Are chickadees good listeners? Anti-predator responses to raptor vocalizations

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Many animals gather information about predators with a variety of cues, such as visual, acoustic, and olfactory. Several species of birds, including chickadees, are good at discriminating between species of raptors using visual cues, and they can encode information about the threat level in their alarm calls. Much less is known about how birds discriminate between the calls of different species of predators. We played back the calls of three species of raptors to black-capped chickadees (*Poecile atricapillus*), mountain chickadees (*Poecile gambeli*) and chestnut-backed chickadees (*Poecile rufescens*) to determine if they can discriminate between them using acoustic cues. We played the calls of two species of small, high-threat raptors, northern pygmy-owl (*Glaucidium gnoma*) and sharp-shinned hawk (*Accipiter striatus*), which have very different hunting strategies (mainly sit-and-wait ambush predator versus very fast surprise attack flights). We also played a larger, lower-threat northern goshawk (*Accipiter gentilis*). Black-capped and mountain chickadees responded much more to the calls of the two small, more dangerous raptors than to northern goshawk; they also responded very differently to the calls of the two small raptors. Chestnut-backed chickadees did not respond differently to the calls of the three raptors. These results indicate that black-capped and mountain chickadees can make specific discriminations between the calls of these three raptors, and encode information in their alarm calls in sophisticated ways.

KEYWORDS: Alarm calls; mobbing calls; acoustics; anti-predator behavior; chickadee; *Poecile*

For many animals, predators account for most mortality (Lima & Dill, 1990; Martin, 1995; Caro, 2005). Furthermore, predation can have large effects on the behavior of prey species. For example, the “landscape of fear” (Laundre et al., 2001) that is created by the perception of risk can change species’ foraging behavior, vigilance, movement patterns, habitat

selection, densities, and reproductive effort (Werner & Peacor, 2003; Preisser et al., 2005; Preisser & Bolnick, 2008; van der Merwe & Brown, 2008; Ohgushi et al., 2012). Thus, how prey species detect and avoid predators is of fundamental importance for understanding the ecology and evolution of predator-prey systems.

How prey species detect and avoid predators involves responses to many types of cues, and there are inherent differences in the information that prey species can gather about predators from different types of cues. For example, visual cues provide unambiguous information about the identity, direction, distance, movement, and general behavior (actively hunting, preening, lounging, etc.) of predators. In contrast, information associated with acoustic or olfactory cues about predators is more ambiguous as there is less certainty about a predator's identity, location, movement and behavioral state. Since the information provided varies with the type of cue, anti-predator behaviors may also vary across cue types. For example, male wolf spiders (*Schizocoas ocreata*) respond to a seismic cue (beak pecking on the substrate) and an acoustic cue (bird vocalization) by not moving. But, in response to a visual cue (bird shadow), wolf spiders will seek cover. The time taken to resume to courtship behavior was also greater after the visual cue than the other cues (Lohrey et al., 2009).

Birds use primarily visual and acoustic cues to gather information about predators. Birds can discriminate between visual cues from different predator species and respond with species-specific anti-predator behaviors (Baker & Becker, 2002; Freeberg & Lucas, 2002; Templeton et al., 2005; Soard & Ritchison, 2009; Bartmess-LeVasseur et al., 2010; Sieving et al., 2010). Much less is known about how birds discriminate between the sounds produced by potential predators (see review by Hettena et al., 2014), but recent studies suggest that birds may be

remarkably sensitive to sounds produced by predators. For example, song sparrows exposed to the vocalizations of predators nested in denser vegetation, laid smaller clutches, spent less time on the nest during incubation and were more skittish, which led to a significant decrease in the number of offspring produced (Zanette et al., 2011).

