

Predator Recognition in the Absence of Selection

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Introduction

Animals are frequently confronted with changing environmental conditions (Houston and McNamara 1992; Komers 1997). When they are no longer exposed to the sources of selection that their ancestors once faced, they experience relaxed selection on these sources (Coss 1999). They may still retain behavior that was shaped to cope with the past selective forces, even though it no longer serves a specific function (Blumstein et al. 2000; Rothstein 2001).

Relaxed selection for predator recognition abilities occurs when animals live in environments which lack predators that previously preyed upon their ancestors. The effects of relaxed predation pressure have been studied in a wide taxonomic range of animals (Curio 1966; Kelley and Magurran 2003; Messler et al. 2007; Peckarsky and Penton 1988; Fullard et al. 2004; Blumstein et al. 2000; Hollén and Manser 2007). Some animals still retain specific antipredator behavior even though they do not coexist with their ancestral predators (Blumstein et al. 2000). The amount of time that has lapsed since animals were exposed to certain predators (Coss 1999; Berger et al. 2001) as well as whether they currently experience predation (Blumstein 2006) are potential factors that may influence the retention of appropriate antipredator behavior.

Compared to other taxa, primates have less often been the focus of studies on relaxed predation pressure (reviewed in Table 10.1). The majority of the studies on naïve primates have investigated the antipredator behavior of captive animals that have been isolated from their predators for only a few generations (van Schaik and van Noordwijk 1985; Takahashi 1997). We know little about predator recognition abilities of wild primates that have been isolated from their ancestral predators for thousands of years.

Indonesian primates offer a unique opportunity to explore this topic because many of them inhabit isolated islands and experience different predation pressures than those experienced by their ancestors. In particular, many primates are no longer exposed to felid predation (Table 10.2). The study described here capitalizes on this fact and asks whether wild, naïve primates that have been isolated from ancestral felid predators for over 0.5 million years are still able to recognize them (Yorzinski and Ziegler 2007).

Table 10.1 Review of the ability of naïve primates to recognize predators when they experience relaxed predation pressure. NA = the study did not provide the relevant information.

