PERCEPTUAL ASPECTS OF LEOPARD RECOGNITION BY WILD BONNET MACAQUES (MACACA RADIATA)

by

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Summary

This study examined the perceptual features of leopards (Panthera pardus) used as recognition cues by bonnet macaques (Macaca radiata) at three sites in southern India. Two of these sites were protected deciduous forest areas, the Mudumalai Wildlife Sanctuary and the Kalakad-Mundanthurai Tiger Reserve. The third study site was a predator-rare urban setting, Bangalore city. Four models were presented for 10-s intervals: (1) upright spotted leopard in a stalking profile with its head facing the subjects; (2) the same spotted model presented upside down; (3) a dark-brown leopard model with the same configuration as the spotted model; and finally (4), the dark-brown model presented upside down. The upright models characterized the two leopard morphs found in the wild — spotted and dark melanic. Inverted presentations of the spotted model examined the effects of the same configuration in an incongruous position to document whether leopard spots were still recognized. Differences between models were examined using alarm calls and flight elicitation as indices of fear. The spotted upright model was found to be the most feared, followed by the spotted upside-down model, the dark upright model, and finally the dark upside-down model. Analysis of when individuals looked at troop members to assess risks revealed that the spotted upright and dark upsidedown models engendered significantly lower frequencies of information seeking; the upright model typically engendered immediate flight and the dark upside-down model was generally ignored. The spotted upside-down model and the dark upright model engendered high rates

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of information seeking. These results appeared to reflect the importance of both spots and felid configuration in leopard recognition. Lower responsiveness to the dark upright model might reflect lack of experience with this rare melanic form.

Introduction

Studies of antipredator behavior have provided fertile topics for examining development, adaptive variation, and the convergent evolution of perceptual systems. Theoretical interest in this area is due, in part, to the ease with which selective regimes can be defined in relation to the functional properties of antipredator behavior. For studies of visual perception, presentations of predator models to prey species have shown that specific facial features, such as two facing eyes, are evocative to some mammals (Coss, 1978; Topál & Csányi, 1994), birds (Scaife, 1976; Inglis *et al.*, 1983), reptiles (Hennig, 1977; Bern & Herzog, 1994), and fish (Coss, 1979; Miklósi *et al.*, 1995). Although a few comparative studies have been conducted on the recognition of the body configuration of avian predators (Curio, 1975; Hanson & Coss, 1997; Kerlinger & Lehrer, 1982), such studies of mammalian carnivore recognition are rare (*e.g.* Kortlandt, 1967).

Leopards (Panthera pardus) constitute a major predatory threat for large and medium-size primates, mostly at night (Busse, 1980; Isbell, 1990; Boesch, 1991; Cowlishaw, 1994; Fay et al., 1995). The current study focuses on leopard recognition by bonnet macaques (Macaca radiata) during less threatening daytime conditions. For medium-sized primates, such as bonnet macaques and vervet monkeys (Cercopithecus aethiops), detection of a leopard during the day is typically followed by vigorous alarm calling, but only after the monkeys have fled up trees (Isbell, 1990; Ramakrishnan & Coss, 2000). In both species, visual surveillance of the leopard is maintained by following it short distances, moving from tree to tree (Isbell, 1990; Ramakrishnan & Coss, 2000). Such visual monitoring with persistent alarm calling might thwart daytime attacks as does direct harassment by larger, more formidable baboons (Papio spp.) and chimpanzees (Pan troglodytes). For example, baboons and chimpanzees will confront leopards during the day by charging them alone and in groups (Altmann & Altmann, 1970; Gandini & Baldwin, 1978; Hiraiwa-Hasegawa et al., 1986), by alarm calling with loud barks (DeVore & Washburn, 1963; Gandini & Baldwin, 1978), and by direct harassment using threatening gestures and sticks as 'weapons'

(Kortlandt, 1967; Boesch, 1991). However at night and at dusk, leopards can be persistent hunters (Busse, 1980) with relatively high kill rates (Boesch, 1991; Cowlishaw, 1994). As such, failure to detect leopards and evade predation during their evolutionary history arguably provided a major source of natural selection for the deterrent effects of persistent vigilance, alarm calling, and mobbing (van Schaik & van Hooff, 1983; Terborgh, 1983; Cheney & Seyfarth, 1990; Isbell, 1994).

