Ethology **86**, 177—190 (1990)

ISSN 0179-1613

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What is Communicated in the Antipredator Calls of Lemurs: Evidence from Playback Experiments with Ringtailed and Ruffed Lemurs

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MACEDONIA, J. M. 1990: What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ringtailed and ruffed lemurs. Ethology **86**, 177—190.

Abstract

Two hypotheses of signal specificity in antipredator calls ("referential signalling" and "response urgency") are discussed in light of prior research on ground squirrels and vervet monkeys. These hypotheses then are examined with data on responses of semi-captive ringtailed and ruffed lemurs to antipredator call playbacks. Although the responses of ringtailed lemurs support a referential-signalling interpretation of their antipredator calls, those of ruffed lemurs do not conform well to either hypothesis. Rather, ruffed lemur antipredator calls seem best viewed as "affective" signals that may only reflect underlying emotional/motivational states.

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Introduction

Different kinds of predators have been noted to elicit different types of antipredator calls from many mammal species (e.g. KLUMP & SHALTER 1984). Interpretation of what is communicated via these vocal signals differs, however, among researchers. For example, observations of vervet monkey (*Cercopithecus aethiops*) responses to naturally occurring predators (e.g. STRUHSAKER 1967; SEYFARTH & CHENEY 1980, 1986) and to playbacks of antipredator calls (e.g. SEYFARTH et al. 1980; CHENEY & SEYFARTH 1988; SEYFARTH & CHENEY 1990) have suggested repeatedly that these vocalizations serve to denote different classes of predators. Termed "referential signals", vervet antipredator calls seem to be analogous to human words in that different objects and events are referred to with structurally-distinctive vocal sounds.

Studies of ground squirrel antipredator calls have precipitated a different view of what is communicated in these vocalizations for the following reason. Whereas the nearby appearance of an airborne raptor presents a response situa-

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tion of "high urgency" for ground squirrels, terrestrial predators usually can be seen approaching and therefore usually require a less urgent response (e.g. ROBINSON 1980, 1981; OWINGS & HENNESSY 1984). Nevertheless, on occasion these sciurids are surprised at close range by terrestrial predators and in this "high urgency" situation they emit the calls that typically are elicited by aerial predators. Likewise, upon sighting distant-flying hawks (i.e. "low urgency"), ground squirrels sometimes utter calls more commonly evoked by terrestrial predators. This "flexibility" in antipredator calling has suggested that different antipredator calls do not refer to different kinds of predators, but rather, that they reflect differences in time constraints that different kinds of predators pose to their prey (e.g. ROBINSON 1980, 1981; OWINGS & HENNESSY 1984). It presently is unclear, however, if the response urgency call system differs fundamentally from one based purely on "affect" (e.g. fear) or merely is a form of an affect-based system.

Although a lack of referential specificity in antipredator calls may rule out referential signalling, nonexperimental evidence does not, however, suffice to prove its existence. Playbacks of antipredator calls provide a means to establish relationships between these vocalizations and their functions.

The referential-signalling and response-urgency hypotheses make opposite predictions for the kinds of vocal responses that predators should elicit from potential prey. The response-urgency hypothesis proposes that antipredator calls vary in structure according to the level of response urgency imposed by predators. The referential-signalling hypothesis, in contrast, proposes that antipredator calls vary in structure according to the types of predators eliciting them but does not rule out the structural encoding of urgency as well. Discriminating between the two hypotheses therefore requires evidence regarding the existence of referential signalling. If the responses of subjects to antipredator-call playbacks support a referential-signalling interpretation, this hypothesis can be tested more stringently by modulating response urgency in predator simulations.

Like vervets and ground squirrels, many species of lemurs (Primates, Prosimii) emit different vocalizations in response to aerial and terrestrial predators (e.g. ANDREW 1963; JOLLY 1966; POLLOCK 1975; RICHARD 1978; PETTER & CHARLES-DOMINIQUE 1979). However, details of lemur antipredator behavior have been lacking until recently (e.g. MACEDONIA & POLAK 1989; PEREIRA & MACEDONIA 1990; SAUTHER 1990). Most extant lemurs are relatively small compared to their primary mammalian predator (*Cryptoprocta ferox*, 7—12 kg; ALBIGNAC 1972), and Malagasy hawks (e.g. *Polyboroides radiatus, Buteo platypterus*) probably also represent a lethal threat to adults as well as immatures of some lemur species (SAUTHER 1990).

In this study, antipredator calls of two semi-captive species of Malagasy prosimians, ringtailed lemurs (*Lemur catta*) and black-and-white ruffed lemurs (*Varecia variegata variegata*), were played back to evaluate the likelihood of referential-signalling in these vocalizations. In a separate report (PEREIRA & MACEDONIA 1990), several experiments are described that employed a variety of predator models to test the response-urgency hypothesis where referential signalling had been suggested by responses to playbacks.

