# VISUAL ASSESSMENT OF AVIAN THREAT IN SEMI-CAPTIVE RINGTAILED LEMURS (LEMUR CATTA)

by

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## Introduction

For well over half a century ethologists have been intrigued by the apparent discrimination shown by avian subjects between raptor and non-raptor flight silhouettes (see SCHLEIDT, 1961; GRAY, 1966, and MÜLLER & PARKER, 1980 for reviews). Early observational work led HEINROTH (1928, as cited in SCHLEIDT, 1961) to propose that the short neck of raptors, in conjunction with their relative rarity, was of primary importance in recognition by birds of the raptor flight silhouette. Later, LORENZ and TINBERGEN (e.g. LORENZ, 1939; TINBERGEN, 1939) examined this idea experimentally by pulling cardboard flight silhouettes of various bird species along a wire overhead of young geese, ducks, and turkeys. These experiments included their well-known "hawk/goose" configuration that appeared as a hawk moving in one direction and as a goose moving in the other. Whereas young geese and ducks did not respond differentially to the two flight directions, young turkeys emitted more

warning calls in response to the hawk direction of flight (LORENZ, 1939).

Although LORENZ (1939) stressed the correlation between a silhouette's relative speed (*i.e.* speed measured in silhouette lengths) and the reaction that it elicited, the appeal of the "short-neck hypothesis" led to its wide acceptance in explaining how birds recognize the raptor shape (*e.g.* TINBERGEN, 1939). Experience of test subjects to naturally-occurring birds, however, was not well-controlled in these early experiments.

SCHLEIDT (1961) addressed the issues of experience, silhouette shape, and silhouette relative speed in a comprehensive study with experienced and inexperienced turkey hens. He showed that the relative rarity with which a silhouette was presented determined the level of response observed: infrequent silhouettes elicited the strongest responses, regardless of neck length. The stronger responses shown by some birds to the hawk shape in prior experiments therefore was interpreted as a result of subjects' greater exposure (*i.e.* habituation) to long-necked than to short-necked silhouettes in nature.

To date, experimental research into raptor/non-raptor flight silhouette discrimination has been limited to a few species of birds as test subjects. Also, whereas many species emit vocalizations in response to avian stimuli perceived as threatening, only a few studies have used antiraptor calls as a measure of such perception (*e.g.* LORENZ, 1939; SCHLEIDT, 1961).

Ringtailed lemurs possess two types of antiraptor calls that are elicited only by aerial/avian stimuli. The "rasp" (Fig. 1a-c) is a relatively low-amplitude but highly-localizable vocalization that typically is elicited by raptors outside of immediate attack range. The rasp's apparent function is to inform nearby group members of a raptor's presence without attracting the predator's attention. In contrast, the "shriek" (Fig. 1e, f) is a high-amplitude call that is given when raptors are near enough to make escaping their detection unlikely. Shrieks often are emitted synchronously by several group members, and seem to function to broadcast detection of a nearby raptor to group members as well to inform the predator that is has been seen.

Here we report the results of an experimental investigation of raptor/nonraptor visual discrimination in semi-captive ringtailed lemurs (*Lemur catta*). Because the study group's long tenure in a forested environment (approximately seven years) had exposed its members to many kinds of brids, our work cannot address any potentially innate capacity for recognition of the raptor shape. Rather, we investigated the lemurs' abilities to classify overhead silhouettes as potentially threatening or not
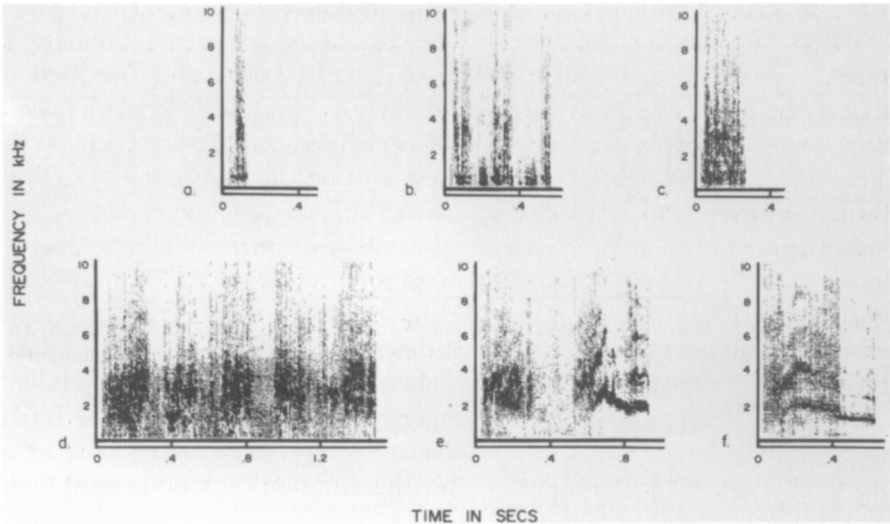
Fig. 1. Audiospectrograms of ringtailed lemur antiraptor vocalizations. (a) rasp; (b) three rapid and consecutive rasps emitted by a single individual (lower frequency pulses between rasps are inhalations); (c) longer rasp; (d) five rasp/shriek hybrids (several individuals); (e) rasp/shriek hybrid followed by shriek; (f) typical shriek: wide-band noise component overlays tonal bands only during first part of call.

