

# Do Naïve Primates Recognize the Vocalizations of Felid Predators?

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## Abstract

Traits that were adaptive under previous conditions may no longer have fitness benefits. However, some species still retain appropriate antipredator behaviors even though they do not coexist with the predators that their ancestors once faced. Studies have examined the responses of a variety of naïve species to these predators, but none have specifically investigated whether naïve primates retain antipredator behaviors against felid predators. We studied the pig-tailed langur (*Simias concolor*) to determine whether it still recognizes felids as predators even though dangerous felids do not exist on the islands on which it inhabits. The responses of the langurs to the playbacks of the vocalizations of felids (an ancestral predator), elephants (an unknown animal but not a predator), humans (a known predator) and, pigs and birds (known animals but not predators) were compared. Langurs fled more slowly and looked at the speaker less in response to the felid and elephant calls than they did in response to the human voices. Similar numbers of langurs fled in response to all playback treatments except the pig and bird. The results suggest that langurs are afraid of novel vocalizations but have not retained specific acoustic knowledge of felid predator vocalizations. For long-lived species that have extended periods of learning, being able to modify general behavioral responses, such as antipredator behaviors, based on individual experiences may be more adaptive than having fixed behavioral strategies.

## Introduction

Many species experience relaxed sources of natural selection that affect the evolution of their morphologic, physiologic, and behavioral traits (Fong et al. 1995). Relaxed selection can occur when environmental or social conditions change. These changes may no longer favor traits that were adaptive in the previous conditions (Coss 1999). The persistence of these traits will depend on trade-offs and evolutionary constraints associated with maintaining them (Fong et al. 1995).

Despite relaxed sources of selection, some species still retain appropriate antipredator behaviors even though they do not coexist with the predators that their ancestors once faced (Caine & Weldon 1989; Coss 1993, 1999; Byers 1997; Blumstein et al. 2000; Barros et al. 2002; Blumstein & Daniel 2002). Multiple hypotheses (not all on the same levels of analysis) have been proposed to explain this variation in behavior. The 'ghost of predators past' (Byers 1997), 'pleiotropic' (Byers 1997; Coss 1999), and 'functional integration' (Coss 1999) hypotheses posit that species retain antipredator behaviors when they are

easy to maintain, are genetically linked, or have multiple functions, respectively. The fourth 'multi-predator' hypothesis (Blumstein 2006; Blumstein et al. 2006) suggests that antipredator behavior persists when the prey species is still subject to predation by at least one predator. Preliminary evidence supports the latter hypothesis (Blumstein et al. 2004; but see Stankowich & Coss 2007).

While studies have examined the response of a wide range of prey species to their former predators, we know almost nothing about how our closest taxonomic relatives respond to felid predators when they are no longer exposed to them (but see Davis et al. 2003). Primates have a long evolutionary history of being preyed on by felids (Hart & Sussman 2005). When attacked by these predators, they exhibit intense antipredator behaviors (e.g. Boesch 1991; Zuberbühler 2001). Predation has been such a dominant process in the evolution of primates that it has been suggested to have influenced their group size and composition, ecological niche, reproductive and vocal behavior, body size, and cognitive abilities (van Schaik & van Noordwijk 1985; reviewed in Zuberbühler & Jenny 2002).

We studied the pig-tailed langur (*Simias concolor*) to determine whether primates that have been isolated from their felid predators are still able to recognize them. The pig-tailed langur is endemic to the Mentawai Islands of Indonesia and has likely been isolated from its mainland predators for over 0.5 Myr (Rohling et al. 1998; Abegg & Thierry 2002). It is a medium-sized leaf monkey that usually lives in one-male one-female or one-male multi-female groups composed of two to five individuals (larger groups exceeding 20 individuals have also been observed; Tilson 1977; Watanabe 1981; Tenaza & Fuentes 1995). Although it is mostly arboreal, it also forages on the ground (J. Yorzinski, pers. obs.). No dangerous felids inhabit the islands on which it lives (World Wildlife Fund. 1980). However, related langur species living on the mainlands experience high rates of predation by tigers (*Panthera tigris*), clouded leopards (*Neofelis nebulosa*), and leopards (*Panthera pardus*; Seidensticker 1983; Rabinowitz et al. 1987; Karanth & Sunquist 1995; Støen & Wegge 1996; Sankar & Johnsingh 2002) and react strongly when seeing these predators or models of these predators (Thapar 1986; Ramakrishnan & Coss 2000; Wich & Sterck 2003). Humans are the main and only confirmed predator of the pig-tailed langur. The serpent eagle (*Spilornis cheela sipora*) and reticulated python (*Python reticulatus*) also likely prey on it