	Common name	Scientific name	Current predator(s)	Novel predator type(s) tested ^a	Time passed (yr) ^b	Antipredator behavior? ^c	Novel control	Novel predator recognized? ^d	Compared to experienced conspecific? ^e	Reference(s)
Auditory	Mantled howler monkey	<i>Alouatta palliata</i>	None	Bird	50–100	Y	Bird	N [§]	Milder	Gil-da-Costa et al. (2003)
	Ringtailed lemur	<i>Lemur catta</i>	Mammal, bird	Bird	– ^f	Y	Bird	Y	NA	Macedonia and Young (1991)
	Cotton-top tamarin	<i>Saguinus oedipus</i>	None	Bird, mammal	– ^f	Y	Bird, mammal	N	NA	Friant et al. (2008)
	Pig-tailed langur	<i>Simias concolor</i>	Human, bird, snake	Mammal	0.5 million	Y	Mammal	N	NA	Yorzinski and Ziegler (2007)
Olfactory	Gray mouse lemur	<i>Microcebus murinus</i>	None	Bird, mammal	– ^f	Y	Bird, mammal	Y	NA	Sündermann et al. (2008)
	Red-bellied tamarin	<i>Saguinus labiatus</i>	None	Mammal	– ^f	Y	Mammal	Y	NA	Caine and Weldon (1989)
	Cotton-top tamarin	<i>Saguinus oedipus</i>	None	Mammal	– ^f	Y	Mammal	Y	NA	Buchanan-Smith et al. (1993)
Visual	Common marmoset	<i>Callithrix jacchus</i>	None	Snake	– ^f	Y	NA	NA	NA	Clara et al. (2008)
	Black tufted-eared marmoset	<i>C. penicillata</i>	None	Bird, mammal, snake	– ^f	Y	Toy	N	NA	Barros et al. (2002)
	Tufted capuchin	<i>Cebus apella</i>	None	Snake	– ^f	Y	NA	NA	NA	Vitale et al. (1991)
	Vervet monkey	<i>Cercopithecus aethiops</i>	None	Bird, mammal, snake	– ^f	Y	Bird	Y	NA	Brown et al. (1992)
	Sooty mangabey	<i>Cercocebus atys</i>	None	Mammal	– ^f	Y	NA	NA	NA	Davis et al. (2003)
	Greater galago	<i>Galago crassicaudatus</i>	None	Mammal, snake	– ^f	Y	NA	NA	NA	Jaenicke and Ehrlich (1972)
	Crab-eating macaque	<i>Macaca fascicularis</i>	None	Snake	– ^f	Y	NA	NA	NA	Vitale et al. (1991)
	Rhesus macaque	<i>M. mulatta</i>	None	Snake	– ^f	Y	Tube	Y	Milder	Joslin et al. (1964), Mineka et al. (1984), Nelson et al. (2003)
	Rhesus macaque	<i>M. mulatta</i>	None	Mammal	– ^f	Y	NA	NA	NA	Davis et al. (2003)
	Pig-tail macaque	<i>M. nemestrina</i>	None	Mammal	– ^f	Y	NA	NA	NA	Davis et al. (2003)
	Bonnet macaque	<i>M. radiata</i>	None	Mammal, snake	– ^f	Y	NA	NA	Less specific	Coss et al. (2007)
	Mandrill	<i>Mandrillus sphinx</i>	Bird, snake	Mammal	30	Y	NA	NA	NA	Yorzinski and Vehrencamp (2008)
	Slow loris	<i>Nycticebus coucang</i>	None	Mammal, snake	– ^f	Y	NA	NA	NA	Jaenicke and Ehrlich (1972)
	Cotton-top tamarin	<i>Saguinus oedipus</i>	None	Snake	– ^f	Y	Mammal	N	Milder	Hayes and Snowdon (1990)
	Cotton-top tamarin	<i>Saguinus oedipus</i>	None	Bird	– ^f	Y	NA	NA	NA	Moodie and Chamove (1990)
	Squirrel monkey	<i>Saimiri sciureus</i>	None	Snake	– ^f	Y	Fish	Y	Milder	Murray and King (1973), Levine et al. (1993)

^a The type of predator(s) the naïve primate was shown in the experiment but had never experienced before.

^b The minimum amount of time that passed since the primate was last exposed to the novel predator.

^c An indication (Y = yes or N = no) of whether the naïve primate exhibited general antipredator behavior (avoidance, alarm and mobbing calls, piloerection and/or changes in vigilance) toward the novel predator.

^d An indication (Y = yes or N = no) of whether the naïve primate treated the novel predator differently than it treated a novel control.

^e An indication of how the naïve primate responded to the novel predator compared to how an experienced conspecific that still lives with that predator responds

Table 10.1 (continued)

^f Because the exact date that this individual was brought into captivity (or moved to an urban setting) is unknown, it is likely that it was last exposed to its natural predators within the past 150 years.

^g The authors conclude that the predator-naïve howler monkey no longer recognize the vocalizations of a native predator that it has not been exposed to for 50-100 years. However, the monkeys exhibited a greater response toward the vocalizations of a novel, native predator (harpy eagle) compared to the vocalizations of a novel, non-native predator (bald eagle) during the playback period.

Case Study: Relaxed Predation Pressure in a Wild Primate

Pig-tailed Langurs

The pig-tailed langur (*Simias concolor*) is endemic to the Mentawai islands in Indonesia, which are located about 150 km off the west coast of Sumatra. Belonging within an Asian colobine clade (also consisting of species within the genera *Nasalis*, *Pygathrix* and *Rhinopithecus*), it is thought to be most closely related to the proboscis monkey (*N. larvatus*; Groves, 1970; Delson, 1975; Whittaker et al., 2006). Two subspecies of the pig-tailed langur are recognized: *S. c. siberu* on Siberut Island (Chasen and Kloss 1927) and *S. c. concolor* on Sipora, North Pagai, South Pagai, and a few small islets off of South Pagai (Miller 1903; Mittermeier et al. 2007); the difference between these two subspecies is based on pelage coloration. Pig-tailed langurs are critically endangered (IDCN Red List 2008) and are considered one of the 25 most endangered primates (Mittermeier et al. 2007).