by measuring antiraptor calling in response to silhouette presentations.

Like immature vervet monkeys (*Cercopithecus aethiops*; SEYFARTH & CHENEY, 1980, 1986), immature ringtailed lemurs are less discriminating of predators and non-predators than are adults (see Results). Inclusion of responses from immatures in our analyses therefore provides a conservative estimate of adult ringtailed lemurs' discriminative abilities.

**Methods and materials**

*Subjects and housing.*

A group of ringtailed lemurs (Lc1 Group) inhabiting a 3.5 ha natural habitat enclosure (NHE-2) at the Duke University Primate Center (DUPC) served as study subjects. Subjects' ages ranged between 9 months and 17 years (median = 4 years; n = 31), and all but the oldest male and female in Lc1 Group had lived in the Duke Forest since weaning or birth. The DUPC natural habitat enclosures have been described in detail elsewhere (*e.g.* PEREIRA et al., 1987).

*Apparatus and silhouette presentation.*

Five silhouettes were presented to the lemurs in nine configurations (Table 1; Fig. 2). Each shape was cut from 3/8-in plywood and painted black. The proportions of the stylized hawk/goose shape (Fig. 2b) were derived from TINBERGEN's original figure (1939; his Fig. 5).

TABLE 1. Dimensions of experimental aerial silhouettes[1-4])

| Shape | Size | Length | Width |
|-------|------|--------|-------|
| *Buteo* silhouette | large | 48 | 107 |
| Hawk/goose silhouette | large | 85 | 70 |
| | small | 42 | 34 |
| Diamond silhouette | large | 85 | 85 |
| | small | 42 | 42 |
| Square silhouette | large | 60 | 60 |
| | small | 30 | 30 |

1) Measurements in cm. 2) Realistic hawk shape traced from a museum specimen of an adult red-tailed hawk (*Buteo jamaicensis*). 3) Stylized hawk and goose are same silhouette flown in opposite directions. 4) Diamond and square are same silhouette presented in different orientations.

The silhouettes were presented on horizontal flight path runs constructed at three sites visited frequently by Lc1 Group (Fig. 3). For each run, a length of 1.6 mm aircraft cable was strung between two trees above a platform (0.9 x 1.2 m) affixed to each tree (platform height: median = 8.7 m; range = 8.0 m-9.5 m; n = 6). The tops of the platforms also were painted black to reduce visibility of the silhouettes from above. When a cord attached to the front of a silhouette was pulled downward two pulleys on the cable transported the silhouette between platforms (Fig. 4). This mode of operation made it difficult to control precisely silhouette flight speed. Therefore, potential effects of relative flight speed on responses were addressed statistically.

The "test arena" for each apparatus was defined in length by the trees supporting the run and in width by other natural objects (*e.g.* trees or logs; #1: 18.9 m x 13.8 m; #: 15.2 m x 8.8 m; #3: 18.3 m x 14.6 m). Silhouettes readied for presentation rested 2-3 cm above their platforms and could not be seen from the ground.

Thirty-five trials were conducted between late November, 1987 and early May, 1988 with a median interval between trials of three days (range = 1-23 days). Trials were ordered to minimize repetition of silhouette shape, size, and direction of presentation. Recent ranging patterns of the lemurs dictated to some extent where a trial would be carried out on a given day. Trials were conducted 10 to 15 minutes after a subgroup of Lc1 Group had settled in a test arena and was unaccompanied by another lemur species. All subjects were required to be on the ground. Impending trials were aborted if an antipredator call was emitted, a large bird was sighted by the group, or some other notable disturbance occurred beforehand. Following a trial the presented silhouette was replaced with a different one after all subjects had vacated the area.