Many bird species are known to produce anti-predator alarm calls in response to visual cues. Two common types of alarm calls are “seet” calls and “mobbing” calls (Marler, 1955; Gyger et al., 1987; Griesser, 2009; Bradbury & Vehrencamp, 2011). Seet calls are typically produced in response to flying raptors or in high threat situations. They tend to be relatively high-frequency (typically 6-12 kHz) tonal signals, of short duration, and low to medium amplitude. In contrast, mobbing calls are produced when birds detect a stationary or perched predator that is not actively hunting. They tend to be loud, harsh (broadband with complex overtone structure), and with a high repetition cycle. Therefore, visual cues about a predator’s specific behavior (flying versus perched) can completely alter anti-predator responses. For example, Templeton et al. (2005) exposed black-capped chickadees (*Poecile atricapillus*) to models and live bird predators (visual cue) and found that black-capped chickadees alter their chick-a-dee mobbing call by adding more -dee elements to predator species that pose a higher threat (Templeton et al., 2005). There are far fewer examples of birds altering their anti-predator responses to acoustic cues from predators (see review by Hettena et al., 2014).

Chickadees and their relatives (Parids) are an ideal group to investigate acoustically-based discrimination among predator species and their anti-predator responses. Chickadees are highly vigilant, susceptible to several avian predator species, can discriminate different predator species by sight, and can encode information to others about predator threat levels (Baker &

Becker, 2002; Freeberg & Lucas, 2002; Templeton et al., 2005; Soard & Ritchison, 2009; Bartmess-LeVasseur et al., 2010; Courter & Ritchison, 2010). However, there is little known about their ability to discriminate between predator species based on acoustic cues.

We designed this study to experimentally test if three species of chickadees can discriminate between the vocalizations of different types of raptors, and whether such discrimination influences their anti-predator responses. We played back the calls of raptors that varied in threat level to black-capped chickadees, mountain chickadees (*Poecile gambeli*) and chestnut-backed chickadees (*Poecile rufescens*).

The threat level of the raptors was assigned *a priori* using size, hunting strategy, and diet. The allometric risk hypothesis states that the risk a raptor poses to another bird is strongly influenced by their relative sizes. This is a natural consequence of the aerodynamics of flight: small birds have smaller turning radii, accelerate faster, and use more of the three-dimensional world compared to larger birds (Dial et al., 2008). The allometric risk hypothesis predicts that raptors that are about the same size as their potential prey pose the greatest risk, whereas raptors that are either much larger or much smaller pose much less of a risk because the larger predators are not mobile enough to catch them and the smaller predators are not able to subdue them. We chose two small raptors that are highly threatening to chickadees, but that differ greatly in their hunting strategies. Northern pygmy-owls (*Glaucidium gnoma*) are small (approx. 50-70 g) and hunt mainly by using a sit-and-wait strategy. They are slow fliers and often plummet down on small chickadee-sized birds below them (Holt & Leroux, 1996; Holt & Peterson, 2000). Sharp-shinned hawks (*Accipiter striatus*) are mid-sized raptors (approx. 85-200 g), extremely fast and maneuverable in flight, and specialize on small- to medium-sized birds (Bildstein & Meyer,

2000). Northern goshawks (*Accipiter gentilis*) are large raptors (approx. 650-1 400 g) that are a low threat to chickadees. They are also fast fliers and bird specialists, but are less maneuverable than chickadees (Dial et al., 2008), and rarely attack birds as small as chickadees (Squires & Reynolds, 1997).

Following the allometric risk hypothesis, we predicted that chickadees would respond less to the large northern goshawk than to the smaller, more dangerous northern pygmy-owl and sharp-shinned hawk. We also predicted that the anti-predator responses of chickadees would differ between the two small predators because of their different hunting strategies. And finally, we predicted the encoding strategy to be similar across the three species of chickadees. Our specific research questions were: 1) Can chickadees discriminate between the vocalizations of these different raptor species? 2) If so, how is this encoded in their anti-predator acoustic responses?

