Ethology

Threat-Related Acoustical Differences in Alarm Calls by Wild Bonnet Macaques (*Macaca radiata*) Elicited by Python and Leopard Models

Richard G. Coss*, Brenda McCowan† & Uma Ramakrishnan‡

* Department of Psychology, University of California, Davis, CA, USA
† California National Primate Center, University of California, Davis, CA, USA
‡ Department of Environmental Science and Studies, Juniata College, Huntingdon, PA, USA

Correspondence
Richard G. Coss, Department of Psychology,
University of California, Davis, CA 95616, USA.
E-mail: rgcoss@ucdavis.edu

Received: September 21, 2006
Initial acceptance: October 27, 2006
Final acceptance: October 27, 2006 (S. Forbes)

doi: 10.1111/j.1439-0310.2007.01336.x

Abstract

Wild and urban bonnet macaques (*Macaca radiata*) were studied in southern India to record alarm calls during presentations of realistic models of spotted and dark leopards (*Panthera pardus*) and an Indian python (*Python molurus*). Recordings of alarm calls were made from members of four forest troops at feeding stations who observed brief and prolonged presentations of fully exposed spotted and dark leopard morphs and partially concealed views of the spotted morph. Four different forest troops were presented a slowly moving python near feeding stations. Two predator-inexperienced urban troops from the city of Bangalore were presented either the spotted leopard morph briefly or the python. Analyses of alarm calls revealed differences in acoustic structure, such as a lower harmonic to noise ratio, which can be interpreted as reflecting the level of perceived threat rather than predator type. Noisy alarm calls likely indicate high states of physiological arousal that might provide eavesdropping troop members with information useful for assessing the urgency of the predatory threat. Lack of alarm-call distinctiveness characterizing predator type is complemented by explicit contextual information in which alarm calling to leopards never occurred on the ground whereas nearly all initial python-elicited alarm calls were made by individuals on the ground monitoring the python. The alarm calls of Bangalore monkeys distinguished the leopard and python models, with the latter engendering the noisiest calls and immediate flight to trees. Such flight is unnecessary with the python and suggests that, without appropriate experience with pythons, bonnet macaques adopt less predator specific refuge-seeking behavior.

Introduction

The ability to react quickly to the presence of a predator reflects an effective coupling of perceptual and cognitive systems capable of appraising the threat in different circumstances. Some circumstances have a high degree of urgency and entail the rapid flight to refuge. When predators are detected at safe distances, prey can monitor them while announcing their presence by postural displays of focused attention, conspicuous movement, and deliberate noise making, such as snorting or alarm calling that might inform the predator that it has been detected (e.g. Zuberbühler et al. 1999; Caro 2005). In social primates foraging on the ground, the emission of alarm calls can elicit nearly synchronous flight to arboreal refuge or the adoption of vigilance postures depending on the spatial and temporal properties of predator dangerousness. When the predator has been detected by only a single individual within a group, the acoustical properties of his or her alarm call might convey the level of urgency perceived by the caller, a property that could trigger immediate flight or initiate periodic scanning. Under low-urgency condition, California ground squirrels (*Spermophilus beecheyi*) emit snake-specific alarm calls somewhat similar to those emitted under the less-urgent circumstance of detecting a mammalian predator at a distance. A markedly different alarm call is emitted during the high-urgency condition of spotting an aerial predator (see Leger et al. 1980).

Several primate species employ distinct alarm calls that appear to inform troop members of the type of predator in the vicinity. For example, vervet monkeys, *Cercopithecus aethiops*, are preyed upon by several mammalian and avian predators as well as pythons, and emit alarm calls that are unique to each class of predator (Seyfarth et al. 1980a,b). Diana monkeys (*C. diana*; Zuberbühler et al. 1997) and ringtailed lemurs (*Lemur catta*; Pereira & Macedonia 1991) also have distinct alarm calls associated with different predators. Although such alarm calls may be distinctive, the information they convey may not be perceived as differentially meaningful when these calls are heard in the absence of seeing the source of the threat. Barbary macaques (*Macaca sylvanus*) living in a large enclosure emit acoustically different shrill barks when they detect snakes and nearby domestic dogs. However, the differential urgency seemingly apparent in their behavior and alarm calling is not reflected by their behavior when they hear playbacks of these alarm calls (Fischer & Hammerschmidt 2001). Conversely, calls that are acoustically similar can still convey different information depending on the action of other troop members. During encounters with snakes, common chimpanzees (*Pan troglodytes verus*) exhibit barks somewhat similar to their hunting barks; albeit, both of these barks are distinctly different from travel and aggressive barks (Crockford & Boesch 2003).

Finally, acoustically similar alarm calls with higher noise levels might convey immediate public information on the caller's level of physiological arousal as is apparent in the alarm barks of chacma baboons (*Papio cynocephalus ursinus*) when they detect predators (Fischer et al. 2001). Other alarm-call attributes that might signify to others the level of perceived threat are the abruptness of call onset, call duration and call intensity (cf. Le Roux et al. 2001; Randall & Rogovin 2002; Digweed et al. 2005).

In previous research (Ramakrishnan & Coss 2000a,b), we have recorded the alarm calls of bonnet macaques during occasional encounters with leopards, numerous encounters with domestic dogs (*Canis familiaris*) and, in one unique circumstance, an encounter with an Indian python (*Python molurus*). As pythons constitute the only snake predator of bonnet macaques, it was important to determine if our observation of bonnet macaque alarm calling was python specific or reflected a pattern of alarm calling to snakes in general. Bonnet macaques in southern India encounter a variety of highly venomous snakes (Daniel 1983), such as the Indian cobra (*Naja naja*), common Indian krait (*Bungarus caeruleus*), banded krait (*Bungarus fasciatus*), saw-scaled viper (*Echis carinatus*), Russell's viper (*Daboia russellii*), and green pit viper (*Trimeresurus gramineus*). To examine the breadth of antisnake behavior exhibited by bonnet macaques, we constructed realistic models of an Indian python, Indian cobra, common Indian krait, and two non-venomous snakes, the green keelback (*Macropisthodan plumbicolor*) and rat snake (*Ptyas mucosus*). Among these snake models, bonnet macaques alarm called *only* during presentations of the Indian python (Ramakrishnan et al. 2005).

Experimental Rationale and Predictions

The current research on acoustical variation in bonnet macaque alarm calls is retrospective, the consequence of our collection of audio recordings of alarm calls emitted during experimental presentations of realistic-looking models of spotted and dark leopards and the Indian python mentioned above (Coss & Ramakrishnan 2000; Coss et al. 2005; Ramakrishnan et al. 2005). Juvenile alarm calls are not included because they exhibit much less low-frequency energy than subadult and adult calls (see Ramakrishnan & Coss 2000b). Several leopard presentations, such as upside-down and partially occluded dark leopards, did not elicit alarm calling from enough individuals for statistical comparisons. To include alarm calls emitted under lower perceived threat, we examined alarm calls recorded from individuals who observed a dark leopard morph presented for a longer time period at a safe distance in an unpublished study of bonnet macaque habituation. The python model was presented closer to feeding stations than the leopard models because the python was compared with smaller snakes that remained undetected by bonnets macaques at greater distances (Ramakrishnan et al.

2005). As natural encounters with predators are difficult to observe (Ali 1981; Eckardt & Zuberbühler 2004), controlled presentations of these predator models for different time periods and at different distances from feeding stations engendered relative consistency in the situational context for predator detection.