Materials and Methods

Study Groups and Environment

One semi-captive group each of ringtailed lemurs (Lc1 Group) and ruffed lemurs (Vv1 Group) inhabiting a 3.5 ha natural-habitat enclosure (NHE-2) were observed. NHE-2 is a mixed pine and hardwood forest containing well over 3000 mature trees (for dominant tree species and a diagram of NHE-2, see PEREIRA et al. 1987). The enclosure is surrounded by a chain-link fence topped with mildly-electrified wire netting. A 10 m swath between the fence and the forest vegetation prevents the lemurs from escaping. Although the lemurs are provisioned twice weekly with mixed cut fruit and receive daily allotments of monkey chow, they spend much of their time ~~with mixed~~ foraging for and supplementing their diet with local flora (e.g. GANZHORN 1986). Excluding young infants, who are identified by patterns of tail shaves, all lemurs in the NHE's are fitted with individually-identifiable collars and tags.

Lc1 Group was introduced into NHE-2 in 1983, after living in another enclosure (NHE-1 : 0.5 ha) since 1981. All members of Lc1 Group, other than the oldest male and female, were born in the enclosures or have lived there since weaning. Vv1 Group was introduced into NHE-1 from an outdoor run in 1983. In 1985 they were moved to NHE-2 where they have lived since that time. The oldest adult male and female of Vv1 Group were born in captivity at other institutions, and their offspring, some of which were born in NHE-2, comprised the rest of this group. During the study period (Aug. 1986 through Apr. 1987), Lc1 Group contained from 4 to 8 adult females, 6 to 13 adult males, and 15 to 16 immatures; Vv1 Group contained 1 to 2 adult females, 2 adult males, and 3 to 4 immatures. Adult (≥ 3 yrs of age) ringtailed lemurs weigh roughly 2 kg; adult ruffed lemurs weigh approximately 75 % more (about 3.5 kg; DUPC records). The ringtailed and ruffed lemur study groups shared NHE-2 with a group of brown lemurs (*Eulemur fulvus fulvus*) in 1986 and with a group of red-fronted lemurs (*E. fulvus rufus*) in 1987. The three species ranged independently but aggregated at feeding stations.

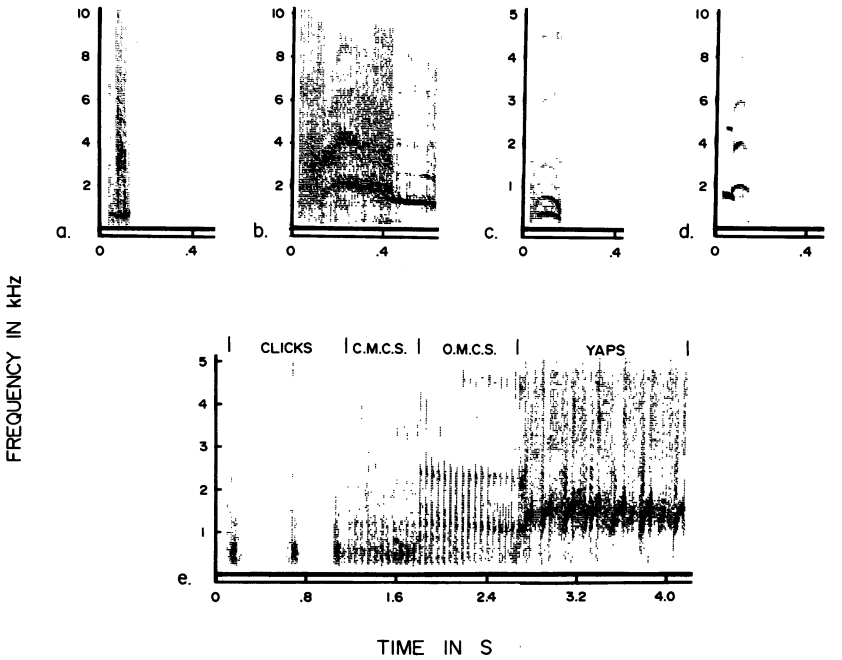

Fig. 1: Ringtailed lemur vocalizations: a. rasp, b. shriek, c. gulp, d. chirp, e. clicks, closed-mouth click series, open-mouth click series, yaps

Playback Protocol

Calls played back (Figs. 1, 2; Table 1) were recorded from identified adults during encounters with actual or simulated predators (e.g. MACEDONIA & POLAK 1989; PEREIRA & MACEDONIA 1990). The number of exemplars of each call type played back was as follows: *L. catta* — antiraptor call (4 rasps from two individuals; 4 shrieks from 2 or more individuals); anticarnivore call (7 yaps from the group); *V. variegata* — antiraptor call (11 abrupt roars from 4 individuals); anticarnivore call (11 pulsed squawks from 2 individuals). The same call types were played to subjects on the ground and in the trees with the exception of the ringtailed lemur "rasp" (Fig. 1 a; Table 1) which, due to its relatively low amplitude in conjunction with the fact that the playback speaker was placed on the ground, was not played to subjects in the trees. Playbacks were not conducted to "mixed species groups", and it was a prerequisite for playbacks that the species being tested was not (as far as could be discerned) in visual contact with the other study species. Subjects in Lc1 Group were tested once per playback type on a given substrate. Due to the small size of Vv1 Group, however, each subject was tested up to three times per playback type on a particular substrate.