*Recording and analysis of vocalizations.*

Audio recordings during trials were made with a Sony TC-D5M cassette recorder onto TDK-ADX recording tape using a highly-directional Sennheiser ME-88 microphone. The frequency response of this equipment is linear between 50 Hz and 15 kHz. All trials were video taped with a Panasonic PK-958 video camera and PV-4500 recorder. Durations of antiraptor calls (Fig. 1) were measured on a Uniscan II real-time audio spectrum analyzer (Unigon Industries) at a time resolution of 6.5 ms. Low-amplitude sounds of the silhouettes leaving one platform and arriving at the other allowed flight durations also to measured.

As in other studies of antipredator calls (*e.g.* OWINGS *et al.*, 1986) callers could not always be identified. Therefore, the calls themselves (*cf.* individual subjects) comprise our
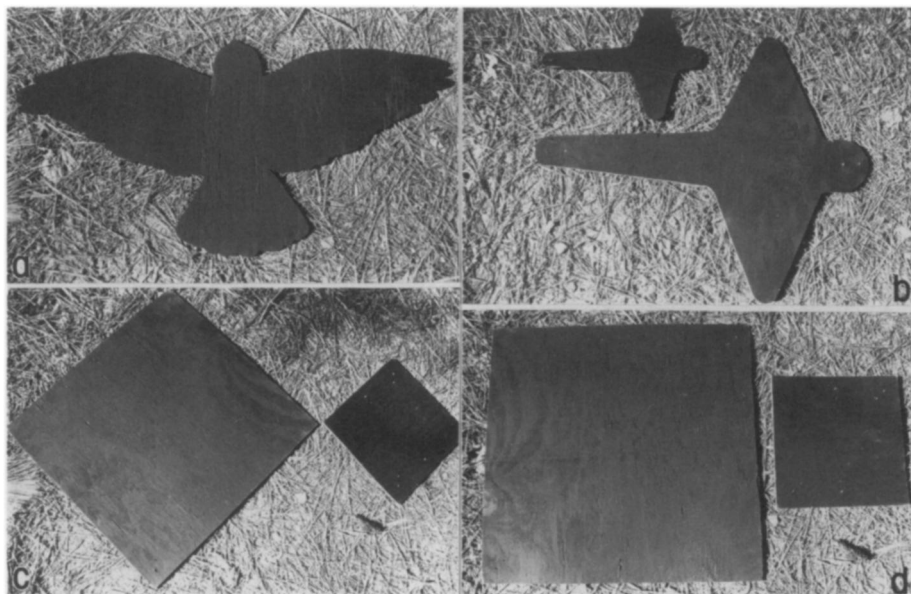
Fig. 2. Plywood silhouettes used as test stimuli: (a) *Buteo* sp. silhouette traced from museum specimen of a red-tailed hawk (*Buteo jamaicensis*); (b) stylized hawk/goose silhouettes; (c) diamond silhouettes; (d) square silhouettes.
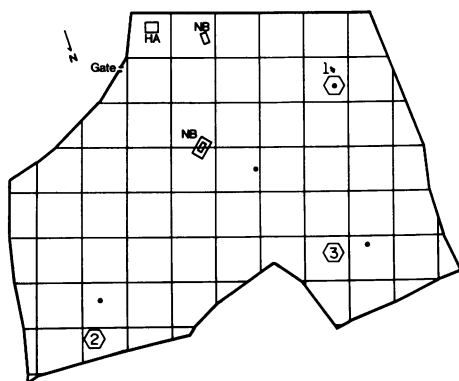


Fig. 3. Diagram of study site (NHE-2). Hexagons indicate the three test apparatus locations. The small black dots indicate locations of chow hoppers. HA = heating area used by the lemurs in cold weather; NB = heated shelters.

units of analysis. Non-parametric significance tests (Kruskall-Wallis One-Way ANOVA, Mann-Whitney U test) carried out with SPSS-PC software (SPSS, Inc.) were used to analyze antiraptor call responses according to (a) call duration (*i.e.* durations of discrete calls), and (b) total calling per trial (*i.e.* the sum of call durations for a trial). Where n > 30

Fig. 4. View from the ground of (a) *Buteo* silhouette; (b) stylized hawk leaving or goose arriving at a platform.