There are few daytime observations of leopards attacking primates (Isbell, 1990; Bailey, 1993), and virtually nothing is known about the perceptual aspects of leopard recognition. For macaques, the genus receiving the most intense laboratory investigation, both innate perceptual processes and learning are likely to play a role in leopard recognition. Because leopards often hunt primates under low-light conditions, detection of a leopard might rely on its overall configuration. In exploratory study of alarm-call provocation, Brown et al. (1992) reported that a moving leopard silhouette elicited alarm calling in captive-born and wild-caught vervet monkeys. During the day, the most invariant cues for detecting partially occluded leopards and those in full view would be the black flecks, spots, and rosettes on a yellow coat. These features might be conspicuous, in part, because the macaque visual system is attuned to yellowish hues (569-577 nm), which for the visual spectrum elicit the strongest neural activity in macaque visual cortex (Yoshioka, & Dow, 1996; Yoshioka et al., 1996). Yellow and green discrimination is also useful for finding edible leaves (Lucas et al., 1998). Some neurons in macaque visual cortex are also attuned to texture regularity (Tanaka, 1996), especially an orderly arrangement of spots (Tanaka et al., 1991).

It is conceivable that the spotted texture of leopards alone provides a consistent cue for leopard recognition among leopard prey. McRae (1997) provides photographic documentation that hunters in Cameroon occasionally wear yellow masks with leopard spots to pinpoint the location of alarm-calling guenons in the canopy. Thus, rather than affording concealment in the dappled light of leaf shadows in the forest, the spotted yellow coat of leopards might be highly conspicuous to primates with trichromatic vision. Ungulates with dichromatic vision, however, would have difficulty differentiating yellow and green (*e.g.* Neitz & Jacobs, 1989; Smith & Goldman, 1999) and might have to rely on detecting leopards via the regularity of the leopard spot pattern. According to Mottram (1915, 1916),

the high regularity of leopard spots does not blend effectively with irregular leaf shadows in the forest. Consistent with this idea of spot conspicuousness, the dark melanic leopard has been reported to hunt ungulates in the open (Rice, 1986), a behavior that would force reliance on detecting leopards by their configuration and movement.

The ancestors of bonnet macaques have likely experienced leopard predation for more than 3 million years, based on the oldest leopard fossils (Barry, 1987), the oldest fossil macaque in south Asia (Szalay & Delson, 1979; Delson, 1980) and current sympatry (Brain, 1981). The aforementioned perceptual cues might have been perceived unvaryingly by ancestral macaques and acted upon differentially to promote the evolution of leopard recognition. In keeping with this view of cue invariableness, it must be noted that both phylogenetic and developmental analyses of felid spots and rosettes suggest that these textures are an ancestral trait in the felid lineage (Ortolani & Caro, 1996; Werdelin & Olsson, 1997; Ortolani, 1999). Availability of these potential recognition cues would not preclude their involvement in learning, especially when they are paired with arousing alarm vocalizations (e.g. Herzog & Hopf, 1984; Ramakrishnan & Coss, in press). Indeed, Herzog & Hopf (1986) have argued that learning accounts for the responsiveness of captive squirrel monkeys (Saimiri sciureus) that alarm called to moving spotted textures on yellow backgrounds. These patterns characterise the coat textures of many neotropic felid predators and would be available for learning. Taken together, these neurobiological and behavioral studies suggest that form, color, and texture regularity might play an important role in leopard recognition.

To select field sites for the current study, we analyzed leopard scat in two parks in southern India to look for evidence of leopard predation on bonnet macaques (Ramakrishnan *et al.*, 1999). Evidence of bonnet macaques was found in one scat sample, and this analysis complemented our field observations of natural encounters of bonnet macaques and leopards (also see Ali, 1981). Because these observations were rare, we developed a leopard model (see Methods) to generate alarm vocalizations in a variety of species (Ramakrishnan & Coss, in press). This model was very effective in eliciting alarm vocalizations by bonnet macaques, Nilgiri langurs (*Trachypithecus johnii*), Hanuman langurs (*Semnopithecus entellus*), sambar deer (*Cervus unicolor*), chital deer (*Axis axis*), and Malabar giant squirrel (*Ratufa indica*). We also presented this model to an urban troop of bonnet macaques that had probably never encountered a leopard. This troop reacted by alarm calling vigorously. The strong reactions of bonnet macaques to our leopard model, irrespective of experience with leopards, led to the present study examining the perceptual properties of leopards used by bonnet macaques in leopard recognition and the social dynamics influencing their escape responses. Our experimental design addressed two questions: (1) Do bonnet macaques react differently to the spotted yellow leopard morph and the dark melanic leopard morph? (2) Are there social influences affecting the response of individuals in the presence of a leopard?