Playbacks of a given type of antipredator call for a given species were separated by at least 24 h and typically by several days or weeks. No evidence of habituation to playbacks was seen in the responses of either species during the study. Playback amplitude was standardized to natural sounding

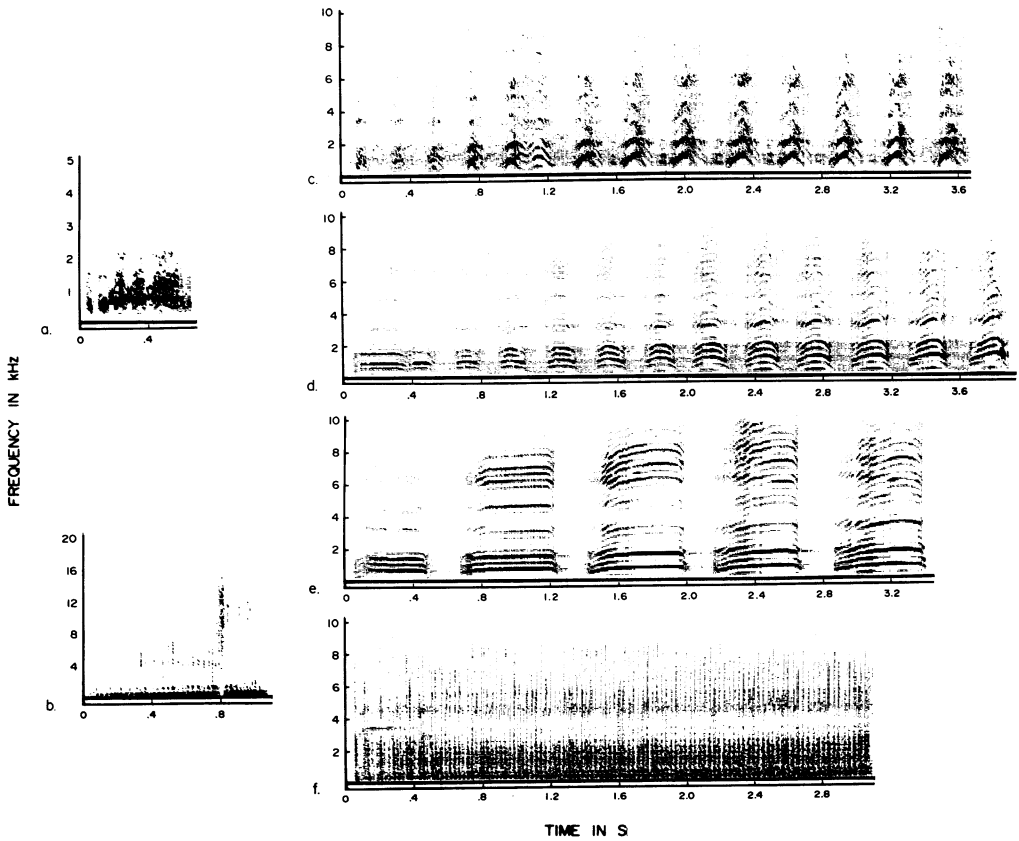

Fig. 2: Ruffed lemur vocalizations: a. abrupt roar, b. growl-snort, c. pulsed squawk, d. pulsed squawk/wail intermediate, e. wail, f. growl

levels over the same approximate distance range (5—15 m) from the playback speaker (Mineroff Electronics Field Speaker) as were subjects during actual trials (Table 2). Trials were aborted or data discarded if some notable disturbance occurred just prior to or during a playback.

Each observer (usually two) chose a single subject on the basis of its activity, location, and ageclass from a continually updated list of potentially available subjects. Only alert individuals at rest, or those engaged in quiet activities (e.g. grooming), were chosen as subjects. Subjects were required to

Table 1: Definitions of ringtailed and ruffed lemur responses to antipredator-call playbacks

Response	Defintion
Look up:	Look skyward
Run: up into tree	Running from the ground up into the *branches* of a tree
Run: not into tree	Running to any location except into a tree
Climb higher in tree	Subject in tree moves upward in response to playback
Climb lower in tree	Subject in tree moves downward in response to playback
Bipedal locomotion (*L. catta* only)	Standing and walking or trotting bipedally (see PEREIRA & MACEDONIA 1990, for example)
Scan and roar (*V. variegata* only)	Antiphonal response to abrupt roars while shifting body in quarter turns and scanning for stimulus (MACEDONIA, in prep)
Vocalizations: *Lemur catta*	
Antiraptor call (Fig. 1 a, b)	Rasp (conspecific-directed) and/or shriek (predator- and conspecific-directed);
Gulp (Fig. 1 c)	General-context group alert call
Chirp (Fig. 1 d)	Elicits moderate-to-rapid group relocation and maintains contact among group members during same
Clicks (Fig. 1 e)	Indicates seeming "apprehensive curiosity" of emitter; focuses attention of group members on emitter
Anticarnivore call (Fig. 1 e)	Yaps: call used in vocally "mobbing" mammals
Varecia variegata	
Antiraptor call (Fig. 2 a)	Abrupt roar: emitted in contexts of high-level aggression; used to vocally mob avian predators
Growl-snort (Fig. 2 b)	Location marker in high arousal disturbances
Anticarnivore call (Fig. 2 c)	Pulsed squawk: vocal response to mammal carnivores; may signal high-urgency need for group reaggregation
Wail (Fig. 2 e)	"All clear" call; may signal low-urgency desire for group reaggregation
Growl (Fig. 2 f)	Location marker in low/moderate arousal disturbances

