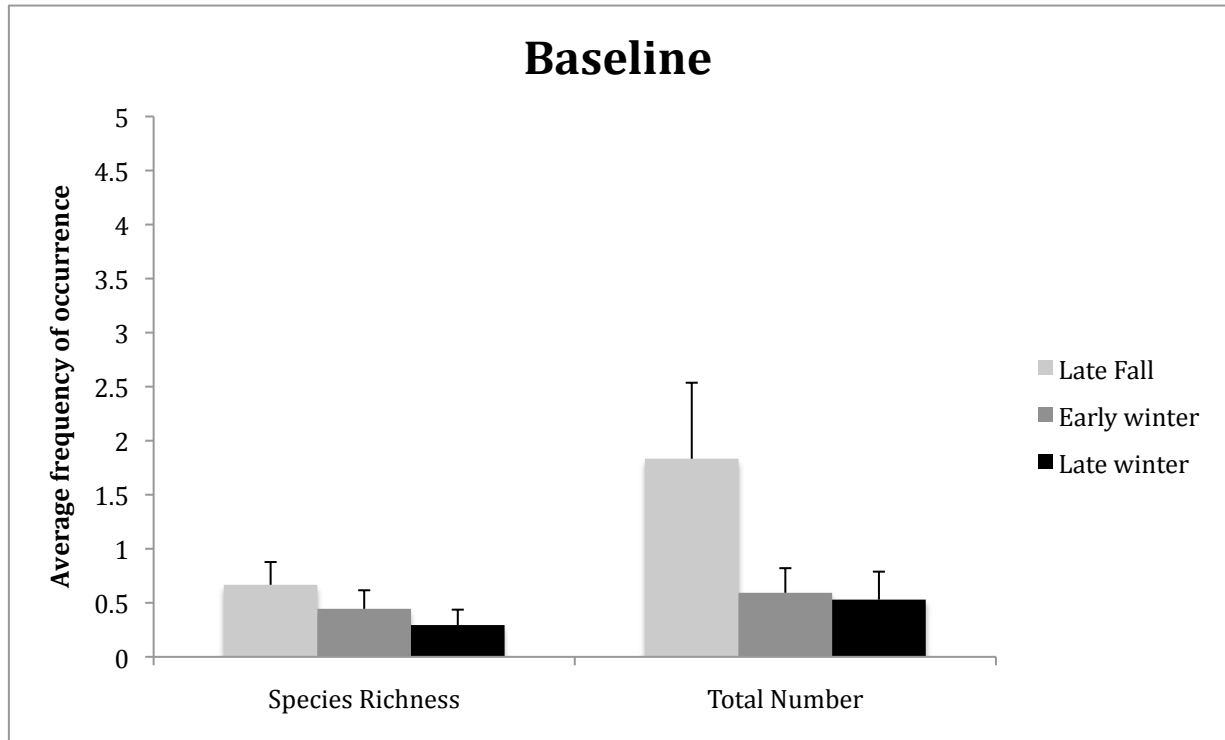


Figure 4. Average (+ SE) number of species and total number of birds present at baseline in different seasons ($n = 6, 27, 17$). Late fall refers to experiments done in mid-November through the end of December, early winter refers to experiments done in January through mid-February, and late winter refers to experiments done from mid-February to the end of March.

