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ORIGINAL ARTICLE

Predator-risk-sensitive foraging behavior of Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) in response to the head orientation of snake predator models

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Abstract The risk of predation varies with behavioral cues and body characteristics of potential predators. One such body characteristic is the head/face orientation of the predator. However, a prey individual's ability to detect the head may be more difficult when the predator's body is serpentine, with little distinguishing the head from the tail. Here, we tested whether individuals in mixed-species flocks of Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) distinguish the head orientation of predator snake models. We conducted behavioral observations at multiple sites each having a bird feeder stocked with seed. Each chickadee and titmouse flock was exposed to two counterbalanced trials: a snake model with head closest to the seed area of the feeder and with tail closest to the seed area of the feeder. Observers recorded the number of seeds taken by each species and also the number of unsuccessful feeder visits. Chickadees and, to a lesser extent, titmice took fewer seeds and had more unsuccessful feeder visits when the head of the snake model was closest to the seed, compared to when the tail was closest to the seed. Titmice, furthermore, had more unsuccessful feeder visits to the black snake model type representing a real snake nest predator for these small songbirds. Therefore, head orientation seems an important factor that some species use to assess predation risk, even for predatory species where head orientation may be a subtle cue.

Keywords Anti-predatory behavior · *Baeolophus* · Chickadees · *Poecile* · Predator-risk-sensitive foraging · Snake predators · Titmice

Introduction

Predation pressure is one of the leading factors influencing prey behavior (Caro 2005). Animals must frequently assess their surroundings for danger and respond appropriately to the perceived risk and so are frequently on alert and vigilant (Bednekoff and Lima 1998). However, this increased vigilance comes at the cost of lost time that could be spent foraging (Lima and Dill 1990). Consequently, animals have evolved various ways of efficiently distinguishing variation in predation risk, such as by discriminating threatening cues from non-threatening cues (Kavaliers and Choleris 2001). Perceived risk may depend on physical or behavioral cues of the predator (Helfman 1989). Responses to noticeable threatening cues, such as looming predators, directness of approach, speed of movement, or fleeing conspecifics, are well documented (Stankowich and Blumstein 2005; Griesser 2008).

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Significance statement Prey species should pay attention not only to the presence of a predator in the environment, but also to the predator's behavior. One predator behavioral cue to which prey individuals pay attention is the predator's head and body orientation. However, this behavioral cue may be difficult to assess if the predator is a snake. Here, we demonstrate experimentally that Carolina chickadees and, to a lesser extent, tufted titmice, forage less from a feeder if the head of a snake model is closer to the feeder than if the tail of a snake model is closer to the feeder. Along with other studies, this work suggests that small songbirds are highly sensitive to the head orientation of potential predators, even in serpentine species where the head location may be difficult to perceive.

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It is clear that head/face orientation of predators influences predator risk assessment by prey individuals in many species (Karplus and Algom 1981; Leopold and Rhodes 1983; Clucas et al. 2013). For example, a predator approaching with its head and gaze averted is often perceived as less threatening than one staring directly at the focal animal (Burger et al. 1991, 1992). In recent studies of tufted titmice (*Baeolophus bicolor*; one of the focal species of our current study), researchers found that birds reduced foraging when a mask-wearing human (Freeberg et al. 2014) or a cat model (Book and Freeberg 2015) faced toward a feeder that the birds were using, compared to when the potential predator was facing away from the feeder. However, little is known about birds' ability to discriminate body orientation in snake predators that have no legs and that exhibit fairly similar body morphology from head to tail.

In some areas, bird and nest predation by snakes is a common occurrence, which reduces survivorship of hatchlings and fledgling birds (Weatherhead and Blouin-Demers 2004). Recent evidence suggests that some birds from the Paridae family (the chickadees, tits, and titmice) perceive snakes as a threat. In Japanese tits, *Parus minor*, individuals produce snake-specific mobbing calls when they perceive a predatory snake in their environment, and receivers respond to these snake-specific mobbing calls by gazing at the ground (Suzuki 2012). Tufted titmice vary the note composition of their *chick-a-dee* calls when they detect snake models as opposed to avian and cat predator models (Sieving et al. 2010). Because snake predators typically face their prey when stalking or attacking them, the head orientation of a snake relative to the prey should be a significant predatory cue and cause the prey to be more vigilant. It would therefore seem beneficial for birds to recognize when a snake predator is facing toward them rather than away (see also Etting and Isbell 2014).