Table 2: Amplitude ranges of antipredator-call playbacks

Call type	db Range
Lemur catta	
Antiraptor (rasp)	76— 78
Antiraptor (shriek)	95— 96
Anticarnivore (yap)	95— 97
Varecia variegata	
Antiraptor (abrupt roar)	99—100
Anticarnivore (pulsed squawk)	97— 99

Natural-sounding amplitude at 1 m; db measurements: realistic sound level meter: "A" weighting, fast response.

be more than 5 m from one another and facing in different directions. The playback speaker was concealed behind a tree or in ground vegetation at a position roughly equidistant between subjects. Each observer watched their subject during and for the first 5 s immediately following a playback, and then scored responses into predetermined behavioral categories (Table 1) on a standardized check sheet. All categorical responses exhibited by a subject during that time period were counted in data tallies, but no subject exhibited more than three (and usually fewer) total categorical responses to a playback. Ad libitum comments on subjects' behavior outside the playback-plus-5-s time window also were recorded.

Terminology

The term "antipredator calls" is preferred here to "alarm calls" (see OWINGS & HENNESSY 1984) because several of these vocalizations appear to function in ways other than to alarm conspecifics to danger (see Discussion). To minimize ambiguity, "antiraptor call" and "anticarnivore call" are used wherever possible. "Anticarnivore" refers explicitly to members of the mammalian order Carnivora.

Predictions

Based on responses of ringtailed and ruffed lemurs to naturally occurring and simulated predators (PEREIRA & MACEDONIA 1990; MACEDONIA, in prep), as well as responses to predators by vervet monkeys (see SEYFARTH et al. 1980), the following predictions were made for the study species under the referential-signalling hypothesis.

Prediction 1: Significantly more ringtailed and ruffed lemurs *on the ground* will (a) look up (skyward), and/or (b) run, but not into trees, in response to playbacks of antiraptor calls than in response to playbacks of anticarnivore calls. Significantly more ringtailed lemurs *on the ground* will locomote bipedally, and significantly more ruffed lemurs *on the ground* will exhibit the "scan and roar" behavior in response to playbacks of antiraptor calls than in response to playbacks of anticarnivore calls (see Table 1).

Prediction 2: Significantly more ringtailed and ruffed lemurs *in the trees* will look up, and significantly more ringtailed lemurs will climb lower or out of trees, in response to playbacks of antiraptor calls than in response to playbacks of anticarnivore calls.

Prediction 3: Significantly more ringtailed and ruffed lemurs *on the ground* will look toward the playback speaker before exhibiting another response to playbacks of antiraptor calls than to playbacks of anticarnivore calls, and/or more will look toward the playback speaker only after exhibiting another response to playbacks of anticarnivore calls than to playbacks of antipredator calls.

Prediction 4: Significantly more ringtailed and ruffed lemurs *on the ground* will run up into trees, whereas when *in the trees* significantly more will climb higher, in response to playbacks of anticarnivore calls than in response to playbacks of antiraptor calls.

No predictions for vocal responses to playbacks were made (aside from the "roar" component of the ruffed lemur "scan and roar" response) because, although different call types may be highly correlated with one antipredator call or another, these other vocalizations do not provide strong evidence in examining the referential signalling hypothesis.

Data Analysis

The 2 × 2 G-test of independence with William's correction (chi-squared distribution; alpha = .05; SOKAL & ROLF 1981) was used to compare response frequencies to playbacks of different antipredator-call types. Because some subjects were unavailable for exposure to playbacks of both types (antiraptor and anticarnivore) on both substrates (ground and trees), the distribution of subjects who were sampled for one or both playback types for a given substrate was uneven. Thus, statistical outcomes should be viewed with caution. Nevertheless, if a species' antipredator calls denote different classes of predators that require different escape tactics, then, per definition, playbacks of antipredator calls elicited by different classes of predators should evoke response differences evident enough to make statistical inference unnecessary for their interpretation.

Results

Ringtailed Lemurs

The number of times that antiraptor and anticarnivore calls were played back to each lemur species is displayed in Table 3. Most responses of the ringtailed lemurs to playbacks of their antipredator calls met predictions. More adults on the ground looked up and locomoted bipedally in response to playbacks of antiraptor calls than to playbacks of anticarnivore calls, and more adults ran into trees in response to anticarnivore calls than to antiraptor calls (Fig. 3 a). Differences in running elsewhere than into trees did not meet predictions because responses did not differ between the two call types. Results for immature subjects on the ground in the categories "look up" and "run: up into tree" were the same as those for adults (Fig. 3 b). Immatures generally did not respond with bipedal locomotion to playbacks of antiraptor calls, however, and there was a tendency to "run: not into tree" in response to antiraptor call playbacks.

