

Alarm calls of tufted titmice convey information about predator size and threat

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Many birds utter alarm calls when they encounter predators, and previous work has revealed that variation in the characteristics of the alarm, or “chick-a-dee,” calls of black-capped (*Poecile atricapilla*) and Carolina (*P. carolinensis*) chickadees conveys information about predator size and threat. Little is known, however, about possible information conveyed by the similar “chick-a-dee” alarm call of tufted titmice (*Baeolophus bicolor*). During the winters of 2008 and 2009, free-ranging flocks ($N = 8$) of tufted titmice were presented with models of several species of raptors that varied in size, and titmice responses were monitored. Smaller, higher threat predators (e.g., eastern screech-owl, *Megascops asio*) elicited longer mobbing bouts and alarm calls with more notes (D-notes) than larger lower threat predators (e.g., red-tailed hawk, *Buteo jamaicensis*). During playback experiments, titmice took longer to return to feeding after playbacks of alarm calls given in response to a small owl than to playbacks given in response to a large hawk or a robin (control). Like chickadees, titmice appear to utter alarm calls that convey information about predator size and threat. Titmice, however, appear to cue in on the total number of D-notes given per unit time instead of the number of D-notes per alarm call. The broadband alarm calls of titmice, containing D-notes uttered in an unpredictable manner that may make it difficult for predators to determine the number of titmice calling, may be particularly well suited for deterring predators. *Key words:* alarm calls, call characteristics, mobbing, predation risk, predator size. [*Behav Ecol* 21:936–942 (2010)]

Many animals utter alarm calls when they encounter predators (Arnold and Zuberbuhler 2006; Frederiksen and Slobodchikoff 2007; Botham et al. 2008), and these calls may alert group members and kin of danger, call for assistance, or inform predators that they have been spotted and are no longer a threat (Hill 1986; Langham et al. 2006). For some species, alarm calls may provide specific information about the type of predator present (functionally referential; Pereira and Macedonia 1991; Kirchoff and Hammerschmidt 2006), the level of threat a predator poses (urgency based; Welbergen and Davies 2008), or both (Manser et al. 2002; Griesser 2008). Accurately interpreting the information encoded in alarm calls can decrease the likelihood of predation for conspecifics (Baker and Becker 2002; Templeton et al. 2005), heterospecific group members (Hurd 1996; Templeton and Greene 2007); and heterospecific eavesdroppers (Lea et al. 2008; Schmidt and Ostfeld 2008; Schmidt et al. 2008).

Alarm calling by birds in the family Paridae has been widely documented (Hailman 1989), with most studies focusing on the remarkable complexity of the alarm calls of chickadees (genus *Poecile*, Baker and Becker 2002; Freeberg and Lucas 2002; Clucas et al. 2004; Lucas and Freeberg 2007). Chickadees utter a high-frequency low-amplitude “seet” call to alert group members to the presence of aerial predators and a broadband “chick-a-dee” alarm call in response to perched predators (Templeton et al. 2005). “Chick-a-dee” calls are composed of a combination of 4 ordered note types that can be repeated, omitted, and uttered at different rates to generate numerous unique call types that can potentially convey enormous amounts of information (Hailman 1989; Lucas and Freeberg 2007). Templeton et al. (2005) found that the

acoustic structure of the “chick-a-dee” alarm calls of black-capped chickadees (*Poecile atricapilla*) varied with the size and degree of threat posed by a predator, with a negative correlation between the number of “dee” notes in the “chick-a-dee” alarm call and predator size. This variation appears to convey information about the extent of a threat, with smaller and more maneuverable predators (i.e., high threat) eliciting calls with more “dee” notes (Templeton et al. 2005). A similar degree of alarm call specificity has recently been reported for Carolina chickadees (*P. carolinensis*; Soard 2008).

