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Notes and Discussion Piece

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ABSTRACT.—During routine surveys of owl distributions on St. Catherines Island, we observed naturalized ring-tailed lemurs displaying antipredator responses to owl auditory cues. In the 32 y since the introduction of ring-tailed lemurs to the island, two successful depredation events by two different owl species have been documented. We investigated the behavioral response of ring-tailed lemurs to determine if they responded consistently to social calls from all three owl species present on St. Catherines Island despite size differences among the owl species that could affect the likelihood of them serving as predators on ring-tailed lemurs. We observed while ring-tailed lemurs responded to all the auditory owl calls, they exhibited more intense, longer and more consistent responses to the two larger owl species – the barred owl and great horned owl – relative to the small Eastern screech owl. These data suggest naturalized species are capable of learning threat-sensitive antipredator behaviors to novel predator communities.

INTRODUCTION

St. Catherines Island is a privately-owned and largely undeveloped semitropical barrier island located off the coast of Georgia, U.S.A. In 1984 ring-tailed lemurs (*Lemur catta*) were introduced to St. Catherines Island by the Wildlife Conservation Society as an assurance colony (Keith-Lucas *et al.*, 1999). At the time of introduction, ring-tailed lemurs were recognized by the International Union for Conservation of Nature Red List as near threatened but presently are recognized as an endangered species (Andriaholinirina *et al.*, 2014). This introduced population originated from animals held in captivity and now represents one of the few free-ranging populations of lemurs outside of Madagascar (Keith-Lucas *et al.*, 1999). In order to be successful, the introduced ring-tailed lemur population was required to establish appropriate social behaviors and avoid toxic plants and potential predators (Keith-Lucas *et al.*, 1999). In their native range, they exhibit strong antipredator behaviors in response to avian visual and auditory cues, suggesting raptors represent a common predator even though documented observations are rare (Goodman, 1994; Gould and Sauther, 2007). On St. Catherines Island, caretakers have observed evidence of lemurs being predated by two nocturnal raptor species - the great horned owl (*Bubo virginianus*) and the barred owl (*Strix varia*; D. Belgio pers. comm.).

While on St. Catherines Island conducting research on the distributions of native owl species, we observed that ring-tailed lemurs responded to owl calls during the day despite lacking the long co-evolved relationships typical of most predator-prey interactions. Although it may be expected that antipredator behaviors that evolved in response to native avian predators may carry over to novel predators in an introduced range (Griffin and Evans, 2003; Ferrari *et al.*, 2008), excessive use of antipredator behaviors in response to nonpredatory organisms may come at the cost of other activities, such as foraging or mating (*i.e.*, threat sensitivity hypothesis; Helfman, 1989). In addition to the two large nocturnal raptors already observed to consume ring-tailed lemurs (barred owl, 99-110 cm tall; great horned owl, 101-143 cm tall; Rusch *et al.*, 1972), St. Catherines Island also hosts a much smaller species of owl, the Eastern screech owl (*Megascops asio*, 45–60 cm tall; Belthoff, 1993). To observe if ring-tailed lemurs had the ability to distinguish among the size-dependent predation threats of these three owl species after 32 y or approximately two to three generations, we employed an owl auditory callback survey protocol to observe ring-tailed lemurs reactions to each potential predator.

METHODS

We surveyed four different ring-tailed lemur troops (N = 4–6 individuals per troop) over 2 d on St. Catherines Island (31.668617, -81.159898; N = eight observations). We placed a Jet Sylvania bluetooth speaker behind a tree or bush approximately 10 m away from where the troop was located and counted the number of visible individuals in the troop. We moved approximately 30–40 m away from the troop and waited 10 min prior to conducting observations to allow the ring-tailed lemurs to resume natural

social behaviors, such as grooming, sunning, or sitting. We randomly determined the order in which we played the three owl species' territorial calls during each visit to each troop. Calls were obtained from The Cornell Bird Lab website (www.allaboutbirds.org). Each call was repeated three times in 60 sec separated by at least 180 sec from the call of another species, which exceeded the time necessary for the animals to return to their previous behaviors. We recorded how many individuals of the troop physically responded to the call, exhibiting vigilant behavior that included standing on their hind legs, alert head movement, fleeing into the trees, or verbal communications between group members, such as clicks and chirps. For each response, we recorded the length of time before the first individual initiated a reaction to the call, the proportion of the group that exhibited a response behavior, as well as the length of time until all members of the troop returned to their behaviors prior to the call. Logistical constraints, including the small number of troops and limited time available for observation, prevented a formal statistical analysis of these outcomes, although behavioral patterns were observed.