More adult ringtailed lemurs in trees climbed lower in response to playbacks of antiraptor calls than to anticarnivore calls (Fig. 3 c). Contrary to prediction, however, more adults in trees did not "look up" or "climb higher in tree" to

Table 3: Number of times each type of antipredator call was played (n) and number of individuals observed in each location

Antipredator call	Location on ground	Location in trees
Lemur catta		
Avian (n = 23)	28	20
Mammalian (n = 23)	33	15
Varecia variegata		
Avian (n = 16)	16	17
Mammalian (n = 18)	21	17

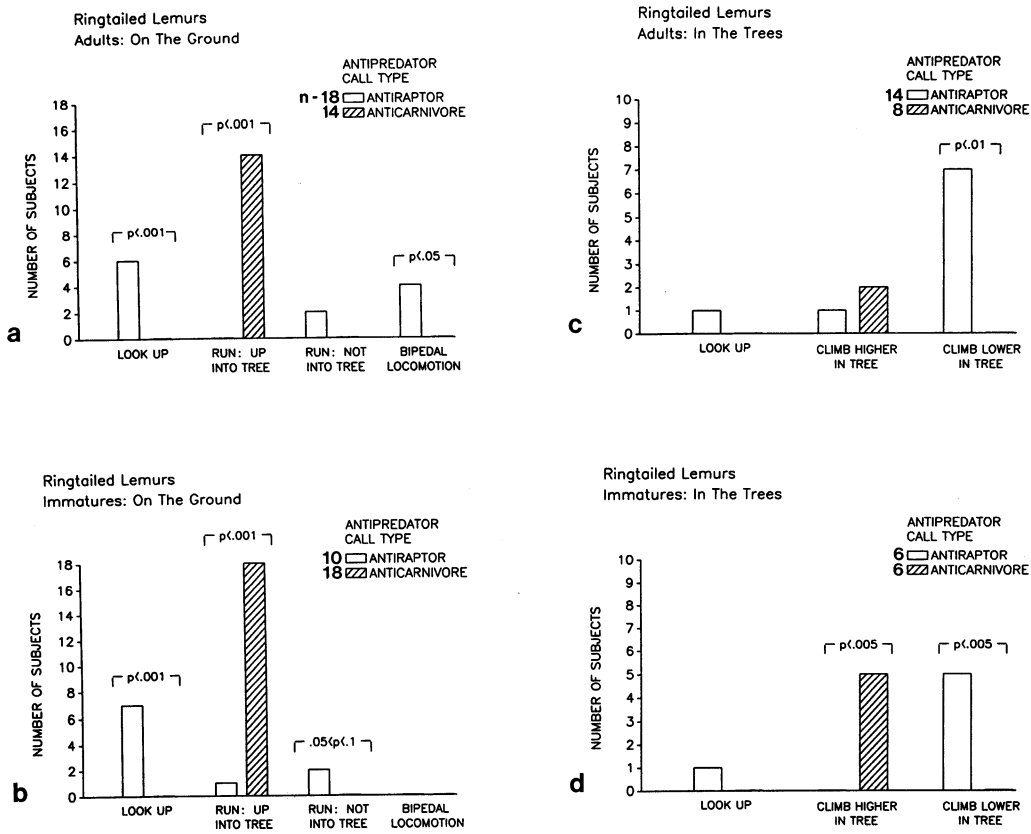

Fig. 3: Responses of ringtailed lemur adults (a) and immatures (b) on the ground and in the trees (c, d) to playbacks of their antipredator calls; n = number of subjects

playback of one call type over another. More immatures in trees climbed lower in response to playbacks of antiraptor calls than to anticarnivore calls (Fig. 3 d) and, like adults, they did not "look up" more often to one call type than to another when in trees. Unlike adults, more immatures climbed higher in trees in response to playbacks of anticarnivore calls than to antiraptor calls.

When on the ground, but not when in the trees, more Lc1 Group subjects looked toward the playback speaker before exhibiting another response to antiraptor calls than to playbacks of anticarnivore calls (Fig. 4). Likewise, when on the ground, but not when in the trees, more ringtailed lemurs looked toward the speaker only after a prior response to playbacks of anticarnivore calls than to antiraptor calls. Both these responses thus met predidictions.

Finally, ringtailed lemurs never responded to an antipredator call playback by emitting the same vocalization (Fig. 4 b). The frequency with which "gulps" (Fig. 1 c; Table 1) were emitted in response to playbacks did not differ between playback types. In contrast, "clicks" (Fig. 1 e; Table 1) were emitted only in response to anticarnivore call playbacks, and "chirps" (Fig. 1 d; Table 1) were emitted only in response to antiraptor call playbacks (Fig. 4 b).

