# Ringtailed lemur anti-predator calls denote predator class, not response urgency

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The referential signalling hypothesis proposes that in some prey species different anti-predator vocalizations denote different classes of predator (Seyfarth et al. 1980). The response urgency hypothesis proposes that different anti-predator calls denote different levels of escape urgency that predators impose on their prey (Owings & Hennessy 1984). An issue not fully addressed in previous research is that anti-predator systems based on response urgency converge in appearance with those based on referential signalling when predators of different classes characteristically impose different levels of response urgency on their prey. All claims of referential anti-predator signalling therefore remain essentially equivocal until observations are made for each class of predator that rule out response urgency as the determinant of call selection.

We presented models of avian and mammalian predators to the forest-living ringtailed lemurs, *Lemur catta*, at the Duke Primate Center under conditions of minimal and maximal response urgency to determine whether a predator class/response urgency correlation causes the false appearance of referential signalling in this species (Macedonia, in press). The primary study group, Lc1 group, had 21–31 members, roughly two-thirds of which were mature. Lc2 group had nine mature members and one juvenile. We conducted only one or two trials of each of the four types (minimal/maximal urgency × avian/mammalian predator) to minimize both the disruptive effects of maximal urgency trials and overall habituation to predators. To maximize the independence of the observations, we conducted any two trials using a given predator model with one study group at least 4 months apart, except the two trials in experiment 1, which were conducted 2 weeks apart using different models at different locations. The occurrence and non-occurrence of each anti-predator behaviour in the ringtailed lemur repertoire were audio- and/or video-recorded during trials. All vocalizations recorded have been positively identified through spectrographic and contextual analyses (J. M. Macedonia, unpublished data).

Experiment 1: avian predator, minimum response urgency. We placed a museum specimen of a perched hawk, *Buteo lineatus*, or owl, *Bubo virginianus*, on a branch 2–3 m above one of the traditional paths of Lc1 group. Each model elicited generalized alert vocalizations ('gulps'), responses normally evoked by soaring raptors (bipedal locomotion; 'chirps'), lunges, 'plosive barks' and frequent male tail-rubbing. Most lemurs remained at least 10 m away from the models, but seven or eight approached to within 1 m to threaten them. All lemurs remained within 15–25 m of the models for the duration of each trial (20 min).

Experiment 2: avian predator, maximum response urgency. A generalized raptor silhouette (plywood painted black) was attached to a 13-m wire run pitched 52° up from horizontal and fastened to a tree trunk 10 m above the ground. The model's starting position was flush against the trunk and its manner of attachment allowed rapid descent in the final attack posture of a stooping raptor upon release. We conducted two trials with Lc1 group. No lemur ever sighted the model before its release. In each trial, most lemurs first crouched to the ground and uttered 'rasps', 'shrieks' and/or multiply-frequency-modulated shrieks before running for cover. One female stood bipedally and shrieked, and a few unidentified lemurs issued plosive barks. 'Chirping' began as the group departed after 5–10 s.

Experiment 3: mammalian predator, minimum response urgency. A moderately large domestic dog, *Canis familiaris* (boxer, 27 kg), on a 20-m lead was introduced through an enclosure gate far from Lc1 group and allowed to walk slowly toward the lemurs. This procedure was also followed with Lc2 group. The lemurs of the two groups sighted the dog at about 30 and 50 m, respectively, remained on the ground for 3 and 6 s respectively, and stared and gulped toward the carnivore. Thereafter,

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the lemurs leapt into trees, uttering 'clicks' and 'closed-mouth click series' while staring at the dog. 'Yapping' and 'open-mouth click series' began about 30 and 50 s after first gulp and continued for 1–2 min after the dog departed each enclosure (20 min trials).

Experiment 4: mammalian predator, maximum response urgency. Sixteen months after experiment 3, the dog was hidden in the storage room of a structure that Lc1 group visits for provisions. Its 10-m lead was attached to a fixed eye-screw by a heavy 0·5-m elastic cord. We delivered provisions about 11 m away and around the corner from the door hiding the dog. After the lemurs fed for 4–5 min, we opened the door and the dog charged the lemurs from about 7 m. Every lemur sprinted immediately and silently toward the surrounding trees and was 10–15 m up into one within 4 s. Clicks and closed-mouth click series began as soon as the lemurs were arboreal. Open-mouth click series and yapping began about 40 s later and stopped about 5 min after the dog departed (2-min trial).

In all four permutations of predator class by urgency condition, responses conformed in detail to patterns seen during natural sightings of predators (Macedonia & Pereira, unpublished data). Rasps, shrieks, chirps, plosive barks and bipedal walking were restricted to the anti-raptor context: none occurred during any group response to the carnivore (see also Sauther 1990; Macedonia, in press). The multiple modulation of shriek frequencies, never witnessed under conditions of lower urgency, may signal high escape urgency, but only for raptors. Both extremes of carnivore response urgency ultimately invoked flight into trees followed by open-mouth click series and yapping, three responses that ringtailed lemurs restrict to the anti-carnivore context (Macedonia, in press; see also Jolly 1966; Sauther 1990).

Response urgency appears not to determine anti-predator call selection in ringtailed lemurs. Rather, the lemurs' consistent use of different calls in response to different classes of predator seems convergent with the anti-predatory behaviour of vervet monkeys, *Cercopithecus aethiops* (Cheney & Seyfarth 1990). For both species, not only do optimal modes of escape differ for raptors as opposed to terrestrial carnivores but each mode can increase vulnerability to predators of the alternate class. In contrast, ground squirrels evade all types of predators by running into their burrows. The anti-predator calls of at least some species (*Spermophilus beecheyi*; *S. beldingi*) denote response urgencies (Owings & Hennessy 1984), which allows efficient budgeting of time, energy and stress.

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