Because only a handful of studies have systematically documented their behavior, we know very little about these rare primates. They are medium-sized leaf monkeys that commonly live in one-male one-female or one-male multifemale groups (Tilson 1977; Watanabe 1981; Tenaza and Fuentes 1995; Radi et al. 2009). They share their habitat with up to three other primate species: Siberut or Mentawai macaques (*Macaca siberu* or *Macaca pagensis*, respectively), Mentawai langurs (*Presbytis potenziani*), and Kloss gibbons (*Hylobates klossii*). Males emit long distance calls that may function as intergroup communicative signals (Tenaza 1989; Erb 2006).

Pig-tailed langurs have likely been separated from their mainland predators for over 0.5 million years (Rohling et al. 1998; Abegg and Thierry 2002). No dangerous felids currently live in their environment (World Wildlife Fund 1980). However, related langur species living on the mainlands experience high rates of predation by felids (Seidensticker 1983; Rabinowitz et al. 1987; Karanth and Sunquist 1995; Støen and Wegge 1996; Sankar and Johnsingh 2002) and exhibit antipredator behavior when

Table 10.2 List of Indonesian monkeys and whether they live in environments with felid predators. Y = they live with felid predators (although some populations may no longer live with them due to relatively recent declines in felid populations or due to isolation from the main population) and N = they have not lived with felid predators for over 0.5 million years

Common name	Scientific name	Felid predators?
Muna-Butung macaque	<i>Macaca brunescens</i>	N
Heck's macaque	<i>M. hecki</i>	N
Moor macaque	<i>M. maura</i>	N
Sulawesi macaque	<i>M. nigra</i>	N
Gorontalo macaque	<i>M. nigricens</i>	N
Ochre macaque	<i>M. ochreata</i>	N
Mentawai macaque	<i>M. pagensis</i>	N
Siberut macaque	<i>M. siberu</i>	N
Tonkean macaque	<i>M. tonkeana</i>	N
Mentawai langur	<i>P. potenziani</i>	N
Pig-tailed langur	<i>Simias concolor</i>	N
Crab-eating macaque	<i>M. fascicularis</i>	Y
Pigtailed macaque	<i>M. nemestrina</i>	Y
Proboscis monkey	<i>Nasalis larvatus</i>	Y
Grizzled langur	<i>Presbytis comata</i>	Y
Banded langur	<i>P. femoralis</i>	Y
White fronted langur	<i>P. frontata</i>	Y
Hose's langur	<i>P. hosei</i>	Y
Mitered langur	<i>P. melalophos</i>	Y
Maroon langur	<i>P. rubicunda</i>	Y
Thomas's langur	<i>P. thomasi</i>	Y
Javan langur	<i>Trachypithecus auratus</i>	Y
Silvered langur	<i>T. cristatus</i>	Y

seeing these predators or models of these predators (Thapar 1986; Ramakrishnan and Coss 2000b; Wich and Sterck 2003). Humans are their primary and only confirmed predator; serpent eagles (*Spilornis cheela sipora*) and reticulated pythons (*Python reticulatus*) are probably predators (Whitten and Whitten 1982; C. Abegg pers. comm.), but predation events have never been documented.

Hypotheses and Predictions

A series of auditory playbacks was conducted to investigate the predator-recognition abilities of the pig-tailed langur. The reactions of langurs to the vocalizations of different animals were evaluated to test hypotheses regarding their acoustic predator-recognition abilities. The first hypothesis is that pig-tailed langurs recognize the vocalizations of dangerous felids. If this hypothesis is supported, then these langurs will exhibit antipredator behavior toward the calls of felids and humans because they recognize both as predators (the human voices are presumed to convey information about human predators because only nonhabituated monkeys were tested). Their responses to the felid calls will be different from their responses to the vocalizations of elephants (novel animals but not predators) and pigs (familiar animals but no predators) because these latter two mammals are not predators of primates (pigs freely roamed the rainforest but were not common).