Methods

Study sites

The experiments were carried out between April and October, 1997, at three study sites in southern India. The Mudumalai Wildlife Sanctuary is located between $11^{\circ} 32'$ to $11^{\circ} 43'$ N latitude and $76^{\circ} 22'$ to $76^{\circ} 45'$ E longitude and covers an area of 321 km^2 . Three troops (Theppakadu, Bandipur, Kargudi) were selected for the study from this site (Table 1). The second study site, the Kalakad-Mundanthurai Tiger Reserve, is located between $8^{\circ} 25'$ to $8^{\circ} 53'$ N latitude and $77^{\circ} 10'$ to $77^{\circ} 35'$ E longitude, and covers an area of 817 km^2 . One troop (Mundanthurai) was selected for study from this site. Both spotted and dark melanic leopard morphs are found at these two sites; albeit, the dark melanic morph is rarely seen. The aforementioned urban troop was located in Bangalore. This troop was included for study because individuals reacted strongly to our leopard model, providing the broadest generality of findings to monkeys with markedly different life histories. All troops in this study were human habituated, thus permitting close-range study.

Individuals from the five study troops were identified and classified into one of six sex and age (demographic) categories based on size: infants (unweaned animals that were less than 1 year of age); juveniles (weaned animals 1-2 years of age); subadult females (2-4 years of age, smaller than adult females and larger than juveniles); subadult males (same size as adult females, smaller than adult males); adult females (females older than 4 years of age with at least one offspring); adult males (older than 5 years of age, larger than adult females). Troop composition is presented in Table 1. The demographic categories of all monkeys in camera view for each model and troop appear in Table 2. Infants were not included in the statistical analyses.

Troops	Habitat	Adult male	Adult female	Subadult male	Subadult female	Juvenile	Infant	Total
Mundanthurai	Forest	8	8	5	3	7	3	34
Theppakadu	Forest	6	10	4	5	3	7	35
Bandipur	Forest	5	7	4	6	3	5	30
Kargudi	Forest	5	9	2	4	6	2	28
Bangalore	Urban	9	12	6	8	9	10	54

TABLE 1. Number of individuals in each troop and demographic category

Leopard models	Troop ID	Adult male	Adult female	Subadult male	Subadult female	Juvenile	Unclassi- fied	Total
Spotted upright	1	2	2	0	1	1	0	6
	2	3	0	1	0	1	0	5
	3	2	1	0	1	1	0	5
	4	3	1	0	0	0	0	4
	5	3	2	1	1	1	1	9
	Total	13	6	2	3	4	1	29
Dark upright	1	5	4	1	3	3	0	16
	2	2	2	2	0	0	0	6
	3	2	2	0	2	0	3	9
	4	1	3	1	3	2	0	10
	5	2	2	0	2	2	0	8
	Total	12	13	4	10	7	3	49
Spotted upside-down	1	2	1	0	1	0	0	4
	2	0	1	0	0	0	0	1
	3	0	1	0	0	1	0	2
	4	0	1	0	0	1	0	2
	5	1	2	1	0	1	0	5
	Total	3	6	1	1	3	0	14
Dark upside-down	1	3	2	1	2	1	0	9
	2	0	1	3	1	0	2	7
	3	0	2	0	2	0	3	7
	4	3	3	0	1	3	0	10
	5	3	4	2	0	1	1	11
	Total	9	12	6	6	5	6	44

 TABLE 2. Number of individuals in camera view when models were presented

Troop identification: (1) Mundanthurai, (2) Theppakadu, (3) Bandipur, (4) Kargudi, (5) Bangalore. Small sample sizes precluded statistical comparisons among demographic categories within each model.