We tested whether the foraging behavior of Carolina chickadees, *Poecile carolinensis*, and tufted titmice is sensitive to the presence of snake models and the orientation of those models (snake head or tail closest to a source of highly preferred food). We expected that chickadees and titmice would reduce foraging in response to the head orientation of a snake predator compared to the tail orientation of a snake predator, based upon earlier work with titmouse responses to human and cat models (Freeberg et al. 2014; Book and Freeberg 2015).

Methods

We conducted behavioral experiments with 24 flocks at four locations in eastern Tennessee (Knox and Anderson Counties). One location was a single residential site, and the other three locations had multiple sites. All sites had a stocked bird feeder (112 cm × 28 cm wooden boards mounted on top of a 1.5-m steel pole). On one end of the bird feeder was a small framed section (28.5 cm × 16 cm) that created a seed area for the birds. On the other end of the bird feeder, we would place the snake models, with a line on the feeder to position the closest part of the snake model body 60 cm from the closest section of the seed area (Fig. 1a; after Book and Freeberg 2015). The three locations with multiple sites included ten sites at the University of Tennessee Forest Resources, Research, and Education Center (36.11° N, 84.20° W), four sites at Ijams Nature Center (36.96° N, 83.93° W), and nine sites at Norris Dam State Park (36.41° N, 84.15° W). Within each location, each of the individual sites was at least 400 m from the other sites and therefore represented independent flocks, given the territoriality of these overwintering flocks (Bartmess-LeVasseur et al. 2010). Observations were conducted between 0800 and 1400 h from 6 October 2014 to 18 December 2014.

We used eight replicates each of three different snake model types (Fig. 1b). All 24 snake models were realistic and identical in size and shape (relaxed serpentine length ~45.7 cm, stretched length ~114.3 cm, body circumference at the widest girth ~6 cm). Two of the three model types resembled snakes whose geographic ranges overlap the locations of the study sites and snakes that we have observed active in the field in Knox County as late as early November. The black snake model resembled Northern black racers (*Coluber constrictor constrictor*), Eastern black kingsnakes (*Lampropeltis nigra*), and gray rat snakes (*Pantherophis spiloides*), which are all native to our study sites (Burbrink 2001; Scott and Redmond 2008; Faust and Blomquist 2011) and prey on young birds and bird eggs, including Carolina chickadees (Mostrom et al. 2002; Niemiller et al. 2013). The green snake model resembled rough green

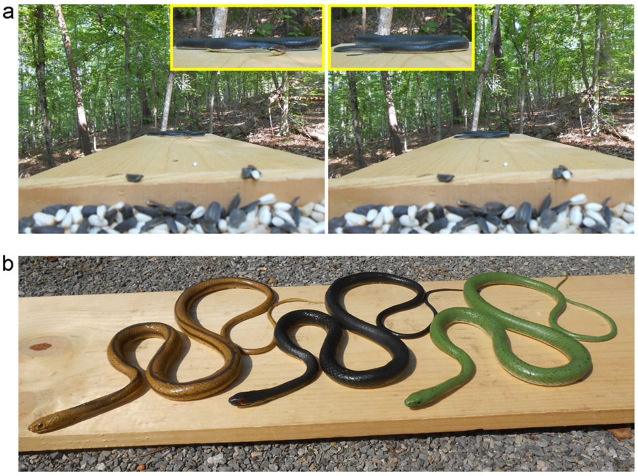

Fig. 1 Photos of snake model types used in study and feeding station manipulations. View of snake models from perspective of chickadee or titmouse in the seed area of the feeding station (**a**): black snake model with head oriented toward seed area (*left panel*) and away from seed area (*right panel*). A close-up view of the snake model on the stand is included in the *boxed portion* at the *top* of each photo in **a**. Overhead view of three snake model types on feeding station (**b**): yellow snake model (*left*), black snake model (*middle*), and green snake model (*right*)