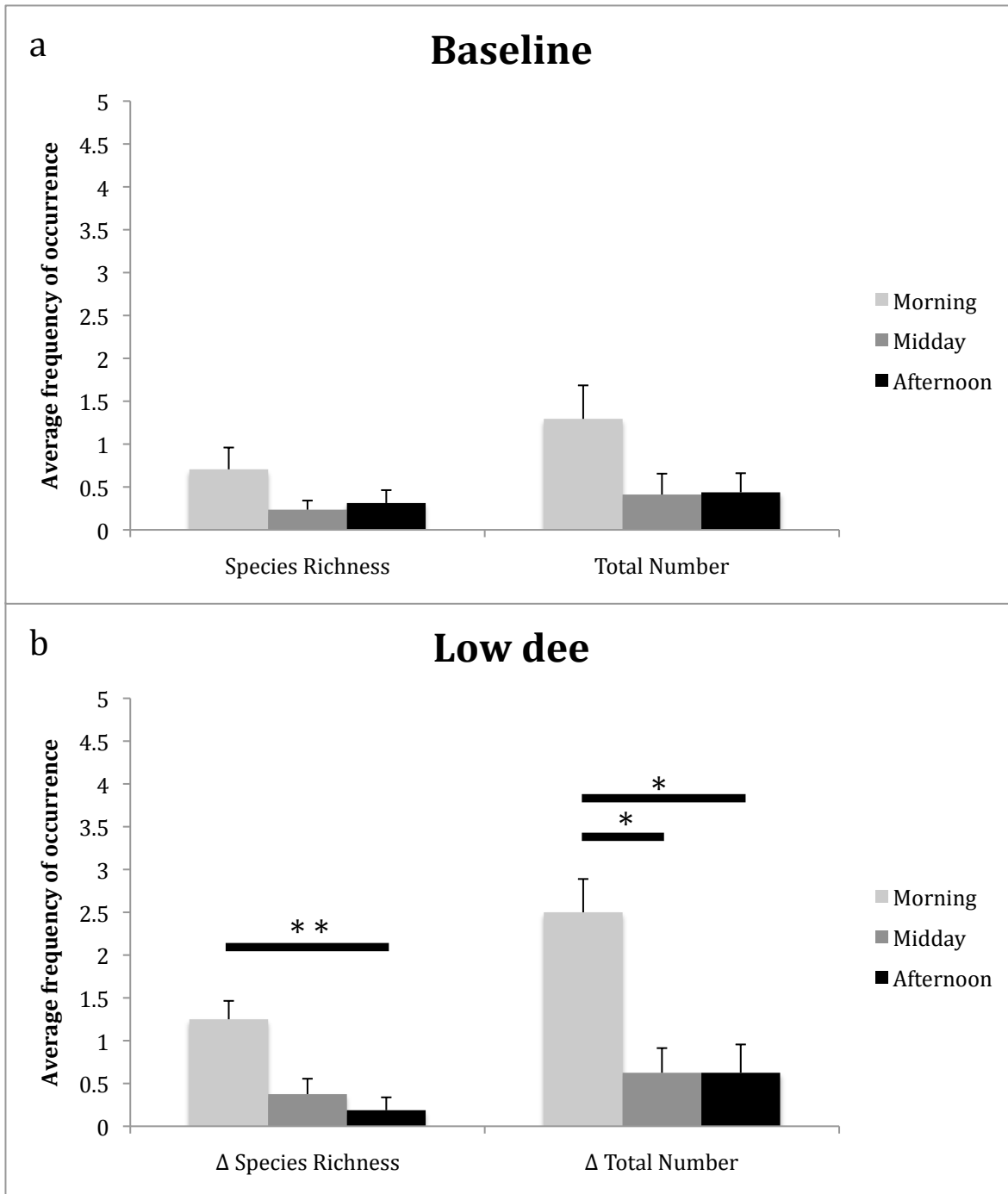


Figure 5. Average (+ SE) number of species and total number of birds at baseline (a) and average change in species richness and total numbers of birds responding to low *dee* calls (b) at different times of day (n = 17, 17, 16). Stars represent significance ($p < 0.05$ and $p < 0.01$, one-way ANOVA).