Leopard models

Four models (Fig. 1) were used in this experiment: (1) upright spotted leopard in a stalking profile with its head facing the subjects; (2) the same spotted model presented upside down; (3) a dark-brown leopard model with the same configuration as the spotted model; and finally (4), the same dark-brown model presented upside down. The upright models characterized the two leopard morphs found in the wild — spotted and dark melanic. Inverted presentations of the spotted model examined the effects of the same configuration in an incongruous position to document whether leopard spots retained their provocative properties when perceptually disassociated from the appropriate leopard configuration. Model head and body length was 1.21 m with the following dimensions: shoulder height: 63 cm; height at pelvis: 61 cm, facial



Fig. 1. Upright leopard models presented briefly to bonnet macaques. Clockwise from top: spotted upright leopard model; detail of face of dark upright model painted on Masonite hardboard; detail of face of spotted upright model painted on yellow cloth covering the Masonite hardboard.

height: 29 cm, and maximum head width: 23 cm. Total model length including tail was 1.5 m. The model was constructed of Masonite hardboard covered with cloth and assembled in three sections. Without the cloth, the dark-brown Masonite provided the background color for the dark melanic morph. For the spotted morph, the cloth was painted to resemble a leopard in full sun. The following model colors are based on the 1963 Munsell Book of Color, Neighboring Hues Edition Matte Surface Samples: Spotted morph; yellow background body color, 5Y7/4, yellow body shading and shadows: range 5Y6-7/4, black rosettes, lips, and eyelids, golden rosette centers and irises: 10YR7/8, and tongue: 7.5R6/6; dark melanic morph, dark-brown color, 5YR3/4, with the same colors used for the spotted model to paint the dark morph's lips, eyelids, and irises.

Experimental layout

To create a similar motivational context for presenting the experimental treatments (*e.g.*, Hanson & Coss, 1997), feeding stations were set up and food (split peas) was scattered in a \sim 1-m radius, which caused bonnet macaques to aggregate for video recording. All troops were fed periodically throughout the study period to preclude any reliable association of food with the experimental treatments. A Panasonic AG-185U VHS camcorder was used for video taping behavioral and auditory responses from a 20-m distance to the center of the feeding station. Camera field of view encompassed the entire feeding area.

Experiments were conducted between 6:00 a.m. and 10:00 a.m. and between 3:00 p.m. and 5:00 p.m., corresponding to the peak foraging periods of this species. Video recording was initiated after the animals arrived at the feeding station. After 2 min of video recording, the animals were presented with one of the four models. All models were presented once to each of the five troops. Models were presented in random order, with minimum and maximum intervals of 4 and 14 days, respectively, between presentations. Video recording continued for 3 min after the model was removed. The model was suspended from two monofilament lines attached to a 100-m long rope strung over a tree branch. Prior to model erection, the model was transported to the presentation site in a green cloth envelope with vegetation print. The model was then positioned on its side concealed in grass, approximately 25 m from the feeding station. To erect the model, the cloth cover was removed and repositioned on top of the model and the monofilament lines were hooked to the rope. When the assistant pulled the rope on cue, the model popped up and the cloth dropped over a 1-s period, simulating the motion of a leopard standing from a crouched position. The model was presented for 10 s and then lowered out of sight. After the monkeys reacted to the model by running up nearby trees, the assistant covered the model with its cloth envelope to prevent its further detection.

Behavioral measures and statistical analyses

Alarm calling

The time interval between model presentation and model detection was measured by recording the onset of the first alarm call. To examine model conspicuousness, we treated each troop as the unit of analysis (N = 5) and applied a one-factor repeated measures analysis of variance (ANOVA). The number of alarm calls was counted for the first 30 s after the onset of model presentation. This time frame was selected for analysis because persistent high rates of alarm calling by individuals that observed the leopard models recruited others into the chorus after this time frame. In this analysis, the number of alarm calls of each troop constituted the unit of analysis to compare response differences to the four leopard models using a one-factor repeated measures ANOVA.

Flight latency

The latencies to flee after model presentations were examined for all individuals in camera view. We measured the time between the onset of model presentation and the shift in the activity of an individual to flight. This shift in behavior was measured irrespective of the processes triggering flight initiation; this included individuals that fled after detecting the model themselves, individuals that fled after observing neighboring monkeys running, and individuals that fled after hearing the alarm calls of the individuals that observed the models. Comparisons of the responses to the four leopard models were made using Survival Analysis

with right-censored data coupled with pairwise comparisons using conservative Log-ranked tests. As in epidemiological studies of patients who outlive the sampling period (*e.g.*, Gehan, 1975; Gail *et al.*, 1980), such censoring permitted the inclusion of animals that failed to flee during a 1-min sampling period.