Although the vocal system of titmice shares many characteristics with those of chickadees (Cimprich and Grubb 1994; Grubb and Pravosudov 1994; Grubb 1998), little is known about the possible information encoded in the alarm calls of tufted titmice (*Baeolophus bicolor*; Hill 1986; Hailman 1989). Like chickadees, titmice utter a high-frequency low-amplitude “seet” call in response to aerial predators (Hailman 1989; Krama et al. 2008) and a broadband “chick-a-dee” alarm call in response to perched predators (Figure 1). The alarm calls of tufted titmice are typically shorter in duration than those of chickadees (Owens and Freeberg 2007), and the interval between “dee” notes in their calls (sometimes referred to as “broken-dee” notes; Smith 1972) is often more variable than similar notes in chickadee alarm calls, making it more difficult for researchers to accurately distinguish between calls (Freeberg T, personal communication). Owens and Freeberg (2007) identified 4 notes (Z, A, Dh, and D) that tufted titmice can include in their “chick-a-dee” calls. These notes typically occur in the same sequence (Z → A → Dh → D), but, as with the “chick-a-dee” calls of chickadees, notes can be repeated, omitted, and uttered at different rates to generate numerous unique call types (Owens and Freeberg 2007). Such variability in call structure suggests that titmice, like black-capped and Carolina chickadees, may alter the information encoded in “chick-a-dee” calls by varying the number of notes.

Our objective was to determine if tufted titmice in natural mixed-species flocks encode information about the size and

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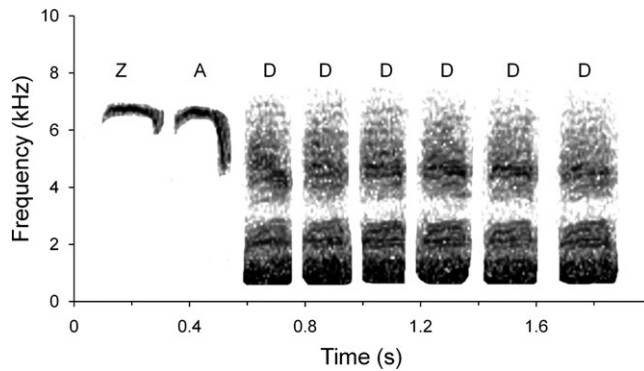


Figure 1
Sonogram illustrating the “chick-a-dee” call (with the different note types designated as Z, A, and D, respectively) of a tufted titmouse.

degree of threat posed by potential avian predators by varying the characteristics of their “chick-a-dee” calls. Our methods were similar to those used by Templeton et al. (2005) in a study of black-capped chickadees, but we studied free-living titmice rather than birds in an aviary. Although aviaries provide a more controlled environment for experimentation, they may also eliminate interactions among natural groups of species in mixed-species flocks that can affect mobbing responses.

We hypothesized that tufted titmice, like black-capped and Carolina chickadees, vary the number of notes in their “chick-a-dee” call when responding to predators that differ in the threat they pose to titmice. To test this hypothesis, we exposed titmice to a variety of avian predators, recorded their vocal responses, and then analyzed the “chick-a-dee” calls uttered to determine if their characteristics varied predictably with the type of predator. We also conducted playback experiments to determine if flocks of tufted titmice responded differently to different types of “chick-a-dee” calls.

MATERIALS AND METHODS

Tufted titmice were studied at 8 locations in Madison County, Kentucky (lat 37°41'58''N, long 84°16'20''W), from 5 January to 27 February 2008 and from 12 December 2008 to 26 January 2009. Study sites were selected based on the presence of apparently suitable habitat and included private residences ($N = 6$), a campground ($N = 1$), and a private farm ($N = 1$). Feeding stations were placed in woodlots on 15 December 2007, separated by a minimum distance of 1.5 km, and stocked with black oil sunflower seeds to attract tufted titmice. Feeding stations consisted of 1 m² sections of plywood hung 1 m above ground with nylon rope.

In our experiments, we used study skins of 5 raptors that differed in the potential threat they posed to tufted titmice, including an eastern screech-owl (*Megascops asio*), sharp-shinned hawk (*Accipiter striatus*), Cooper's hawk (*A. cooperii*), great horned owl (*Bubo virginianus*), and red-tailed hawk (*Buteo jamaicensis*). Great horned owls and red-tailed hawks rarely, if ever, prey on tufted titmice; thus, they were considered “low-threat” predators, whereas the other 3 species are known predators of tufted titmice (Gaddis 1980; Grubb 1998; Roth and Lima 2007), and were considered “high-threat” predators. An empty platform (Baker and Becker 2002; Templeton et al. 2005) and a study skin of a ruffed grouse (*Bonasa umbellus*; a nonpredatory bird) were used as control presentations.

