Auditory Assessment of Avian Predator Threat in Semi-captive Ringtailed Lemurs (*Lemur catta*)

JOSEPH M. MACEDONIA and PAMELA L. YOUNT

Duke University

ABSTRACT. Antiraptor responses from forest-living ringtailed lemurs to advertisement calls of naturally-occurring red-tailed hawks suggested that the lemurs discriminated these calls from other environmental sounds. A series of playback experiments, using real animal sounds and synthetic sound probes, was conducted to investigate the acoustic basis of this putative discrimination. Two semi-captive groups of ringtails served as study subjects: one group had many years of experience living in the forest, whereas the other group had relatively little such experience. Responses to playbacks suggested that both groups used the same acoustic criteria to discriminate "calls of large hawks" from other sounds, but the range of auditory stimuli that evoked antiraptor responses was broader for the experienced group than for the inexperienced group. Although several interpretations of the experimental results are possible, one that seems particularly compatible with the data is the "prototype" concept of stimulus categorization.

Key Words: Lemur catta; Hawk calls; Acoustic discrimination; Antiraptor behavior; Playback experiments.

INTRODUCTION

Predation poses a relentless threat to existence for most free-ranging animals. For some species of primates, predation is the primary cause of death (see Cheney & Wrangham, 1987). Although a number of brief reports have described interactions of primates with predators (e.g. Gouzoules et al., 1975; Chapais & Schulman, 1980; Chapman, 1986; Bartecki & Heymann, 1987; Heymann, 1987; Gautier-Hion & Tutin, 1988), the ways in which dangerous predators are discriminated from non-threatening animals by primates has received little attention (cf. Seyfarth & Cheney, 1980, 1986; Macedonia & Polak, 1989). The loud, piercing cries that characterize many species of large hawks (e.g. Buteo sp., Figs. 1 & 2) provide a case in point. Although these vocalizations are used primarily in territorial advertisement, they also may serve a dual role in flushing prey from cover (e.g. Brown & Amadon, 1968). This hunting technique has been documented for several species of forest falcons (Micrastur sp.) who use their advertisement calls to provoke movement in concealed passerine prey (Smith, 1968). Recognition of raptor calls by undetected primates potentially could provide the forewarning necessary to escape predation. To date, however, no studies have investigated whether such recognition occurs.

In Madagascar, the semi-terrestrial ringtailed lemur (*Lemur catta*) inhabits an open, arid landscape (see TATTERSALL, 1982) where concealment from predators is difficult. Although ringtailed lemurs live in relatively large social groups and possess a sophisticated system of antipredator vocalizations (e.g. MACEDONIA, 1990; PEREIRA & MACEDONIA, in press), Malagasy carnivores (the fossa: *Cryptoprocta ferox*) and raptors (e.g. Madagascar harrier hawk: *Polyboroides radiatus*) are known to take ringtails or similar-sized lemurs as prey (e.g. WILSON et al., 1989; SAUTHER, 1989).

Ringtailed lemurs living in forested enclosures at the Duke University Primate Center

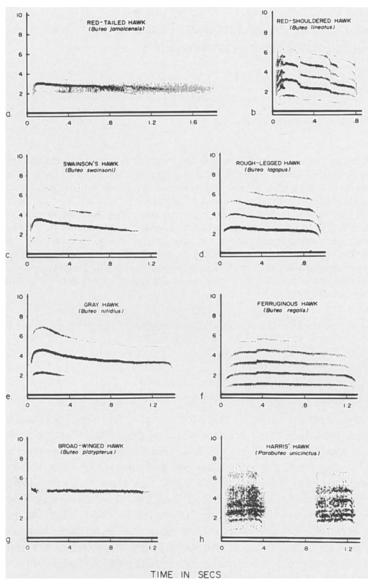


Fig. 1. a-g. Advertisement calls of large North American hawks (Genus: *Buteo*); h. a related genus (*Parabuteo*) with a different call structure.