(Whitten & Whitten 1982) but predation events have never been recorded.

The aim of this study was to investigate the predator-recognition abilities of the pig-tailed langur. We evaluated the reactions of langurs to the vocalizations of different animals to test two hypotheses regarding their acoustic predator-recognition abilities. Our first hypothesis is that pig-tailed langurs have retained the ability to recognize the vocalizations of dangerous felids. And, our second hypothesis is that langurs are afraid of novel vocalizations that they have had no prior experience hearing.

## Methods

### Subjects and Location

We studied the acoustic predator-recognition abilities of the pig-tailed langur (*S. concolor*) between Jan. and July 2006. One researcher (JLY) systematically searched the forest for experimental subjects (see below) during two of their peak foraging times in the morning (7:00–11:00 hours) and afternoon (15:00–18:00 hours). Adult males could be distinguished from females based on their larger and stockier body builds (Tenaza & Fuentes 1995); the sex of juveniles could not be determined. All subjects were of the dark phase coloration (Tilson 1977), were unmarked, and not habituated to the presence of humans.

This study was conducted at the Siberut Conservation Project field site (SCP; 1°01'34'S, 98°50'16'E; elevation: 8–180 m above sea level) in northeast Siberut Island which is located 150 km off the west coast of Sumatra, Indonesia. The field site encompasses 10.7 km<sup>2</sup> of primary and secondary dipterocarp and mixed rainforest. The local people stopped hunting primates at the field station 2 yr before the onset of this study. Fifteen transects (mean length: 1600 ± 80 m; range: 900–2000; total: 24 km) radiate from the central field site and circular intertransects connect these transects at 200 and 600 m from the field site. Additional semi-circular intertransects connect 10 of these transects at 400, 800, and 1000 m. The transects were marked every 50 m with aluminum tags.

### Hypotheses and Predictions

We evaluated the reactions of langurs to seven different playback treatments of the vocalizations of animals to test two hypotheses regarding their acoustic predator-recognition abilities (Table 1).

**Table 1:** Summary of the treatments, call types of the playbacks, hypotheses, and predictions

Treatment	Call type (x, y) <sup>a</sup>	Primate predator? <sup>b</sup>	Present on Siberut? <sup>b</sup>	Hypotheses and predictions <sup>c</sup>		
				H1 <sup>d</sup>	H2 <sup>e</sup>	Ho <sup>f</sup>
Tiger ( <i>Panthera tigris</i> )	Loud calls (5, 3) Growls (1, 1)	Y	N	X	X	X
Clouded leopard ( <i>Neofelis nebulosa</i> / <i>N. diardi</i> )	Mews/main calls (2, 2)	Y	N	X	X	X
Leopard ( <i>Panthera pardus</i> )	Sawing (4, 3)	Y	N	X	X	X
Elephant ( <i>Elephas maximus</i> )	Trumpets (4, 3) Roars (4, – <sup>g</sup> )	N	N		X	X
Person ( <i>Homo sapiens</i> )	Speaking in Mentawai (6, 6)	Y	Y	X	X	
Pig ( <i>Sus scrofa</i> )	Grunts (6, 6)	N	Y			X
Bird ( <i>Pycnonotus melanoleucos</i> , <i>Pycnonotus atriceps</i> , <i>Culicicapa ceylonensis</i> )	Songs (4, 4)	N	Y			X

<sup>a</sup>The number of (x) different playback segments emitted by (y) different individuals.

<sup>b</sup>'Y' indicates that the animal is a primate predator or present on Siberut; 'N' indicates the opposite.