Predator presentations

Trials were conducted at each location from 5 January to 27 February 2008 and during the period from 09:00 to 14:00 h,

with at least 48 h between successive trials (Hill 1986). To eliminate the possibility that interobserver differences would influence our results, all observations were made by J.R.C. Each trial began by placing a randomly selected raptor (or control) in a life-like position (i.e., study skin at an angle of about 70° to mimic a perched raptor) on a platform 1 m above the ground and 1 m from the feeder (Baker and Becker 2002). Specimens were initially covered with a white sheet to hide their identity during a 5-min prepresentation period, while the observer was positioned 5 m away. The prepresentation period began as soon as titmice were heard or observed within 25 m of the covered raptor or control and was intended to acclimate birds to the observer's presence and ensure that birds would remain near a feeding station long enough for an experiment to be completed. After 5 min, the observer walked to the feeder and removed the sheet to expose the raptor or control and then returned to the observation site to monitor the behavior of titmice for 6 additional minutes.

During each trial, the observer noted 1) the number of titmice present; 2) the closest distance any titmouse approached the raptor or control; and 3) the time needed for flock members to return to non-mobbing behavior, that is, no alarm calls uttered for at least 15 s. During all trials, all “chick-a-dee” calls uttered by focal titmice were recorded using a cassette recorder (TCM-500DV; Sony, Tokyo, Japan) and a unidirectional microphone (ATR55; Audio-Technica, Stow, OH).

Acoustic analysis

Raven software (Cornell Lab of Ornithology, Ithaca, NY) was used to analyze the calls recorded during each trial. Mobbing behavior of titmice in response to study skins was generally most intense during the first 2 min of trials (Gaddis 1980) and, therefore, best indicated the threat level perceived by the responding titmice.

For each trial, we attempted to identify, count, and analyze all alarm calls, but when multiple titmice were calling at high rates, calls uttered by different birds sometimes overlapped, and we were unable to identify each unique call. So for each trial, we first counted the total number of D-notes uttered by all titmice in the first 2 min of each recording. We then selected 10 individual calls to analyze using a 120 digit random number table. Random numbers corresponded to a tape location (in seconds, e.g., if the number 15 was selected, we used the first distinct [i.e., not overlapping other calls] titmouse alarm call uttered 15 s after the start of the trial). If there were no calls at or after the selected tape location or if the call had already been analyzed, we selected another number, and corresponding tape location until 10 different calls were analyzed. If fewer than 10 calls were uttered in response to a predator during a trial ($N = 4$), means were calculated using all calls uttered.

For each call, we noted the number and duration of each note type (Z, A, Dh, and D). However, because Dh-notes are given infrequently by titmice and have an acoustic structure similar to D-notes (Owens and Freeberg 2007), we combined them with D-notes for statistical analysis. Most calls could be easily distinguished from other calls by the order of notes and distinct breaks or intervals between calls. However, some calls consisted of only D-notes and lacked Z-notes that typically indicate the start of a different call. When such calls were given in quick succession, distinct breaks between the D-notes of successive calls were not clear. These notes are referred to as “broken-dee” notes (Smith 1972) and make it difficult to identify unique titmice alarm calls (Figure 2). When “broken-dee” notes were observed, notes separated by >0.147 s were identified, and the first of these designated the end of one call and the second designated the start of a successive call. This value (0.147 s) represents the mean duration between second and

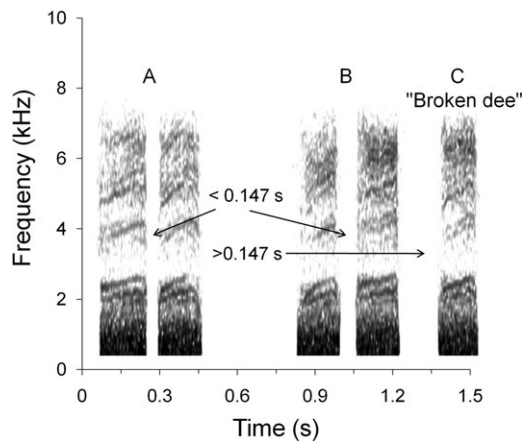


Figure 2

Sonogram illustrating alarm calls uttered by tufted titmice during a predator presentation. D-notes in call (A) and call (B) are each separated by $< 0.147\text{ s}$ and were grouped together within call (A) and call (B), respectively. Call (C) is separated from the second D-note of call (B) by $> 0.147\text{ s}$ and was considered a unique call. Individual D-notes, either single notes or added to the end of calls at variable intervals, are referred to as “broken-dee” notes. Call (C) illustrates a “broken-dee” call.