Our comparisons are presented in two parts, the first of which examines bonnet macaques living in forest sites where leopards and pythons are major predators. The second part compares the alarm calling of forest monkeys with predator-inexperienced urban monkeys during leopard and python model presentations with the aim of determining if predator experience shapes the acoustical properties of alarm calling. Based on our listening to alarm calls in the field and post hoc audio recordings, we predicted that bonnet macaque alarm calls to the leopard and python models would be acoustically similar. As in chacma baboons (Fischer et al. 2001), bonnet macaque alarm calls were predicted to differ in noisiness, a property that might reflect the level of urgency or danger posed by each predator type and model-presentation context. As the behavior of callers provides public information that complements the acoustical properties of alarm calls, and as leopards and pythons constitute different terrestrial threats, we will report whether alarm calling occurred initially on the ground or after individuals had fled to trees.

Part 1: Risk-Related Alarm Calling to Python and Leopard Models

Study Sites

All bonnet macaque troops in this study were habituated to humans and could be studied at close range. Presentations of leopard models were carried out at two study sites in southern India, between April and October 1997. The Mudumalai Wildlife Sanctuary is located between 11°32′–11°43′N latitude and 76°22′–76°45′E longitude and covers an area of 321 km^2. Three troops were selected for study from this site. An additional troop was examined at the Kalakad–Mundanthurai Tiger Reserve, which is located between 8°25′–8°53′N latitude and 77°10′–77°35′E longitude, and covers an area of 817 km^2. Presentations of the python model occurred between February and March, 2000, using four troops at the Bandipur National Park adjacent to the Mudumalai Wildlife Sanctuary. Spotted leopards and pythons are common predators at all these field sites. In contrast, the dark melanic leopard morph is relatively rare.

To acquire large enough samples for comparative study of predator effects, the alarm calls of subadult and adult individuals were examined as a single age class. This age class consisted of: non-reproducing subadult females (2–4 yr of age, smaller than adult females and larger than juveniles); non-reproducing subadult males (same size as adult females, smaller than adult males); adult females (females older than 4 yr of age with at least one offspring); adult males (older than 5 yr of age, larger than adult females). The composition of caller age and sex was similar across predator-model treatments.

Experimental Layout

To engender close aggregation of bonnet macaques for video recordings of antipredator behavior and to create a similar motivational state (e.g. Hanson & Coss 1997), feeding stations were set up and food (split peas) was scattered in a approx. 1-m radius. All troops were fed periodically throughout the study period to preclude any reliable association of food with the experimental treatments. A Panasonic VHS camcorder model AG-185U or model PVD-209 (Matsushita Kotobuki Electronic Industries Ltd, Osaka, Japan) was placed at a distance of 12 m from the center of the feeding station and used to record behavioral responses and vocalizations. The microphones on these video cameras have approximately the same sensitivity in the frequency range of bonnet macaque alarm calls. Camera field of view encompassed the entire feeding area until all individuals had fled to trees in which case the camera was quickly removed from its tripod and focused on individuals who were alarm calling. Experiments were conducted between 6:00 AM and 10:00 AM and between 3:00 PM and 5:00 PM, corresponding to the peak foraging periods of this species. Video recording was initiated after the animals arrived at the feeding station. After 3 min of video recording, the models were presented to monkeys gathered at their feeding station. Video recording continued for 3 min after the each model was no longer in view.

Python and Leopard Model Presentations

The Indian python model studied by Ramakrishnan et al. (2005) was made of cotton-filled fabric with a python scale print and painted patterns (Fig. 1a). This model had a length of 200 cm, a maximum width of 15.2 cm, and a maximum head width of

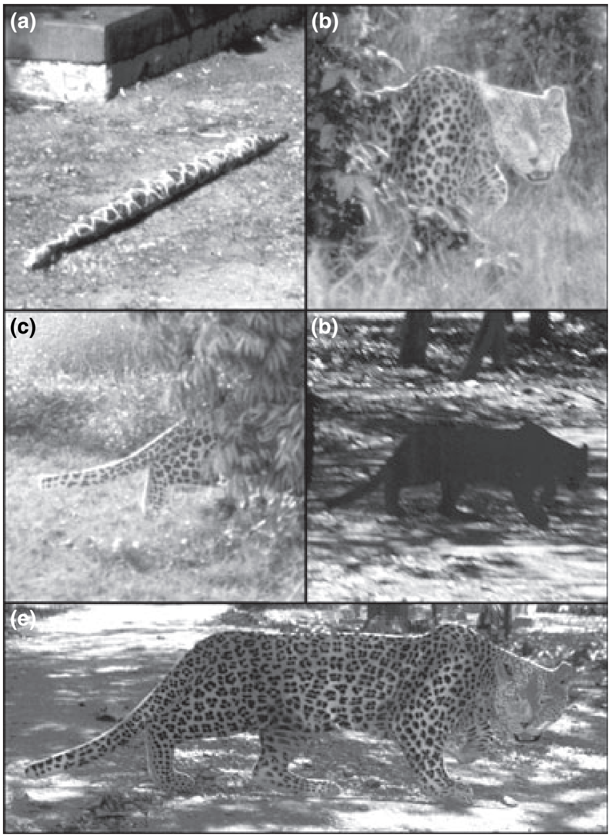


Fig. 1: Predator models presented to bonnet macaques to elicit alarm calling. (a) Indian python (*Python molurus*); (b) Forequarter view of spotted yellow leopard morph (*Panthera pardus*) presented for 1 min at 25 m distance; (c) Hindquarter view of spotted yellow leopard morph presented for 1 min at 25 m distance; (d) Dark leopard morph in full view presented for 3 min at 60 m distance; (e) Spotted yellow leopard morph in full view presented for 10 s at 25 m distance

10.2 cm. The python model was transported to the site in a green cloth envelope with vegetation print and positioned perpendicular to the feeding station at distances between 4 and 5 m. After animals had gathered at the feeding station, the python was pulled slowly from its cloth enclosure via a thin monofilament line into view of the monkeys. At the end of the 3-min presentation trial, the python was covered by its cloth enclosure.

The antipredator behavior elicited by models of the spotted yellow and dark melanic leopard morphs has been reported elsewhere (Coss & Ramakrishnan 2000; Coss et al. 2005). Both morphs exhibited the same stalking profile with their heads facing the subjects (Fig. 1d and e). The model frame was constructed of Masonite hardboard covered with cloth and assembled in three sections. For the spotted yellow morph, the cloth was painted to resemble a leopard in full sun. The spotted and dark morphs consisted of the following dimensions and colors: Model head and body length was 1.21 m with the following dimensions: shoulder height: 63 cm; height at pelvis: 61 cm, facial height: 29 cm, and maximum head width: 23 cm. Total model length including tail was 1.5 m. 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 centres 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.

The leopard models were transported to the presentation sites in the same cloth enclosure used for python presentations. Leopard model presentations consisted of the following: (i) A spotted yellow morph that appeared for 10 s in full view at approx. 25 m distance and then disappeared (Fig. 1e); (ii) A dark morph presented in full view for 3 min at approx. 60 m distance (Fig. 1d); (iii) A forequarter view of the spotted morph presented for up to 1 min at approx. 25 m distance (Fig. 1b); (iv) A hindquarter view of the spotted morph presented for up to 1 min at approx. 25 m distance (Fig. 1c).