MATERIALS AND METHODS

Study sites

We conducted this study on 5 mixed-species flocks in the Missoula Valley, MT, USA (46.8625° N, 114.0117° W) and 4 flocks in the Methow Valley, WA, USA (48.4736° N, 120.1789° W). During the winter in our study areas, mixed species flocks tend to be very stable in composition and numbers of individuals (Morse, 1970; pers. obs.). We have observed that flocks travel together in fairly tight groups, they stay acoustically connected (giving contact calls), and have fairly small home ranges. We conducted our playback experiments near bird feeders, since these are useful hubs to reliably relocate flocks.

The feeders were located a minimum of 2 km from one another, so it is unlikely the same flock visited more than one feeder. The experiments were performed in the winter months (December-March) of 2012-2014 when the mixed-species flocks regularly visit feeders. Four of the nine feeders were replicated across consecutive years ($N = 52$ experiments; 13 experimental blocks). All three chickadee species were not present at every feeder, so sample sizes varied (black-capped chickadees, $N = 50$ experiments; mountain chickadees, $N = 46$ experiments; chestnut-backed chickadees, $N = 32$ experiments).

Stimuli

The birds at each feeder were exposed to four acoustic stimuli treatments. We chose the vocalizations of Townsend's solitaires (*Myadestes townsendi*), a common, non-predatory songbird, as a control and three common raptors: northern pygmy-owl, sharp-shinned hawk, and northern goshawk. These species differ in their seasonal production of vocalizations. Sharp-shinned hawks and northern goshawks are mostly silent during the winter (when we conducted our playback experiments), and call mainly during the breeding season (Squires & Reynolds, 1997; Bildstein & Meyer, 2000). In contrast, northern pygmy-owls and Townsend's solitaires vocalize throughout the year (Bowen, 1997; Holt & Peterson, 2000). However, like chickadees, all of the stimuli species are year-round residents at our study sites, so it is probable that the chickadees were exposed to the vocalizations of all the stimuli at some point during the year.

To make the playback stimuli, we chose the highest quality recordings from the Macaulay Library of Natural Sounds at Cornell's Lab of Ornithology. The accession numbers and recording locations for the stimuli are: Townsend's solitaire (ML47553, California (Herr, 1990); ML119411, California (Keller, 2001); ML120266, California (Keller, 2002)), northern

pygmy-owl (ML45192, Montana (Keller, 1987a); ML40576, Arizona (Keller, 1987b)), sharp-shinned hawk (ML4153, New York (Kellogg, 1953); ML139421, New York (D'Alessandro, 1996)) and northern goshawk (ML63118, Oregon (Herr, 1992); ML40509, Arizona (Keller, 1987c), ML105702, Oregon (Keller, 1995). Although most of the sounds we used were not recorded near our study sites, there is no evidence for geographic structure in the calls of these species.

To avoid pseudoreplication, we created multiple playback samples (exemplars) for each stimulus (Hurlbert, 1984; Kroodsma, 1989; Kroodsma, 1990). The exemplars were randomly assigned to each feeder. Vocalizations from the recordings were kept at their natural length to create the stimuli. To standardize across stimuli and exemplars we used a 50% duty cycle (stimulus and equal length of silence alternating for the duration of the playback). We made the stimuli in Raven Pro 1.4 (Charif et al., 2008) and saved the audio files as 24-bit WAV files.

Playback design

The calls were played from an Apple iPhone 4 (Model No. A1349, EMC No. 2422, frequency response curve is flat between 20 Hz – 20,000 Hz, Apple, Cupertino, CA, USA) connected to a PigNose Legendary 7-100 field speaker (frequency response curve is flat between 500 Hz – 17,000 Hz, PigNose Ind., Las Vegas, NV, USA). This equipment produces good playback characteristics in the hearing range of chickadees (Henry & Lucas, 2010; Vélez et al., 2015) and is commonly used in playback experiments to birds (e.g. Greig & Webster, 2013). We hid the speaker in vegetation that was 10 and 20 m from the feeder and about 2 m off the ground. We calibrated the peak amplitude of each playback stimulus to 80 dB SPL A-weighting at 1 meter using an Extech 407730 sound level meter (Extech Instruments, Nashua, NH, USA). The

154 acoustic responses of the chickadees were recorded with Sennheiser 67 shotgun microphones
155 (Sennheiser, Wedemark, Germany) into Marantz PMD 661 recorders at 48kHz sampling rate and
156 24-bit depth (Marantz, Kanagawa, Japan).