SPSS-PC transformed the Mann-Whitney U into a normally distributed Z statistic. Because intermediate forms of rasps and shrieks sometimes occurred (Fig. 1d), the two call types were grouped together for analysis. Explicit predictions of test outcomes were not made *a priori*, and all significance tests were two-tailed.

Correlations (Pearson's r) between the two call measures and three potentialy confounding variables were examined: (a) number of subjects present in a trial, (b) silhouette flight duration, and (c) position of a trial in the 35-trial sequence. Antiraptor calls emitted in response to naturally-occurring stimuli were noted as well.

## Results

None of the three uncontrolled variables differed significantly across the large or small silhouette types (df = 4: large silhouettes, df = 3: small silhouettes; all p's > .05). Therefore, the correlations shown below did not influence the outcomes of the pairwise significance tests. Relative flight speed differed significantly across the nine silhouette configurations (H = 24.10, df = 8, p < .01). However, when taking into account the antiraptor call responses of the lemurs to the different silhouettes no consistent relationship between relative flight speed and antipredator call duration was evident.

Total calling per trial (n = 35) was not significantly correlated with number of subjects (mean = 10.3 subjects/trial, S.D. = 4.7, r = .05, p = .77) or with silhouette flight duration (mean = 9.0 s, S.D. = 2.5 s, r = .13, p = .48). Earlier trials, however, elicited more calling than later trials (r = -.32, p = .06). Individual call durations (n = 121) were not significantly correlated with trial number (r = -.02, p = .85) or silhouette flight duration (r = -.04, p = .65), but were significantly correlated with number of subjects (r = .20, p = .03).

The only shape whose large and small sizes elicited significantly different responses was that of the stylized hawk. The large hawk elicited both significantly more calling per trial ($n_1 = 5$, $n_2 = 5$, U = 0, p < .01) and longer individual call durations (n1 = 44, n2 = 10, Z = -3.25, p < .01) than did the small hawk. Differences in total calling per trial were not significant between any pairs of the small silhouettes, but differed among the large silhouettes between the hawk shapes and the square shape (Fig. 5).

Individual calls did not differ significantly in duration between the two large hawk shapes, but both hawk shapes elicited significantly longer calls than did the large goose shape and the large square shape (Fig. 6a). Call durations did not differ, however, between the large hawk shapes and the diamond shape. Similarly, the large goose shape elicited significantly longer calls than the large square but not the large diamond shape. The

Fig. 5a, b. Median and range values for total calling per trial (sum of calls) in response to large and small silhouettes. Sample size (n) is total number of trials of a given silhouette type. Asterisks denote values out of graph range (large hawk: 737 msecs; small diamond: 68 msecs). Trials in which no calling occurred were assigned a value of 0 (*e.g. small quare*).

small hawk shape elicited significantly longer individual calls than did the small square shape (Fig. 6b). No other comparisons of individual call durations among the small silhouettes were significant, although the goose shape typically elicited longer calls than the square shape.