Frequency of flight

The number of individuals in video view that fled to the different models within the first minute after model presentation was counted, irrespective of the processes triggering flight. Flight behavior was defined as a shift in activity to running off camera view. Responses of individuals were summed across troops to generate behavioral frequencies for multinomial log-linear analyses with maximum likelihood estimations of the interaction of model type and frequency of flight (see Agresti, 1990).

Flight reaction time and frequency of flight after observing model

The flight reaction time measure was calculated as the interval between lifting or turning the head in the direction of the model and initiation of flight. Monkeys already looking in the direction of the models during their presentations were not included in this analysis. Because reaction times are typically skewed to the right due to the inherent physiological limits on information processing and recognition (Rogal *et al.*, 1985), the data are usually not normally distributed. Therefore, nonparametric tests were applied to the data. Again we used Survival Analyses coupled with pairwise comparisons using Log-ranked tests to measure differences in flight reaction times after individuals detected the models. Individuals were censored if they did not flee within the 1-min sampling period. The proportion of individuals fleeing to each model was examined by multinomial log-linear analysis.

Circumstances associated with flight

We recorded the responses of individuals that were exposed to one of three circumstances promoting flight. These circumstances were: (1) sighting the model and fleeing prior to looking at another troop member or hearing alarm calls, (2) looking at another troop member and fleeing prior to sighting the model or hearing alarm calls, and (3) hearing alarm calls and fleeing prior to sighting the model or looking at another troop member. Multinomial log-linear analysis examined the proportion of individuals fleeing (the dependent variable) as a function of the three circumstances promoting flight (the independent variables). The effects of each model were examined separately.

Looking at others during risk assessment

We recorded individuals that had sighted the model and those that also looked at their neighbors after sighting the model. The focus of our question of social facilitation addressed the issue of how troop members used each other as sources of information for assessing risks; thus, we examined the effects of each model using logistic regression. This statistical modeling approach examines the relationship of several predictor variables to a dichotomous response variable (Kleinbaum, 1994). In our study, the response variable was whether the subjects looked at their neighbors and the single predictor variable was whether the subjects had observed the model before looking at their neighbors.

We also recorded the behavior of all individuals that did not see the model, but looked at other troop members. We then recorded the behavior of the those troop members during the time frame in which the subjects look at them. We applied a logistic regression model in which the response variable was whether the individuals fled and the predictor variable was whether the troop members they look at fled. Since the subjects did not see the models, this analysis included data from all model presentations.

Results

Alarm calling

Only individuals in trees alarm-called, either after detecting the model from their arboreal perch or after observing it and running up trees. The intervals between model presentations and the first alarm calls did not differ significantly among models ($F_{3,12} = 2.072$; p = 0.158). Despite variation in the latency to call, comparison of the four leopard models (Fig. 2) revealed that they differed significantly in the number of alarm calls produced ($F_{3,12} = 12.020$; p < 0.0005). Pairwise comparisons showed that the spotted upright model produced a significantly greater number of alarm calls than the spotted upside-down, dark upright, and dark upside-down models (respectively: $F_{1,4} = 19.590$, 18.762, 13.675; p < 0.025). None of these latter models differed significantly from each other.



Fig. 2. Average number of alarm calls with standard errors produced by 5 troops for a 30-s interval after the onset of model presentation.

Flight latency

Analysis of the interval between model presentation and flight using the Kaplan-Meier estimate of the survivor function (Fig. 3A) revealed that the models differed significantly ($\chi^2 = 33.416$; df = 3; p < 0.0001), irrespective of the processes triggering flight. The latency to flee to the spotted upright model (N = 29) was significantly faster than the latencies to all other models (spotted upright compared with: (1) spotted upside-down (N = 14), Log-ranked test = 4.592; p < 0.0001; (2) dark upright (N = 49), Log-ranked test = 3.867; p < 0.0005; (3) dark upside-down (N = 44), Log-ranked test = 5.368; p < 0.0001). The spotted upside-down model engendered a significantly faster flight latency than the dark upside-down model (Log-ranked test = 2.039; p < 0.05), but this spotted model did not differ significantly from the dark upright model (Log-ranked test = 1.369; p = 0.171). Finally the dark upright model elicited a significantly faster flight latency than the dark test = 3.214; p < 0.005).