157 We waited at least 10 min after hiding the speaker to allow the birds to return to natural
158 activity. However, since all these experiments were performed near feeders, the birds were
159 habituated to human activity and did not seem disturbed by our presence. There can be large
160 variation in the numbers and species of birds active at bird feeders even during relative short
161 times. However, we broadcast the playback stimuli into the woods around the feeders. We did
162 this to maximize the chances that members of that flock would be able to hear and respond to the
163 playback stimuli, not just birds that happened to be at the feeder during a particular minute of the
164 experiments. Even if flock members were not actively feeding, they were still likely to be in the
165 vicinity to be recorded during the pre-playback, to hear the playback, and to be recorded during
166 the playback and post-playback periods. We designed our experiments to probe the acoustic
167 responses of birds in each flock, rather than just the individual birds that happened to be at a
168 feeder.

169 We were not able to measure the number of individuals of each species within a flock
170 because the birds were not banded. In addition to short-term variation in the numbers of
171 individual birds visiting a feeder, there could have been some changes within a flock due to
172 mortality during the study periods. To control for these differences, each experiment was paired
173 with a baseline period. Before each experiment, we recorded a 2 min pre-playback recording for
174 a baseline level of acoustic activity of a particular flock. The playback stimulus lasted 2 min.
175 Once the playback ended, we continued to record for 5 min (post-playback). We chose these

times to ensure we captured accurate activity levels during each playback time period. The order of the stimulus presentation was randomized for each feeder, and if multiple stimuli were presented at a feeder in one day we waited at least 20 min between each presentation to allow the birds to return to normal activity.

Ethical Note

We simulated the presence of raptors by playing their calls to wild, free-living birds. Although in some cases the playbacks changed the vocal behavior of the birds (which is the focus of this study), we do not feel that these experiments were unduly stressful. Birds seemed to return to normal activity relatively quickly after our experiments. Our experiments conform to the standards outlined in the ASAB/ABS Guidelines for the Use of Animals in Research, and were approved by the University of Montana IACUC (AUP 049-14EGDBS-080814).

Acoustic Analysis

The three species of chickadees that we studied (black-capped, mountain, and chestnut-backed chickadees) produce vocalizations that are acoustically similar (Smith, 1993; McCallum et al., 1999; Dahlsten et al., 2002). All three species produce chick-a-dee calls that consist of chicka- elements followed by -dee elements (**Figure 1A-C**). For full chick-a-dee calls, we could distinguish the three species. All three species can also produce independent chicka- calls without any following -dee elements (**Figure 1D**). We could not distinguish black-capped and mountain chickadees using only chicka- calls, but we could distinguish chestnut-backed chickadee chicka- calls from the two other species. Finally, all three species produce a wide variety of high-frequency calls (seet and others **Figure 1E**). We could not distinguish species using these calls.