snakes (*Opheodrys aestivus*), which are also native to the study sites but typically feed on smaller prey such as insects, spiders, and young frogs and lizards (Scott and Redmond 2008; Niemiller et al. 2013). The yellow snake model resembled yellow rat snakes (*Pantherophis alleghaniensis quadravitta*) whose geographic range does not overlap with the study area (they are found as far north as northern Florida) but is known to prey on young birds and bird eggs (Conant and Collins 1998). The yellow snake model may represent a novel snake predator to the birds observed in our study. The eight replicates within each model type varied in subtle color patterns and markings, and each was positioned in slightly different ways on the feeders, providing within-type phenotypic variation in the snake models, which, along with the use of three different snake model types, helped to minimize pseudoreplication (Kroodsma 1989).

Each of the 24 flocks experienced the same time frame for testing: a 5-min first pre-stimulus baseline period, a 5-min first stimulus orientation trial, a 30-min inter-trial interval, a 5-min second pre-stimulus baseline period, and a 5-min second stimulus orientation trial. Order of snake orientation was randomly determined across sites, resulting in 13 sites where the snake's head was closest to the seed area of the feeder in the first stimulus orientation trial and 11 sites where the snake's tail was closest to the seed area of the feeder in the first stimulus orientation trial. We used a 30-min inter-trial interval because other studies have found that 15 to 30 min is sufficient for parids (chickadees, tits, and titmice) to return to their normal behavior after exposure to a predator stimulus (Tvardíková and Fuchs 2012; Book and Freeberg 2015). Prior to pre-stimulus baseline observations, one observer walked to the feeder and back to the observation point to control for the presence of the observer when placing the snake model during the stimulus trials. At the start of each stimulus period, one observer walked up and placed the model snake predator on the board 60 cm (closest distance) from the seed area from which the birds were feeding. Immediately after model placement, both observers moved to a distance behind vegetation and at least 10 m from the feeder to reduce effects of observer presence on the birds' behavior. For all test periods, we recorded the following: (1) the total number of feeder visits when seed was taken, (2) the total number of feeder visits in which seed was not taken (unsuccessful feeder visits), and (3) the species of each bird involved (after Bartmess-LeVasseur et al. 2010; Freeberg et al. 2014; Book and Freeberg 2015). Unsuccessful feeder visits suggest extreme instances of approach-avoidance conflict, in which a bird landed on the feeder and then, typically, immediately flew away again without taking a seed (Freeberg et al. 2014). Trials were recorded with a Sony digital video camera (Sony Electronics Inc., San Diego, CA, USA; model no. HDR-XR160). We did not record or code the data blind but did have high inter-observer agreement when different authors independently coded the data for 16 (roughly 16 %) of the 5-min video files (Kaufman and Rosenthal 2009). Inter-observer reliability scores were calculated using Spearman's rho and ranged from $\rho = 0.933$ ($N = 16$, $p < 0.001$) for titmouse unsuccessful feeder visits to $\rho = 0.996$ ($N = 16$, $p < 0.001$) for chickadee seed-taking rates.

For each species separately, we analyzed relative rates of seed-taking and relative rates of unsuccessful feeder visits. Relative rates of these behavior patterns were obtained by subtracting the rates of the behavior in the 5-min pre-stimulus baseline period from the 5-min stimulus orientation period. Thus, relative rates of behavior below zero would represent instances of the stimulus inhibiting the behavior, and relative rates of behavior above zero would represent instances of the stimulus increasing the behavior. Relative seed-taking rates were only weakly correlated with relative rates of unsuccessful feeder visits and so were analyzed independently (chickadees: $N = 48$ trials at 24 sites, Spearman correlation $= -0.336$, $p = 0.019$); titmice: $N = 46$ trials at 23 sites, Spearman correlation $= +0.069$, $p = 0.648$). Relative rates of behavior data were analyzed using mixed model analysis of variance in SPSS (IBM SPSS Statistics Version 20.0; Armonk, New York). All tests were two-tailed. Normality of residuals was confirmed with Kolmogorov-Smirnov tests. Stimulus orientation (snake head closest, snake tail closest; within-site factor) and snake type (black, yellow, green; between-site factor) were fixed effects, and site was a random effect in the models. We included each fixed effect and the stimulus orientation × snake type interaction term in the models. When significant effects of snake type were observed, we assessed possible pairwise differences with additional ANOVAs, using an adjusted alpha level of 0.017 to correct for three different pairwise comparisons.