RESULTS

Ring-tailed lemurs on St. Catherines Island did not appear to exhibit differences in latency to respond to calls of any of the three owl species tested (Fig. 1A), and all ring-tailed lemur responses occurred in less than 4 sec from the initiation of the owl call. However, ring-tailed lemurs exhibited predator-specific reactions in the length of response (Fig. 1B) and proportion of the troop responding to calls of the three owl species (Fig. 1C). Response length was 3.7 times longer for the barred owl relative to the Eastern screech owl and 1.7 times longer than that for the great horned owl (Fig. 1B). Response length for the great horned owl was 2.2 times longer than the Eastern screech owl (Fig. 1B). The proportion of the troop responding to the call was similar between the barred owl and great horned owl, which were both 1.25 times larger than the response to the Eastern screech owl (Fig. 1C).

We also observed that behavioral intensity increased in responses to barred owl and great horned owl calls relative to Eastern screech owl calls. Specifically, the ring-tailed lemurs made more intense vocalizations of shrieks and loud yelps following calls of the larger two species relative to chirps, clicks, and short barks following the calls of the Eastern screech owl. Furthermore, the ring-tailed lemurs stood up on hind limbs scanning the sky before fleeing into nearby trees following calls of the two larger species, whereas all of the troops only scanned the sky following the calls of the Eastern screech owl (Table 1).

DISCUSSION

Although studies have demonstrated risk-sensitive behaviors of ring-tailed lemurs in their native range (Goodman, 1994; Gould and Sauther, 2007), this is the first documentation of risk-sensitive threat responses in an introduced context. Ring-tailed lemurs scaled their antipredator response to the size of the potential avian predator, demonstrating the ability to distinguish among predator auditory cues of which they had no prior experience before release onto St. Catherines Island. The ring-tailed lemur population originated from lineages held in captivity in which their exposure to predators was deliberately limited and, as a result, they failed to exhibit natural behaviors (Keith-Lucas *et al.*, 1999). Short-term observations demonstrated the lemurs returned to natural social behaviors quickly after introduction to the new site (Keith-Lucas *et al.*, 1999), showing increased sensitivity to novel predators that fell within size ranges and the visual profiles of native avian predators (Goodman *et al.* 1993; Gould and Sauther 2007). Our observations of ring-tailed lemur antipredator behaviors suggest successful development of accurate detection and responses within two to three generations after exposure to a novel wildlife community. Despite being tested for their response to social calls rarely used by owls during hunting, ring-tailed lemurs demonstrated their ability to associate this nonpredatory cue with the presence of a predator. In addition, ring-tailed lemurs responded to these predator cues during the day despite crepuscular and nocturnal hunting behaviors by owls. More research is needed to determine how ring-tailed lemur threat responses vary throughout the day and to a wider array of avian and nonavian predators in nonnative locations.

Limited anecdotal observations prevent us from being able to accurately assess the predation risk posed by each owl predator. However, current responses to predators may provide information about

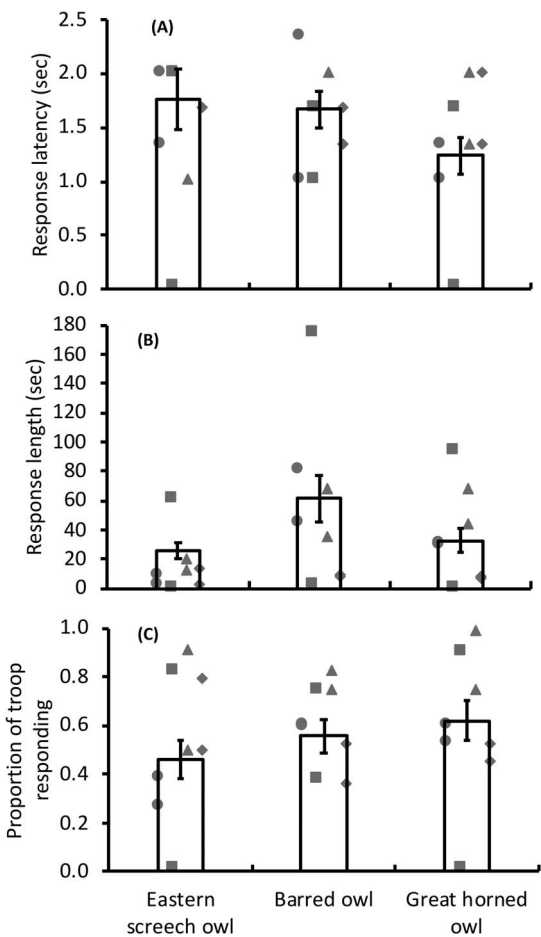


FIG. 1.—Mean (\pm standard error) latency to respond to a call (A), response length (B), and proportion of the ring-tailed lemur (*Lemur catta*) troop (C) responding to diurnal auditory playback of social calls by three owl species native to St. Catherines Island, Georgia, U.S.A. Grey symbols each represent repeated observations of each troop in this study