198 All recordings were analyzed using Raven Pro 1.4 (Charif et al., 2008). Spectrograms
199 were made of each recording using Hann window type with a 50% overlap and a window size
200 between 512 – 1 150 samples. The analysts would visually and acoustically identify the various
201 chickadee calls. All the variables were tallied for each minute so each recording had a count of
202 each of the variables broken into nine 1-min increments. We measured 11 acoustic variables: (1)
203 The total number of complete black-capped chick-a-dee calls (**Figure 1A**, 1 complete call
204 shown), (2) the number of chicka- element pairs per black-capped chick-a-dee call (**Figure 1A**, 1
205 chicka element pair shown), and (3) the number of -dee elements per black-capped chick-a-dee
206 call (**Figure 1A**, 3 -dee elements shown). (4) The total number of complete mountain chick-a-
207 dee calls (**Figure 1B**, 1 complete call shown), (5) the number of chicka- element pairs per
208 mountain chick-a-dee call (**Figure 1B**, 2 chicka- element pairs shown), and (6) the number of -
209 dee elements per mountain chick-a-dee call (**Figure 1B**, 2 -dee elements shown). (7) The
210 number of complete chestnut-backed chick-a-dee calls (**Figure 1C**, 1 complete call shown). We
211 did not count the number of chestnut-backed chicka- element pairs or -dee elements within the
212 complete chick-a-dee call because sample sizes were small and there was little variation in the
213 makeup of the chestnut-backed chickadee call. (8) The number of chicka- calls given without -
214 dees by black-capped or mountain chickadees (**Figure 1D**, 1 chicka- call shown). (9) The
215 number of chicka- element pairs within each chicka- call (**Figure 1D**, 2 chicka- element pairs
216 shown). (10) The number of chestnut-backed chicka- calls without -dees (**Figure 1D**, 1 chicka-
217 call shown). We did not analyze the number of chestnut-backed chickadee chicka- element pairs
218 because samples sizes were small and there was little variation in the number of elements. And

219 (11) the number of high-frequency calls given (**Figure 1E**, 3 high-frequency calls shown). We
220 defined a high-frequency call as a tonal call between 6 500 – 12 000 Hz.

Figure 1

Figure 1: Spectrograms of **A.** one full black-capped chick-a-dee call, **B.** one full mountain chick-a-dee call, **C.** one full chestnut-backed chick-a-dee call, **D.** independent chicka- calls from black-capped/mountain chickadees and chestnut-backed chickadees, and **E.** high-frequency calls from black-capped/mountain/chestnut-backed chickadees. All acoustic elements used for analysis are indicated with brackets, labeled, and numbered. Spectrograms made with Raven Pro 1.4.

Statistical Analysis

For each variable, we averaged the count across each playback period. Counts of each variable in the first and second minute of the pre-playback were added together and divided by two to give an average number of each variable per minute in the pre-playback. Counts of each variable in the third and fourth minute were added together and divided by two to give an average of each variable per minute in the playback. Counts of each variable in the fifth through ninth minute were added together and divided by five to give an average of each variable per minute in the post-playback.

The pre-playback was a paired measure of the baseline acoustic activity for a particular experiment at a particular feeder. To standardize both within and across feeders and remove confounding effects such as differences in flock size and activity, differences across days, or differences due to weather, we subtracted the average of each variable in the pre-playback from the average of that variable in the playback and the average in the post-playback. This provided an average change in each of the 11 variables given during the playback and the post-playback relative to the baseline or pre-playback period. Thus, a positive number indicates more calls were

given than baseline, a negative number indicates fewer calls were given than baseline and zero means no difference in the number of calls than baseline.

We constructed linear mixed effects models using maximum likelihood for each of the 11 variables. Stimuli (4 levels: Townsend's solitary, northern pygmy-owl, sharp-shinned hawk, northern goshawk) and playback period (2 levels: playback, post-playback) were assigned as fixed effects and the feeder location (9 levels) and the time in the season (2 levels: winter=December, January and February, late winter=March) were assigned as random effects. Although we controlled for differences within and between flocks using the pre-playback baseline, we also included the feeder location in all the statistical models to account for any variation that was not taken care of by the pre-playback control. All fixed and random effects were tested for significance using likelihood-ratio tests. Residuals from the models failed a Shapiro-Francia test for normality, so following Faraway (2004) and Galecki & Burzykowski (2013), we used parametric bootstraps on each variable. To identify how the response differed between all stimuli and playback categories, any models that were significant from the bootstraps were run with a Tukey Kramer post hoc test. This is a conservative correction and is the best available when doing all pairwise comparisons when sample sizes are small and unequal. Because Tukey Kramer tests also assume a normal distribution, we ran parametric bootstraps on all pairwise comparisons. All statistical analyses were done in R using the *lme4* package with an alpha of 0.05 (Bates et al., 2010).

