Predator-Prey Dynamics: Prey Responses to Heightened Risk of Native and Exotic Predators in Urban and Rural Environments

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Although the dynamics of predator-prey have fascinated scientists for several decades, factors influencing behavioral responses to predation risk remain relatively unknown. With ongoing environmental change, two key issues that may alter perceived risk by prey are the presence of non-native predators and if (and how) urban environments may alter perceived risk. We tested the tufted titmouse (*Baeolophus bicolor*) reactions toward similar sounding but non-native predator calls, as well as how they would react to differences in predation risk in urban and rural environments. Predator calls of two local and nonlocal species were broadcasted to titmice in both urban and natural areas and their behaviors recorded. Latency to approach and minimum distance were the two variables that produced significant results, showing that the titmice would generally come in closer and more quickly in rural areas. We found that titmice altered their behaviors in response to different predators and effects varied in rural and urban environments.

INTRODUCTION

Predation can affect the fitness of organisms by both consumptive and non-consumptive aspects. Aside from direct consumption of an individual, the habitat choice, foraging behavior, social behavior, reproductive effort, and other behavioral characteristics may be altered in accordance to predation risk. Prey species' alterations of behavior due to the perception of predation risk can result in adverse effects on fitness (Parsons and Blumstein 2010, Travers et al. 2010, and Large et al. 2011). Many prey species have modified their behavior in accordance to predator-specific cues (Ghalambor and Martin 2001, Rainey 2004, Orrock et al. 2004, Apfelbach 2005).

While prey can alter their behavior in response to predation risk, the introduction of non-native predators poses a formidable problem for native prey species (Case 1996). Non-indigenous predators are becoming more frequent due to urbanization and shifting biogeographical ranges (Case 1996, Williamson, M 1996, Vitousek 1997). Native prey may not immediately percieve a predation threat from foreign predator species, resulting in increased population vulnerability of prey. It is unclear how these novel predator species will affect prey behavior and how they will react behaviorally to new predation pressures.

The urban to rural gradient of landscapes can also have implications on the behaviors of prey species (Chace and Walsh 2006, Marzluff and Neatherlin 2006, Bodey et al. 2011). As an effect of increasing urbanization, more non-native species are being introduced into urban areas, proliferating in these human-dominated habitats (McKinney 2006). Urbanization can lead to an increase in several types of predators, such as some raptor species (Chace and Walsh 2006, Stout and Rosenfield 2010), which could influence predation risk for prey living in increasingly urban environments. For example, fitness of avian species in urban areas is directly related to predator occupancy (Chace and Walsh 2006).

We performed a field experiment to test if nonnative predators have adverse effects on the behavior of the tufted titmouse (*Baeolophus bicolor*), as well as how urbanization may affect behavior. Non-native versus local predator calls may affect how the titmice respond behaviorally. The degree of human occupation may also affect the detection and behavioral response to these calls due to surrounding noise, differences in canopy and matrix structure, and potential differences in predator density in urban environments. These factors may affect behavior because of their unnatural origin and relatively recent appearance in evolutionary time (Chace and Walsh 2006). We expect the titmouse not to respond as strongly to the foreign predator calls as the native predator calls because they have not evolved with nonnative predators and would not as easily identify those calls as a threat. For the effect of urbanization, we expect that the titmice will be more wary in the natural environment because they would be more habitualized to foreign noises in an urban area.

METHODS

Study Area

This study was done in neighborhoods around Gainesville, Florida and at the Ordway-Swisher Biological Station located in Melrose, Florida. These areas consist mostly of live oak (*Quercus virginiana*) hammocks, pine flatwoods, and riparian areas.

Focal Species

Tufted titmice are a passerine species, and in northern Florida are found most commonly in the hardwood hammock habitat (Langham et al. 2006). The most common avian predators of this species include Eastern Screech Owls (*Otus asio*) and Cooper's hawks (*Accipiter cooperii*). The tufted titmouse has very pronounced reactions to threats posed by predators and therefore is an ideal candidate for the study of predator-prey interaction and the effects of urbanization on prey species. This species uses a mobbing behavior for protection from predators (Sieving et al. 2010). Detection of a predator may result in mobbing, in which the predator is chased away by all individuals, thus protecting the family unit.

Experimental Design

I conducted a field experiment to test the effects of native and non-native predator cues on behavioral responses of titmice in urban and rural environments. I manipulated predator cues of avian predators using a playback experiment (Rainey et al. 2003, Templeton et al. 2005, Templeton and Greene 2007, Sieving et al. 2010). Playback experiments are effective designs for understanding the role of predation risk because they mimic examples of predation situations by broadcasting calls that prey species may encounter and allow the researcher to observe prey behavior.

I collected calls of local frog species (*Acris gryllus, Anaxyrus terrestris, Gastrophryne carolinensis, Hyla andersonii, Hyla cinerea, Hyla femoralis, Hyla gratiosa,* and *Hyla squirella*), Western Screech Owls (*Megascops kennicottii*), Eastern Screech Owls (*Otus asio*), Cooper's Hawks (*Accipiter cooperii*), and Northern Goshawks (*Accipiter gentilis*). For each species, I collected multiple examples of calls from various sources so that I could determine if one call had varying effects on prey behavior (Kroodsma 2001). I assigned playlists to be played randomly during each trial. The order of the playlist of the predator (treatment) and frog (control) calls were also randomly assigned. The playlists were set up as follows: 30 seconds silence, 30 seconds treatment/control, 1 minute silence, 2 minutes buffer silence, 30 seconds treatment/control, 1 minute silence. I took verbal notes in the first 30 seconds of silence, the 30 seconds of treatment/control, and the 1 minute silences. The 2 minutes buffer silence between the first and second calls was to reduce carryover reaction from the first call (cf. Martin et al. 1996, Martin and Martin 2001).