Frequency of flight

The application of a multinomial log-linear analysis to examine differences between models (Fig. 3B) revealed a significant interaction between models and the frequency of flight (Likelihood ratio $\chi^2 = 43.487$; df = 3; p < 0.001). The pattern of results revealed in the pairwise comparisons of frequency of flight to the models is identical to that of flight latency. The proportion of individuals that fled in response to the spotted upright model was significantly greater than the proportions of individuals that fled to all other models (spotted upright compared with: (1) spotted upsidedown: Likelihood ratio $\chi^2 = 9.886$; df = 1; p < 0.002; (2) dark upright: Likelihood ratio $\chi^2 = 13.00$; df = 1; p < 0.001; (3) dark upside-down: Likelihood ratio $\chi^2 = 40.820$; df = 1; p < 0.001). The spotted upsidedown model elicited a significantly greater proportion of individuals fleeing than that of the dark upside-down model (Likelihood ratio $\chi^2 = 8.867$; df = 1; p < 0.005), but this spotted model did not differ significantly from the dark upright model (Likelihood ratio $\chi^2 = 0.010$; df = 1; p > 0.5). Lastly, the dark upright model engendered a significantly greater proportion of individuals fleeing than that of the dark upside-down model (Likelihood ratio $\chi^2 = 13.205$; df = 1; p < 0.001).



A. Time to Flee After Model Presentation

Fig. 3. Latency to flee and the proportion of individuals fleeing after the onset of model presentations. (A) Cumulative proportion of individuals in camera view as a function of time before they fled, with censoring of individuals that did not flee during the 1-min sampling period. (B) Proportion of individuals fleeing to the models and the circumstances that promoted flight. Significance values are for cumulative proportions of individuals fleeing to each model. The contribution of each of the three flight-promoting circumstances is shown. Whereas alarm calls contributed to less that 40% of flight, all individuals that heard alarm calls flee, irrespective of model type.

Circumstances promoting flight

This analysis compared the proportion of individuals that fled as a result of three primary causes of flight: (1) after model detection (including individuals facing the models during their presentations); (2) after looking at neighbors; (3) after hearing alarm calls (Fig. 3B). For the spotted upright and upside-down models, the interaction of flight-promoting circumstances and flight was not significant (spotted upright: Likelihood ratio $\chi^2 = 0.002$; df = 2; p > 0.5; spotted upside-down: Likelihood ratio $\chi^2 = 4.138$; df = 2; p = 0.126). All individuals in camera view fled in the three circumstances eliciting flight for the spotted upright model, whereas the spotted upside-down model engendered flight in 70% that looked at it, 50% that looked at neighbors, and 100% that heard alarm calls. In contrast, the interaction of flight-promoting circumstances and flight was significant for the dark upright and upside-down models (dark upright: Likelihood ratio χ^2 = 19.103; df = 2; p < 0.001; dark upside-down: Likelihood ratio $\chi^2 = 19.400$; df = 2; p < 0.001). For both dark models, hearing alarm calls induced flight in 100% of individuals in camera view, which was significantly greater than either the proportions of individuals fleeing under the circumstances of looking at the models or looking at neighbors [dark upright model, Likelihood ratios for hearing alarm calls vs looking at the model (53.6% flight) and hearing alarm calls vs looking at a neighbor (50% flight), respectively: $\chi^2 = 16.759$ and 14.698; df = 1; p < 0.001; dark upside-down model, Likelihood ratios for hearing alarm calls vs looking at the model (15.8% flight) and hearing alarm calls vs looking at a neighbor (22.2% flight), respectively: $\chi^2 = 18.072$ and 15.227; df = 1; p < 0.001].

Flight reaction time and frequency of flight after observing model

Analysis of the interval between model detection and the onset of flight, using the Kaplan-Meier estimate of the survivor function (Fig. 4A), showed that the models differed significantly ($\chi^2 = 15.684$; df = 3; p < 0.005). Pairwise comparisons revealed that the flight reaction times after seeing the spotted upright model (N = 11) and spotted upside-down model (N = 4) did not differ significantly (Log-ranked test = 1.017; p = 0.309). Similarly, the flight reaction times after seeing the dark upright model (N = 14) and dark upside-down model (N = 9) did not differ significantly (Log-ranked test = 1.405; p = 0.160). However, the flight reaction time to the spotted upright model (Log-ranked test = 3.168; p < 0.005) and the dark upside-down model (Log-ranked test = 3.504; p < 0.005). Finally, the