<sup>c</sup>If the hypothesis is supported, an 'X' indicates in which treatments the langur is expected to respond similarly.

<sup>d</sup>The langurs are afraid of felid vocalizations.

<sup>e</sup>The langurs are afraid of novel vocalizations.

<sup>f</sup>The langurs are unafraid of felid and novel vocalizations.

<sup>g</sup>These vocalizations were all recorded by the same organization but it is unknown whether they were emitted by the same individual or multiple individuals.

Previous research has shown that primates cohabiting environments with predators can recognize the predators by their vocalizations (e.g. Hauser & Wrangham 1990; Zuberbühler et al. 1997). The first hypothesis is that pig-tailed langurs have retained the ability to recognize the vocalizations of dangerous felids. If this hypothesis is supported, then their responses toward the calls of tigers, clouded leopards, and leopards will be similar to their responses toward human voices because they recognize all four treatments as predators (the human voices are presumed to convey information about human predators because we only tested non-habituated monkeys). Their responses to the felid calls will be different from their responses to the vocalizations of elephants and pigs because these latter two mammals are not predators of primates.

The second hypothesis is that langurs are afraid of novel vocalizations that they have had no prior experience hearing. If this hypothesis is supported, then they will respond to the tiger, clouded leopard, and leopard vocalizations in a manner similar as their response to the elephant calls because all of these vocalizations are novel. We would expect their response to the felid calls to be more similar to their response toward the human vocalizations than toward the pig vocalizations. The langurs may still be fearful of the novel vocalizations but react less intensely than they do toward the known human predators.

The null hypothesis is that langurs are not afraid of the felid or elephant vocalizations. If this is the

case, then their response to the calls of tigers, clouded leopards, and leopards will be different from their response to the voices of their known human predator. We would expect their reactions to all novel vocalizations (tiger, clouded leopard, leopard, and elephant) to be the same and also be similar to their responses toward known and non-predatory animals (pig and bird).

In addition, if the langurs display no fear toward any of the vocalizations (particularly in response to the playbacks of human voices), then the experimental procedure failed to elicit natural behaviors and no conclusions can be drawn. Likewise, the experimental procedures failed if the langurs respond to the songs of birds (bird song did not naturally elicit any behavioral changes in the langurs).

### Playback Stimuli and Experimental Protocol

Each playback segment consisted of 10 s of vocalizations from one treatment of the same call type and had 10 s of silence both before and after it. The segments usually included only the vocalizations of one individual. We used vocalizations emitted by multiple individuals to provide variation in the vocalizations within each acoustic category. The vocalizations of some segments were produced by the same individual but on different occasions (Table 1). Segments were imported into a Mayah<sup>®</sup> Flashman<sup>®</sup> Professional MPEG and linear digital audio recorder. (Mayah Communications GmbH, Hallbergmoos, Germany) Sound levels were adjusted to a mean of

80–85 dB at 1 m from the speaker (Radioshack sound level meter, model 33-2050, C-weighting; Radio Shack Corp., Fort Worth, TX, USA). The clouded leopard and leopard vocalizations as well as most of the tiger vocalizations were recorded by Gustav Peters and obtained from the Animal Sound Archives at the Zoological Research Museum Alexander Koenig. The elephant and other tiger vocalizations were purchased from the Wildlife Section of the British Library Sound Archive. We recorded the human, pig, and bird vocalizations using a Sennheiser K6 microphone (Sennheiser Electronic Corp., Old Lyme, CT, USA) connected to the Mayah® Flashman® on Siberut Island.

To conduct the playbacks, a field assistant and the researcher systematically searched the study area for groups of pig-tailed langurs. Groups were often located because we heard them vocalizing or saw them moving. Because the estimated home range of the langur is 3–5 ha (Watanabe 1981), we tested groups that were about 600 m (mean  $600 \pm 50$  m; range: 300–1100) away from groups that were previously tested with the same stimulus type. It is therefore unlikely that the same group was tested on multiple occasions with the same stimulus type. However, it is possible that some of the same individuals were repeatedly tested with different stimuli; even so, this type of resampling would have minimal effects on the statistical analyses (Coss et al. 2005).