For brief presentations of the spotted yellow morph in full view, the model was positioned on its side concealed in grass, approx. 25 m from the feeding station prior to luring monkeys with food to the feeding station. While hidden from view, the model was suspended from two monofilament lines attached to a 100-m long rope strung over a tree branch. 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. The dark leopard morph was presented for 3 min at a 60 m distance from the feeding station. Unlike the pop-up presentation of the spotted morph, this model was suspended by pulleys on a thin cord attached to two trees. The cloth enclosure concealing the model was similarly suspended, permitting the leopard to emerge into view when the leopard's cord was pulled by an assistant hidden from view of the monkeys. The dark morph was presented for 3 min, following which the cloth enclosure was pulled over the model by its cord to conceal it.

The spotted leopard forequarter exposed the leopard's face, shoulder, and one foreleg (Fig. 1b). The spotted leopard hindquarter exposed the leopard's tail and one hind leg (Fig. 1c). For these presentations, an assistant, hidden behind thick vegetation, removed the green cloth envelope used for transporting the model. On cue, the assistant moved the front or rear section of the model forward into view and withdrew the model after all monkeys at the feeding station responded by flight or after a 1-min interval if any individuals remained at the feeding station. This procedure simulated a leopard emerging from behind a bush into partial view of the monkeys, freezing and then retreating from view after being detected.

Results

Qualitative Description of the Situational Context of Alarm Calling

In these analyses, we use the term 'context' as in Smith (1977), p. 225) who employed the term to 'refer only to sources of information that are available to a recipient *in addition* to some particular display source.' In all leopard model presentations, alarm calls were not emitted until individuals who observed the models had reached the safety of trees or were already in trees when they detected the models. For the latter circumstance, arboreal alarm calling triggered immediate flight in troop members at nearby feeding stations, many of whom never oriented toward the leopard model until they reach arboreal refuge. The rapid latency to flee after hearing these arboreal-based alarm calls has been reported elsewhere (Ramakrishnan & Coss 2000b).

Prior to the emission of the first alarm calls, all individuals on video at feeding stations who looked at the spotted leopard that appeared briefly in full view at 25 m distances (Fig. 2a) fled in rapid succession to the nearest trees (Coss & Ramakrishnan 2000). Similarly, all individuals in video view who looked at the dark leopard morph in a prolonged stationary position at 60 m distance fled to nearby trees. Partially occluded views of the spotted leopard morph presented at 25 m distances yielded markedly different effects depending on which leopard body features were visible. Ninety percent of individuals in video view who looked at the spotted leopard's forequarter fled to trees, with flight-reaction times reliably similar to the flight-reaction times elicited by the spotted leopard in full view (Coss et al. 2005). In contrast, the leopard's hindquarter elicited flight with reliably slower reaction times in only 31.3% of individuals who looked at the model (Coss et al. 2005). Individuals who remained on the ground did not alarm call.

Unlike the leopard-model presentations, the sight of the python model caused initial episodes of alarm calling almost exclusively on the ground. The one exception was an adult female accompanied by her juvenile offspring who quietly observed the python for 28 s and then ran toward a tree, delaying her repetitive alarm calling until she was safely in the tree. In two of the four troops, adults and subadults remained on the ground throughout the trial. After the first alarm call was emitted, four juveniles in one troop and two juveniles in another who had seen the python emerged from its cloth cover ran up a nearby tree, only to descend after watching the adults and subadults gather on the ground at a safe distance from the python (Fig. 2b). None of the juveniles alarm called when the python first appeared, and the small number of juveniles who alarm called later did so from an arboreal vantage point.

Both callers and non-callers alike adopted vigilance postures after they detected the python (Ramakrishnan et al. 2005). For example, after sighting the python, many individuals feeding in quadrapedal postures or moving about typically froze for a several seconds. This brief immobility was followed by individuals raising their heads and bodies by stiffening their legs. Other individuals stood erect and on their hindlegs, a posture that afforded a better view of the python. Similar enhanced vigilance and passive avoidance has been reported for wild long-tailed macaques (*Macaca fascicularis*) during exposure to a python model (van Schaik & Mitrasetia 1990). Analyses of video tapes later revealed that individuals close to the video camera exhibited piloerection of their body and tail hair, indicating that they were in a high state of sympathetic nervous system arousal (Fuchs et al. 1985; Ennis & Coss 2006).

In contrast to the effects of persistent ground-based alarm calling by adults and subadults in two troops, all six individuals at one feeding station progressively climbed a tree overhanging the python model. Watching others run is very contagious (see Coss & Ramakrishnan 2000) and the excitatory effects of simultaneously hearing an increasing

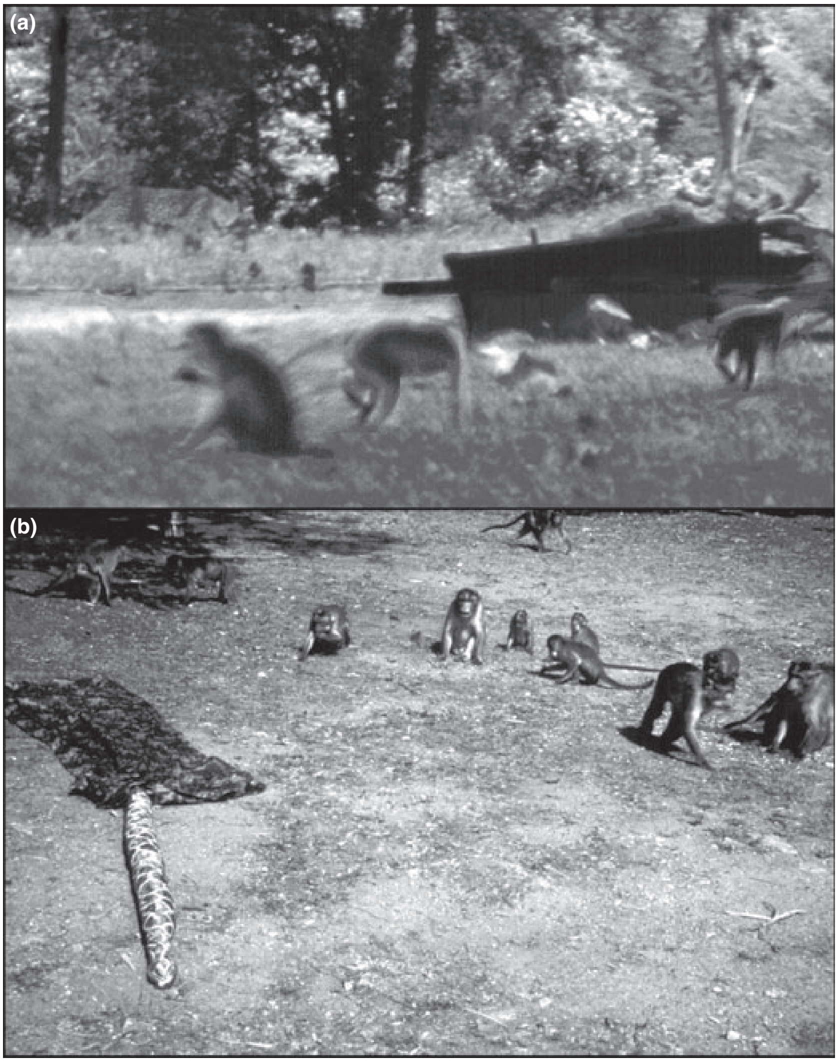


Fig. 2: Differences in spatial location of bonnet macaques when leopard and python models first appear. (a) Leopard model in full view for 10 s elicits immediate flight to the nearest tree before the initiation of alarm calling. (b) Alarm calling at python model on the ground while it emerges from its cloth cover. Three juveniles appear in the background

chorus of alarm calls from this tree and seeing neighboring individuals climbing apparently outweighed the perceived risk of monitoring the python on the ground. Despite this intense alarm calling, two adult males near the python remained on the ground, indicating some inherent understanding that pythons on the ground do not pose the imminent threat that leopards that can sprint do.