(DUPC) regularly see and hear red-tailed hawks (*Buteo jamaicensis*) while these raptors are soaring above the forest canopy. Although no forest-living lemur at the DUPC is known to have fallen prey to a hawk, red-tailed hawks do attack small mammals in these enclosures (J.M.M., pers. obs.) and are capable of taking prey roughly the same size and weight as adult ringtailed lemurs (2 kg jackrabbits, *Lepus californicus*; J.M.M., pers. obs.). Responses shown by the semi-captive ringtails when sighting a red-tailed hawk nearby (see below) leave no doubt that the lemurs consider these birds of prey threatening. Moveover, the fact

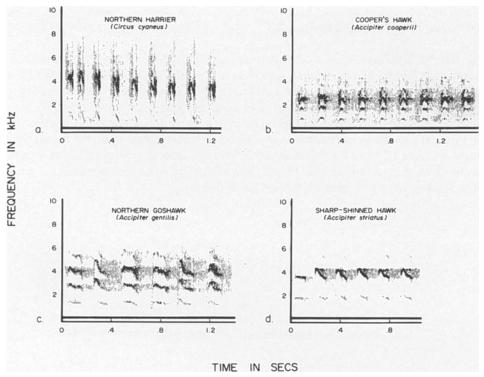


Fig. 2. Advertisement calls from a. A medium-sized North American harrier hawk, *Circus cyaneus*; b-d. some smaller North American hawks (Genus: *Accipiter*).

that the hawks' cries alone elicited antiraptor behavior suggested that the lemurs discriminated these calls from other sounds in the forest. Playback experiments therefore were conducted to elucidate which acoustic features of hawk calls might be serving as recognition cues.

STUDY GROUPS AND ENVIRONMENT

Two groups of ringtailed lemurs (Lc1 and Lc2 Groups) at the DUPC served as study subjects. These lemur groups live year-round in natural habitat enclosures (NHE-2: 3.5 ha; NHE-4: 5 ha) composed of mixed pine/hardwood forest surrounded by a mildly electrified fence. A 10-m swath between the fence and the forest vegetation prevents the lemurs from escaping. The lemurs are provisioned with monkey chow and mixed cut fruit twice weekly, and spend much of their time daily foraging for local flora. All lemurs in the NHE's wear individually-indentifiable collars and tags.

Lc1 Group was introduced into NHE-2 in 1983 after living in another enclosure (NHE-1: 0.5 ha) since 1981. During the study period (November 1988 – April 1990), Lc1 Group contained 11 adults (3 or more years of age) and between 10 and 24 immatures, and Lc2 Group contained 5 adults and 6 immatures. Lc2 Group was introduced into NHE-4 in two stages: adult females and dependent offspring in 1987 and adult males in 1988.

EXPERIMENT 1

MATERIALS AND PLAYBACK PROTOCOL

In the first experiment, calls of three avian species (red-tailed hawk: Buteo jamaicensis; Madagascar harrier hawk: Polyboroides radiatus; wood thrush: Hylocichla mustelina) and one mammal species (Eastern gray squirrel: Sciurus carolinensis) were broadcast to the lemurs to investigate the effects of call structure, call amplitude, and experience (i.e. prior association of calls with their producers) on elicitation of antiraptor behavior (Fig. 3). Each call type permitted one of the three variables to be manipulated while the others were held constant (Table 1). Note that whereas all individuals in both ringtailed lemur groups were familiar with the red-tailed hawk, thrush, and squirrel calls, no member of either group had heard the call of a Madagascar harrier hawk previously.