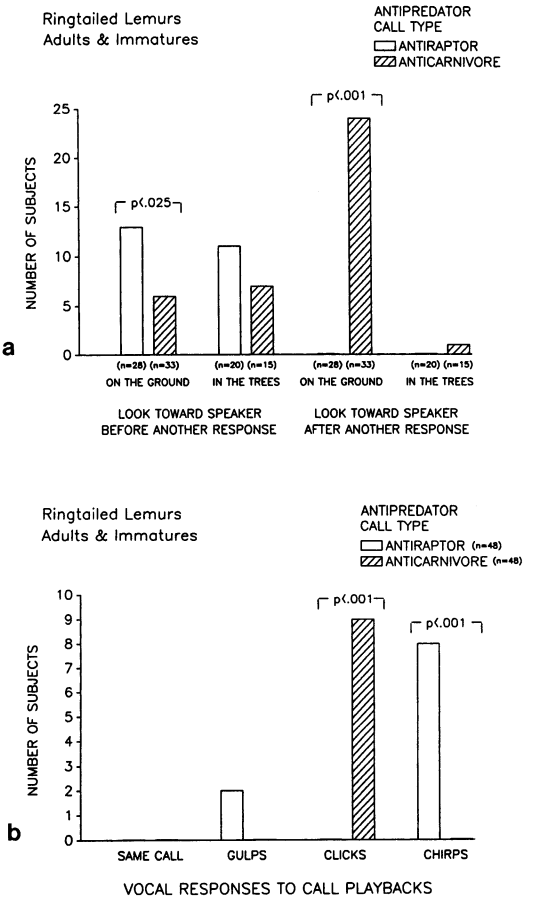

Fig. 4: a. "Look toward speaker" responses and b. vocal responses of ringtailed lemurs to playbacks of their antipredator calls; n = number of subjects

Ruffed Lemurs

More adult ruffed lemurs on the ground exhibited the "scan and roar" behavior (Table 1) in response to playbacks of antiraptor calls than to anticarnivore calls (Fig. 5 a). Contrary to prediction, however, more adults on the ground did not look up in response to playbacks of antiraptor calls than to anticarnivore calls. Although no explicit prediction was made, more adults did not run elsewhere than into trees in response to one playback type than to another. Like adults, more immatures scanned and roared in response to playbacks of antiraptor calls than to anticarnivore calls (Fig. 5 b), and did not often look up in response to either call type. Although neither adults nor immatures ran into trees differentially in response to playbacks of the two call types, immatures ran into trees more often than did adults. Also as predicted, more adult ruffed lemurs in the trees exhibited the "scan and roar" behavior in response to playbacks of antiraptor calls than to anticarnivore calls (Fig. 5 c). Just as when on the ground, however, more adults in the trees did not look up in response to playbacks of one antipredator call type than to another.