RESULTS

Chickadees were able to distinguish the different predators by their vocalizations. In response to the experimental stimuli, chickadees produced vocalizations that differed across

multiple acoustic variables. We did not find the random effects of feeder location or season to be significant in any of the models ($p < 0.05$). Also, how chickadees encoded information about the different predators varied by acoustic variable, chickadee species and playback period.

Chick-a-dee calls (Figure 1A-C):

Black-capped chickadees altered the number of full chick-a-dee calls given in response to different stimuli (**Figure 2A**; $\chi^2 = 17.48$, $df = 3$, $p < 0.001$). Specifically, black-capped chickadees marginally increased the number of chick-a-dee calls in response to northern pygmy-owls during the playback period [control:pygmy-owl $p = 0.082$; goshawk:pygmy-owl $p = 0.184$; sharp-shinned:pygmy-owl $p = 0.380$] and significantly increased the number of full chick-a-dee calls in response to northern pygmy-owls during the post-playback period [control:pygmy-owl $p < 0.001$; goshawk:pygmy-owl $p < 0.001$; sharp-shinned:pygmy-owl $p < 0.001$]. However, they only showed a marginal trend in the number of chick-a- elements and the number of -dee elements within their chick-a-dee call (chicka-: $\chi^2 = 3.9753$, $df = 3$, $p = 0.069$; -dees: $\chi^2 = 6.2286$, $df = 3$, $p = 0.07$; graphs not shown), and the post hoc pairwise comparisons did not reveal any significant differences between stimuli within a playback period.

Mountain chickadees also altered the number of full chick-a-dee calls given in response to different stimuli (**Figure 2B**; $\chi^2 = 36.572$, $df = 3$, $p < 0.001$). Mountain chickadees gave significantly more full chick-a-dee calls in response to northern pygmy-owls than the other stimuli species during the playback period [control:pygmy-owl $p = 0.003$; goshawk:pygmy-owl $p = 0.007$; sharp-shinned:pygmy-owl $p = 0.005$] and post-playback period [control:pygmy-owl $p < 0.001$; goshawk:pygmy-owl $p < 0.001$; sharp-shinned:pygmy-owl $p < 0.001$]. Within the chick-a-dee call, mountain chickadees did not alter the number of chick-a- elements ($\chi^2 = 3.4047$, $df = 3$,

286 p=0.144; graph not shown), but did alter the number of –dee elements ($\chi^2=14.776$, df=3,
287 p<0.001; graph not shown). Mountain chickadees added significantly more –dee elements to
288 their chick-a-dee call in response to the northern goshawk stimulus than other stimuli during the
289 playback period (control:goshawk p=0.009; sharp-shinned:goshawk p=0.014; pygmy-
290 owl:goshawk p=0.046), but not during the post-playback period.

291 Chestnut-backed chickadees marginally altered the number of full chick-a-dee calls given
292 in response to the stimuli ($\chi^2= 6.0311$, df=3, p=0.081; graph not shown) but the post-hoc
293 pairwise comparisons did not reveal any significant differences among stimuli within a playback
294 period.

295 **Figure 2:** The number (mean $\pm$ SE) of full chick-a-dee calls given by (A) black-capped
296 chickadees; and (B) mountain chickadees during the playback period (closed circles) and post-
297 playback period (open circles). Lower-case letters indicate differences significant at p<0.1. The
298 y-axis is the difference in the number of calls from the baseline or pre-playback. Note the y-axis
299 scales differ between (A) and (B).

300 *Chicka- calls and chicka- element pairs (Figure 1C):*

301 Black-capped and mountain chickadees altered the number of independent chicka- calls
 302 given in response to the different stimuli (**Figure 3A**; $\chi^2=26.56$, $df = 3$, $p<0.001$). Specifically,
 303 they significantly increased the number of independent chicka- calls they gave to northern
 304 pygmy-owls during the playback period [control:pygmy-owl $p<0.001$; goshawk:pygmy-owl
 305 $p=0.022$; sharp-shinned:pygmy-owl $p=0.004$] and post-playback period [control:pygmy-owl
 306 $p=0.003$; goshawk:pygmy-owl $p=0.015$; sharp-shinned:pygmy-owl $p=0.033$].