Results

Chickadees Chickadee flocks were observed at all 24 sites. Chickadees took fewer seeds from the feeding stations when the snake models were presented compared to the pre-stimulus baseline periods (95 % confidence intervals do not encompass 0; Fig. 2a). Furthermore, we obtained a significant main effect of stimulus orientation for relative seed-taking rates, with chickadees taking fewer seeds when the snake model was oriented toward the seed area compared to when the snake model was oriented away from the seed area ($F_{1,21} = 4.715$, $p = 0.041$; Fig. 2a). We detected no effect of snake type on relative seed-taking rates ($F_{2,21} = 0.860$, $p = 0.437$; Fig. 2b) and no significant stimulus orientation × snake type interaction term ($F_{2,21} = 0.536$, $p = 0.593$). We also found a significant main effect of stimulus orientation for relative rates of unsuccessful feeder visits, with chickadees having more unsuccessful feeder visits when the snake model was oriented toward the seed area compared to when the snake model was

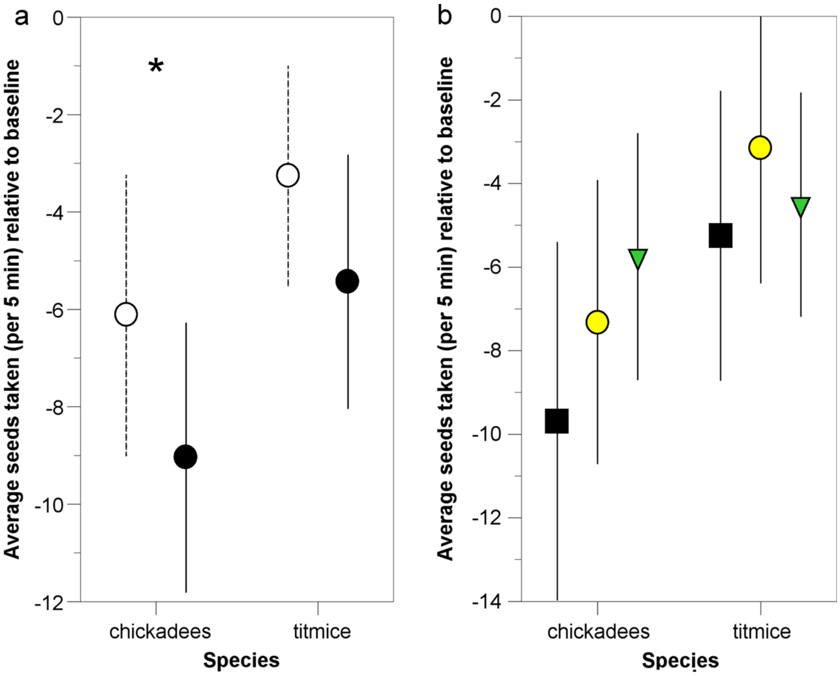

Fig. 2 Carolina chickadee and tufted titmouse average seed-taking rates relative to pre-stimulus baseline periods. **a** Seed-taking rates related to snake model orientation: snake tail closest to seed area (*open circles with dashed whiskers*) and snake head closest to seed area (*closed circles with solid whiskers*). **b** Seed-taking rates related to snake model type: black snake model (*black squares*), yellow snake model (*yellow circles*), and green snake model (*green triangles*). Data are plotted as means (*circles*) and 95 % confidence intervals (*whiskers*). Significant overall effects are indicated by *asterisk*

oriented away from the seed area ($F_{1,21} = 5.732$, $p = 0.026$; Fig. 3a). We detected no effect of snake type on relative rates of unsuccessful feeder visits ($F_{2,21} = 0.748$, $p = 0.486$; Fig. 3b) and no significant stimulus orientation × snake type interaction term ($F_{2,21} = 0.620$, $p = 0.547$).