third D-notes plus 2 standard deviations (SDs) from an initial subsample ($N = 150$) of alarm calls that were uttered in response to high- and low-threat predators and clearly grouped together.

Statistics

We used repeated measures analysis of variance to examine differences in the characteristics of “chick-a-dee” alarm calls among predator treatments. When differences were significant, a Student–Newman–Keuls (SNK) post hoc test was used to identify differences among treatments. All analyses were conducted using the Statistical Analysis System (SAS Institute 2002–2004). To examine the possible effect of raptor size on the responses of titmice, the body length of each predator was determined using information provided by Bump et al. (1947), Gehlbach (1995), Houston et al. (1998), and Clark and Wheeler (2001), and the relationships between body length and the mean number of each type of note (Z, A, and D) in “chick-a-dee” calls uttered by titmice and the mean duration of mobbing responses were examined using linear regression. We used average body length rather than simply measuring the study skins because we assumed a priori that titmice likely cued on a combination of species identity and relative size rather than on individual size alone (Kullberg and Lind 2002; Soard 2008).

Playback experiments

To determine if encoded information was accurately characterized, playback experiments were conducted from 12 December 2008 to 26 February 2009 at the same 8 locations in Madison County, Kentucky, where presentation trials had been conducted previously. All experiments were conducted during the period from 09:00 to 14:00 h. Beginning on 20 November 2008, feeding stations were stocked with black oil sunflower seeds to attract tufted titmice. Playback tapes were made using high-quality calls of titmice recorded from each location during the previous field season, responding to an eastern screech-owl, a high-threat predator, and to a red-tailed hawk, a low-threat predator. Because the calling rate and length of

alarm calls varied in response to the 2 different predators, we standardized the total duration of playback (1 min) instead of the total number of D-notes. Playback tapes of calls given by titmice in response to the eastern screech-owl (high threat, $N = 8$) contained an average of 44 ± 4.8 (SD) and 183 ± 17.6 D-notes, and tapes of calls given in response to the red-tailed hawk (low threat, $N = 8$) contained an average of 29 ± 5.9 calls and 57 ± 23.6 D-notes. Mobbing calls of American robins (*Turdus migratorius*) ($N = 4$) were used as controls. American robins also utter alarm calls in response to raptors (Shedd 1982) but do not typically associate with parids. High-quality calls recorded in response to predators from the previous winter (5 January to 27 February 2008) were played back to flocks at the same location during the next winter (12 December 2008 to 26 January 2009) at consistent amplitudes that approximated the natural volume of titmice alarm calling.

All playback experiments ($N = 24$; a high threat, low threat, and control at each feeding station) were conducted by J.R.C., and each experiment began when titmice were detected within 25 m of a feeder. Each experiment began with a 5-min acclimation period and was followed immediately by a 60-s playback period. Tapes were played with a cassette recorder (Sony TCM-400DV, Sony), and the speaker (SME-AFS portable speaker; Saul Mineroff Electronics, Elmont, NY) was hidden in vegetation 5 m from the feeder, and its location was moved for each trial. To prevent possible differences in response due to habituation, trials at particular feeders were conducted at least 2 days apart, and the order of presentation (high-threat, low-threat, and American robin calls) was randomized. During each trial, the observer remained 5 m from the playback speaker and recorded 1) the number of titmice present; 2) the closest distance any titmouse approached the speaker; 3) the percentage of birds in the flock that came within 3 m of the speaker; 4) the percentage of birds in the flock that came within 1 m of the speaker; and 5) the time from the start of the playback trial to when flock members returned to normal behavior, that, at least one titmouse landing on the feeder and selecting a seed. During all trials, all “chick-a-dee” calls uttered by focal titmice were recorded.