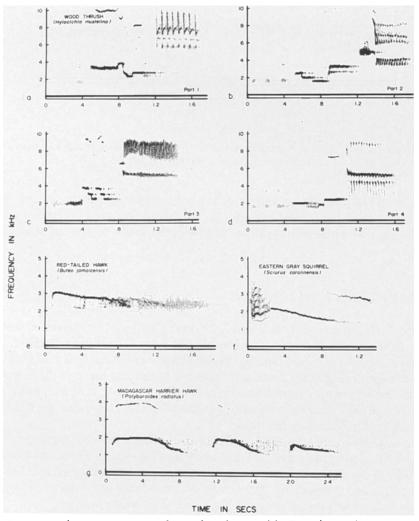


Fig. 3. Representative spectrograms of sound probes used in Experiment 1.

| Table 1. | Relationships | of call ty | ypes broadcast | and variables | investigated in | Experiment 1. |
|----------|---------------|------------|----------------|---------------|-----------------|---------------|
| | | | | | | |

| Vocalization | Structure | Relative amplitude | Prior experience |
|--------------------|-----------------------------|--------------------|------------------|
| Red-tailed hawk | Simple, descending whistles | High | yes |
| Madagascar harrier | Simple, descending whistles | High | no |
| Gray squirrel | Simple, descending whistles | Low | yes |
| Wood thrush | Complex | Intermediate | yes |

Table 2. Playback amplitudes in Experiments 1 and 2.*

| Vocalization | Playback amplitude label | Relative playback amplitude | Decibel range |
|--------------------|--------------------------|-----------------------------|---------------|
| Red-tailed hawk | Natural | High | 71 – 72 |
| | Experimental | Low | 55 – 56 |
| Madagascar harrier | Natural | High | 70 - 72 |
| - | Experimental | Low | 55 - 56 |
| Gray squirrel | Natural | Low | 54 – 56 |
| | Experimental | High | 70 - 73 |
| Wood thrush | Natural | Intermediate | 66 - 68 |
| | Experimental | High | 78 - 80 |

^{*}Amplitude measured at 11 m from source (see text).

A playback cassette containing exemplars of calls from the bird and mammal species was assembled from field recordings. Although red-tailed hawk and gray squirrel calls each contained a single continuous sound unit (Figs. 3e & 3f), Madagascar harrier hawk calls contained three sound units (Fig. 3g). Each part of the wood thrush song (Figs. 3a – 3d) was separated by a natural pause of two to four seconds. Natural call repetition rate was similar for avian call exemplars (red-tailed hawk: .220 calls/sec; Madagascar harrier: .139 calls/sec; wood thrush: .191 calls/sec), and the squirrel call was dubbed at an equivalent repetition rate (.184 calls/sec). Playbacks were conducted at two quantified amplitude levels: one that was considered "natural" sounding at a distance of 11 m (i.e. "natural amplitude", or NA), and an experimental amplitude (EA) (Table 2). Decibel measurements were made with a Realistic sound level meter ("A" weighting, fast response). For calls of relatively high natural amplitude (those of the hawks), the experimental amplitude was reduced to foster the impression of a hawk calling in the distance; for calls of relatively lower natural amplitudes (those of the squirrel and thrush), experimental amplitudes were increased to the NA level of the hawk calls or greater.

In playback trials, approximately 60 sec of a given call type was broadcast from a Sony TC-D5M cassette recorder over a speaker (Mineroff Electronics Field Speaker or Acoustic Research "Powered Partners") that was concealed in ground vegetation 10-15 m from most subjects. Selection of the call to be played back on a given day was randomized, and at least 24 hr separated trials for each group. Playbacks were not conducted if the study groups were in visual contact, and were aborted if some significant disturbance occurred during location of a study group or during preparation for a trial. Sixteen trials, all of which were video taped (Panasonic PK-958 video camera with on-screen chronometer), were completed successfully for each group between late November and mid-December 1988.