Titmice Titmouse flocks were observed at 23 of the 24 sites. Like chickadees, titmice took fewer seeds from the feeding stations when the snake models were presented compared to the pre-stimulus baseline periods (95 % confidence intervals do not encompass 0; Fig. 2a). However, for relative seed-taking rates, we detected no main effect of stimulus orientation ($F_{1,20} = 2.956$, $p = 0.101$; Fig. 2a). We also detected no effect of snake type ($F_{2,20} = 0.363$, $p = 0.700$; Fig. 2b) and no significant stimulus orientation × snake type interaction term ($F_{2,20} = 0.907$, $p = 0.420$), for relative seed-taking rates. For relative rates of unsuccessful feeder visits, we detected no main effect of stimulus orientation (though there was a trend for

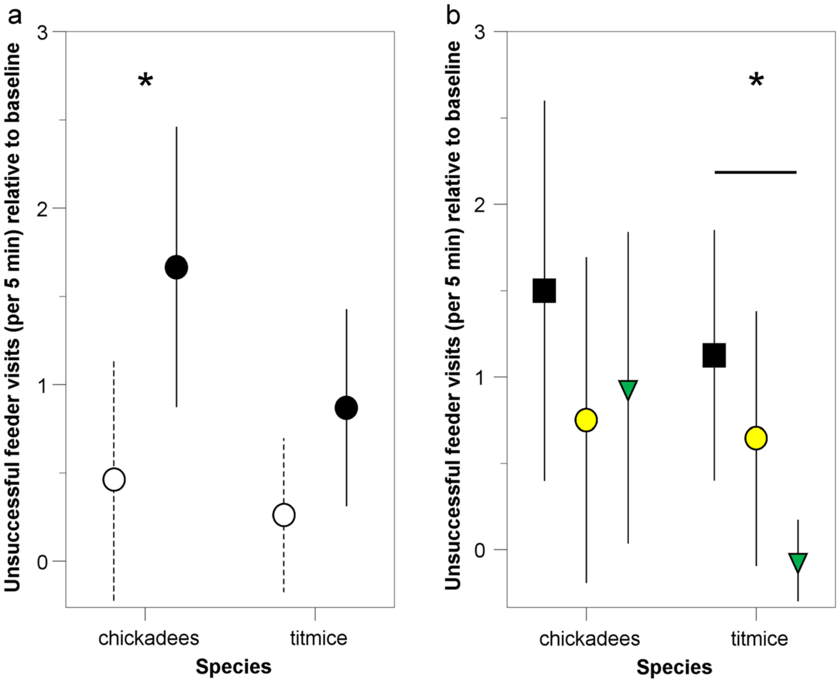

Fig. 3 Carolina chickadee and tufted titmouse average unsuccessful feeder visits relative to pre-stimulus baseline periods. Data plotted as in Fig. 2. Significant overall effects are indicated by *asterisks*, and significantly different pairwise differences related to snake model type are indicated by the *horizontal line*

more unsuccessful feeder visits when the snake model's head was oriented toward the seed area: $F_{1,20} = 3.306$, $p = 0.084$; Fig. 3a) but did detect a significant effect of snake type ($F_{2,20} = 5.729$, $p = 0.011$; Fig. 3b). Titmice had more unsuccessful feeder visits to the black snake model than they did to the green snake model ($F_{1,14} = 21.974$, $p < 0.001$) and tended to have more unsuccessful feeder visits to the yellow snake model than they did to the green snake model ($F_{1,13} = 3.413$, $p = 0.088$); relative rates did not differ between the black snake model and the yellow snake model ($F_{1,13} = 1.222$, $p = 0.289$). Finally, we did not detect a significant stimulus orientation × snake type interaction term ($F_{2,20} = 1.076$, $p = 0.360$).