If the monkeys detected us before the playback began, we moved at least 300 m away before searching for another group. For each trial, the researcher randomly chose an adult langur that was engaged in a stationary activity (e.g. resting, grooming, or eating), hid within the understory, and began filming this focal individual with a Canon ZR-60 (Canon USA, Inc., Lake Success, NY, USA) or Sony DCR-HC32E PAL digital video camcorder (Sony Corp., Tokyo, Japan). Occasionally, two individuals were filmed because they were sitting beside one another. Meanwhile, the field assistant placed the speaker (Anchor mini-vox PB-25; frequency response: 100 Hz to 12 kHz; Anchor Audio, Torrance, CA, USA) in a concealed spot on the ground at about 35 m (mean  $34 \pm 1$  m) from the closest individual of the group. He connected the speaker and flashman with a 3 m cord and then hid in the understory while holding the flashman. After scanning the area, he noted the position, sex, age, and behavior of all visible monkeys. Because of the dense canopy, it is likely that he did not observe all individuals within each group. He initiated the playback with the flashman and noted the reaction (flee or remain within 10 s of the start of the playback) of each individual that was observed before

the playback began. Individuals that were only observed after the playback began (most often because we saw them flee) were not included in the analyses. The researcher continued filming the focal animal until it left its original position (in which case visual contact was usually lost). The equipment was disassembled and the distance between the speaker and the initial position of each monkey was measured (Rangemaster Leica Laf 800; Leica Camera AG, Solms, Germany). All tested langurs were in the canopy of the forest. Only one playback was ever conducted within the same observation period. The playback treatments were randomized across trials.

### Measurements and Statistical Analysis

We compared the gaze direction of the focal langurs before and after the start of the playbacks. For each focal langur, we measured the total amount of time it (1) looked in the direction of the speaker (speaker), (2) scanned in all directions other than the speaker (scanning), and (3) neither looked at the speaker nor scanned in other directions (i.e. the focal was resting, grooming, or feeding; self-directed). The gaze direction of the focal langur always fell within one of these three categories. The pre-playback period consisted of 10 s before the playback began. Because the monkeys often moved out of view when we lengthened the pre-playback period, we decided to maximize the number of trials by only using this 10 s pre-playback period. The post-playback period varied depending on the behavior of the focal langur. If the focal langur did not flee, we measured its gaze direction for 1 min after the start of the playback; if the focal langur fled, we measured its gaze direction only during the time before it fled. Because the pre- and post-playback periods were of different durations, the percentage of time the focal langurs spent gazing in each of the categories was calculated for each period. The percentage of time gazing in each category in the pre-playback period was then subtracted from the percentage of time gazing in each category in the post-playback period; this difference was used to compare treatments.

We calculated the amount of time between the start of the playback and the initial reaction to the playback (latency to respond). For those focals that fled within 10 s of the start of the playback, we calculated their latency to flee (difference between the start of the playback and the first movement away from the speaker). Non-parametric Kruskal–Wallis tests (PROC NPAR1WAY) compared the differences in gaze direction and generalized linear models (PROC

GLM) were used to compare latency to respond and latency to flee. Responses were compared across treatments, sex of the focal subject, behavior of the focal subject before the trial began (i.e. looking, foraging, grooming, or sleeping), and number of visible monkeys in the group. A Fisher's exact test was also performed to compare the number of focal monkeys responding to the novel, dangerous, and/or uncommon treatments (felid, elephant, person, and pig) and the bird control.

Finally, a multinomial logistic regression compared the total number of individuals fleeing within 10 s of the start of the playback across treatments. A Fisher's exact test compared the number of individuals fleeing in response to the novel and/or dangerous treatments (felid, elephant, and human) and the non-dangerous treatments (bird and pig). In all analyses, the responses to the tiger, clouded leopard, and leopard treatments were pooled because no statistically significant differences existed among them. Planned comparisons were made to investigate differences in the behavior of the langurs in response to the felid vocalizations and the other treatments; because we made multiple comparisons, we used the Bonferroni method to appropriately adjust our p-values. Incomplete data exists for some trials because the video recordings were not completely free of visual occlusion from vegetation. All analyses were performed with SAS (version 9.1; SAS Institute 2003); videos were analyzed frame-by-frame (33.333 ms increments) with Microsoft Windows Movie Maker 2001 (version 5.1). Mean  $\pm$  SE are provided in graphs to illustrate effect sizes.