RESPONSES SCORED AND DATA ANALYSIS

Data were gathered on two variables, "bipedal locomotion" and "leaping onto tree trunks," both of which had been exhibited by Lc1 group in response to airborne and perched hawks. Bipedal locomotion was restricted almost solely to Lc1 Group, where it was

a reliable indicator of perceived avian predator threat (MACEDONIA, in prep; PEREIRA & MACEDONIA, in press). Ringtailed lemurs that leap onto tree trunks in response to low-flying hawks use the tree as a shield against a potential attack. The number of subjects exhibiting these responses during playback trials was quantified by reviewing the video tapes. In all trials, subjects exhibited one response or the other, not both. For bipedal locomotion to be scored as a response, subjects were required only to stand bipedally and take one step, although once initiating this behavior most subjects traveled at least several meters bipedally. Positive identification of all respondents was not always possible; care was taken, however, to score each respondent only once per trial. Pairwise significance tests (2 × 2 G-test with Williams' correction: Sokal & Rolf, 1969) were used to compare response frequencies of subjects to all NA vs NA, and NA vs EA playbacks.

Because playbacks lasted approximately 60 sec and the number of respondents in trials was scored across the duration of the playback, the responses of some subjects may have been influenced by those of others. Nevertheless, opportunity for intersubject influence was roughly equivalent across trials. Several trials were conducted with each acoustic probe and the number of respondents to each type of probe exceeded, only in Experiment 1, the total number of subjects in the groups tested. Thus, statistical outcomes of this experiment should be viewed with a degree of caution (e.g. MACHLIS et al., 1985).

RESULTS

Bipedal Response

Although the propensity of bipedal locomotion was consistent within each study group across NA playbacks of red-tailed hawk and Madagascar harrier hawk calls, the level of responsiveness differed dramatically in the two groups: Lc1 Group subjects responded bipedally to playbacks of both species' calls (Fig. 4a), whereas Lc2 Group members did not respond bipedally to either species' call (Fig. 4b). Further examination of Lc1 Group's responses showed that NA playbacks of the hawk calls (both species combined) elicited significantly more bipedal locomotion than did EA (low amplitude) playbacks of the same calls or playbacks of thrush song at any amplitude (Fig. 5a). More individuals exhibited

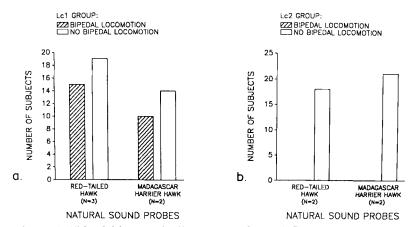


Fig. 4. Experiment 1: "bipedal locomotion" response of a. Lc1 Group; b. Lc2 Group to "natural amplitude", or "NA" playbacks (see text), of red-tailed hawk and Madagascar harrier hawk calls. N=No. of playbacks.

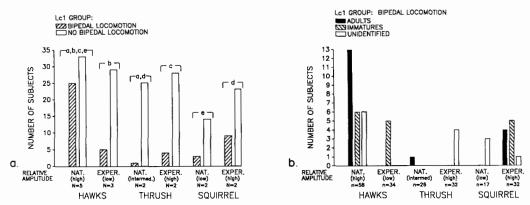


Fig. 5. Experiment 1: "bipedal locomotion" response of Lcl Group to a. NA and experimental amplitude (EA) playbacks of all sound probes; N=number of playbacks; bars with same letter are significant at the following levels: a=p<.001: b, c=p<.005; d=p<.025; e=.05< p<.1; b. bipedal locomotion response by age-class: n=total number of subjects.

bipedal locomotion in response to NA hawk call playbacks than to NA (low amplitude) squirrel call playbacks, but not to EA (high amplitude) squirrel call playbacks. EA squirrel call playbacks elicited significantly more bipedal locomotion than NA (intermediate amplitude) thrush call playbacks. Adults and immatures appeared to respond with bipedal locomotion similarly across call types except that, unlike adults, immatures also responded to EA (low-amplitude) hawk call playbacks (Fig. 5b). Bipedal locomotion by ageclass was not examined statistically due to inability to verify identities (and thus ageclasses) of all subjects.