Fig. 4. Latency to flee and the proportion of individuals fleeing after looking at the models. (A) Cumulative proportion of individuals in camera view as a function of time before they fled, with censoring of individuals that saw the models but did not flee during the 1-min sampling period. Since the longest latency to flee within this period was about 22 s, the graph

is terminated at 25 s. (B) Proportion of individuals fleeing after observing the models.

spotted upside-down model engendered a faster flight reaction time than that of the dark upside-down model which was nearly significant (Log-ranked test = 1.905; p = 0.057); this spotted upside-down model did not differ significantly from the dark upright model (Log-ranked test = 1.097; p = 0.273).

To examine the proportions of individuals that fled after seeing the four models, we used a multinomial log-linear analysis (Fig. 4B). The interaction

between models and the frequency of flight was significant (Likelihood ratio $\chi^2 = 29.061$; df = 3; p < 0.001). The proportion of individuals that fled after looking at the spotted upright model was significantly greater than the proportions of individuals that fled after looking at all the other models (spotted upright compared with: 1) spotted upside-down: Likelihood ratio $\chi^2 = 5.594$; df = 1; p < 0.05; (2) dark upright: Likelihood ratio $\chi^2 = 12.547$; df = 1; p < 0.001; (3) dark upside-down: Likelihood ratio $\chi^2 = 27.787$; df = 1; p < 0.001). The spotted upside-down model elicited a significantly greater proportion of individuals fleeing after they sighted this model than that of the dark upside-down model (Likelihood ratio $\chi^2 = 8.573$; df = 1; p < 0.01), but this model did not differ significantly from the dark upright model (Likelihood ratio $\chi^2 = 0.839$; df = 1; p = 0.360). A significantly greater proportion of monkeys fled after seeing the dark upright model than after seeing the dark upside-down model (Likelihood ratio $\chi^2 = 7.312$; df = 1; p < 0.01).

Looking at others during risk assessment

Logistic regression revealed that looking at the spotted upright model (N = 18) was not a significant predictor of looking at nearby troop members ($\chi^2(\beta = 0) = 2.44$; p = 0.118). Similarly, looking at the dark upsidedown model (N = 22) was not a significant predictor of looking at nearby troop members ($\chi^2(\beta = 0) = 2.32$; p = 0.128). However, looking at both the spotted upside-down model (N = 21) and the dark upright model (N = 21) was a significant predictor of looking at nearby troop members (spotted upside-down model: $\chi^2(\beta = 0) = 6.18$; p < 0.025; dark upright model: $\chi^2(\beta = 0) = 4.09$; p < 0.05). The behavior of all individuals that did not see the models (N = 24), but looked at other troop members revealed that the flight response of troop members was a significant predictor of the flight response of individuals that looked at them ($\chi^2(\beta = 0) = 16.85$; p = 0.001).

Discussion

Spotted yellow and dark melanic leopard models were presented briefly to bonnet macaques to examine their reactions to the common and rare leopard morphs. Inverted presentations of these models further examined the perceptual coupling of leopard form, color, and texture in leopard recognition. Social facilitation of flight behavior was also evaluated to determine the influence of troop members.

Perceptual effects of spotted and dark melanic leopard morphs

On the whole, the spotted upright model was the most provocative, eliciting the greatest number of alarm calls and the greatest proportion of individuals fleeing with the fastest reaction times. Evidence that spots on a yellow coat might be important in leopard recognition was apparent in the comparisons of the models in the same upright or inverted orientations. For those individuals that actually looked at these models and fled, only the spotted and dark upright models generated reaction times within the 200-300 ms time frame, which approximated the fastest reaction times to learned visual targets recorded from macaques in laboratory study (e.g., Rogal et al., 1985; Sato, 1995). Although few individuals reacted this quickly after seeing the upright models, all 11 individuals that looked at the spotted upright model fled, whereas only 8 of 14 that looked at the dark upright model fled. For those that did flee, the average reaction time was 1.44 s for the spotted upright model and 7.24 s for the dark upright model. As apparent in Fig. 4A, this longer reaction time included individuals that watched the dark upright model disappear from view. Compared with the more skewed distribution of flight reaction times to the spotted upright model, the broader distribution of flight reaction times to the dark upright model suggests some uncertainty in leopard recognition, possibly related to its unfamiliar appearance.