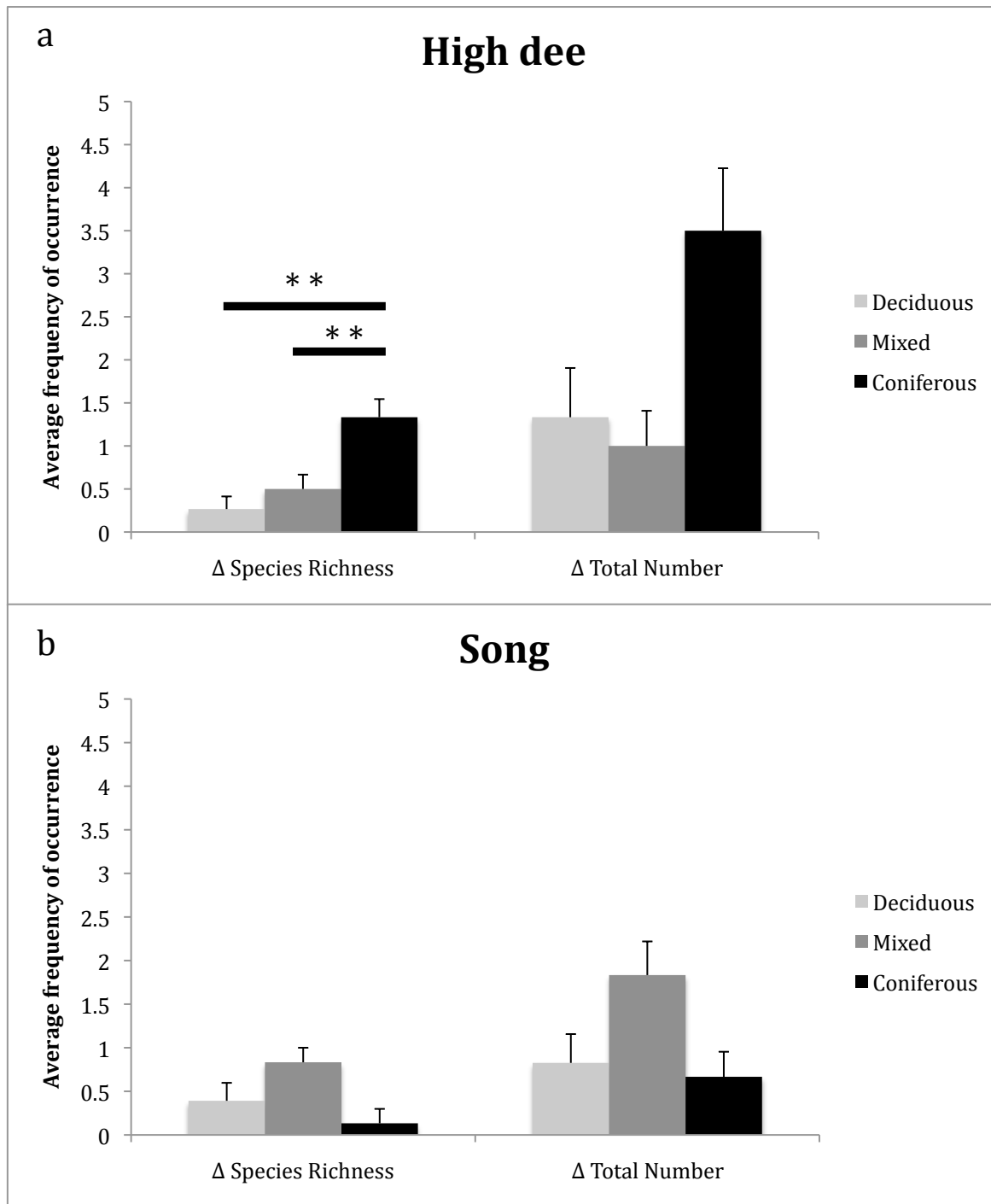


Figure 6. Average (+ SE) number of species and total number of birds responding to chickadee vocalizations in different types of forest cover ($n = 23, 15, 12$), as a change from baseline levels. (a) High *dee* calls. (b) Song. Stars indicate significance ($p < 0.01$, one-way ANOVA).