All non-experimental stimuli that elicited antiraptor calls from adult lemurs (excluding low-flying helicopters: see below) were birds hawk-sized or larger (Fig. 7a). On the occasions (n = 7) where birds smaller than hawks elicited antiraptor calls from immatures (Fig. 7b) each caller had been startled by the sudden appearance of one of these birds at close range (approx. 2-10 m).
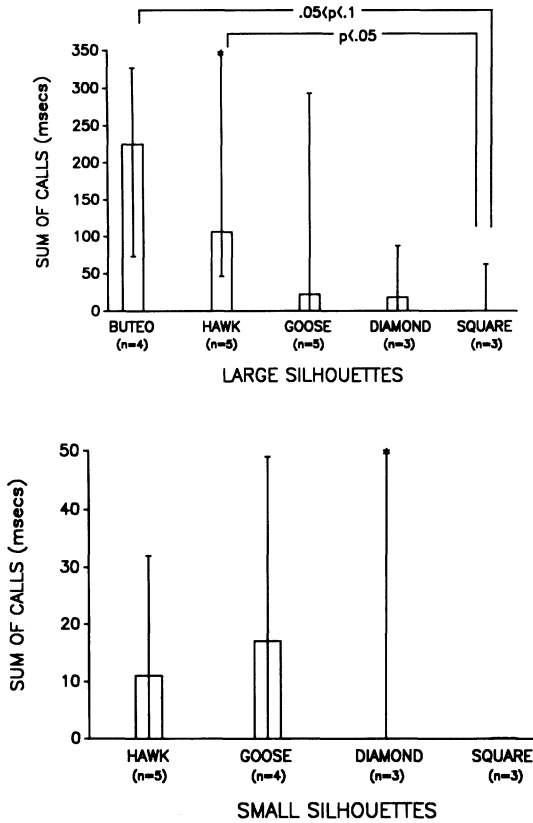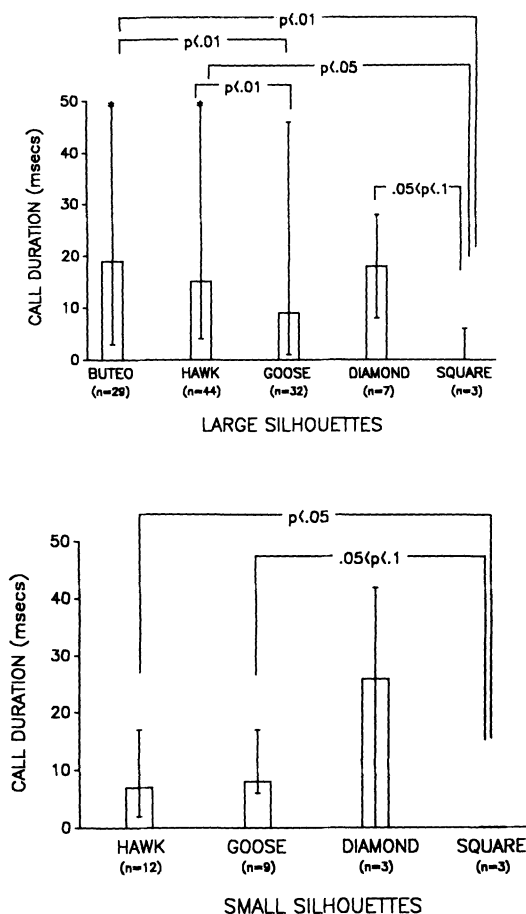
Fig. 6a, b. Median and range values for individual calls emitted in response to large and small silhouettes. Sample size (n) is total number of calls for a given silhouette type. Asterisks denote values out of graph range (*Buteo:* 68 msecs; large hawk: 80 msecs). Trials in which no calling occurred were assigned a value of 0 (*e.g.* small square).

The two types of non-raptorial birds that elicited antiraptor calls from adults, vultures and great blue herons, are larger than resident North Carolina raptors (Table 2). The silhouettes of vultures and raptors are very similar and may account for the apparent lack of discrimination. Likewise, herons fly with their necks looped back between their shoulders and present a "short-necked" (*i.e.* raptor-like) flight silhouette as well.

The "short-necked" hypothesis cannot extend, however, to antiraptor

calling elicited by low-flying helicopters. Although diverse aircraft regularly pass over the DUPC natural habitat enclosures, non-infant Lc1 Group members called only in response to low-flying helicopters (Fig. 7a). The sounds of approaching helicopters, but not those of other aircraft, also elicited other antiraptor responses from this lemur group.

Each aircraft passing overhead was noted between mid-March and early June 1989. Only aircraft judged qualitatively to be both low in altitude and within approximately 30 degrees of vertical were counted. In 29 h of observation a total of 22 airplanes, 18 jets, and 2 helicopters met the above criteria. Thus, in comparison to the other aircraft low-flying helicopters were rare (less than 5% of the sample).

ADULTS and
IMMATURES

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                           ANTIRAPTOR CALLS
                     ┌─────────── 39 ───────────┐
                   Avian                      Non–Avian
           ┌─────── 31 ───────┐                   │
          15                  16                   │
           │                   │                   │
        Raptors           Non–Raptors             │
        ┌────┐          ┌──────┬──────┐           │
       13     2         2      6      8            8
      red–   red–     black  turkey  great      low–
      tailed shouldered vulture vulture blue     flying
      hawk   hawk                      heron    helicopter
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IMMATURES
ONLY