The second hypothesis is that langurs are afraid of novel vocalizations that they have never heard before. If this hypothesis is supported, then they will respond similarly to the felid and elephant calls because both of these vocalizations are novel. Because they will still exhibit fear towards the vocalizations, their response to the novel sounds should have some similarities to their response toward human voices. 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 felids and elephants will be different from their response to the voices of their known human predator. We would expect their reactions to all novel vocalizations (felid and elephant) to be the same and also be similar to their responses toward known and nonpredatory animals (pig and bird). Preliminary visual presentations were also conducted to determine whether the predator-recognition abilities the monkeys exhibited in response to the auditory stimuli were similar to their response to visual stimuli (Yorzinski unpublished data). Two-dimensional visual models of a felid (*Panthera tigris*) and rhinoceros (*Rhinoceros unicornis*) were used. The rhinoceros represented a nonpredatory, novel animal that was not present on the island but exists on the mainland (similar to the elephant vocalizations in the auditory experiments).

Field Site and Experimental Procedure

The langurs were studied at the Siberut Conservation Project (SCP) field site in northeast Siberut Island. The Siberut Conservation Project collaborates with local people to protect the rainforest from logging and hunting activities. The field site encompasses 10.7 km² of primary and secondary mixed lowland rainforest. An extensive trail system allows researchers to navigate through the dense understory. Even though the monkeys were not hunted for two years prior to the onset of this study, they were not habituated to the presence of humans. Over 300 h were spent searching the rainforest for pig-tailed langur groups. When a group was found, I randomly chose an adult langur that was relatively still (i.e., it was resting, grooming, or eating), hid within the understory, and began filming this focal individual. Meanwhile, the field assistant placed the speaker in a concealed spot on the ground at about 35 m from the closest individual of the group and initiated the playback. A 10 s segment of a felid, elephant, person, pig or bird vocalization was broadcast (the particular vocalization that was played was randomized across trials and only one trial was conducted within a given

observation period). I continued filming the focal animal until it left its original position (in which case visual contact was usually lost). The video recordings were analyzed frame-by-frame to quantify the behavior of the focal individual. Sound levels of the playback stimuli were adjusted to a mean of 80-85 dB at 1m from the speaker. Most of the felid vocalizations were recorded by Gustav Peters and obtained from the Animal Sound Archives at the Zoological Research Museum Alexander Koenig. The elephant and other felid vocalizations were purchased from the Wildlife Section of the British Library Sound Archive. I recorded the human, pig, and bird vocalizations on Siberut Island.

Because the estimated home range of the langur is 3-5 ha (Watanabe 1981), we tested groups that were about 600 m (mean 600 ± 50 m; range: 300-1,100) 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). Planned comparisons were made to investigate differences in the behavior of the langurs in response to the felid vocalizations and the other treatments.

Two preliminary visual experiments were conducted. The two-dimensional visual models were based on copies of high quality photographs (tiger: Whittaker 2002; rhinoceros: McHugh 2003) that were enlarged to approximate the actual size of the animals (tiger: 95 cm length, 70 cm height; juvenile rhinoceros: 141 cm length, 86 cm height (Stankowich and Coss 2007)). Two blinds were built about 1,100 m apart and only one experiment was conducted at each blind. Based on their home range size (Watanabe 1981), it is likely that two different langur groups were tested. The field assistant and I waited inside of the blinds for over 100 h. When a group of langurs (at least two individuals) randomly passed in front of the blind, a model was displayed for 90 s. One individual in each group was filmed and the video was later analyzed frame-by-frame.

Results and Discussion

The results supported the second hypothesis (langurs are afraid of novel vocalizations). Langurs that heard felid vocalizations spent similar amounts of time looking in the direction of the speaker compared to the langurs that heard the elephant vocalizations (both novel vocalizations); in contrast, langurs that heard the felid vocalizations spent less time looking in the direction of the speaker compared to langurs hearing human voices. Langurs spent similar amounts of time looking at the speaker in response to the felid and pig vocalizations. The langurs likely spent a substantial amount of time looking at the speaker in response to the pig vocalizations because pigs were present in the forest but not abundant enough to ensure frequent interactions between the two species (Fig. 10.1).