## Results

Thirty-seven playback trials were successfully conducted on 88 pig-tailed langurs. A field assistant and the researcher searched the study area for experimental subjects for over 300 h. Over 75% of all trials were aborted because the monkeys detected us or moved out of visual range. Only one focal langur ever emitted an alarm vocalization within 1 min of the start of a playback (this alarm call was emitted by an adult male in response to hearing tiger vocalizations).

### Gaze Direction

The gaze direction was unaffected by the sex of the focal subject (speaker:  $X^2 = 0.001$ ,  $df = 1$ ,  $p = 0.975$ ; scanning:  $X^2 = 0.183$ ,  $df = 1$ ,  $p = 0.669$ ; self-directed:  $X^2 = 0.0044$ ,  $df = 1$ ,  $p = 0.947$ ), the behavior of focal subject before the trial began (speaker:  $X^2 = 4.83$ ,  $df = 3$ ,  $p = 0.185$ ; scanning:  $X^2 = 1.165$ ,  $df = 3$ ,  $p = 0.762$ ; self-directed:  $X^2 = 3.013$ ,  $df = 3$ ,  $p = 0.390$ ), and the number of visible monkeys (speaker:  $X^2 = 0.596$ ,  $df = 4$ ,  $p = 0.964$ ; scanning:  $X^2 = 2.094$ ,  $df = 4$ ,  $p = 0.719$ ; self-directed:  $X^2 = 1.05$ ,  $df = 4$ ,  $p = 0.902$ ). The gaze direction was only affected by the treatment type (speaker:  $X^2 = 17.45$ ,  $df = 4$ ,  $p = 0.0016$ ; scanning:  $X^2 = 9.412$ ,  $df = 4$ ,  $p = 0.0516$ ; self-directed:  $X^2 = 9.346$ ,  $df = 4$ ,  $p = 0.0530$ ). The gaze behavior of focal subjects before the trials began did not differ significantly across treatments (speaker:  $X^2 = 0.000$ ,  $df = 4$ ,  $p = 1.00$ ; scanning:  $X^2 = 4.885$ ,  $df = 4$ ,  $p = 0.299$ ;

**Table 2.** Selected comparisons of gaze directions and behavioral responses of pig-tailed langurs. The first line in each row shows the test statistics along with the p-values; the second line in each row shows the value of Cohen's  $d$ .

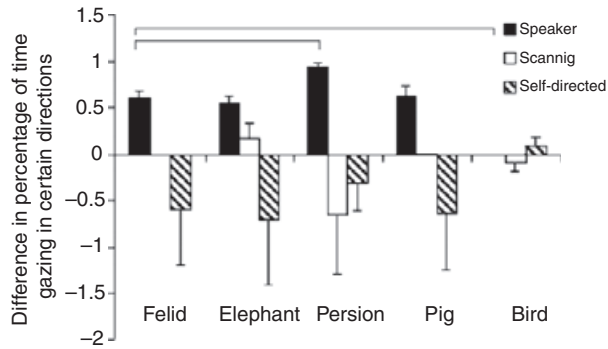
	Felid vs. elephant ( $n = 21$ ) <sup>c</sup>	Felid vs. person ( $n = 18$ )	Felid vs. pig ( $n = 19$ )	Felid vs. bird ( $n = 17$ )
Gaze directions <sup>a</sup>				
Speaker	0.222 (0.638) 0.217	6.852 (0.0089) 1.603	0.0692 (0.793) 0.0724	7.570 (0.0059) 2.882
Scanning	1.103 (0.294) 0.305	4.939 (0.0263) 1.229	0.0308 (0.861) 0.0208	1.044 (0.307) 0.220
Self-directed	0.402 (0.526) 0.248	1.453 (0.228) 0.646	0.291 (0.590) 0.0690	5.772 (0.0163) 1.965
Speaker+scanning	0.1507 (0.698) 0.248	2.255 (0.133) 0.646	0.291 (0.590) 0.0690	5.772 (0.0163) 1.965
Latency to flee <sup>b</sup>	0.15 (0.704) <sup>d</sup> 0.243	8.48 (0.017) <sup>d</sup> 2.598	–	–

<sup>a</sup>Analyzed with non-parametric models ( $X^2$  values).