RESULTS

The mean number of titmice present during presentation trials ($N = 56$) was 2.42 ± 0.79 (SD) birds (range = 1–5), and flocks often included other species, including Carolina chickadees, white-breasted nuthatches (*Sitta carolinensis*), and downy woodpeckers (*Picoides pubescens*). Study skins of raptors elicited longer bouts of mobbing behavior ($F_{6,42} = 9.4$, $P < 0.0001$) than controls during the 6-min trial period, and mobbing bouts were generally longer for smaller raptors (Figure 3). There was no difference in distance of closest approach by titmice to study skins and controls ($F_{6,42} = 1.3$, $P = 0.29$).

Acoustic analyses

Overall, we found that the mean number of notes in alarm (chick-a-dee) calls uttered by tufted titmice in response to the study skins of predators was 4.1, including an average of 0.58 Z-notes, 0.59 A-notes, and 2.91 D-notes. The mean number of D-notes uttered per titmouse during the first 2 min differed among predator treatments ($F_{6,42} = 10.1$, $P < 0.0001$), with significantly more D-notes uttered in response to the eastern screech-owl, Cooper’s hawk, and sharp-shinned hawk. Multiple titmice were typically calling simultaneously, especially in response to these 3 species of raptors; as a result, values reported for these raptors likely underestimate actual

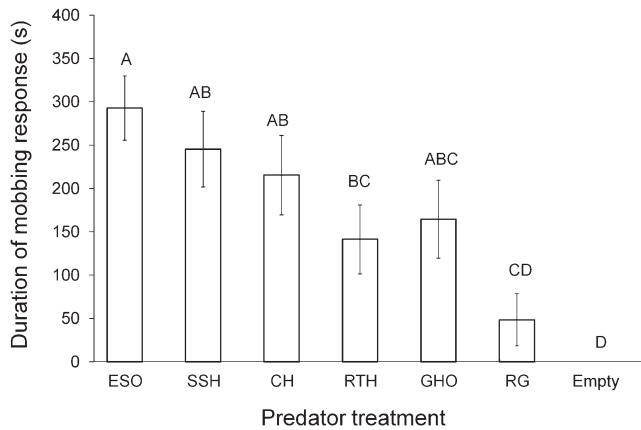


Figure 3 Mean duration (\pm standard error) of mobbing responses (in seconds) of tufted titmice responding to raptors and controls during 6-min presentation periods. Inset letters over bars show multiple comparisons from the Student–Newman–Keuls post hoc test ($\alpha = 0.05$), with different letters indicating significant differences. Raptors are listed in order of increasing body length from left to right and controls are listed on the far right. ESO = eastern screech-owl, SSH = sharp-shinned hawk, CH = Cooper’s hawk, RTH = red-tailed hawk, GHO = great horned owl, RG = ruffed grouse, and empty = empty platform.

values. Overall, we found an inverse relationship between total number of D-notes in the first 2 min of mobbing and predator body length ($r^2 = 0.81$, $P < 0.0001$), with smaller raptors eliciting more D-notes (Figure 4).

The mean number of notes in titmice alarm calls also varied among predator treatments ($F_{5,30} = 3.0$, $P < 0.025$), with more notes per call during trials with eastern screech-owls and sharp-shinned hawks. No differences, however, were found among predator treatments in the number of different note types per call, including Z-notes ($F_{5,30} = 1.21$, $P = 0.33$), A-notes ($F_{5,30} = 0.72$, $P = 0.61$), and D-notes ($F_{5,30} = 0.93$, $P = 0.47$). In general, the mean number of each note type uttered per call tended to be higher (although not significantly higher) when titmice were responding to smaller raptors, and the additive effect (i.e., more notes of each note type) explains why smaller raptors elicited calls with a significantly greater number of total notes. The mean duration of