Acoustical Analyses of Alarm Calls

Audio tracts of VHS video tapes were digitized in 16-bit mode at a sampling frequency of 48 kHz by a Sony Media Converter Model DVMC-DA2 (Sony Corporation, Tokyo, Japan) and captured by a Macintosh G4 computer running Peak DV 3.0 software (Berkley Integrated Audio Software, Inc., Petaloma, California, USA). Alarm calls were examined initially for artifacts (overlapping calls and high background noise) and then converted to separate WAVE files. The unit of analysis for comparisons of leopard and python alarm calls was the first high-quality alarm call emitted in a series. Alarm calls were measured from 25 individuals during python-model presentations, 17 individuals during brief presentations of the spotted morph in full view, 11 individuals during sustained presentations of the dark morph full view, 13 individuals during spotted leopard-forequarter presentations, and 11 individuals during spotted leopard-hindquarter presentations. These calls were quantified using the methods described by McCowan (1995); McCowan & Reiss (2001) and McCowan & Hooper (2002).

Over the length of each call, sixty equidistant measurements were digitally extracted from the spectrogram (sampling rate of 44.1 kHz; 1024-point

Table 1: Acoustic variables of bonnet macaque alarm calls quantified for predator model comparisons

Duration
Minimum fundamental frequency
Maximum fundamental frequency
Mean fundamental frequency
Standard deviation in fundamental frequency
Position of maximum frequency in call, expressed as a percentage of call
Position of minimum frequency in call, expressed as a percentage of call
Overall change in frequency across the duration of call divided by its duration
Percentage of samples that were identified as tonal (vs. pulsed) characteristics
Amount of frequency modulation in a call
Amount of amplitude modulation in a call
Minimum harmonic to noise ratio
Maximum harmonic to noise ratio
Mean Harmonic to noise ratio
Standard deviation in harmonic to noise ratio

FFT spectrum with a Hamming filter; time resolution of 23 ms; frequency resolution of 43 Hz). For each of these 60 measurements across time, the frequency with the highest amplitude was recorded using Cool Edit Pro software (rebranded as Adobe Audition, Adobe Systems, Inc., San Jose, California, USA) and automated customized macros developed by McCowan. Fifteen acoustic variables defining various call spectral and temporal parameters were calculated from these call measurements (see Table 1 for a list and description of variables).

Single factor analyses of variance revealed statistically significant main effects for model differences for four acoustical measures. These variables were: (i) the duration (ms) of the alarm call ($F_{4,72} = 3.613$, $p < 0.01$, Fig. 3a), (ii) the percentage of 60 measurements across time with tonal vs. pulsed characteristics ($F_{4,72} = 4.030$, $p < 0.01$, Fig. 3b), (iii) mean harmonic to noise ratio for 60 measurements across time ($F_{4,72} = 6.160$, $p < 0.0005$, Fig. 3c), (iv) standard deviation of the harmonic to noise ratio for 60 measurements across time ($F_{4,72} = 3.350$, $p < 0.025$, Fig. 3d).

To distinguish the alarm calls elicited by the five types of model presentations, the four aforementioned dependent variables were analyzed together using discriminant function analysis coupled with group classification (Statistica software, Statsoft, Inc., Tulsa, OK, USA). Discriminant analysis indicated a statistically significant main effect for alarm-call differences (Wilks' Lambda = 0.535, approx. $F_{16,211} = 3.003$, $p < 0.0005$). Alarm calls elicited by the python and leopard forequarter exhibited the longest squared Mahalanobis distance ($F_{4,69} = 5.640$, $p = 0.0005$), followed by the python and spotted leopard hindquarter ($F_{4,69} = 4.444$, $p < 0.005$). The python alarm calls were not reliably distinguishable from those engendered by the spotted and dark leopard morphs in full view. Alarm calls elicited by the spotted leopard forequarter also differed appreciably in distances from the spotted hindquarter ($F_{4,69} = 3.482$, $p < 0.025$) and dark leopard in full view ($F_{4,69} = 4.473$, $p < 0.005$). Finally, the spotted leopard hindquarter exhibited a statistically significant distance from the dark morph in full view ($F_{4,69} = 5.330$, $p < 0.001$).

A scatter plot of individual alarm calls distributed on the first and second roots is shown in Fig. 4, accompanied by spectrograms of python (Fig. 4b) and spotted leopard forequarter alarm calls (Fig. 4c) with unstandardized canonical scores closest to the first and second root averages (group centroids). It must be noted that among the four dependent variables, the mean harmonic to noise ratio over time yielded the largest standardized coefficient for canonical variables on the first root, illustrating its strong contribution to group discrimination. Examples of alarm call spectrograms approximating group mean values for the mean harmonic to noise ratio variable appear in Fig. 5 in which the noisy property of an alarm call elicited by the spotted leopard's forequarter is visibly apparent (Fig. 5b).

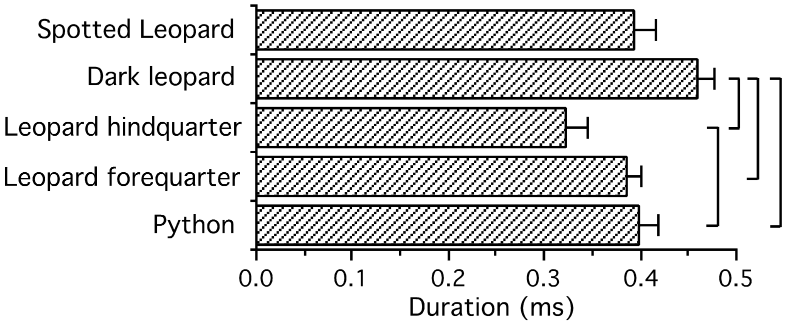
The frequency of correct alarm-call classification appears in Table 2. Here, it can be seen that the spotted leopard forequarter received the highest correct classification (84.62%) for the probability based on sample size (0.169) and the highest correct classification (76.92%) for an equal likelihood among the five groups of alarm calls. Alarm calls elicited by the python received the highest correct classification (72.00%) for the probability based on sample size (0.325), but a relatively low correct classification (32.00%) for an equal likelihood (0.20%) among the five groups of alarm calls.

Part 2: Effects of Predator Inexperience on Alarm Calling

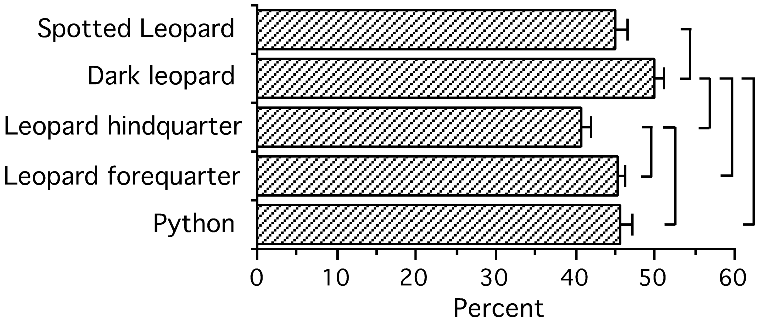
Study Sites

As reclusive predators, leopards and pythons avoid large human settlements whereas bonnet macaques do live in predator-rare urban settings in which they find food and shelter. Since there are no forests adja-