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                           ANTIRAPTOR CALLS
                     ┌─────────── 9 ────────────┐
                     7                          2
                     │                          │
                   Avian                     Non–Avian
        ┌──────┬──────┬──────┬──────┐      ┌──────┬──────┐
        1      2      1      3             1             1
     mourning red–  pileated blue       low–        airborne
     dove   headed woodpecker jay      flying       trashbag
      (i)  woodpecker  (a)   (i,j,a)   airplane       (j)
            (j)                          (i)
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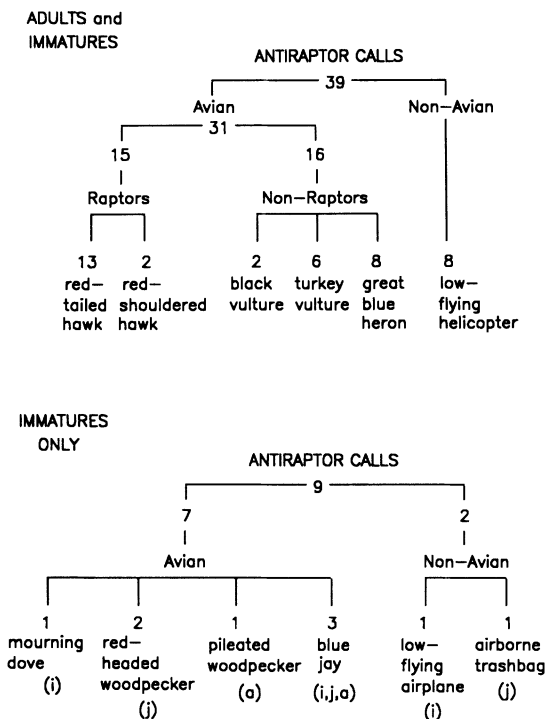
Fig. 7. The number of *incidents* where one or more ringtailed lemurs emitted an antiraptor call during behavioral observations between August 1987 and June 1989. Lower case letters in parentheses (bottom of figure) refer to cases where only certain ageclasses of immatures were observed calling: i = infant (<1 yr of age); j = juvenile (1-2 yrs of age); a = adolescent (2-3 yrs of age).

TABLE 2. Large birds encountered by the study group[1])

| Birds | Approximate mean wing length (cm) |
| --- | --- |
| Red-tailed hawk (*Buteo jamaicensis*) | 38 |
| Red-shouldered hawk (*Buteo lineatus*) | 33 |
| Turkey vulture (*Cathartes aura*) | 54 |
| Black vulture (*Coragyps atratus*) | 43 |
| Great blue heron (*Ardea herodias*) | 46 |

[1]) Wing lengths of hawks and vultures: BROWN & AMADON, 1968; wing length of heron: GODFREY, 1966.

## Discussion

Comparisons of individual call durations elicited by the large silhouettes suggest that (a) the realistic and stylized hawk shapes were perceived as equally threatening, (b) the hawk shapes were perceived as more threatening than the goose shape, and (c) the bird shapes were perceived as more threatening than the square, but not the diamond shape. Because total calling per trial was consistently low among the small shapes it appears that these silhouettes were perceived as relatively harmless overall.

The fact that the only significant comparison among the small silhouettes involved the hawk shape suggests that the variables of size and shape are additive in their effect on antipredator calling. Because large aerial objects warrant more initial caution than small ones they may elicit more calling in general and may stimulate more calling "mistakes" (*e.g.* SEYFARTH & CHENEY, 1980, 1986). This study has shown that, given suffi-cient raptor-like attributes, an aerial silhouette can elicit antiraptor call-ing even when small. It appears also that, regardless of its size, a square shape simply lacks too many raptor-like attributes to be classified as threatening by ringtailed lemurs. In contrast, the large diamond shape, with its relatively short and pointed leading edge, was perceived as raptor-like by at least some of the study subjects.

It could be argued, however, that the square shape elicited less calling per trial than when oriented as a diamond because of its shorter length and width (60 cm) relative to its path of motion (as diamond: 85 cm). This seems unlikely, given that small hawk, goose, and diamond silhouettes (dimensions in Table I) elicited more calling than did the large square.