It is reasonable to assume that individuals that did not flee after looking at the spotted upside-down, dark upright, and dark upside-down models were perceiving these models as ecologically unimportant even though others ran away. Longer visual assessment of the dark upright model was indeed complemented by the tendency to look at nearby troop members, possibly to capitalize on their assessment of any potential threat. This interpretation of information seeking is supported by the similar tendency to look at neighbors after individuals looked at the spotted upside-down model. Failure to identify a model as something dangerous would not lead to further concerns as appeared to be the case for those that observed the dark upside-down model and did not look at other troop members. On the other hand, if the model was recognized, but the context of the threat was ambiguous, individuals might be expected to seek information from others. From this perspective, a dark-brown leopard in daytime might have been recognized by some as incongruous. Further, recognition of a spotted yellow pattern on an irrelevant form might have engendered sufficient ambiguity that some individuals chose not to flee.

Perhaps the strongest evidence that the spotted yellow coat acted as a leopard-recognition cue emerged from the comparisons of the inverted models. In this context, the spotted upside-down model was clearly more provocative than the dark upside-down model even when other flightpromoting circumstances, such as alarm calling, were considered (*cf.* Figs 3B and 4B). This difference between the inverted models is critical because it characterizes the importance of the spotted yellow coat in signifying danger, irrespective of the overall shape exhibiting this pattern. As discussed previously, partially concealed leopards might be recognized by prey via visible patches of spots unoccluded by vegetation or rocks. In light of phylogenetic and developmental evidence that spots are a primitive trait in the felid lineage (Ortolani & Caro, 1996; Werdelin & Olsson, 1997; Ortolani, 1999), it is reasonable to consider that natural selection might operate on the ability to recognize this spotted texture in different microhabitats independent of seeing it on the entire felid form.

Preliminary study of the role of experience governing leopard recognition was conducted on the urban troop of bonnet macaques that had no apparent exposure to leopards. In trials conducted several months before the present study, this urban troop was exposed to the spotted upright model and later exposed to a resting leopard model constructed of towels with a leopard print. The vigorous alarm calling and cautious investigative behavior of these individuals in response to these models support the hypothesis that experience is not a prerequisite for leopard recognition by bonnet macaques. These responses were analogous to those exhibited by leopard-experienced forest troops, the rationale for including the urban troop in the current study.

Perceptual effects of leopard configuration

Comparisons of upright and inverted models matched for texture and coloration provide evidence that bonnet macaques are attuned to recognizing the appropriate leopard body orientation. In the absence of a specific expectation of figure orientation, humans tend to perceive the uppermost contour of a figure as its top (Rock, 1973; Parks *et al.*, 1986). Such assignment of top might be somewhat specialized for shapes that were ecologically important historically. For example, Overman & Doty (1982) report that macaques have greater difficulty recognizing inverted faces than inverted scenery. More specifically to faces, Tomonaga (1994) found that photographs of conspecific and heterospecific macaques were less distinguishable when they were presented upside down. If generalizable to the current study, these findings support the argument that the dark upside-down model was generally ignored. As discussed above, failure to recognize this model as a threat might explain why there was no predictive association between the event of looking at this model and the likelihood of looking at a nearby troop member.

Social facilitation of flight behavior

Alarm vocalizations were first emitted by individuals in nearby trees that either fled up these trees after looking at the model or after detecting it from within these trees. The average latencies for the first alarm call after model presentations were not substantially different due to the high variation among troops, indicating that model detection was stochastic. Alarm calling, however, induced flight in all individuals, irrespective of the type of model presented. Because the onset of alarm calling was often delayed, the effects of other circumstances, such as looking at the model or looking at a neighbor could be evaluated before the occurrence of alarm calls. Even though some individuals did not see the models, they were likely to flee if they saw other individuals fleeing. This result is important because its characterizes the significance of monitoring the behavior of other troop members as a antipredator tactic in addition to its utility in social contexts.

In conclusion, our results suggest that bonnet macaques recognise leopards by their configuration and the color and pattern of their coat. This recognition ability of primates with trichromatic vision would likely impact the hunting success of leopards in daytime. Hunting at night would preclude at least one recognition cue potentially used by prey to detect leopards thus enhancing leopard stealth. Other aspects of leopard recognition will be the subject of future studies on primate antipredator behavior.

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