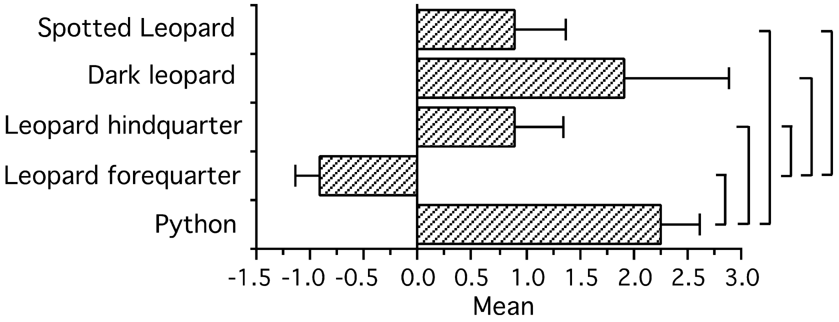
(a) Alarm Call Duration



(b) Proportion Tonal versus Pulsed



(c) Mean Harmonic to Noise Ratio



(d) Standard Deviation of Harmonic to Noise Ratio

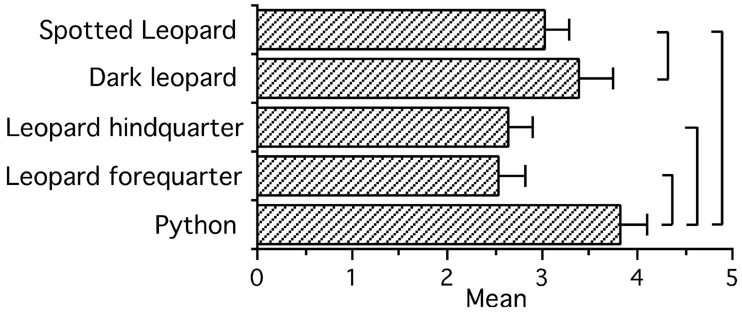


Fig. 3: Differences in the acoustic structure of alarm calls engendered by predator models. Vertical lines adjacent to the horizontal bars indicate statistically significant differences ($p < 0.05$) between specific models. Note that the forequarter view of the spotted leopard elicited the noisiest alarm calls indicative of high physiological arousal

cent to the city of Bangalore, we are reasonably confident that bonnet macaques living in Banglore have never encountered leopards and pythons. Thus, the availability of predator-inexperienced urban troops afforded the opportunity to compare the acoustic properties of alarm calls emitted during presentations of a novel python and leopard with the alarm calls of predator-experienced forest troops examined in

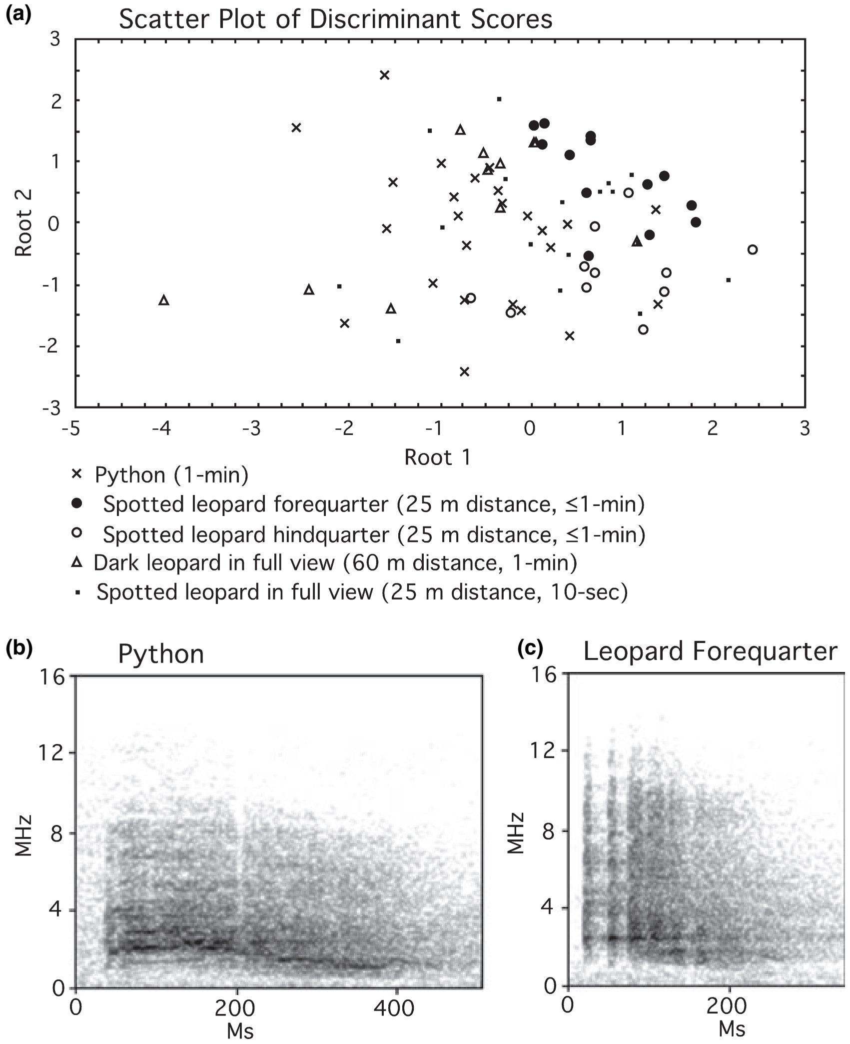


Fig. 4: Discriminant function scores for alarm calls emitted by bonnet macaques in forest settings (a). Spectrograms of alarm calls elicited by the python model (b) and forequarter view of the spotted leopard morph (c) approximating group centroids

Part 1 experiencing the same model-presentation protocol. We had preliminary evidence that leopard-naïve bonnet macaques would alarm call when they saw a leapord because, prior to selecting the current protocol using ground-based feeding sites, we first presented the model of the spotted morph on the rooftop of a building used for sleeping. In 1997, individuals in one free-ranging troop living at an agricultural college campus on the periphery of the city were presented the spotted leopard model in full view for 10 s at approx. 25 m distance from their feeding station (Coss & Ramakrishnan 2000). Three years later, members of a second troop living on this campus were presented the python model approx. 4 m from a feeding station using the same procedure employed for the python model shown to forest troops. The urban habitat in which these models were observed consisted of forest plantations interspersed with agricultural fields and buildings. Juveniles, subadults and adults emitted alarm calls during these predator presentations, yielding high-quality calls for acoustic analyses. As the venomous Indian cobra (*Naja naja*) and a several non-venomous species of snake are encountered occasionally on this campus, it was assumed that subadult and adult Bangalore monkeys were snake experienced, but not leopard or python experienced. In previous study of snake-species discrimination (Ramakrishnan et al. 2005), forest monkeys were presented realistic looking, animated models of four species of snake near their feeding stations, including the provocative Indian cobra. Bangalore monkeys were also shown the same snake models for exploratory purposes. Unlike the python model presented much later, none of these snake models engendered alarm calling in either forest or Bangalore monkeys, albeit,