SCHNEIRLA (1959) proposed that the differential responses of some bird species to hawk and goose shapes could be caused by different rates of change in retinal stimulation when viewing the two shapes: the hawk shape produces a more abrupt darkening of the visual field than does the goose shape. However, GREEN *et al.* (1968) found for mallards that neckless hawk and goose silhouettes, which produced very abrupt retinal darkening, did not elicit responses as great as those elicited by an unaltered hawk silhouette. Likewise, although our square silhouette produced a more abrupt rate of darkening across the retinas of the ringtailed lemurs than did the diamond shape, the responses to the "less abrupt" diamond shape were far greater than those elicited by the square. The results of these studies indicate that retinal stimulation "abruptness" is not the means whereby hawk and goose shapes are discriminated. Nevertheless, recognition of the raptor shape still must result from some particular pattern of retinal stimulation even if beyond that of abrupt retinal darkening.

It also could be argued that, because eagles are absent from mainland Madagascar, responses to the diamond shape may indicate that selection for predator discimination has been weaker in the lemurs than for some other primates (*e.g.* vervets: SEYFARTH *et al.*, 1980). Given Madagascar's size and proximity to the African continent, however, the absence of eagles from the island seems explainable only in light of the megafaunal extinctions known to have occurred there within historical times (see DEWAR, 1984, for a review). The current lack of a large raptorial avifauna on Madagascar therefore may be a consequence of the relatively recent disappearance of suitably-sized prey. If so, this would not reflect accurately the levels of predator pressure exerted on the lemurs throughout their evolutionary history. Regardless, several species of Malagasy hawks are large enough to take immature lemurs (see BROWN & AMADON, 1968), although only the Madagascar harrier hawk (*Polyboroides radiatus*) has so far been observed to do so. Given that the somewhat smaller redtailed hawk (Table 2) is capable of taking prey similar in size and weight to adult *L. catta* (*e.g.* a jackrabbit, *Lepus californicus:* JMM, pers. obs.) the Madagascar harrier probably can dispatch adults as well as immature ringtailed lemurs.

We cannot rule out the possibility, however, that the antiraptor calls elicited by the large diamond shape came primarily from immature subjects. The importance of experience in refining predator/non-predator discrimination has been addressed previously for several species of primates (*e.g.* SEYFARTH & CHENEY, 1980, 1986; MASATAKA, 1983;

MINEKA *et al.*, 1984). Like free-ranging vervet monkeys in East Africa (*e.g.* SEYFARTH & CHENEY, 1986) immature ringtailed lemurs, both in Madagascar and in this study, were more likely than adults to emit antiraptor calls in response to innocuous birds – particularly when those birds appeared suddenly at close range.

SCHLEIDT (1961) proposed that antipredator responses of naive turkeys were based primarily on differential amounts of exposure to different shapes: the rarest shapes elicited the strongest responses. SEYFARTH & CHENEY (1980) suggested, to the contrary, that SCHLEIDT's hypothesis is unlikely to be generally applicable: animals should respond to all types of predators that pose a threat to them regardless of the frequency with which each type is encountered. Actually, these two views are not incompatible. In ecological terms, raptors and other large carnivores are relatively rare because the energy available to consumers decreases with increasing trophic level. Carnivores therefore must be less common than herbivores. All else being equal, this could provide a basic means for animals to discriminate between potential predators and non-predators. On the other hand, a smaller, more common predator species might pose a greater threat to potential prey by virtue of sheer numbers than would a larger, more rare predator species.

Helicopters were the rarest of low-flying aircraft at the DUPC and were the only aircraft to elicit antiraptor calls from the study group. This finding supports SCHLEIDT's (1961) hypothesis. Why the large square silhouette did not evoke comparable antiraptor calling may be that (a) the additive effects of size and shape were not great enough for the square to be viewed as threatening, and/or (b) a completely novel stimulus may be perceived differently from one that simply is rare (*i.e.* hawk silhouettes were seen by the study group outside of experimental intervention). These issues currently are being investigated in the auditory mode by quantifying antiraptor responses of Lc1 Group to playbacks of acoustically-modified and unmodified raptor and non-raptor vocalizations.

**Summary**

Visual assessment of avian stimuli as threatening or non-threatening was investigated experimentally in semi-captive, forest-living ringtailed lemurs (*Lemur catta*). Subjects were presented silhouettes of different sizes and shapes on overhead runs. Antiraptor calls elicited by the silhouettes were recorded and quantified. Realistic and stylized hawk shapes elicited more total calling per trial than did a square shape. Large hawk shapes elicited longer individual calls than a large goose shape, and all bird shapes elicited longer calls than did a square but not a diamond shape. We suggest the observed response patterns reflect a differential in perceived avian threat and that they support an ecologically-oriented view of the "short neck" interpretation for raptor shape recognition.

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