Asymmetries in Mobbing Behavior Among Nuclear Flockmates

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ABSTRACT.—Tufted Titmice (Baeolophus bicolor) and Carolina Chickadees (Poecile carolinensis) often occur together in mixed species flocks during the non-breeding season and, as nuclear species, often initiate mobbing bouts. We compared the mobbing behavior of Tufted Titmice and Carolina Chickadees and, specifically, their tendency to approach five potential predators. We exposed flocks of chickadees and titmice to study skins of five species of raptors in 2008; raptors were categorized as either low-threat (rarely preying on chickadees or titmice) or high-threat (more likely to prey on chickadees or titmice). We noted the distance of closest approach by titmice and chickadees during trials, and whether a chickadee or titmouse spent more time within 5 m of the raptor. Titmice were more likely to remain within 5 m of both low (P = 0.0008) and high-threat (P = 0.0015) raptors. Titmice approached low-threat raptors closer than chickadees (P = 0.014). There was no difference in the mean distance of closest approach by chickadees and titmice during high-threat trials (P = 0.34). Titmice generally approached and remained closer to raptors during mobbing bouts than chickadees, possibly because larger titmice (~21 g) are more likely targets of aerial predators than smaller chickadees (~11 g). Titmice may be willing to take greater risks because the potential benefits (reduced risk of predation) are greater if mobbing causes potential predators to leave an area. Received 30 September 2011. Accepted 14 April 2012.

Mixed-species flocks during the non-breeding season in the southeastern United States are often composed of nuclear species including Tufted Titmice (Baeolophus bicolor) and Black-capped (Poecile atricapillus) or Carolina (P. carolinensis) chickadees and attendant species (Moyrihan 1962). Nuclear species direct group movements toward food, maintain flock cohesion, and are typically the first to approach potential predators and initiate mobbing bouts (Dolby and Grubb 1999, Templeton et al. 2005, Bartmess-LeVasseur et al. 2010).

Mobbing can be beneficial, causing a predator to leave an area, but such behavior can also be costly, including the risk of being injured or killed for birds that closely approach a predator (e.g., Denson 1979, Sordahl 1990). The costs and benefits of mobbing may vary among species depending on the identity of the predator. For example, because larger predators tend to take larger prey (Vézina 1985), larger raptors may represent more of a threat to larger species in mixed-species flocks. Roth and Lima (2007) found that Cooper’s Hawks (Accipiter cooperii) generally prefer larger avian prey, while Roth et al. (2006) found that Sharp-shinned Hawks (A. striatus) typically do not target prey species weighing <20 g. Thus, the potential benefits of mobbing larger raptors may be lower for smaller species in mixed-species flocks (e.g., Carolina Chickadees: ~11 g; Mostrom et al. 2002) than for larger species (e.g., Tufted Titmice: ~21 g; Grubb and Pravasudov 1994).

Both Tufted Titmice and Carolina Chickadees utter ‘chick-a-dee’ alarm calls when mobbing perched aerial predators. Carolina Chickadees vary the number of ‘dee’ notes per call to potentially convey information to conspecifics about the threat posed by different predators (Soard and Ritchison 2009). Tufted Titmice vary the rate at which ‘dee’ notes are uttered which may convey information about predator threat; this variation in call rate may also deter predators by causing them to overestimate the number of titmice present (Courter and Ritchison 2010). Thus, the alarm calls of Tufted Titmice may differ functionally from those of chickadees, conveying information to conspecifics and ‘misinformation’ to predators. These species also differ in size and other aspects of their mobbing behavior may also differ. Our objective was to compare the mobbing behavior of Tufted Titmice and Carolina Chickadees responding to different species of raptors. We examined their spatial relationships relative to potential predators because proximity to predators, i.e., approach distances and time spent near potential predators, may be related to risk (Krams et al. 2010) or willingness to accept greater potential costs.
METHODS

Study Area.—Free-ranging flocks of Carolina Chickadees and Tufted Titmice were studied at eight locations in Madison County, Kentucky (37° 41' 58" N, 84° 16' 20" W) from 5 January to 27 February 2008. Study sites included private residences (n = 7) and a public campground (n = 1) and were separated by a minimum distance of 1.5 km. A feeding station, if not already present at a site, consisting of a 1-m² section of plywood was placed 1 m above ground at each site in December 2007. All feeding stations were regularly stocked with black-oil sunflower seeds.