exposure to owl predation. As expected, fewer individuals responded to the smallest owl (Eastern screech owl) relative to the two larger species. Unexpectedly, the response was significantly longer to calls by barred owls relative to calls by great horned owls. Effective antipredator behaviors should balance the risk of predation with the frequency of encountering predators (Lima and Bednekoff, 1999; Pecor and Hazlett, 2003; Brown *et al.*, 2006). During our routine owl surveys, we detected more callbacks from barred owls than great horned owls suggesting barred owls are more common on St. Catherines Island. More common species are likely to interact with ring-tailed lemurs more frequently and contribute to learned antipredator responses by ring-tailed lemurs.

Ring-tailed lemurs use similar habitats on St. Catherines Island as the owl species and are within the size range of their prey. The ring-tailed lemurs are best described as semi-terrestrial, and much of their time on St. Catherines Island is spent foraging in the trees or around the feeding stations that provide supplemental food. Daily feedings result in troops that move only short distances away from the feeding

TABLE 1.—Qualitative descriptions of ring-tailed lemur (*Lemur catta*) responses to diurnal auditory playbacks of social calls by three owl species native to St. Catherines Island, Georgia, U.S.A.

Call type	Vocal response	Behavioral response
Eastern screech owl	Chirps, short barks, series of clicks	Visually searching sky/ground, ear movements
Barred owl	Shrieks, loud yelps	Fleeing into tree, standing on hind legs, visually searching sky/ground
Great horned owl	Shrieks, loud yelps	Fleeing into trees, standing on hind legs, visually searching sky/ground

stations, making their locations predictable for predators. Additionally, ring-tailed lemurs on St. Catherines Island travel terrestrially along corridors, such as roads, which match preferences for corridors in the gallery forests of Madagascar (LaFleu and Sauther, 2015). Great horned owl and barred owl are also likely to use these corridors in which they may find high perches to observe open areas like a road or field (Nicholls and Fuller, 1987). Finally, the two larger owls typically feed on small to medium-sized mammalian prey. The larger great horned owl feeds on slightly larger prey than the barred owl, and its diet includes mammals as large as striped skunks (*Mephitis mephitis*, 1.5–5.5 kg; Fergus, 1993) and Virginia opossums (*Didelphis virginiana*, 1.5 - 3.7 kg; Jenkins, 1979; Johnson, 1993). The slightly smaller barred owl feeds on smaller mammalian prey, such as cottontail or marsh rabbits (*Sylvilagus*, 1.2–2.2 kg; Bailey, 1968; Mazur and Paul, 2000). The weight of ring-tailed lemurs (2.3–3.4 kg; Pereira, 1993) overlaps that of all of these potential prey items, making it likely that these avian predators perceive them as prey.

Based on our observations, we hypothesize owls to be one of the primary predators of the ring-tailed lemurs on St. Catherines Island. There are no bobcats or coyotes on the island, hence American alligators (*Alligator mississippiensis*) are the apex predators of the freshwater and marginal marine ecosystems on St. Catherines Island. Shortly after introduction, a ring-tailed lemur was predated by an American alligator (D. Belgio, pers. comm.). However, this was the only documented interaction between the two species, as they occupy different habitats on the island. Because ring-tailed lemurs receive supplemental food and water, they do not frequent the freshwater ponds, tidal creeks, salt marshes, or beaches where they are likely to encounter American alligators. Other potential predators could include diurnal avian species, such as red-tailed hawks (*Buteo jamaicensis*) and red-shouldered hawks (*Buteo lineatus*; Thomas, 1978). Yet in the 32 y ring-tailed lemurs have occupied the island, there have been no documented interactions between the lemurs and these avian species. Similarly, mesopredators, such as striped skunks (*Mephitis mephitis*) or raccoons (*Procyon lotor*), could also potentially pose a threat to juvenile ring-tailed lemurs, but interactions of these species with the ring-tailed lemurs is undocumented.

The observations made in this contribution provide foundational information that introduced prey species can develop threat-sensitive antipredator behaviors to a novel set of predators within a few generations, increasing their survival and success rates. This is promising for future wildlife conservation efforts, specifically species translocation. As the world’s biodiversity faces the incessant threats of habitat loss, invasive species, and climate change, this type of conservation intervention will become more frequent (Griffith, 1989). Continued monitoring and management of other translocated species will provide more information about the abilities of introduced species to adapt and succeed in novel environments.

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