The langurs that heard felid vocalizations fled more slowly than those hearing human voices. Langurs fled at similar latencies for both of the novel vocalizations (felid and elephant vocalizations; Fig. 10.2). As indicated by this flight behavior, the langurs appeared to quickly recognize the human vocalizations, while their delayed responses to novel playbacks indicated sensitivity to novel sounds. Similar numbers of individuals fled in response to the novel and/or dangerous stimuli (felid, elephant, and human), but none fled in response to the familiar and nondangerous stimuli (pig and bird). The total numbers of monkeys that fled did not differ among the felid, elephant, and person playbacks (Fig. 10.3). 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. The preliminary experiments with visual models also supported the second hypothesis (although the results are speculative because only two experiments were conducted).

Langurs exhibited fear toward the felid and rhinoceros visual models by alarm calling (emitted over 25 calls to each model) and fleeing (waited at least 15 s before fleeing). Although no visual models of humans were presented, the response of the langurs to the felid and rhinoceros models was qualitatively different from their response to actual encounters with humans. When langurs encounter humans, they tend to alarm call less frequently or not at all (pers. obs.); this behavior is adaptive because humans can easily kill langurs with their bow and arrows if the monkeys remain conspicuous. In contrast, a group of pig-tailed langurs was observed mobbing a snake by gathering around it and alarm calling frequently (Pak Tarzan, pers. comm.). Although different from their response toward humans, their response to the model felid and rhinoceros was more similar to their response toward the snake and may be better suited to countering the attacks of nonhuman predators.

Antipredator behavior may persist in populations under relaxed selection that are still exposed to at least one predator (i.e., the multipredator hypothesis; Blumstein et al. 2004). The persistence of these behaviors would probably only occur if the remaining predator elicits the same type of antipredator response (e.g., fleeing or mobbing) as the historical predator. However, a remaining predator may not even be necessary for some aspects of predator recognition. For example, perceptual

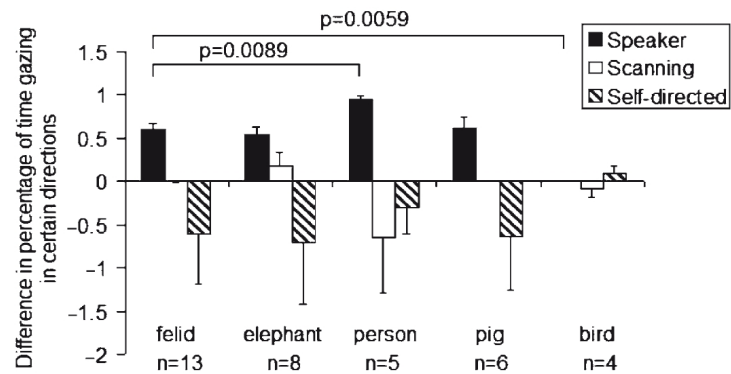


Fig. 10.1 Difference in the percentage of time pig-tailed langurs spent gazing in certain directions before and after different playback treatments: looking in the direction of the speaker (*speaker*), scanning in different directions (*scanning*), and looking at their own body (resting, grooming, or feeding; *self-directed*). The percentage of time the langur was engaged in each of the three categories in the pre-playback period was subtracted from the percentage of time gazing in each category in the post-playback period. Positive values indicate that the monkeys spent more time gazing in specific directions after the playback compared to before the playback. Means \pm SE are displayed

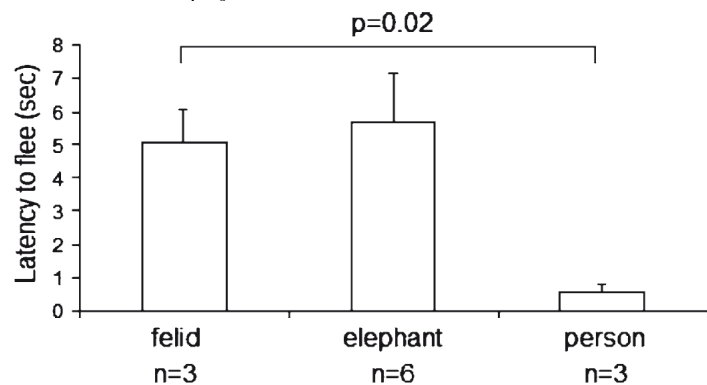


Fig. 10.2 Latency to flee in response to different playback treatments. Means \pm SE are displayed