The experimental calls were produced through a speaker with a 5 meter long wire hooked up to an MP3 player. I would recognize an individual in either a wilderness area (The Ordway-Swisher Biological Station) or suburban/urban environment (neighborhoods around Gainesville). I took verbal notes on a voice recorder of the number of calls, the number of psh calls, the number of peter calls, the number of call types, the number of flights, and the latency to approach the speaker. Titmice psh calls are used when they are mobbing a predator and help to draw in other passerines to force the predator to flee (Langham et al. 2006). If this call were used during a playback, it may be due to the individual's perception of risk toward that call. Peter calls are the song call of the species and may be used to assert territories or call to mates. If this call were made during a playback, it would suggest that the individual did not assess the playback as a risk (Sieving et al. 2010). To ensure independence among replicate trials, all trials were > 100m apart. I conducted 160 trials at both the Ordway-Swisher Biological Station and in neighborhoods around Gainesville (80 trials for each habitat type).

Analysis

I used repeated measures analysis of variance to test for the effects of treatment, urban versus rural environment (hereafter referred to as location), and their interaction on the six component behaviors described above. I initially checked if these behaviors measured were highly correlated with each other but found no evidence for strong correlations ($r < 0.4$), so I tested each behavior separately. This experimental design can be considered a cross-over design due to the sequential nature of treatments and controls within a trial. I tested for potential cross-over effects in the experiment, following Littell et al. (2006), and considered measurements within trials as repeated measures.

RESULTS

None of the six variables tested varied greatly enough from the control value to be considered statistically significant. For all of the variables, F-value <1.91 and P>0.09.

DISCUSSION

Percieved predation risk directly relates to behavioral responses and results in changes in choices of habitat, foraging, and reproductive effort (Ghalambor and Martin 2001, Orrock et al. 2004). I observed varying responses of titmice to different predator cues, however, none were considered statistically significant.

The hypothesis that native predator calls (Eastern Screech Owl and Cooper's hawk) would elicite more of a response than the non-native predator calls (Western Screech Owl and Northern Goshawk), was not supported by the statistical evidence. This occurance could be explained by the timing of the experiment. Avey (2011) found that black-capped chickadees' calls varied according to season, and that one call type occurred more often in spring, the breeding season. The titmice calls that I

witnessed were observed during the breeding season, and the birds could have been expending more energy on defending territories than searching for predators. If the experiment occurred during the non-breeding season, results may have been more significant. More interest in breeding would lead to similar reactions to both native and non-native predator calls. Parsons and Blumstein (2010) studied effects of novel predator cues on small mammals and found that the mammals had similar avoidance responses to both foreign and native cues. According to Sih et al. (2010), invading predators have a "novelty advantage" when it comes to the naivety of native prey species, and community similarities may increase this advantage. This may suggest that passerine prey species may be at higher risk to foreign predators due to the similarities in communities selected by passerines and due to differences seen in the reactions of mammal prey species and passerine prey species to novel predator cues. More research should be conducted in order to more effectively determine behavioral effects of non-native predators on tufted titmice.

The location effect was also not significant because there were only two examples of each area type (one urban area and one rural area). To actually determine a significant effect, multiple rural and urban areas would need to be studied. However, abundance of bird species in urban areas has been shown to generally improve with a decrease in urban infrastructure, an increase in old-growth trees, and an increase in the use of native shrubs in landscaping (Ortega-Alvarez and MacGregor-Fors 2010). This could mean that predation risk (perceived and actual) is higher in urban areas, and birds may stay further away from any sign of a predator.

All vocal responses also had mostly inconclusive results. Though we expected to observe the greatest reaction rate in the vocal response, we could have not accounted for impacts of the family group (such as dominance) or environmental factors. The vocal behaviors exhibited by titmice could be used mostly when the risk is visually recognized. Titmice may hear a predator, move in to assess the risk, and then after recognizing the predator visually, use auditory calls to drawn in other members to mob the predator.

Lack of significant effects could also be explained by the lack of data or faulty research design. The number of trials conducted resulted in nearly, but not quite significant results. If I had conducted more trials for each playlist, predator type, and habitat type, I may have seen more significance in the results. The playlist design also may have been too short or long to obtain appropriate behavioral responses. My presence also may have affected the bird's responses, especially in the rural areas because these individuals would not be as accustomed to humans as birds in urban environments.

The results obtained cannot be used for management implications for all passerine species and can only be directly applied to tufted titmice in Northern Florida. There may be some continuations of this study that would help to solidify these results and provide more information on predator-prey interactions and behavior of species in urban vs. rural environments. If in addition to the auditory cue a visual cue were added to this experiment, it could be determined if titmice use alarm calls more often for the visual representation of a predator. This study could also be expanded to include more urban and rural areas to ensure that the effects seen here can be applied to a broader region. More species may also be included to determine differences in reactions to risk posed by avian predators. Another direction for this study may include the use of more predators, including depredating predators such as corvids, snakes, and mammals.

Predator-prey interactions and urbanization are of great interest to ecologists because of their influences on multiple aspects of prey behavior. In this study, we saw that tufted titmice will respond differently to the similar auditory cues of native and non-native predators and also have varying responses to predators in urban and rural areas. These results may have implications for the management of urban areas and the introduction of novel predators to native prey ranges. Urban areas may be managed to provide enough cover for prey species, and prey species may not initially assess the risk level of novel predators, which may have its own implications in the ever-changing ranges of species.

ACKNOWLEDGMENTS

I would like to acknowledge and thank Irina Skinner, the University Scholars Program, and the Ordway Swisher Biological Station for making this project a possibility.

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