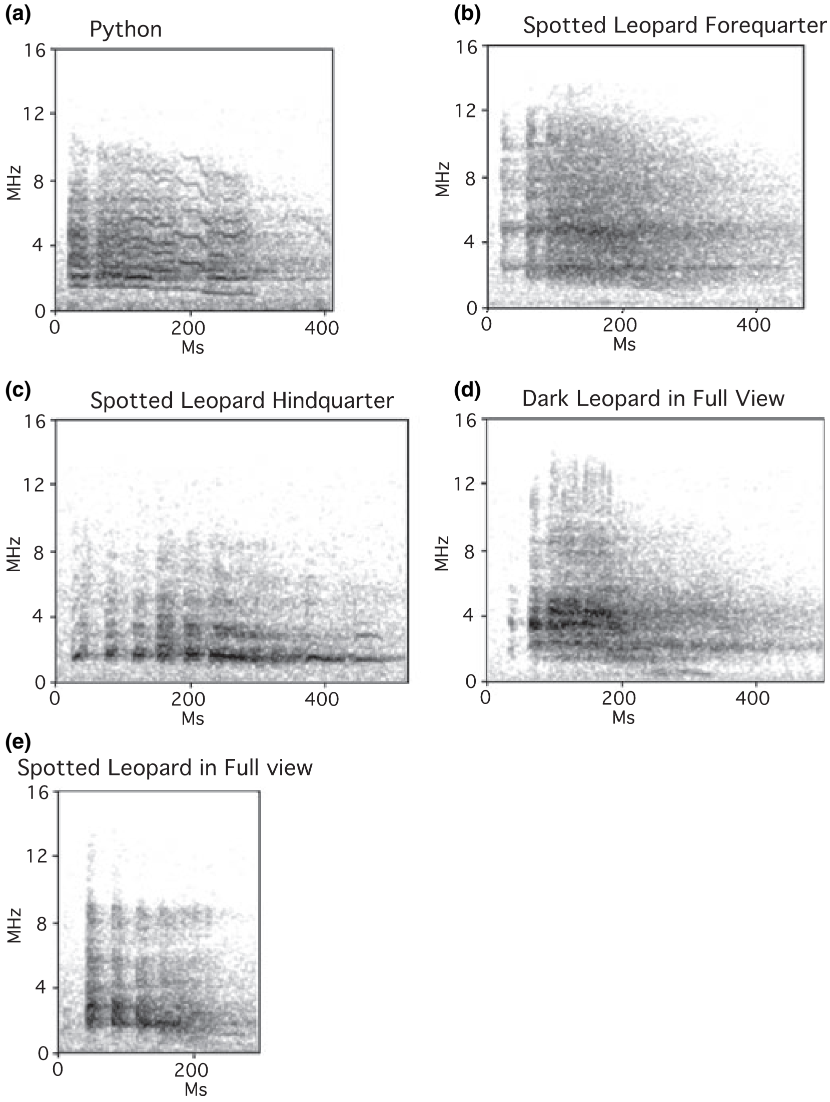


Fig. 5: Spectrograms of alarm calls approximating group mean values for the mean harmonic to noise ratio. Note for the spotted leopard's forequarter (b) the noisy appearance across the duration of the call

Table 2: Discriminant function analysis on predator type, coat color, and visibility

	Python (p = 0.32)	Spotted leopard forequart (p = 0.17)	Spotted leopard hindquart (p = 0.14)	Dark leopard (p = 0.14)	Spotted leopard full view (p = 0.22)	Correct classification (%)
Python	18	1	2	3	1	72.00
	8	*1*	*3*	*10*	*3*	*32.00*
Spot. leop. foreq.	0	11	1	0	1	84.62
	0	*10*	*3*	*0*	*0*	*76.92*
Spot. leop. hindq.	2	1	6	0	2	54.55
	1	*1*	*7*	*1*	*1*	*63.64*
Dark leopard	8	2	0	0	1	0.00
	1	*2*	*1*	*6*	*1*	*54.54*
Spot. leop. full V.	7	3	3	2	2	11.76
	4	*4*	*4*	*4*	*1*	*5.88*

Italicized numbers indicate an equal probability of correct classification.

these monkeys became jumpy immediately after they detected the snake models.

Results

Effects of Predator Inexperience on the Situational Context of Alarm Calling

Consistent with the arboreal alarm calling by forest monkeys after a leopard has been sighted, all alarm calls emitted by Bangalore monkeys during the leopard model presentation were made by individuals who had fled to trees or were already in trees when the model was erected into view. Because the first alarm call was emitted by an individual in a tree who spotted the leopard when it first appeared, all individuals at the feeding station fled to trees without orienting toward the leopard. Many of these individuals, however, would have had time to run up a tree and look at the leopard model before it was lowered out of sight.

Several facets of the situational context of alarm calling by Bangalore monkeys during the python presentation resembled the situational context of alarm calling by forest monkeys. For example, the first alarm was made on the ground by an adult male who observed the python for 5 s before calling. Although retreating after he made his first alarm call, this adult remained on the ground near the base of a tree, facing the python for another 13 s during which he heard a succession of alarm calls without ascending the tree. Nevertheless, his initial alarm call had triggered the immediate flight of four individuals in video view who ran up a nearby clump of trees even though these monkeys were already looking at the python with alert postures for 3–6 s as it emerged from its cloth cover. When the python was no longer in view within 88 s from the first alarm call, the four monkeys at the feeding station who had fled up trees returned to the feeding station and resumed feeding. A subadult and adult also ran to the initial alarm call, but they remained on the ground near the base of two trees. These individuals remained on the ground for another 47–53 s, following which they climbed a tree several meters away to join others who were alarm calling vigorously from low branches while they tracked the python as it was pulled away from the feeding station.

Acoustical Analyses of Alarm Calls

The first high-quality alarm calls in a series by subadults and adults from the Bangalore troops, yielded nine alarm calls from the leopard presentation and eight alarm calls from the python presentation. These calls were compared with 17 and 25 calls from forest monkeys elicited by the leopard and python models, respectively. The Bangalore individuals emitting these alarm calls were the same as those compared for their arboreal or terrestrial locations during emission of their initial alarm calls. Two-factor between subjects (predators and forest-Banglore locations) ANOVAS were applied to each acoustic measure. Statistically significant interactions of predator type and forest and Banglore locations were evident for the four acoustic measures that differed reliably as main effects in Part 1, with the addition of the minimum harmonic to noise ratio across time. These statistical interactions were: (i) the duration (ms) of the alarm call ($F_{1,55} = 4.965$, $p < 0.05$), (ii) the percentage of 60 measurements across time with tonal vs. pulsed characteristics ($F_{1,55} = 6.340$, $p < 0.025$), 3) the minimum harmonic to noise ratio for 60 measurements across time ($F_{1,55} = 4.055$, $p < 0.05$), (iv) the mean harmonic to noise ratio of 60 measurements across time ($F_{1,55} = 4.825$, $p < 0.05$), and (v) the standard deviation of the harmonic to noise ratio for 60 measurements across time ($F_{1,55} = 7.442$, $p < 0.01$).

Tests of simple effects revealed the sources of these statistical interactions of predator type and forest and Banglore locations. For example, the mean duration of the leopard alarm calls from Bangalore monkeys was shorter than the mean duration of either the python calls from Bangalore monkeys ($F_{1,55} = 7.427$, $p = 0.01$) or the leopard calls from forest monkeys ($F_{1,55} = 4.334$, $p < 0.05$). The average percentage of tonal vs. pulsed properties of the python calls from Bangalore monkeys was markedly higher than the average of Bangalore leopard calls ($F_{1,55} = 10.152$, $p < 0.0025$). The minimum harmonic to noise ratio was higher for the leopard calls from forest monkeys compared with Bangalore monkeys ($F_{1,55} = 5.086$, $p < 0.05$). As evinced by their mean harmonic to noise ratios, the python alarm calls of Bangalore monkeys were reliably noisier than their leopard calls ($F_{1,55} = 4.416$, $p < 0.05$) and the python calls of forest monkeys ($F_{1,55} = 4.253$, $p < 0.05$). Finally, forest monkeys emitted python alarm calls with a higher harmonic to noise ratio standard deviation throughout the duration of the call than the python calls from Bangalore monkeys ($F_{1,55} = 4.370$, $p < 0.05$), the latter of which were also reliably lower in the standard deviation in harmonic to noise ratio than Bangalore leopard calls ($F_{1,55} = 4.510$, $p < 0.05$).