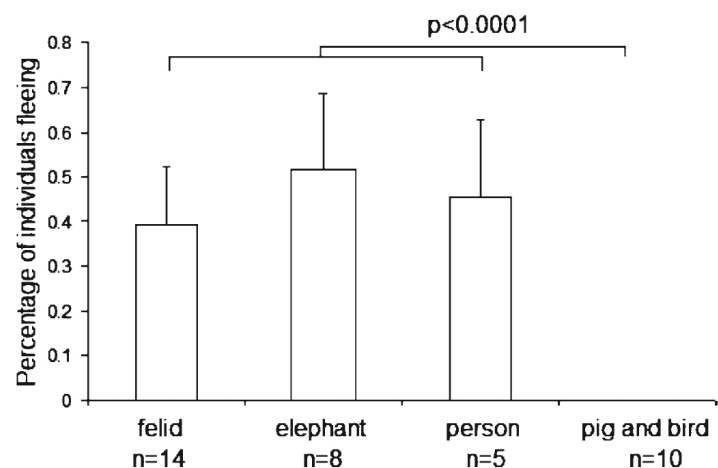


Fig. 10.3 Total number of individuals fleeing in response to different playback treatments. Means \pm SE are displayed

features indicating danger, such as two facing eyes, are shared by felid predators and conspecifics. Aggressive social contexts might maintain the provocative aspects of these perceptual features (Coss et al. 2005).

Because the pig-tailed langur has been heavily hunted by humans for centuries (Tenaza and Tilson 1985) and is the likely prey of native eagles and pythons (Whitten and Whitten 1987; C. Abegg pers. comm.), it may be particularly sensitive to potentially dangerous sight and sounds. Indeed, the langurs often reacted with rhinoceros models) but did not react strongly to familiar, nondangerous animals (pigs and birds). Because the felid vocalizations were not treated differently than other novel vocalizations (elephant), the langurs did not appear to retain specific recognition of felid predators.

Evaluating Predator Recognition

Studies that conduct predator presentation experiments (see above case study), monitor reintroductions, and track developmental changes can all contribute to our knowledge of naïve animals' responses to predators. While these types of studies have been conducted on diverse species, relatively little is known about primates.

Predator Presentations

We can investigate predator recognition abilities by presenting predator-naïve animals with predators. When presented with a predator, some naïve animals appear to recognize it (e.g., Hollen and Manser 2007). In contrast, other naïve animals do not identify it as a predator (e.g., Blumstein et al. 2006).

Few studies have explored the abilities of predator-naïve primates to recognize predators. Primates often exhibit generalized antipredator behavior (avoidance, alarm and mobbing vocalizations, piloerection, and/or changes in vigilance) in response to novel olfactory, auditory, and visual predatory stimuli. However, we often do not know whether primates are specifically responding to predators or simply responding to novelty. Very few studies have presented both predator and novel stimuli to primates in order to evaluate their predator recognition abilities. Experiments that present both of these stimuli can help us fill this gap in our knowledge (Table 10.1).

In the few studies that investigated naïve primates and their ability to recognize predators by olfactory cues, the primates demonstrate that they are able to recognize the predators (Caine and Weldon 1989; Buchanan-Smith et al. 1993; Sündermann et al. 2008). In contrast, naïve primates that hear the vocalizations of novel animals fail to make distinctions between predatory species and novel, non predatory species (e.g., Yorzinski and Zeigler 2007 but see Macedonia and Young 1991). Lastly, when primates see novel animals, they are sometimes able to differentiate between the novel and predatory animals (Brown et al. 1992), but not always (Hayes and Snowdon 1990). The limited number of studies investigating this topic makes it difficult to draw general conclusions.