Leaping Response

Where identities were confirmed for this response, most Lc1 Group subjects were immatures. Lc2 Group differed from Lc1 Group in that this was the only response exhibited consistently to playbacks by Lc2 Group adults and immatures. Also in contrast to Lc1 Group

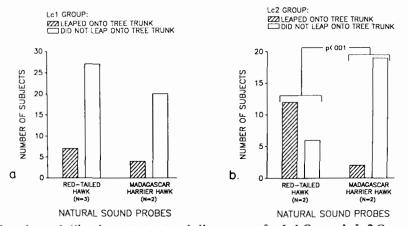
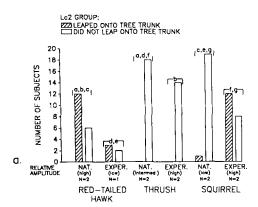


Fig. 6. Experiment 1: "leaping onto tree trunks" response of a. Lc1 Group; b. Lc2 Group to NA playbacks of red-tailed hawk and Madagascar harrier hawk calls. N=No. of playbacks.



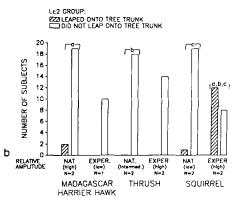


Fig. 7. Experiment 1: "leaping onto tree trunks" response of Lc2 Group to a. NA and EA playbacks of red-tailed hawk, wood thrush, and Eastern gray squirrel calls; N = number of playbacks. Bars with same letter are significant at the following levels: a, b, c, f, g = p < .001; d = p < .005; e = p < .025; b. Madagascar harrier hawk, wood thrush, and Eastern gray squirrel calls. Bars with same letter are significant at the following levels: a, b, c = p < .001; N = number of playbacks.

(Fig. 6a), members of Lc2 Group leapt onto tree trunks significantly more often in response to NA playbacks of red-tailed hawk calls than to playbacks of Madagascar harrier hawk calls (Fig. 6b). More Lc2 Group subjects responded with leaping to NA and EA (low amplitude) red-tailed hawk call playbacks, and to EA (high amplitude) squirrel call playbacks, than did not respond to these calls (Fig. 7a). Responses did not differ significantly among paris of these three playback conditions (i.e. NA red-tailed hawk, EA red-tailed hawk, and EA squirrel) but each differed significantly from all other playback types paired with them (Fig. 7a). Unlike responses to red-tailed hawk call playbacks, significantly fewer Lc2 Group subjects exhibited the leaping response to NA Madagascar harrier hawk call playbacks than to EA (high amplitude) squirrel call playbacks (Fig. 7b).

EXPERIMENT 2

MATERIALS AND PROTOCOL

In the second experiment, the red-tailed hawk calls and wood thrush song were played back normally and in reverse to investigate whether the exact ordering and conformation of call/song components, or simply the presence of the components *per se*, was important for discriminating calls of large hawks from other sounds. This forward/reverse playback design served, in a broad sense, as an acoustic analog to the "hawk/goose" silhouette of Tinbergen and Lorenz (e.g. TINBERGEN, 1939; MACEDONIA & POLAK, 1989) which mimicked a threatening avian stimulus only when presented in the "hawk" direction of motion.

The normal (forward) red-tailed hawk calls and wood thrush song exemplars used were those presented in Experiment 1. The reversed-direction sequences were constructed by dubbing the original cassette recordings onto a stereo reel-to-reel recorder (Tandberg 15-21), turning the tape over, and recording it back onto the cassette deck. A Krohn-Hite low-band-pass filter was used to attenuate introduction of high-frequency tape "hiss." All sound probes played back measured 70-72db at 11 m from the source, and playback order

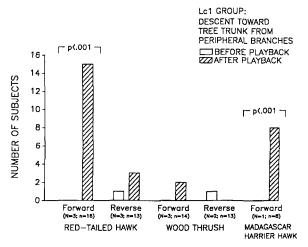
was randomized across the 12 trials. All trials were conducted during the first three weeks of April 1989 with lemurs foraging in the terminal branches of trees. As arboreal foraging was not a group-coordinated activity in Lc2 Group, only Lc1 Group was tested in Experiment 2. Playbacks were concentrated between about 16:30 and 17:30 Eastern Standard Time, when feeding on buds and flowers by the lemurs was maximal and movement within and between trees was minimal.