Discussion

The chickadees and titmice in our study decreased the number of seeds that they took in response to the snake models. Our results suggest that the birds recognized the snakes as predators and distanced themselves from the threat by avoiding the feeder (Weatherhead and Blouin-Demers 2004; Devereux et al. 2006; Tvardíková and Fuchs 2012). Additionally, when the snake models were on the feeders, chickadees, but not titmice, took fewer seeds when the head of the snake model was closer to the seed area than when the tail of the model was closer to the seed area. This indicates that chickadees recognized differences in the model predator's body orientation and responded by changing their foraging behavior. Abrahams and Dill (1989) found that animals are more likely to forage in areas where they are in less danger. By taking fewer seeds when the heads of the snake models were closest to a highly preferred food source, chickadees decreased the amount of energy that they could obtain but would perhaps decrease the likelihood of being preyed upon.

The birds in our study responded in a manner consistent with the threat sensitivity hypothesis (Helfman 1989). In the absence of risk, chickadees and titmice rarely visit our feeders without taking a seed. Pre-stimulus baseline rates of unsuccessful feeder visits are typically on the order of <1 unsuccessful visit per 10-min period (Todd Freeberg unpublished data). However, as risk increases, the birds are more likely to visit the feeder and leave almost immediately without taking seed (i.e., an unsuccessful feeder visit). Risk increased when the snake model stimulus was placed on the feeder and even more so if that snake model stimulus was oriented with its head closer to the seed area. Thus, taking our two dependent measures together, chickadees and titmice were able to distinguish the difference between the head and the tail of a predator even when it is missing limbs or other characteristics that could make it easier to determine body orientation. The responses of these birds to snake models and head orientation of snake models were additionally interesting in that during the time of year that we conducted the study, snakes are not important predators of these birds (and toward the second half of our data collection period—November and December—snakes would not have been in the birds' environments at all). Snakes are thus recognized as potential threats by these small birds even during seasons of the year in which these predators do not naturally occur as a real threat.

Titmice had the most unsuccessful feeder visits to the snake model type representing the one real nest predator (for small songbirds in eastern Tennessee) of the three models that we tested, compared to the other two snake model types that we used. Although Northern black racers and gray rat snakes are likely not serious nest predators of tufted titmice (Ritchison et al. 2015), they are important nest predators of Carolina chickadees (Mostrom et al. 2002). It is curious that we obtained such an effect with titmice but not with chickadees. Perhaps, chickadees perceive any snake of this size as a potential threat, regardless of how "natural" or novel the snake might be (akin to the "better safe than sorry" hypothesis of Haftorn 2000).

We detected strong effects of snake model head orientation on chickadee behavior and possibly parallel, but weaker, effects on titmouse behavior. Further tests are needed to determine the relative sensitivities of chickadees and titmice to snake predators, but we suspect that the relative size differences of the two species might have contributed to our results. Chickadees are roughly 10 g, and titmice are roughly 20 g in size, which is reflected in the fact that over 90 % of the interspecific supplanting behavior that we observed between these two species involves titmice supplanting chickadees from the feeders (TF unpublished data). Perhaps, this relative size difference resulted in titmice not perceiving these snake models to be as risky as chickadees did? If bird size relative to snake model size influences bird responses to snake model head orientation, we would predict titmice to show stronger sensitivity to head orientation of larger snake models, and we would predict chickadees to show weaker sensitivity to head orientation of smaller snake models. Additionally, as mentioned above, snakes like gray rat snakes are predators of chickadee eggs and nestlings and seem to be much less of a threat to titmouse eggs and nestlings. Perhaps, this selective pressure has resulted in chickadees being more sensitive than titmice to the head orientation of this important class of predators. Finally, it also seems likely that the two species may simply respond to different predatory threats in different ways. For example, the calling behavior of chickadees in a western Indiana population varied considerably when owl stimuli were detected, but titmouse behavior was not observed to be so sensitive to detection of the same predator stimuli (Nolen and Lucas 2009). The visual and acoustic owl stimuli from that study represented eastern screech owls, *Megascops asio*, which are potential predators of both chickadees and titmice, so relative size differences between chickadees and titmice cannot account for the species differences observed by Nolen and Lucas (2009). More comparative work on these and related species is needed to determine predator-risk-sensitive foraging and communicative variation and how it might contribute to mixed-species flock dynamics.