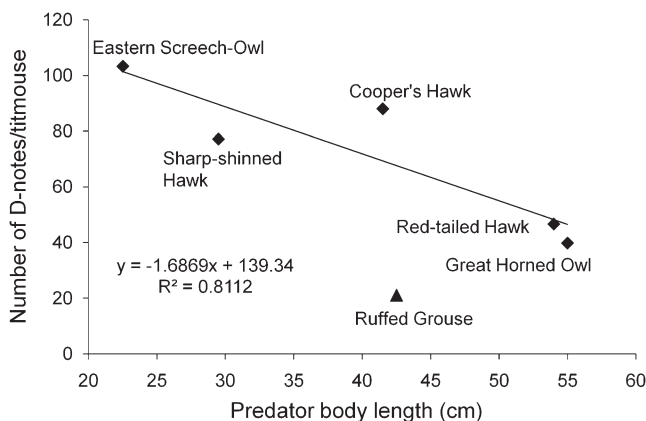


Figure 4 When presented with raptors of varying size, the number of total D-notes uttered per titmouse in the first 2 min of the trial period decreased with increasing body length of raptors. A control treatment, the ruffed grouse (Δ), is also included but omitted from the R^2 calculation.

Z-notes ($F_{1,7} = 0.02$, $P = 0.89$), A-notes ($F_{1,7} = 0.12$, $P = 0.74$), D1-notes (D1 = first D-note; $F_{1,7} = 2.8$, $P = 0.14$), D2-notes ($F_{1,7} = 0.7$, $P = 0.45$), and D3-notes ($F_{1,7} = 0.02$, $P = 0.89$) did not differ between calls given in response to high-threat (eastern screech-owl, sharp-shinned hawk, and Cooper’s hawk) and those given in response to low-threat predators (great horned owl and red-tailed hawk). In addition, we found no differences in the mean interval between D1- and D2-notes ($F_{1,7} = 0.14$, $P = 0.72$) or D2- and D3-notes ($F_{1,7} = 0.7$, $P = 0.44$).

Playback experiments

Tufted titmice took longer ($F_{2,14} = 25.4$, $P < 0.0001$) to return to normal feeding behavior during playback experiments when calls previously uttered in response to a high-threat predator (eastern screech-owl) were played back than during experiments where calls previously uttered in response to a low-threat predator (red-tailed hawk) were played back (Figure 5). The percentage of titmice in flocks that approached within 3 m of the speaker differed among trials ($F_{2,14} = 6.5$, $P = 0.01$), but the difference was between treatments and the control rather than between responses to playback of high-threat calls and low-threat calls (SNK; $P > 0.05$). We found no differences among experimental treatments in the percentage of titmice in flocks that approached to within 1 m of the speaker ($F_{2,14} = 0.5$, $P = 0.61$), the number of calls uttered ($F_{2,14} = 2.7$, $P = 0.10$), or the total number of D-notes uttered ($F_{2,14} = 2.5$, $P = 0.11$).

DISCUSSION

Tufted titmice in our study exhibited greater antipredator responses to predator treatments than to controls, with longer bouts of mobbing and more D-notes uttered during the first 2 min of predator trials. These results indicate that titmice distinguish between predatory and nonpredatory species (i.e., ruffed grouse). More importantly, titmice in our study appeared to correctly assess the degree of threat posed by different predators and conveyed this information in their alarm calls. For small birds, predator’s threat level likely corresponds to predator body size, with smaller more maneuverable raptors presenting more of a threat than larger raptors (Roth and Lima 2007; Dial et al. 2008). In response to smaller raptors (eastern screech-owl, sharp-shinned hawk, and Cooper’s

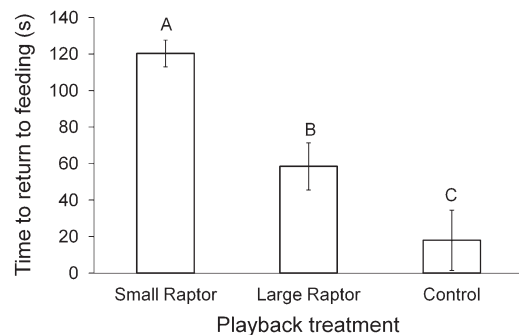


Figure 5 Bar graph showing the mean time (\pm standard error) before tufted titmice returned to normal feeding behavior after playback of “chick-a-dee” calls previously given to a small raptor (eastern screech-owl), a large raptor (red-tailed hawk), and a control (American robin mobbing calls). Inset letters over bars show multiple comparisons from the Student–Newman–Keuls post hoc test ($\alpha = 0.05$), with different letters indicating significant differences.