RESPONSE SCORED

The response scored in this experiment was the number of subjects moving downward and/or inward from peripheral branches toward the tree trunk during the time it took four exemplars of a sound probe to be played back (16 sec), as compared to the number of subjects exhibiting the same behavior in the 16 sec prior to the playback. Mammals seem highly vulnerable to raptorial predation when foraging in the terminal branch milieu because exposure is great and manueverability difficult. Consequently, fleeing terminal branches as an antiraptor response is widespread across primate taxa (e.g. vervets: SEYFARTH et al., 1980; capuchins: VAN SCHAIK & VAN NOORDWIJK, 1989; ringtailed lemurs: JOLLY, 1966; crowned lemurs: WILSON et al., 1989)

RESULTS

A significantly greater number of subjects moved downward and/or inward from peripheral branches toward tree trunks during than before playbacks *only* in the case of forward-played hawk calls (Fig. 8). The single playback of the Madagascar harrier hawk calls was unplanned but the result (Fig. 8) demonstrates that Lcl Group members, whether on the ground or in the trees, responded with equal vigor to both hawk species' calls.



NATURAL AND EXPERIMENTAL SOUND PROBES

Fig. 8. Experiment 2: "Descent toward tree trunk from peripheral branches" response in Lcl Group to forward and reverse sound probe playbacks. N=number of playbacks; n=number of subjects.

EXPERIMENT 3

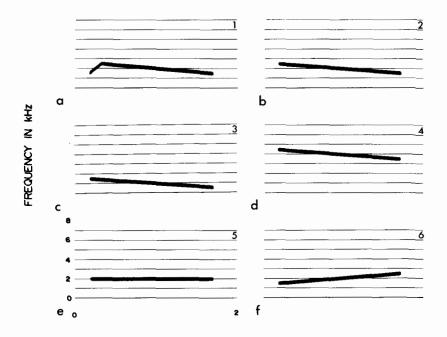
MATERIALS AND PLAYBACK PROTOCOL

In this final experiment, the acoustic cues potentially responsible for evoking antiraptor behavior in Lc1 Group were investigated more precisely by playing back simplified synthetic versions of *Buteo* sp. advertisement calls that varied independently (a) fundamental frequency, (b) frequency slope, and (c) presence/absence of a frequency-modulated call onset. Six synthetic sound probes (Fig. 9) were generated using the acoustic signal analysis program "SIGNAL" (BEEMAN, 1989). Each digital sound was constructed with a sine wave that, with the exception of Probe 5 (Fig. 9e), sloped 1 kHz across a 1.5 sec time window. The sounds were stored first as SIGNAL files, then were converted to analog signals and output to the cassette recorder. The sequences used for playback consisted of five identical (1.5 sec) signals with 2 sec of silence between each signal.

Playbacks were broadcast to Lc1 Group from the last week of March through the third week of April 1990, and were concentrated between 16:45 and 17:15 Eastern Standard Time. Two full sets and one partial set of playbacks of the six synthetic sound probes were conducted. In both sets of six trials the sound probes were presented in the order: b-c-d-f-a-e, with respect to Figure 9. The response scored in this experiment was the same as in Experiment 2 (i.e. fleeing terminal branches).

RESULTS

Due to the apparent occurrence of habituation during Set 2 (see below), results for each set of playbacks are presented separately and were not analyzed statistically (Fig. 10). Over-



TIME IN SECS

Fig. 9. a-f. The six synthetic sound probes broadcast in Experiment 3. The number in the upper right-hand corner of each sonogram corresponds to Probes 1-6 in Fig. 10.