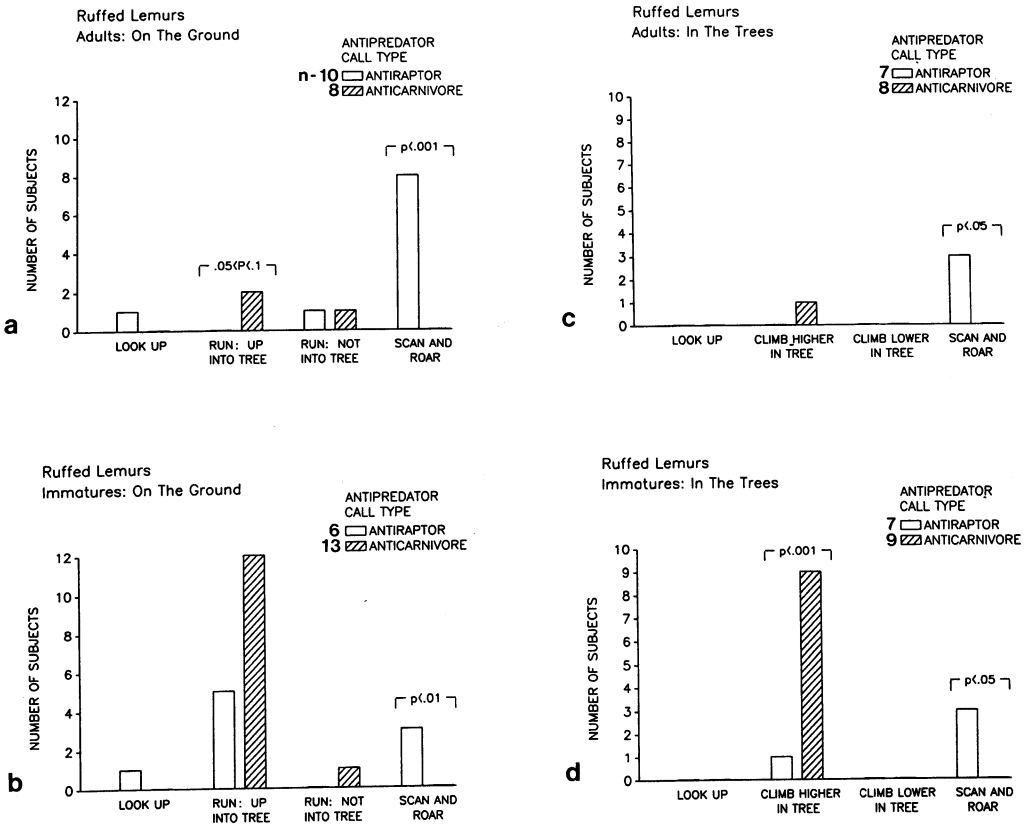

Fig. 5: Responses of ruffed lemur adults (a) and immatures (b) on the ground and in the trees (c, d) to playbacks of their antipredator calls; n = number of subjects

Like adult ringtailed lemurs, more adult ruffed lemurs did not climb higher in trees after playbacks of anticarnivore calls than after playbacks of antiraptor calls. Like immature ringtailed lemurs, more immature ruffed lemurs in the trees showed this predicted differential response (Fig. 5 d).

In contrast to the ringtailed lemurs, the most common first response of the ruffed lemurs to playbacks of either call type was to look toward the speaker (Fig. 6 a). Ruffed lemurs on the ground, however, looked toward the speaker only after another response more often to playbacks of anticarnivore calls than to antiraptor calls.

Playbacks of ruffed lemur antiraptor calls elicited emission of the same call (Fig. 2 a; Table 1) from subjects in over half the trials (Fig. 6 b). Both in absolute terms and relative to antiraptor call playbacks, anticarnivore call playbacks rarely elicited the same calls (Fig. 2 c; Table 1) from ruffed lemur subjects. More "growls" (Fig. 2 f; Table 1), and the combination of growls plus "growl-snorts" (Fig. 2 b; Table 1) were elicited in response to anticarnivore call playbacks than to antiraptor call playbacks.

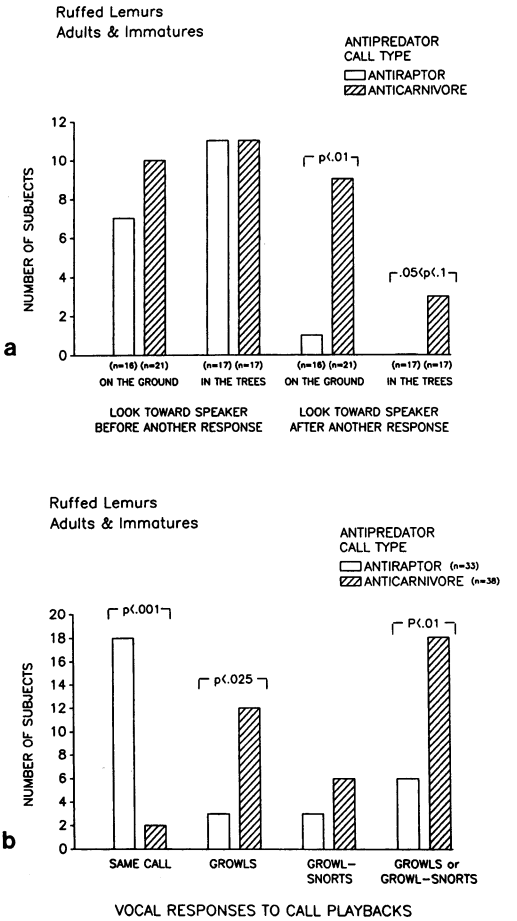

Fig. 6: a. "Look toward speaker" responses and b. vocal responses of ruffed lemurs to playbacks of their antipredator calls; n = number of subjects

Discussion

Ringtailed lemurs responded to playbacks of their antipredator calls as they did when the stimuli that elicited those calls were present. Although not every prediction was supported fully by their playback results, the clear and consistent responses of the ringtailed lemurs lean strongly toward a referential-signalling interpretation of their antipredator calls. Importantly, the nonconfirmation of certain predictions does not constitute evidence against this interpretation. That fewer ringtailed lemurs in the trees looked up after antiraptor than anticarnivore call playbacks may have been due to the fact that (a) it is more important to scan horizontally when in a tree, (b) skyward glances more often went unnoticed by observers on the ground, and/or (c) the predominant response of climbing down largely excludes looking up. More adults may not have climbed higher after anticarnivore than antiraptor call playbacks because adult primates maintain an advantage over mammalian predators in the trees. Immatures may have climbed higher in trees in response to playbacks of anticarnivore calls due to inexperience

both with predation attempts and with arboreal locomotion. Note that climbing upward or downward in a tree in parallel with a particular type of antipredator call is not expected under the response-urgency hypothesis.