hawk), titmice in our study uttered more D-notes during the initial 2 min of mobbing and also uttered calls with more notes. Similarly, Sieving et al. (2010) found that captive titmice responding to a stuffed sharp-shinned hawk and a live eastern screech-owl uttered “chick-a-dee” calls with more D-notes than when responding to a live red rat snake (*Elaphe guttata*). However, based on the assumption that D-note production is a direct measure of perceived threat (Sieving et al. 2010), these authors also found that the captive titmice, in apparent contrast to our results, perceived the sharp-shinned hawk as greater threat than the screech-owl. A likely explanation for this is that, during their experiments, Sieving et al. (2010) placed caged titmice and predators just 0.75 m apart. At that short distance, during the day, a fast-flying maneuverable diurnal predator like a sharp-shinned hawk would likely represent a greater threat to a titmouse than a nocturnal predator like a screech-owl.

We also found that the duration of mobbing bouts was generally longer when titmice were responding to smaller raptors. Longer and more intense mobbing bouts are likely adaptive and may cause a predator to evacuate the area (Pettifor 1990), alert the predator that it has been spotted and is no longer a threat (Haftorn 1999), warn kin of danger (Bergstrom and Lachmann 2001), and facilitate cooperation with conspecifics (Hurd 1996).

Our results suggest that tufted titmice perceive eastern screech-owls as a highly threatening predator. Small nocturnal predators, like screech-owls, may prey on titmice (Allen 1924; Ritchison and Cavanagh 1992) when they are roosting or sleeping and most vulnerable. High-intensity mobbing in response to small owls has also been reported for Carolina (Soard 2008) and black-capped (Templeton et al. 2005) chickadees. However, in contrast to Carolina and black-capped chickadees, the responses of tufted titmice to sharp-shinned and Cooper’s hawks in our study were comparable to their responses with the eastern screech-owl. This suggests that tufted titmice, unlike Carolina and black-capped chickadees, may recognize sharp-shinned hawks, Cooper’s hawks, and eastern screech-owls as equally dangerous predators. One possible explanation for this is that their larger size (mean body mass = 21.5 g for tufted titmice vs. 10.5 g for Carolina chickadees; Dunning 1993; Pyle 1997) may make titmice more vulnerable to predation by sharp-shinned or Cooper’s hawks than chickadees. Roth (2006) noted that sharp-shinned hawks generally do not capture prey weighing less than 20 g. In addition, Cooper’s hawks generally prefer larger birds, feed at sunrise and sunset when titmice most actively forage, and employ unpredictable hunting patterns (Roth and Lima 2007, Roth et al. 2008) that may make them dangerous predators to titmice. Mobbing responses of tufted titmice to the larger great horned owl and red-tailed hawk were generally short lived and less intense than responses to smaller raptors.

We found that the mean number of notes in alarm (chick-a-dee) calls uttered by tufted titmice in response to the study skins of predators was 4.1, including 0.58 Z-notes, 0.59 A-notes, and 2.91 D-notes. By comparison, for “chick-a-dee” calls uttered by tufted titmice under natural conditions (i.e., no predator present), Owens and Freeberg (2007) found that the mean number of notes was 3.2, including 0.9 Z-notes, 0.8 A-notes, and 1.3 D-notes. Although the possible function(s) of different note types in the “chick-a-dee” calls of titmice is(are) not known, Owens and Freeberg (2007) suggested that Z- and A-notes may encode information about individual identity. If so, when responding to predators, it may be more beneficial for titmice to utter calls with more D-notes that convey information about the degree of threat and may also attract conspecifics (Hurd 1996) and cause predators to flee (Pettifor 1990) than to utter calls with more

Z- and A-notes that may convey information about individual identity.

The mean duration of notes in titmice alarm calls did not vary with predator threat level in our study. In contrast, black-capped chickadees increase the duration of the ‘dee’ section (i.e., all D-notes) of their “chick-a-dee” call, shorten the duration of the first D-note, and shorten the intervals between the first and second D-notes of their alarm calls in response to high-threat predators (Templeton et al. 2005). Carolina chickadees also shorten the duration of the first D-note of alarm calls given in response to smaller raptors, particularly the eastern screech-owl (Soard 2008). Physiological constraints may prevent titmice from producing the number and types of calls that closely related chickadees produce and make titmice less able to manipulate elements of their alarm calls to encode fine-tuned predator information (Owens and Freeberg 2007). As noted previously, it is also possible that, in contrast to chickadees, several predators, including eastern screech-owls, sharp-shinned hawks, and Cooper’s hawks, are high-threat predators for larger titmice, and as a result, differences in call elements that convey information about degree of predator threat are less pronounced for titmice than chickadees.