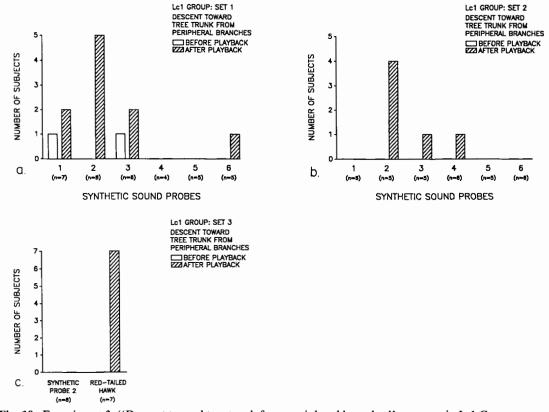


Fig. 10. Experiment 3: "Descent toward tree trunk from peripheral branches" response in Lc1 Group to playbacks of synthetic sound probe; n=number of subjects observed. Probe numbers 1-6 correspond to a-f in Fig. 9.

all responses to the synthetic sound probes were rather weak. In both full sets, the probe that elicited the strongest response was the simple tone descending from 2.5 to 1.5 kHz (Probe 2: Fig. 9b). On the third trial that this sound probe was broadcast, however, it failed to elicit the scored response from any of the eight subjects observed (Fig. 10c). Therefore, on another day five calls from the red-tailed hawk call sequence used in Experiments 1 and 2 were played back to discern whether subjects had habituated to the synthetic sound stimuli or to the playback procedure. All subjects observed (N=7) responded to the playback of the red-tailed hawk call by climbing inward and/or downward from the terminal branches (Fig. 10c).

DISCUSSION

Based on observations that the advertisement calls of red-tailed hawks elicited antiraptor behavior in forest-living ringtailed lemurs at the Duke University Primate Center, this play-back study set out to determine what acoustic cues were being used by the lemurs to discriminate these calls from other environmental sounds. For both study groups, playbacks of wood thrush song rarely elicited antiraptor behavior at any playback amplitude, whereas playbacks of red-tailed hawk and Eastern gray squirrel calls elicited appreciable antiraptor responses when broadcast at an amplitude simulating a hawk calling nearby. Immatures in

Lc1 Group proved to be a minor exception in that they responded with bipedal locomotion on occasion to low-amplitude hawk call playbacks. This result could reflect, among other possibilities, a poorer performance of immatures in estimating distances of calling hawks via call amplitude. Overall results from Experiment 1 seemed to suggest that the long frequency downslope and/or a sharp, frequency-modulated onset (present in both hawk species' calls and in the squirrel call but not in woodthrush song) may be pertinent discrimination cues.

The lack of antiraptor response in Lc1 Group to playbacks of reversed woodthrush song and red-tailed hawk calls in Experiment 2 suggests that stimulus novelty, per se, does not play a role in eliciting antiraptor behavior from these lemurs. Moreover, responses indicate that an acoustic "mirror image" of a red-tailed hawk call is not recognized as a call from a large hawk. The relative importance of call slope direction and FM onset (as well as call fundamental frequency) were examined further in Experiment 3 by playing back synthetic sound probes that manipulated these variables independently. Responses of Lc1 Group to the playbacks suggest that a sharp, frequency-modulated onset, which is a common feature of the advertisement calls of many large hawk species (e.g. Figs. 1 & 3), is relatively unimportant in "hawk call" recognition. Acoustic features that did appear to be important to Lc1 Group were the presence of a (relatively long) tone with a negative frequency slope, and a frequency range (among those tested) between 1.5 and 2.5 kHz. The upper bound of this frequency range must extend at least to 3 kHz, however, which is the onset peak frequency of the red-tailed hawk calls broadcast in Experiments 1 and 2. The list of variables manipulated here was not exhaustive, and other acoustic features (e.g. call bandwidth, call duration, slope descent rate, and unit repetition rate) also may have salience in the discrimination between calls of large hawks and other environmental sounds.