Looking toward the speaker following playbacks also revealed distinctive call-type specificity. More ringtailed lemurs looked toward the speaker before beginning locomotion in response to antiraptor calls than to anticarnivore calls. And, where subjects on the ground looked in the direction of the playback speaker only after another response, the prior response was in every case running into trees. Thus, and in contrast to responses to antiraptor calls, a no-information-necessary response seems workable for anticarnivore calls. The fact that more ringtailed lemurs looked toward the speaker in response to playbacks of antiraptor calls than to playbacks of anticarnivore calls does not imply that their antiraptor calls are less referential. Rather, important information about raptor *location* can be had by following the direction of the caller's gaze. Such information is unnecessary for responding to carnivores if trees are accessible. The overall lower rates of looking toward the speaker by subjects in the trees may have been due to the generally low level of visibility in the arboreal habitat, i.e. one cannot follow a caller's gaze if one cannot see the caller.

That clicks were emitted only in response to anticarnivore-call playbacks illustrates the association between these call types (see Fig. 1 e) but cannot provide evidence for referential-signalling (MACEDONIA, in prep.). Because ringtailed lemurs respond to low flying hawks by relocating terrestrially (PEREIRA & MACEDONIA 1990), chirps, which elicit and appear to maintain rapid group movement, are highly correlated with this particular predator context. The emission of chirps only following playbacks of antiraptor calls suggests an awareness of impending rapid, terrestrial group movement.

The responses of ruffed lemurs to playbacks of their antipredator calls argue against a referential-signalling interpretation for these vocalizations. Although the ruffed lemur anticarnivore call, the pulsed squawk, has been observed only in contexts involving mammals (or where no stimulus was discernable), this call forms one end of a structurally-graded acoustic continuum at whose other end is located the "wail" (Fig. 2 c—e). The ruffed lemur wail appears to serve an "all clear" notification function following high-arousal contexts, as well as apparently stimulating leisurely group reaggregation in low-arousal contexts (PEREIRA et al. 1988; see also IWANO 1989: 242). Therefore, it seems likely that the pulsed squawk/wail acoustic continuum (cf. pulsed squawk/abrupt roar) maps onto a response urgency continuum. Although ruffed lemur growls and growl-snorts may function primarily to localize callers in low to moderate arousal and high-arousal contexts respectively (PEREIRA et al. 1988), they more often seem to occur in conjunction with pulsed squawks than with abrupt roars.

In contrast to the propensity of vervets (SEYFARTH et al. 1980) and ringtailed lemurs on the ground to look up in response to antiraptor calls, ruffed lemurs almost never looked up after playbacks of "abrupt roars", their vocal signal associated with the advent of raptors. Moreover, abrupt roars occur in several generalized, high-arousal nonpredator contexts (e.g. PEREIRA et al. 1988; MACEDONIA, in prep). The ruffed lemur abrupt roar, therefore, seems best viewed

as a signal that neither denotes a predator class nor communicates a level of response-urgency, but rather as an aggressive/defensive disposition toward a disturbing stimulus (see PEREIRA et al. 1988 for a description of the concomitant aggressive/defensive posture).

Also unlike ringtailed lemurs, a strong ageclass difference in running up into trees was observed for the ruffed lemurs: immatures frequently fled into trees in response to anticarnivore *and antiraptor* call playbacks, whereas adults seldom did so to either call type. This difference may reflect selection pressures that, due to factors of reproductive biology, body size, foraging tactics, and activity cycle have been unique to the ruffed lemur among extant primates (see MACEDONIA, in prep.)

There are systems of vocal antipredator behavior other than those described in this report. For example, superb starlings (*Spreo superbus*) appear to designate predators according to substrate; airborne vs earthbound (see SEYFARTH & CHENEY 1990). These birds will emit one type of antipredator call in response to a perched raptor, and another when the same raptor takes wing. This same phenomenon has been reported for arctic ground squirrels (MELCHIOR 1971). As substrate cannot be divorced from response urgency under nonexperimental conditions, however, it is not yet clear if the "substrate" oriented system actually differs from the response-urgency system.

In summary, responses of the ringtailed lemurs to playbacks of their antipredator calls support the interpretation of these calls as referential signals. In contrast, insufficient evidence was found to support a referential-signalling hypothesis for the antipredator calls of the ruffed lemur. The call elicited from ruffed lemurs by raptors appears instead to reflect an aggressive/defensive demeanor, whereas the call elicited by carnivores is interpreted as a high-urgency signal for rapid group reaggregation.

To evaluate the possibility that a strong correlation between types of predators and consistent levels of response urgency generated by those predators might confer the false appearance of referential-signalling in *Lemur catta*, predator simulations were conducted that controlled for response-urgency within predator classes, the results of which are reported elsewhere (see PEREIRA & MACEDONIA 1990).

Acknowledgments

I thank R. H. WILEY for use of his sound laboratory to produce the spectrograms used for illustration. I am most grateful to M. E. PEREIRA for assisting with this project in ways too many to enumerate here. I also express my appreciation to P. MARLER, M. E. PEREIRA, R. M. SEYFARTH, and two anonymous reviewers for constructive comments on earlier versions of this manuscript. This research was supported by an NSF Dissertation Improvement Award (BNS 8912589) to MACEDONIA. This is DUPC publication No. 493.

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Received: February 8, 1990

Accepted: July 10, 1990 (G. Barlow)