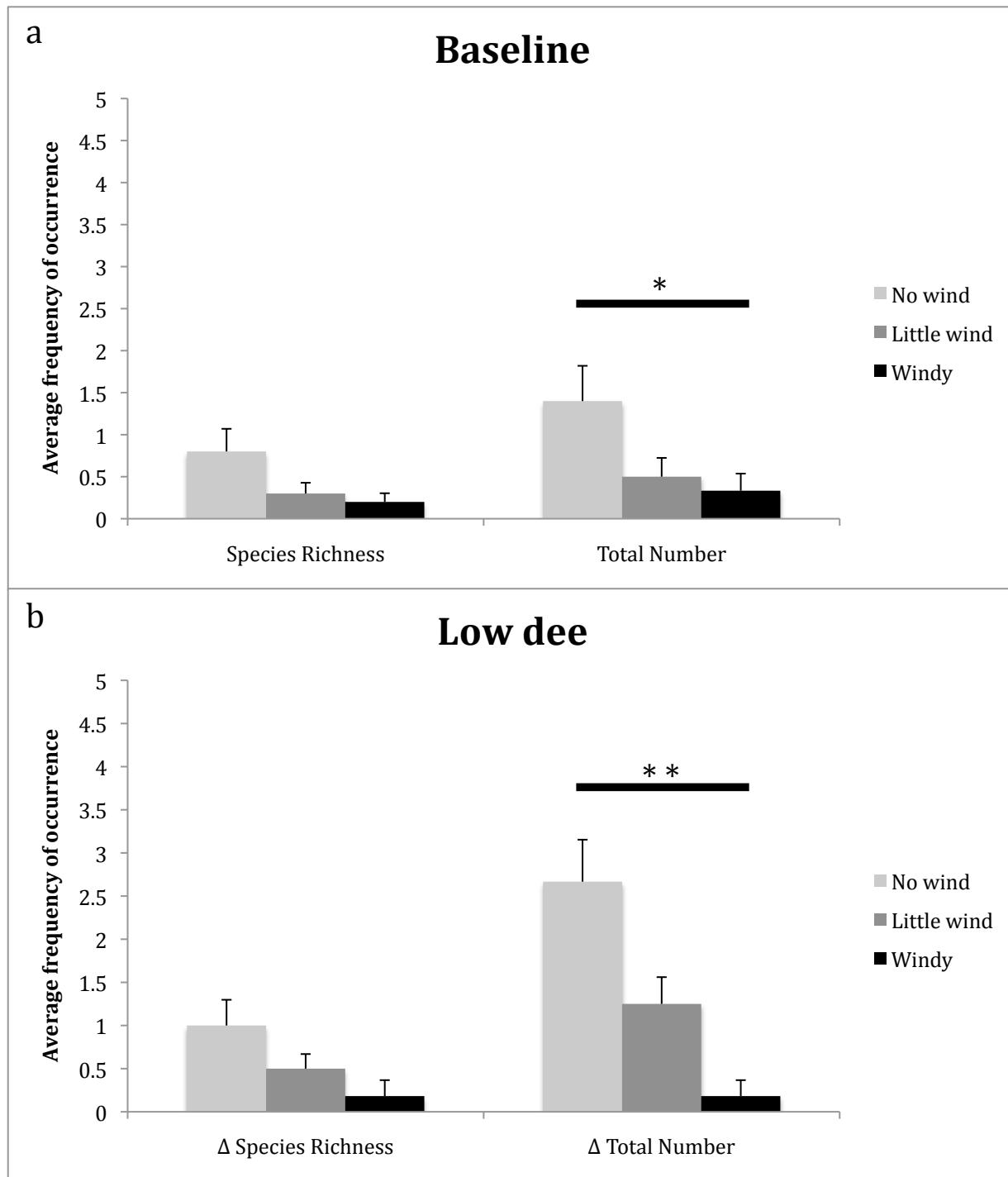


Figure 7. Average (+ SE) number of species and total number of birds at baseline (a) and average change in response to low *dee* calls (b) at different wind conditions (n = 15, 20, 25). Wind conditions were measured on the Beaufort scale: no wind (0-3 mph), little wind (4-12 mph), and windy (13-24 mph). Stars represent significance (p < 0.05 and p < 0.01, one-way ANOVA).