Follow-up discriminant analysis incorporated these five acoustic variables to compare alarm calls elicited by leopard and python model presentations to forest and Bangalore troops. Discriminant analysis yielded a statistically significant main effect for alarm-call differences (Wilks' Lambda = 0.622, approx. $F_{15,141} = 1.766$, $p < 0.05$). As apparent from the standardized coefficients for the canonical variables, the tonal vs. pulse properties of the alarm calls contributed the most to distinguishing the four alarm call groups. Unlike the forest troops that did not emit leopard and python alarm calls that were statistically distinguishable ($p = 0.349$), the Bangalore troops emitted alarm calls to leopard- and python-model presentations that yielded the longest squared Mahalanobis distance ($F_{5,51} = 3.270$, $p = 0.012$). Moreover, the acoustic properties of the leopard alarm calls by members of the forest and Bangalore troops were reliably distinguishable ($F_{5,51} = 2.590$, $p = 0.037$).

Three spectrograms of alarm calls closest to group centroids in discriminant space that are reliably distant are shown with the scatter plot of individual alarm calls distributed on the first and second roots (Fig. 6). These spectrograms exhibit three acoustic features that contributed to group discrimination, as illustrated by a shorter duration leopard alarm call from a Bangalore monkey contrasted by a more tonal python call of longer duration from a Bangalore monkey and a noisier, longer duration leopard call from a forest monkey.

Classification analyses (Table 3) illustrates the disparity of alarm-call classification for comparisons of the two models and locations. None of the python calls from Bangalore monkeys were correctly classified with a probability of 0.136 based on sample size, whereas 88.00% python calls from forest monkeys were correctly classified with a probability of 0.424 based on sample size. Correct classification of the leopard alarm calls from Bangalore monkeys (44.44%) and forest monkeys (35.29%) were somewhat larger than the probabilities based on sample sizes, respectively, $p = 0.153$ and 0.288. With an equal probability of correct classification (0.25%), overall correct classification of the four alarm call groups was 44.07%, with correct classification of the python alarm calls from forest monkeys (28.00%) approximating chance level.

Discussion

Analyses of the acoustic features of bonnet macaque alarm calls revealed differences in acoustic structure that can be interpreted as reflecting the level of perceived threat rather than predator type. Although bonnet macaque alarm calls do not have the distinctive properties associated with specific predator types found in vervet, diana, and Campbell's (*C. campbelli*) monkeys (e.g. Struhsaker 1967; Seyfarth et al. 1980a,b; Zuberbühler 2003), bonnet macaque alarm calls do have graded features that might provide eavesdropping troop members with information useful for assessing the urgency of the predatory threat. Such assessment can include distinguishing juvenile and adult bonnet macaque alarm calls because adults are less likely to flee after hearing playbacks of juvenile calls (Ramakrishnan & Coss 2000b). Moreover, any lack of alarm-call distinctiveness that characterizes predator type would not preclude evaluation of the dangerousness of the situation because more explicit contextual information would be available by observing whether alarm calling was initiated by individuals in trees or by individuals looking at something on the ground. In a similar vein, Fichtel (2004) has suggested that lemurs hearing general alarm calls might determine the nature of the threat by assessing the body posture and gaze of alarm callers. As stealthy, sprinting predators, leopards can run down bonnet macaques in the open and potentially catch them in trees if bonnet macaques fail to reach the thinner branches that cannot support the leopard's weight (cf. Busse 1980; Ramakrishnan & Coss 2001). In contrast, pythons constitute a serious threat to bonnet macaques only at distances in which pythons can lunge and seize them. As such, bonnet macaques were found to monitor the python model at safe distances on the ground (Ramakrishnan et al. 2005). Pythons, however, are facile climbers and could constitute a daytime and nighttime threat in trees; although as with leopards, python access to bonnet macaques would be restricted to weight-bearing branches.

It is important to note that, unlike forest monkeys, all alarm calls by Bangalore monkeys following the first one were made by individuals in trees who moved from branch to branch to keep the python in view. From the point of view of predation risk, the immediate flight to trees by Bangalore monkeys following the first alarm call was unnecessary. Such perceived urgency with the python in view suggests that, without appropriate experience with pythons, bonnet macaques adopt more generalized refuge-seeking behavior appropriate for evading sprinting and cursorial predators. In contrast with forest monkeys, none of the Bangalore monkeys remaining on the ground approached the python after they detec-