What are the salient features of snakes to these birds beyond head orientation? The three model types differed only in color patterns, so clearly, titmice were sensitive to the color markings of these snake models with regard to their rates of unsuccessful feeder visits. Although our study did not test this possibility, research in other taxa suggests that individuals of prey species are particularly sensitive to predator eyes (Gallup et al. 1971; Jones 1980; Burger et al. 1991; Davidson et al. 2014). In addition, snake body posture (striking, coiled, or sinusoidal) is a salient cue to prey individuals (Etting and Isbell 2014). Other salient features of snakes used in risk assessment could include the shape of the head and movement trajectory. For example, many non-avian reptile species have been shown to be sensitive to head orientation, direction of turning, and movement of potential predatory stimuli (Cooper 1997, 2003; Cooper et al. 2010). Future studies are needed to determine the salient predator cues and proximate mechanisms involved in the predation-risk-sensitive behavior toward potential snake predators that we have documented here.

Studies suggest that long-term costs of anti-predator responses select for individuals to delay or reduce feeding only when necessary, adjusting behavior with the current level of risk (Lima 1998). When a snake model was present and facing toward the seed area that the birds were using, they were less likely to forage, likely due to the inherent risk of the minimal distance between them and the mouth of the potential predator. Birds that are able to respond appropriately to the head or tail of a predator may reduce their risk of predation more than individuals that demonstrate an unvaried response (Kleindorfer et al. 2005). Sensitivity to predator behavior should be a driving force for natural selection (Stankowich and Blumstein 2005). This may also be true with respect to predator head/face orientation: effective assessment of risk associated with a predator's head orientation may decrease the probability of mortality (Montgomerie and Weatherhead 1988; Kleindorfer et al. 2005), even for predators like snakes, in which head orientation may be a relatively subtle cue.

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Compliance with ethical standards

Ethical standards This study was conducted under approved University of Tennessee IACUC protocol no. 1248.

Conflict of interest The authors declare that they have no conflict of interest.

References

Abrahams MV, Dill LM (1989) A determination of the energetic equivalence of the risk of predation. Ecology 70:999–1007

Bartmess-LeVasseur J, Branch CL, Browning SA, Owens JL, Freeberg TM (2010) Predator stimuli and calling behavior in Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). Behav Ecol Sociobiol 64:1187–1198

Bednekoff PA, Lima SL (1998) Randomness, chaos and confusion in the study of antipredator vigilance. Trends Ecol Evol 13:284–287

Book DL, Freeberg TM (2015) Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats. Anim Cogn 18:1155–1164

Burbrink FT (2001) Systematics of the eastern ratsnake complex (*Elaphe obsoleta*). Herpetol Monogr 15:1–53

Burger J, Gochfeld M, Murray BG Jr (1991) Role of a predator's eye size in risk perception by basking black iguana, *Ctenosaura similis*. Anim Behav 42:471–476

Burger J, Gochfeld M, Murray BG Jr (1992) Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). J Comp Psychol 106:97–101

Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago

Clucas B, Marzluff J, Makovjak D, Palmquist I (2013) Do American crows pay attention to human gaze and facial expressions? Ethology 119:296–302

Conant R, Collins JT (1998) A field guide to reptiles and amphibians of Eastern and Central North America, 3rd edn. Houghton Mifflin Company, New York

Cooper WE Jr (1997) Threat factors affecting antipredatory behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. Copeia 1997:613–619

Cooper WE Jr (2003) Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. Can J Zool 81:979–984