307 Black-capped and mountain chickadees also altered the number of chicka- element pairs
 308 within their independent chicka- calls (**Figure 3B**; $\chi^2=6.606$, $df = 3$, $p=0.004$). During the

309 playback period, they marginally increased the number of chicka- element pairs per chicka- call
310 to northern pygmy-owls [control:pygmy-owl p=0.066; goshawk:pygmy-owl p= 0.103; sharp-
311 shinned:pygmy-owl p=0.009]. But, there was no difference between stimuli during the post-
312 playback period [control:pygmy-owl p=0.608; goshawk:pygmy-owl p=0.436; sharp-
313 shinned:pygmy-owl p=0.532].

314 Chestnut-backed chickadees did not alter the number of independent chicka- calls given
315 to stimuli ($\chi^2=3.4322$, $df = 3$, $p=0.375$; graph not shown).

316 **Figure 3:** The number (mean $\pm$ SE) of (A) independent chicka- calls and (B) chicka- element
317 pairs per chicka- call given by black-capped and/or mountain chickadees during the playback
318 period (closed circles) and post-playback period (open circles). Lower-case letters indicate
319 differences significant at $p<0.1$. The y-axis is the difference in the number of calls from the
320 baseline or pre-playback. Note the y-axis scale differs between (A) and (B).

321 *High-frequency calls (Figure 1E):*

322 Black-capped, mountain and/or chestnut-backed chickadees altered the number of high-

323 frequency calls given in response to the different stimuli (**Figure 4**; $\chi^2=9.6091$, $df = 3$, $p=0.023$).

324 Specifically, they significantly increased the number of high-frequency calls to the sharp-shinned

325 hawk stimulus during the post-playback period [control:sharp-shinned $p=0.062$; goshawk:sharp-

326 shinned $p=0.117$; pygmy-owl:sharp-shinned $p=0.012$], but not during the playback period

327 [control:pygmy-owl $p=0.550$; goshawk:pygmy-owl $p=0.134$; sharp-shinned:pygmy-owl

328 $p=0.159$].

Figure 4: The number (mean $\pm$ SE) of high-frequency calls given by black-capped, mountain and/or chestnut-backed chickadees during the playback period (closed circles) and post-playback period (open circles). Lower-case letters indicate differences significant at $p < 0.1$. The y-axis is the difference in the number of calls from the baseline or pre-playback.

DISCUSSION

1) Can chickadees discriminate between the vocalizations of different types of raptors?

Our playback experiments showed that black-capped and mountain chickadees distinguished between the vocalizations of different species of sympatric raptors. On the basis of the allometric risk hypothesis, diet, and hunting behavior, we predicted that chickadees would respond differently to the smaller raptors (northern pygmy-owl and sharp-shinned hawk) than to the larger northern goshawk. This prediction was generally supported, since both black-capped

and mountain chickadees responded by changing call elements in response to the vocalizations of both northern pygmy-owls and sharp-shinned hawks, and very little to northern goshawks.

2) How do chickadees alter their anti-predator acoustic responses to the vocalizations of different raptors?

We found that black-capped and mountain chickadees responded differently to the two small, high-threat raptors. In response to northern pygmy-owls, both black-capped chickadees and mountain chickadees gave more complete chick-a-dee calls, more chicka- calls, and more chicka- elements. They produced more chick-a-dee calls and more chicka- calls during both the playback and post-playback periods, but produced more chicka- elements only during the playback period. Templeton et al. (2005) found that in response to visual cues about predators (i.e. models and live birds) black-capped chickadees added more -dee elements to smaller predators (Templeton et al., 2005). This indicates that at least black-capped chickadees respond differently to a visual predator cue versus an acoustic predator cue. They also seem to encode this information differently by altering different characteristics of their mobbing calls.