The number of individual note types (Z-, A-, and D-notes) per titmice alarm call did not vary among predator treatments in our study. For black-capped chickadees, the number of introductory notes (A-, B-, and C-notes) was found to be negatively correlated with predator body size (Templeton et al. 2005), and for Carolina chickadees, a weak positive relationship between the number of introductory notes and predator body size was reported (Soard 2008). For both black-capped and Carolina chickadees, strong positive relationships have been reported between the number of D-notes and predator threat level, with smaller raptors eliciting calls with a great number of D-notes. For tufted titmice, we found great variability in the number of D-notes per call among predator treatments and no relationship between the number of D-notes per call and predator body size. Although it is possible that we incorrectly defined what titmice perceive as a unique call, it seems more likely that titmice perceive and communicate predator information based on the total number of D-notes uttered per unit time (including many “broken-dee” notes) rather than the number of D-notes per call, as reported for black-capped and Carolina chickadees (Templeton et al. 2005; Soard 2008).

In mixed-flock contexts, a combination of different alarming calling techniques may enhance mobbing effectiveness of a group (Goodale and Kotagama 2005, 2008). Chickadee alarm calls, containing D-notes that range from 2 to 4 kHz in frequency and vary in number with respect to predator threat, appear well suited to attract conspecifics and heterospecific flockmates whose auditory sensitivities are typically greatest from 2 to 3 kHz (Henry and Lucas 2008). Although titmice alarm calls also convey information about predators and attract flockmates, D-notes in titmice alarm calls also extend over a wider range of frequencies (1–8 kHz; Owens and Freeberg 2007) that may easily be received by a variety of predators, ranging from small hawks that hear best at low frequencies (1–4 kHz) to larger owls that hear best at high frequencies (7–8 kHz; Krama et al. 2008). Broadband D-notes of titmice alarm calls, with unpredictable breaks between successive notes (i.e., “broken-dees”), may be better suited to confuse and frustrate predators. The unpredictable presentation of these notes in “broken-dee” calls might make it difficult for a predator to identify individual titmouse alarm calls and cause a predator to overestimate the number of titmice calling, thereby increasing the likelihood that a predator would leave an area (Bildstein 1982; Pavey and Smyth 1998).

Titmice in our study took longer to return to normal feeding behavior after the playback of alarm calls previously uttered in response to the presence of a high-threat predator (eastern screech-owl), indicating that information about threat level had been conveyed by the alarm calls. However, in response to playback of alarm calls previously given in response to a high-threat and low-threat predator, titmice in our study, in contrast black-capped (Templeton et al. 2005) and Carolina (Soard 2008) chickadees, exhibited no differences in either approach distance or the number of calls uttered. If they are at greater risk of predation than the smaller chickadees because of their larger size, titmice may be less willing to approach a playback speaker or call when they lack visual cues of predation. For example, Lind et al. (2005) reported that captive great tits (mean body mass = 19.0 vs. 21.5 g of tufted titmouse; Lange and Leimar 2004) that only heard alarm calls remained still, whereas those that saw a perched predator uttered loud mobbing calls.

Like black-capped and Carolina chickadees, tufted titmice encode information in their “chick-a-dee” alarm calls that is both functionally referential and contains information about the level of threat posed by a potential predator. Titmice, however, may be less flexible in manipulating the duration of the various elements of their alarm calls and appear to communicate and perceive information in alarm calls differently than closely related chickadee species. In conveying information about the degree of threat posed by a perched raptor, tufted titmice appear to vary the total number of D-notes uttered per unit time rather than varying other characteristics of their alarm calls. Additional study is needed to determine if this difference between chickadees and titmice translates into a difference in how each species conveys information to heterospecifics and conspecifics in predator defense contexts.

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