Reintroductions

We can learn about predator recognition abilities when naïve animals are reintroduced into predator rich environments. Predation can account for a significant percentage of mortality in reintroduced animals (Short et al. 1992; Miller et al. 1994; Pietsch 1994; Kuehler et al. 1996) but is not always the main cause of death (Wolf et al. 1998). This variation in mortality rate due to predation

may reflect differences in the abilities of animals to recognize predators and respond appropriately to them. Because animals can have higher survival rates if they have experience with live predators before they are released into the wild (van Heezik et al. 1999), some naïve animals may lack detailed predator recognition abilities.

Among primates, predation is also a major cause of mortality in reintroductions. An inability to recognize predators as well as inappropriate antipredator responses may explain this high mortality rate. Relative to other causes of mortality in reintroductions, predation ranks as one of the highest (22% mortality due to predation in *Leontopithecus rosalia*, Beck et al. 1991; 57% in *Callithrix geoffroyi*, Passamani and Passamani 1995; 71% in *Varecia variegata*, Britt et al. 2003). However, the offspring of reintroduced parents suffer reduced predation (0% mortality due to predation in *Leontopithecus rosalia*; Beck et al. 1991). Because primates are able to learn about predators from their conspecifics (Custance et al. 2002; Griffin 2004), it may only take a few generations for naïve primates to become knowledgeable about predators. Wild primates have even been shown to learn appropriate antipredator behavior within their lifetimes after being exposed to a new predator (Gil-da-Costa et al. 2003).

Ontogeny

Immature animals living in environments with predators are also relatively naïve and can teach us about predator recognition abilities. For example, immature California ground squirrels (*Spermophilus beecheyi*) react more intensely to snakes than novel stimuli. This suggests that the young are predisposed to recognizing and responding appropriately to these predators (Owings and Coss 1977). In contrast, great tit fledglings (*Parus major*) do not appear to recognize predators - they respond similarly to dangerous and nondangerous stimuli (Kullberg and Lind 2002).

Only several studies have explored the development of antipredator behavior in immature primates. Immature vervet monkeys, bonnet macaques, and spectral tarsiers emit alarm calls in response to a wider range of potentially dangerous stimuli than adults (Seyfarth and Cheney 1986; Ramakrishnan and Coss 2000a; Gursky 2003). Because they receive feedback from conspecifics after they make these alarm calls (e.g., conspecifics emit further alarm calls or flee if a real danger exists), they can use this information to learn which stimuli are in fact dangerous (Seyfarth and Cheney 1986).

Conclusions

The results from the above types of studies (predator presentation experiments, reintroductions, and developmental changes) provide us with important information about the responses of naïve primates to predators. In general, these studies suggest that primates are often fearful of novel stimuli and can learn to react appropriately to them. When naïve primates are relying on auditory and visual assessments, they may not know whether a novel animal is dangerous or not. However, when they rely on olfactory assessments, they can better make this distinction.

Although we are rapidly accumulating knowledge about the responses of animals to relaxed predation pressures, we still have much to discover. Naïve animals learn to fear certain types of animals faster than others (Öhman and Mineka 2001). For example, naïve rhesus macaques can quickly learn to associate fear with snakes and crocodiles (but not with nondangerous rabbits) when conspecifics are fearful of them (Cook and Mineka 1989). Future studies that explored whether animals learn more quickly with respect to other predator types (not just snakes and crocodiles) would provide us with a better understanding of naïve primates' responses toward predators.

We also know little about the features that are salient for predator recognition in naïve primates. Because animals must first recognize predators before they can respond appropriately, it is critical to understand how naïve animals categorize dangerous and nondangerous animals. When naïve animals recognize predators based on olfactory cues, they may be relying on specific metabolites in the feces that indicate whether the animal was carnivorous (Blumstein et al. 2006; Sündermann et al., 2008). When they categorize novel predators based on visual cues, they may be relying on the relative size of the animal as well as the presence of forward-facing eyes (Coss and Goldthwaite 1995; Coss et al. 2005). And when they make assessments based on auditory cues, the acoustic properties of the calls (e.g., low-pitched vocalizations) may provide information about the size or motivation of the potential threat (Owings and Morton 1998). While all of these factors may influence a naïve primate's ability to recognize a predator, there is little systematic research pinpointing the exact features that are salient for recognition.

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