Predator Presentations.—We used study skins of five raptors in our experiment that differed in potential threat they posed to parids (Templeton et al. 2005, Soard and Ritchison 2009, Courter and Ritchison 2010). Common predators of parids (Gaddis 1980, Grubb 1998, Roth and Lima 2007), including Eastern Screech-Owl (Megascops asio), Sharp-shinned Hawk, and Cooper’s Hawk were considered high-threat predators (Templeton et al. 2005). Great Horned Owls (Bubo virginianus) and Red-tailed Hawks (Buteo jamaicensis), species that rarely, if ever, prey on parids, were considered low-threat predators (Templeton et al. 2005, Nocera and Ratcliffe 2010). An empty platform (Baker and Becker 2002, Templeton et al. 2005) and a study skin of a Ruffed Grouse (Bonasa umbellus; a non-predatory bird) were used as control presentations.

Trials were conducted at each location from 5 January to 27 February 2008 during 0900 to 1400 hrs EST with at least 48 hrs between successive trials. Each trial was conducted by JRC and began by placing a randomly-selected raptor (or control) in a life-like position on a platform 1 m above ground and 1 m from a feeding station. Specimens were initially covered with a white sheet during a 5-min pre-presentation period while the observer sat 5 m away. The pre-presentation period was intended to acclimate birds to the observer’s presence and ensure chickadees and titmice would remain near a feeding station sufficiently long for an experiment to be completed. The observer then walked to the feeder, removed the sheet to expose the raptor or control, and returned to the observation site to monitor the behavior of chickadees and titmice for the 5-min trial period.

The observer noted during each trial: (1) the number of chickadees and titmice present, (2) the distance of closest approach by a titmouse and chickadee, and whether a chickadee or a titmouse (3) first approached within 5 m of the raptor or control, and (4) spent more time within 5 m of the predator. Mean approach distances were estimated (± 0.5 m) using the width of the predator platform (1 m), distance of platform to feeding station (1 m), and the distance between the observer and the feeding station as references.

Statistical Analyses.—We calculated a mean distance of closest approach for chickadees and titmice in each of the eight flocks during the two control trials, the two low-threat predator trials, and the three high-threat predator trials. We ascertained the percentage of control, low-threat, and high-threat trials where titmice and chickadees in each flock were first to approach within 5 m and remained within 5 m of controls or predators the longest. We compared the mean distance of closest approach by chickadees and titmice, and the percentage of trials where each species was first to approach and remain within 5 m of controls and predators using Wilcoxon tests for paired samples. All tests were two-tailed. We used Kruskal-Wallis tests to examine possible differences in flock size during control, low-threat, and high-threat predator trials. We used the Statistical Analysis System for all analyses (SAS Institute 2004). Values are presented as means ± SE.

RESULTS

The mean ± SE number of chickadees present during trials was 3.2 ± 0.2 (range = 1–6) and the mean number of titmice present was 2.6 ± 0.1 (range = 1–5). Mean numbers of chickadees (Kruskal-Wallis \( \chi^2 = 0.1, P = 0.93 \)) and titmice (Kruskal-Wallis \( \chi^2 = 0.5, P = 0.80 \)) present during control, low-threat, and high-threat trials did not differ. Chickadees and titmice were equally likely to be first to approach within 5 m of controls or predators in response to control (\( Z = 1.4, P = 0.08 \)), low-threat (\( Z = 0.2, P = 0.41 \)), and high-threat (\( Z = 0.1, P = 0.50 \)) treatments. Titmice and chickadees did not differ in tendency to remain within 5 m of controls (\( Z = 0.1, P = 0.50 \)). However, titmice were more likely to remain within 5 m during trials with both low-threat (\( Z = 3.2, P = 0.0008 \)) and high-threat (\( Z = 3.0, P = 0.0015 \)) predators. Titmice in the eight flocks tested spent more time within 5 m than chickadees during an average of 81.2 ± 9.0% of all trials with low-threat predators and 79.4 ± 9.1% of high-threat trials.
We found no difference in the mean distance of closest approach by chickadees and titmice during either control ($Z = 0.1, P = 0.50$) or high-threat trials ($Z = 0.4, P = 0.34$). However, titmice approached predators closer than chickadees during low-threat trials ($Z = 2.2, P = 0.014$). The mean distance of closest approach during low-threat trials was $1.4 \pm 0.3$ m for titmice and $3.2 \pm 0.6$ m for chickadees, whereas the mean closest approach distance during high-threat trials was $1.7 \pm 0.2$ m for titmice and $2.4 \pm 0.5$ m for chickadees.