We found that mountain chickadees increased the number of -dee elements in their chick-a-dee call to the northern goshawk stimulus. This may be because mountain chickadees have a different encoding strategy for high and low threat predators than black-capped chickadees. And it raises questions of how mountain chickadees respond and encode information to visual predator cues, but this remains to be tested.

A striking difference in the responses of chickadees to northern pygmy-owls and sharp-shinned hawks was detected only after the acoustic cue stopped (i.e. the post-playback period). After the calls of sharp-shinned hawks stopped, chickadees produced significantly more high-

frequency calls. The difference in anti-predator response between these two raptors may be related to their very different hunting tactics. Northern pygmy-owls are relatively slow fliers, and they rely mainly on perch and pounce ambush tactics (Holt & Leroux, 1996; Holt & Peterson, 2000). In contrast, sharp-shinned hawks are very maneuverable and stealthy, and capture prey mainly by flying very fast (Bildstein & Meyer, 2000). When chickadees see a northern pygmy-owl calling, they tend to approach and engage in vigorous mobbing behaviors (Templeton et al., 2005). This mobbing behavior is generally effective at driving a northern pygmy-owl out of the area. But once a sharp-shinned hawk stops calling, the information giving rough distance and direction is gone. The high-frequency calls produced by chickadees might signal that the sharp-shinned hawk is flying and hunting, which would be very dangerous for chickadees. While these ideas are speculative, the results emphasize that black-capped and mountain chickadees respond to two different species of small and dangerous raptors very differently.

Black-capped chickadees and mountain chickadees responded to the sounds of potential predators in similar ways. However, chestnut-backed chickadees showed no significant difference in any call characteristics we measured. Although we could not distinguish among species in the high-frequency calls, the overall difference in high-frequency calls seems to be driven by black-capped and mountain chickadees (pers. obs. during playback experiments). In fact, we observed that chestnut-backed chickadees made up a very small number of the individuals in the mixed-species flocks. The similar responses of black-capped and mountain chickadees and the lack of response of chestnut-backed chickadees suggest that chestnut-backed chickadees may encode predator information in different ways. Black-capped and mountain

chickadees are sister species, while chestnut-backed chickadees are more distantly related (Johansson et al., 2013). Carolina chickadees (*Poecile carolinensis*), which are closely related to black-capped and mountain chickadees (Johansson et al., 2013), also give more chick-a-dee calls in response to higher threat predators (Bartmess-LeVasseur et al., 2010; Courter & Ritchison, 2010). Therefore, chestnut-backed chickadees may differ simply due to a lack of shared phylogeny.

We did not anticipate that chickadees would respond to the control songs of Townsend's solitaires. Townsend's solitaires defend berry and fruit trees and bushes during the winter, and often sing throughout the winter from tall, exposed perches (Bowen, 1997), especially when predators are not around (pers. obs.). Townsend's solitaires also give harsh alarm calls when they detect a raptor (Bowen, 1997; pers. obs.). Thus, Townsend's solitaires may serve as vigilant sentinel species: when they are singing it may signal to other species that no predators are nearby. We found that black-capped and mountain chickadees gave fewer chicka- calls during the playbacks of Townsend's solitaire songs than the baseline. This implies that the calls of Townsend's solitaires may not be a completely neutral control, but may be interpreted as an "all clear" signal.

Overall, our study demonstrates that black-capped and mountain chickadees are good listeners. Most studies examine if species can discriminate between different classes of predators such as terrestrial versus aerial. Our study is one of the few that examines the subtle differences in anti-predator responses within a predator class (Hettena et al., 2014). Our results also suggest that the classification of predators is not as simple as threatening versus non-threatening raptors, or small versus large raptors. We found that the responses of chickadees are more nuanced,

subtle, and complex than we had predicted: both black-capped and mountain chickadees responded differently to the two small and dangerous raptors. Alarm call systems are complex, and a lot of information about predator size, hunting strategy, predator behavior, and the modality of the predator cue (e.g. visual versus acoustic) may influence the structure and use of alarm calls.

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