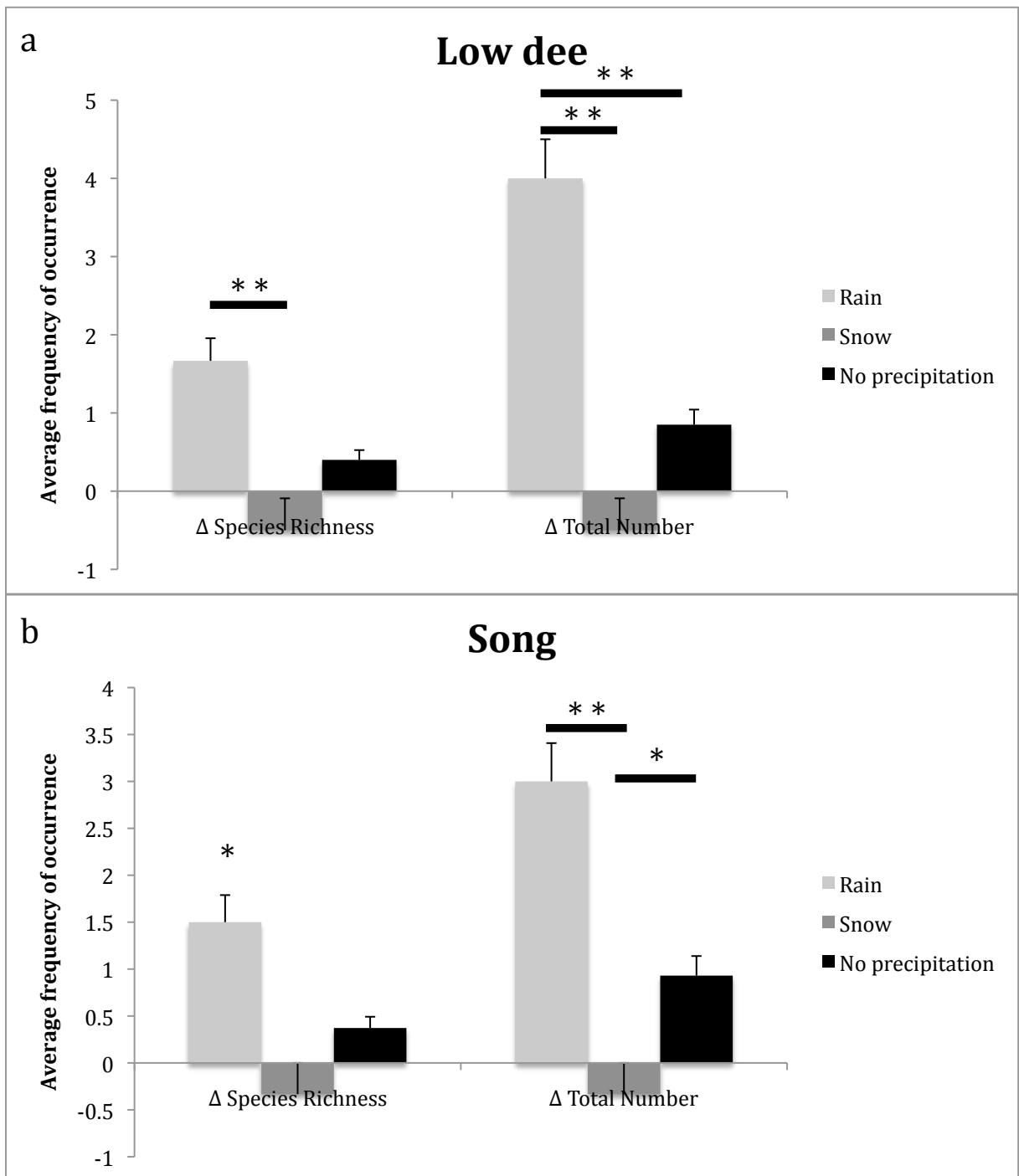


Figure 8. Average (+ SE) number of species and total number of birds as a change from baseline in response to low *dee* calls (a) and song (b) at different precipitation conditions ($n = 4, 3, 43$).