<sup>b</sup>Analyzed with generalized linear models (F values).

<sup>c</sup> $n$ : number of focal samples.

<sup>d</sup> $n = 9$ .



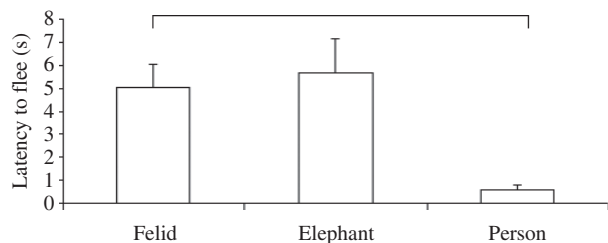
**Fig. 1:** Difference in the percentage of time pig-tailed langurs spent gazing in certain directions before and after different playback treatments. Positive values indicate that the monkeys spent more time gazing in specific directions after the playback compared with before the playback. Statistically significant differences are connected by lines.

self-directed:  $X^2 = 4.885$ ,  $df = 4$ ,  $p = 0.299$  (see Table 2 for sample sizes).

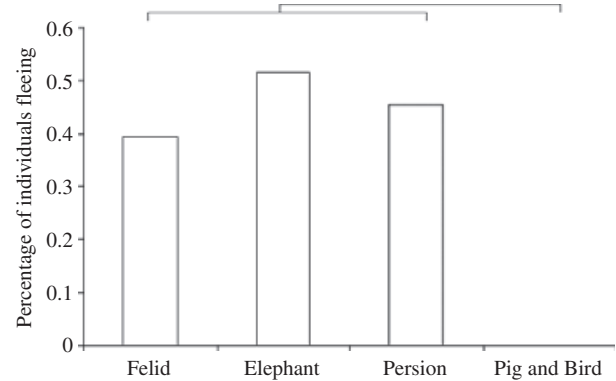
The langurs spent less time looking at the speaker in response to the felid vocalizations than they did toward the human vocalizations; they spent more time looking at the speaker in response to felid vocalizations than in response to the bird vocalizations. Langurs hearing felid vocalizations tended to decrease their self-directed behaviors in comparison with langurs hearing bird vocalizations. The results were similar when the amount of time that the langurs spent scanning and looking in the direction of the speaker were combined (Table 2; Fig. 1).

**Latency to Flee, Latency to Respond, and Number of Individuals Fleeing**

The latency to flee was unaffected by the sex of the focal subject ( $F_{1,10} = 1.95$ ,  $p = 0.193$ ,  $r^2 = 0.163$ ), the behavior of the focal subject before the trial ( $F_{3,8} = 1.01$ ,  $p = 0.438$ ,  $r^2 = 0.275$ ), and the number of visible monkeys ( $F_{4,7} = 3.07$ ,  $p = 0.093$ ,  $r^2 = 0.637$ ). The latency to flee was only influenced by the treatment type ( $F_{2,9} = 5.28$ ,  $p = 0.0303$ ,



**Fig. 2:** Latency to flee in response to different playback treatments. Statistically significant differences are connected by lines.



**Fig. 3:** Total number of individuals fleeing in response to different playback treatments. Statistically significant differences are connected by lines.

$r^2 = 0.540$ ). Langurs hearing the felid vocalizations fled more slowly than langurs hearing human voices but fled with a similar mean latency as langurs hearing elephant vocalizations (Table 1; Fig. 2).