Another important finding in this study was that forest-experienced and inexperienced ringtailed lemur groups responded very differently to playbacks of calls from a large hawk species that was unfamiliar to them. Equivalent amounts of bipedal locomotion in Lcl Group in response to playbacks of calls from familiar (red-tailed hawk) and unfamiliar (Madagascar harrier) hawks might indicate that subjects failed to discriminate between the two species' calls; alternatively, this result could indicate that the two species' calls were discriminated between, but were classified in the same category (i.e. "calls from large hawks"). Although the first explanation may be more parsimonious, evidence suggests that it may not best explain the data. For example, responses of the inexperienced Lc2 Group revealed that they discriminated clearly between the two hawk species' calls. Were the "lack of discrimination" explanation to be favored for Lc1 Group, one must then accept that members of a group established in the forest for seven years were far less capable of discriminating between the calls of the two hawk species than were members of a group living in the same forest for a little over a year. This proposition seems unlikely.

A theoretical model that may shed light on this issue concerns the existence of category "prototypes" in the mind. As suggested by ROSCH (1977) and others (see SEYFARTH & CHENEY, 1986 for references), humans appear to classify stimuli in terms of prototypes, or mental category representatives, where novel stimuli are categorized subsequently on the basis of features shared with the pre-existing prototypes. As categories are filled with increasing numbers of stimuli, the resemblances between those stimuli and the category prototype decrease to the point where a new category with a new prototype must be formed. Thus, if "calls from large hawks" were representative of a category in the minds of the DUPC forest-living ringtailed lemurs, for which the category prototype was the call of the familiar red-tailed hawk, then the breadth of acceptable category members would be expected to covary with experience until new (finer) categorical delineations were required.

Consider the following. The less-common red-shouldered hawk (Buteo lineatus), which has a call somewhat different than that of the red-tailed hawk (Fig. 1), was seen and heard only rarely in the forested enclosures (J.M.M., pers. obs.). Nevertheless, the number of red-shouldered hawks (as well as those of seasonally-present raptor species) that would be seen and heard over the years would accumulate such that the perceptual category of "calls from large hawks" for many Lc1 Group members might be expected to acommodate those of a number of hawk species. By comparison, the same category of "calls from large hawks" in the minds of Lc2 Group members might be expected, due to the lack of experience, to contain few or no members other than the category prototype, i.e. the locally-common red-tailed hawk. If true, this would explain why the gray squirrel's call, with a single, long descending frequency slope evoked antiraptor responses from Lc2 Group of equal strength to those of the red-tailed hawk, whereas the Madagascar harrier hawk's call, with three shorter units, did not. It likewise would explain why, when broadcast at an amplitude simulating that of a nearby hawk, both hawk species' calls as well as those of the gray squirrel elicited antiraptor responses from the more experienced Lc1 Group.

The generally weak responses of Lc1 Group to playbacks of the synthetic sound probes in Experiment 3 might have stemmed from an absence of acoustic subtleties in these sounds which are present in actual animal vocalizations. Although the sound probe that elicited the strongest responses was in the same frequency range as the advertisement calls of many *Buteo* sp. hawks (Probe 2: Fig. 9b), it was surprising that what was designed to be the most "realistic" probe (Probe 1: Fig. 9a) elicited such a low level of antiraptor response. One possible explanation for this result is that, because the Duke Forest is an enclave surrounded by suburban areas, the rising-and-falling, tonal sound of the "realistic" probe may have been perceived by Lc1 Group as more similar to a police siren than to the call of a large hawk.

Although the ringtailed lemurs habituated to the synthetic call playbacks rather quickly, the final playback of red-tailed hawk calls indicated clearly that the habituation was to the sounds being broadcast and not to the playback protocol. One factor promoting habituation may have been that, unlike calling hawks who sometimes also are seen, the synthetic sounds never were associated with the sight of a call emitter. Whether or not ringtailed lemurs would attend preferentially to a synthetic sound probe that was accompanied by the visual image of a raptor would be worth future investigation.

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Authors' Names and Present Addresses: Joseph M. Macedonia, Department of Zoology, University of California, Davis, California 95616-8755, U. S. A.; Pamela L. Yount, Department of Zoology, Duke University, Durham, North Carolina, 27705, U. S. A.