Stars represent significance ($p < 0.05$ and $p < 0.01$, one-way ANOVA).

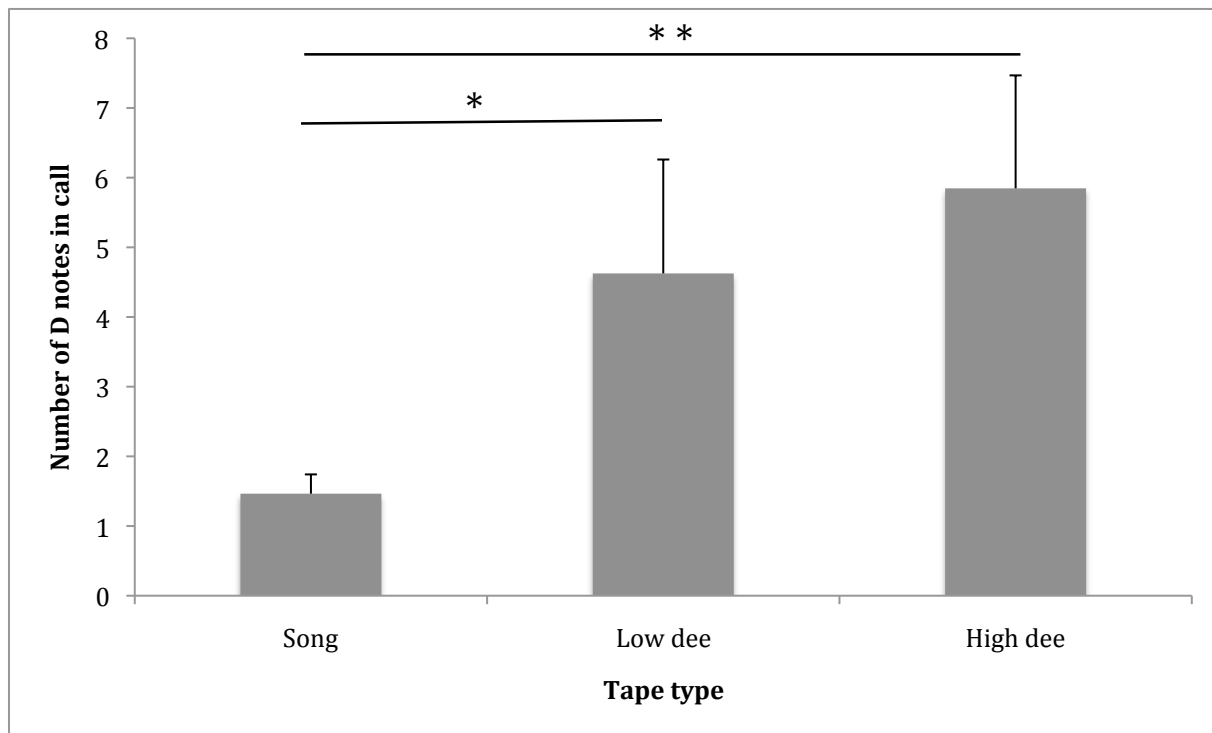


Figure 9. Average (+ SE) number of D notes produced by chickadees in response to various tape types (n = 28, 8, 13). Stars represent significance ($p < 0.05$ and $p < 0.01$, one-way t-tests).