Cooper WE Jr, Hawlena D, Pérez-Mellado V (2010) Escape and alerting responses by Balearic lizards (*Podarcis lilfordi*) to movement and turning direction by nearby predators. J Ethol 28:67–73

Davidson GL, Clayton NS, Thorton A (2014) Salient eyes deter conspecific nest intruders in wild jackdaws (*Corvus monedulan*. Biol Lett 10:20131077

Devereux CL, Whittingham MJ, Fernandez-Juricic E, Vickery JA, Krebs JR (2006) Predator detection and avoidance by starlings under differing scenarios of predation risk. Behav Ecol 17:303–309

Etting SF, Isbell LA (2014) Rhesus macaques (*Macaca mulatta*) use posture to assess level of threat from snakes. Ethology 120:1177–1184

Faust TM, Blomquist SM (2011) Size and growth in two populations of black kingsnakes, *Lampropeltis nigra*, in east Tennessee. Southeast Nat 10:409–422

Freeberg TM, Krama T, Vrublevska J, Krams I, Kullberg C (2014) Tufted titmouse (*Baeolophus bicolor*) calling and risk-sensitive foraging in the face of threat. Anim Cogn 17:1341–1352

Gallup GG Jr, Nash RF, Ellison AL Jr (1971) Tonic immobility as a reaction to predation: artificial eyes as a fear stimulus for chickens. Psychon Sci 23:79–80

Griesser M (2008) Referential calls signal predator behavior in a group-living bird species. Curr Biol 18:69–73

Haftorn S (2000) Contexts and possible functions of alarm calling in the willow tit (*Parus montanus*): the principle of "better safe than sorry". Behaviour 137:437–449

Helfman GS (1989) Threat-sensitive predator avoidance in damselfish–trumpetfish interactions. Behav Ecol Sociobiol 24:47–58

Jones RB (1980) Reactions of male domestic chicks to two-dimensional eye-like shapes. Anim Behav 28:212–218

Karplus I, Algom D (1981) Visual cues for predator face recognition by reef fishes. Z Tierpsychol 55:343–364

Kaufman AB, Rosenthal R (2009) Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. Anim Behav 78:1487–1491

Kavaliers M, Choleris E (2001) Antipredator responses and defensive behavior: ecological and ethological approaches for the neurosciences. Neurosci Biobehav Rev 25:577–586

Kleindorfer S, Fessl B, Hoi H (2005) Avian nest defense behaviour: assessment in relation to predator distance and type, and nest height. Anim Behav 69:307–313

Kroodsma DE (1989) Suggested experimental designs for song playbacks. Anim Behav 37:600–609

Leopold DA, Rhodes G (1983) A comparative view of face perception. J Comp Psychol 124:233–251

Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Stud Behav 27:215–290

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defense by parent birds. Q Rev Biol 63:167–187

Mostrom AM, Curry RL, Lohr B (2002) Carolina chickadee (*Poecile carolinensis*). In: Poole E (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca, http://bna.birds.cornell.edu/bna/species/636

Niemiller ML, Reynolds GR, Miller BT (eds) (2013) The reptiles of Tennessee. University of Tennessee Press, Knoxville

Nolen MT, Lucas JR (2009) Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. Anim Behav 77:1137–1146

Ritchison G, Grubb TC Jr, Pravasudov VV (2015) Tufted titmouse (*Baeolophus bicolor*). In: Poole E (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca, http://bna.birds.cornell.edu/bna/species/086

Scott AF, Redmond WH (2008) Atlas of reptiles in Tennessee. The Center of Excellence for Field Biology. Austin Peay State University, Clarksville, http://apsu.edu/reptatlas/

Sieving KE, Hetrick SA, Avery ML (2010) The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. Oikos 119:264–276

Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. Proc R Soc Lond B 272:2627–2634

Suzuki TN (2012) Referential mobbing calls elicit different predator searching behaviors in Japanese great tits. Anim Behav 84:53–57

Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. J Ethol 30:157–165

Weatherhead PJ, Blouin-Demers G (2004) Understanding avian nest predation: why ornithologists should study snakes. J Avian Biol 35: 185–190