**DISCUSSION**

Titmice in our study generally approached and remained closer to predators than chickadees. One possible explanation is that larger titmice are dominant to smaller chickadees (Waite and Grubb 1988) and, as a result, chickadees may remain some distance from titmice to avoid possible aggression. Another possible explanation, however, is that larger titmice are more likely targets of aerial predators than smaller chickadees and, if so, titmice may mob with greater intensity because those predators represent a greater threat to titmice than chickadees. Gehlbach (1994), in support of this hypothesis, examined the behavior of 17 species of songbirds that mobbed Eastern Screech-Owls in Texas and found a significant positive correlation between how often a species mobbed screech-owls and how often screech-owls preyed upon those species. Previous studies have revealed that Cooper’s Hawks, for example, generally prefer larger avian prey (Roth and Lima 2007), and Sharp-shinned Hawks typically do not target prey species weighing <20 g (Roth et al. 2006). Larger titmice may also be less maneuverable than smaller chickadees (Dial et al. 2008), possibly increasing their vulnerability to aerial predators and providing additional incentive for titmice to aggressively mob predators (Cresswell 1994a, b; Flasckamp 1994; Courter and Ritchison 2010). Nocedal and Ficken (1998) reported that Bridled Titmice (*Baeolophus wollweberi*) in similar mixed-flock contexts in the American southwest aggressively mobbed Northern Pygmy-Owls (*Glaucidium gnoma*), sometimes approaching the owls as close as 30 cm. Intense bouts of mobbing behavior that include close approaches to predators are adaptive strategies that deter predators (Pettifor 1990) and cause raptors to change their roost locations (move-on hypothesis; Sunde et al. 2003, Hendrichsen et al. 2006).

Titmice generally approached closer to predators and remained closer for longer periods than chickadees, but the difference in approach distance by these two species with high-threat predators was not significant. Small raptors such as Sharp-shinned Hawks and Eastern Screech-Owls are unlikely to prey on birds as small as chickadees, but they almost certainly represent a greater potential threat to chickadees than large raptors including Red-tailed Hawks and Great Horned Owls. Thus, for chickadees, the benefit of more vigorous mobbing behavior (i.e., small raptors leaving an area in response to vigorous mobbing) may outweigh the potential costs (i.e., risk of predation by closely approaching a potential predator).

Nolen and Lucas (2009) examined the mobbing behavior of Tufted Titmice, Carolina Chickadees, and White-breasted Nuthatches (*Sitta carolinensis*) and found that chickadees and nuthatches mobbed an Eastern Screech-Owl model with greater frequency and intensity, and typically approached the model closer than titmice. We examined the combined responses of chickadee and titmice to three high-threat predators; titmice in our study exhibited a stronger response to Eastern Screech-Owl, spending more time within 5 m than chickadees during seven of eight trials and, on average, approaching closer (mean approach distances $= 0.7$ m for titmice and $1.6$ m for chickadees). One possible explanation for this apparent difference in responses of titmice and chickadees is that we used study skins to elicit mobbing behavior, whereas Nolen and Lucas (2009) presented a model combined with playback of the screech-owl monotonic trill. Nolen and Lucas (2009) and others (Lind et al. 2005) noted a predator’s behavior may influence mobbing behavior. A calling screech-owl likely represents less of a threat than a silent owl that may be actively hunting and titmice may respond less aggressively to the former than the latter.

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