The treatment type and sex of focal animal did not affect the latency to respond (treatment type:  $F_{3,25} = 0.83$ ,  $p = 0.491$ ,  $r^2 = 0.0904$ ; sex of focal:  $F_{1,27} = 0.44$ ,  $p = 0.511$ ,  $r^2 = 0.0162$ ) but langurs tended to respond more quickly when there were more visible monkeys in the group ( $F_{1,27} = 3.27$ ,  $p = 0.0818$ ,  $r^2 = 0.108$ ) and when the monkeys were performing certain behaviors before the trial began ( $F_{3,25} = 2.50$ ,  $p = 0.083$ ,  $r^2 = 0.230$ ). More monkeys responded to the felid, elephant, person, and pig vocalizations than they did to the bird calls (Fisher’s exact test:  $p < 0.0001$ ; Pearson correlation coefficient = 1).

The total number of monkeys that fled did not differ between the felid, elephant, and person playbacks ( $X^2 = 3.29$ ,  $df = 2$ ,  $p = 0.193$ ; odds ratio of felid and elephant: 3.11; odds ratio of felid and person: 1.90). However, more langurs fled in response to these treatments than the bird and pig treatments (Fisher’s exact test:  $p < 0.0001$ ; Pearson correlation coefficient = 0.486; Fig. 3).

**Discussion**

The results of this study suggest that naive pig-tailed langurs have not retained specific antipredator responses toward the vocalizations of ancestral felid predators. The langurs that heard the felid and elephant vocalizations spent less time looking in the direction of the speaker than the langurs that heard the human voices. They were spending their time scanning in all different directions, possibly trying to

locate the source of the unknown sound or to watch the reactions of conspecifics. The langurs that heard human voices fled much faster than those hearing the vocalizations of the felids and elephants. This suggests that the langurs quickly recognized their known predator and fled but hesitated before fleeing in response to the novel playbacks. With the exception of the bird and pig treatments, similar numbers of individuals fled in response to the playbacks.

The first hypothesis (langurs are afraid of felid vocalizations) was not supported because langurs responded similarly when hearing both the felid and elephant vocalizations but often responded differently when hearing the vocalization of their known predator (humans). The null hypothesis (langurs are not afraid of felid or novel vocalizations) was also not well supported. The langurs often fled to the felid and elephant vocalizations, but never fled in response to the bird and pig playbacks. Therefore, the results best support the second hypothesis that langurs are afraid of novel vocalizations. Further experiments that evaluate the responses of langurs to playbacks of a wider range of novel vocalizations (i.e. not only broadcasting felid and elephant vocalizations) would indicate the extent to which their responses to novel vocalizations can be generalized across different types of sound stimuli. It would also be interesting to evaluate whether the langurs would respond similarly if the lower frequency components (e.g. infrasound) of the playback stimuli were broadcast.

General antipredator behaviors may persist in populations that are still exposed to at least one predator (multi-predator hypothesis; Blumstein et al. 2004). Because the pig-tailed langur has been heavily hunted by humans for centuries (Tenaza & Tilson 1985) and is likely predated on by native eagles and pythons (Whitten & Whitten 1982), it would be expected to retain its antipredator behaviors according to this hypothesis (but see Stankowich & Coss 2007). Indeed, the langurs often reacted with a generalized fear response to ontogenetically novel stimuli (felid and elephant calls) but did not appear to recognize the felid vocalizations *per se*.

Many animals, especially primates, have generalized behavioral responses that they can refine during ontogeny (e.g. Marler 1990; Pereira & Fairbanks 2002). Because environmental and social conditions can change (both within and across generations), animals that can flexibly modify these behavioral patterns can adapt to the current conditions and increase their chances of survival (Komers 1997). In particular, antipredator behaviors often have an innate component that can be modified by experi-

ence (Curio 1993; Griffin et al. 2000). Direct interactions with predators and observations of conspecifics responding to predators can have marked effects on an individual's own antipredator behaviors (Curio et al. 1978; Griffin 2004). These changes in any individual's antipredator behaviors can increase its chances of survival in future encounters with those predators (Griffin et al. 2000). The extent to which innate and learned factors interact in the ability of animals to recognize and respond appropriately to predators remains an intriguing question.

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