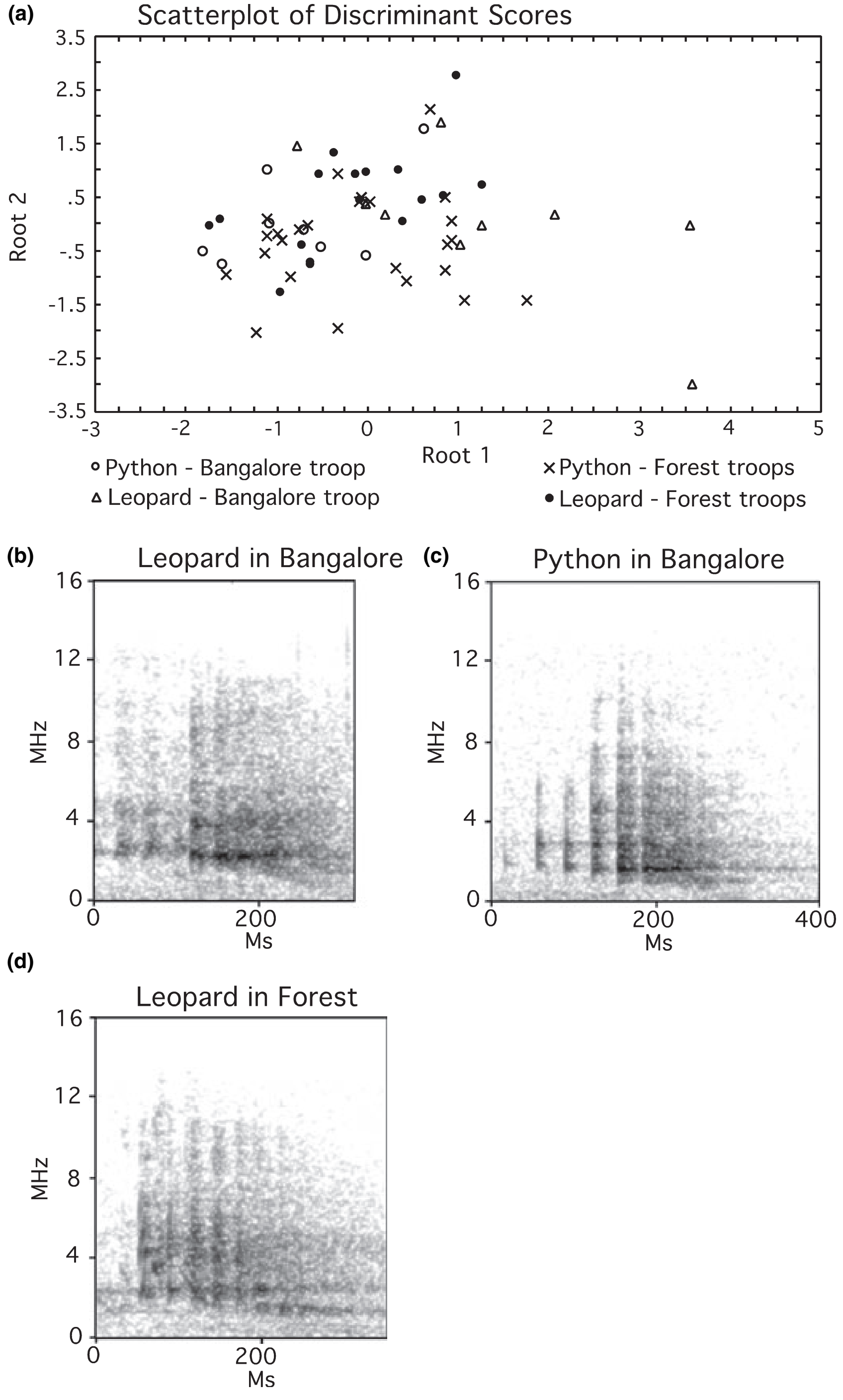


Fig. 6: Discriminant function scores for alarm calls from forest and Bangalore monkeys elicited by a spotted leopard model presented for 10 s at 25 m distance and a python model presented at distances between 4 and 5 m (a). Spectrograms shown are alarm calls approximating the group centroids that differed reliably in discriminant space. Note for Bangalore monkeys, the shorter duration leopard alarm call (b), and more tonal python call (c), contrasted by a noisier, longer duration leopard call from a forest monkey (d)

ted it, which suggests that the chorus of alarm calling inhibited their investigative behavior despite any inherent understanding that pythons are not sprinting predators like leopards and can be monitored safely on the ground. In keeping with this argument for the role of predator experience in moderating perceived urgency, several juvenile members of two forest troops climbed trees after they heard the first alarm call from adults on the ground, but they descended when they saw older monkeys continuing to monitor the python on the ground. Nevertheless, the fact that several Bangalore individuals remained on the ground while others alarm called from trees illustrates common features of python-initiated anti-

Table 3: Discriminant function analysis on predator location and type

	Bangalore		Forest		Correct classification (%)
	Python (p = 0.14)	Leopard (p = 0.15)	Python (p = 0.42)	Leopard (p = 0.29)	
Bangalore python	0	0	6	2	0.00
	5	*0*	*1*	*2*	*62.50*
Bangalore leopard	0	4	3	2	44.44
	0	*5*	*0*	*4*	*55.56*
Forest python	0	1	22	2	88.00
	8	*5*	*7*	*5*	*28.00*
Forest leopard	0	1	10	6	35.29
	4	*2*	*2*	*9*	*52.94*

Italicized numbers indicate an equal probability of correct classification.

predator behavior shared by both experienced and inexperienced bonnet macaques.

With respect to specific acoustic features that might have information properties, a lower mean and standard deviation of the harmonic to noise ratio across the duration of the call probably characterize the caller's level of fearfulness. As apparent in Fig. 3, prolonged viewing of the spotted leopard forequarter by forest monkeys generated alarm calls that were reliably noisier across the duration of the call than calls evoked by the other treatments. On the other hand, predator-inexperienced Bangalore monkeys emitted alarm calls to the python model, which remained in view that were much noisier than their alarm calls elicited by the transient appearance of the spotted leopard morph in full view. Consistent with this noisier calling, the choice of trees by inexperienced Bangalore monkeys to monitor the python instead of the ground suggests that they were much more frightened by the python model than experienced forest monkeys who emitted more harmonic alarm calls. Cumulative experience with snakes as bonnet macaques age generally lowers their excitability during snake encounters (Ramakrishnan et al. 2005), but the python was a large novel snake unlike any encountered before in Bangalore. In forest troops, older individuals would have had the benefit of previous experience watching troop members monitor pythons on the ground and associating the ensuing alarm calls with the dynamics of the situation.

In support of the conjecture that noisy alarm calls reflect higher states of fear, examination of the neurobiology of alarm calling reveals that the midbrain periacqueductal gray (PAG) is the essential structure mediating sympathetic nervous system responses during defensive behavior (e.g., Farkas et al. 1998). Holstege et al. (1997) review evidence that the final common pathway for mammalian vocalizations is the projection from the midbrain PAG and the laterally adjoining tegmentum to the nucleus retroambiguus (NRA). NRA neurons project to motoneurons innervating the pharynx, larynx, diaphragm, and abdominal muscles (Vanderhorst et al. 2000). Neural discharges in the PAG are coincident with macaque alarm barking (Larson & Kistler 1984, 1986). Another source of strong fearful emotions is produced by elevated neural discharges in the amygdala, a structure that sends projections to the PAG and mediates alarm calling indirectly (Jürgens 1982). Thus noisier alarm calling during a higher states of physiological arousal could result from forceful diaphragm contractions, producing turbulence of the airflow through the open glottis and aperiodic vocal-fold vibrations (Owren & Rendall 1997; Bettany 2002). Similarly, Fichtel & Kappeler (2002) argue that differences in the noisy properties of woofs and croaks of redfronted lemurs (*Eulemur fulvus rufus*) during predator encounters indicate different intensities of arousal.

Alarm calls with more harmonic properties that include greater tonal than pulsed properties might also reflect less physiological arousal. For example, the long, tonal barks of chimpanzees when they see snakes probably indicates a lower state of arousal than occurs during social aggression (Crockford & Boesch 2003), and chimpanzees have been observed to exhibit passive avoidance of snakes without alarm calling (Kortlandt 1967). Previous study of the flight responses of bonnet macaques indicates that the dark leopard morph is less provocative than the spotted morph (Coss & Ramakrishnan 2000), and the dark morph observed by forest monkeys at a 60-m distance generated the most tonal and harmonic alarm calls among the four leopard-model presentations. Nevertheless, the dark morph retained the ability to elicit alarm calling after it disappeared from view, and several monkeys traveled across a series of trees to perch near the spot where the leopard was presented.

Alarm calling while moving from tree to tree to locate the predator resembles the behavior of diana monkeys whose repetitive alarm calling appears to deter leopard hunting (Zuberbühler et al. 1999). While it is reasonable to argue that the alarm calling of bonnet macaques serves a similar pursuit-deterrent function by informing mammalian predators that they have been detected, this explanation would not apply to python predators that would have difficulty hearing alarm calls. Research on snake hearing (Young 1997, 2003) indicates that the best hearing range of snakes is 150–600 Hz with a steep dropoff in hearing above 1000 Hz, a frequency which approximates the lowest frequency dropoff of bonnet macaque alarm calls (see Fig. 5). Perhaps in addition to gaining information about the python's activity and hunting motivation (Ramakrishnan et al. 2005), cautious inspection of the python on the ground by small numbers of alarm-calling individuals or mobbing by larger groups (Fig. 2) might compensate for the python's poor hearing by providing the python with conspicuous visual evidence that it has been detected (also see Caro 1986). Whether such mobbing has python-deterrent properties as has been proposed for snake harassment by ground squirrels (Owings & Coss 1977) requires further study.

Acknowledgements

This research was supported by Faculty Research grant D-922 to R.G. Coss and by the Foundation for Ecological Research, Advocacy and Learning, Pondicherry, India to U. Ramakrishnan. We thank the Forest Department of Tamil Nadu for permission to conduct research in the Kalakad–Mundanthurai Tiger Reserve and the Mudumalai Wildlife Sanctuary and their staff for facilitating our research. We thank our field assistants, Anil Kumar, M. Siddhan and V. Yashoda for their contribution in data collection and Heather Austin and Alessandra Lanza for digitizing alarm calls.

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