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ORIGINAL ARTICLE

Scales drive detection, attention, and memory of snakes in wild vervet monkeys (*Chlorocebus pygerythrus*)

Lynne A. Isbell[1,2,3,4] · Stephanie F. Etting[1]

Abstract Predatory snakes are argued to have been largely responsible for the origin of primates via selection favoring expansion of the primate visual system, and even today snakes can be deadly to primates. Neurobiological research is now beginning to reveal the mechanisms underlying the ability of primates (including humans) to detect snakes more rapidly than other stimuli. However, the visual cues allowing rapid detection of snakes, and the cognitive and ecological conditions contributing to faster detection, are unclear. Since snakes are often partially obscured by vegetation, the more salient cues are predicted to occur in small units. Here we tested for the salience of snake scales as the smallest of potential visual cues by presenting four groups of wild vervet monkeys (*Chlorocebus pytherythrus*) with a gopher snake (*Pituophis catenifer*) skin occluded except for no more than 2.7 cm, in natural form and flat, the latter to control for even small curvilinear cues from their unusual body shape. Each of these treatments was preceded by a treatment without the snakeskin, the first to provide a baseline, and the second, to test for vigilance and memory recall after exposure to the snakeskin. We found that (1) vervets needed only a small portion of snakeskin for detection, (2) snake scales alone were sufficient for detection, (3) latency to detect the snakeskin was longer with more extensive and complex ground cover, and (4)

vervets that were exposed to the snakeskin remembered where they last saw "snakes", as indicated by increased wariness near the occluding landmarks in the absence of the snakeskin and more rapid detection of the next presented snakeskin. Unexpectedly, adult males did not detect the snakeskin as well as adult females and juveniles. These findings extend our knowledge of the complex ecological and evolutionary relationships between snakes and primates.

Introduction

Primates and snakes have shared a long, complex evolutionary relationship in which each has been variously predator, prey, and competitor of the other (Headland and Greene 2011). The "Snake Detection Theory" (SDT) argues that as predators, snakes were a major source of selection favoring the origin of primates via visual expansion for rapid snake detection and avoidance (Isbell 2006, 2009). Ecological and behavioral studies have been supportive of the SDT's predictions. For instance, sightings of deadly snakes at primate study sites in Gambia and Senegal occurred once every 44.8 h (or 3.7 days, assuming a 12-h observation day) and 7.2 days, respectively, suggesting that the risk of envenomation or constriction in those habitats is non-trivial for primates on the ground (Starin and Burghardt 1992; McGrew 2015). Among both non-human and human primates, behavioral research also consistently shows that snakes attract visual attention more rapidly than other stimuli (Öhman 2009; Shibasaki and

✉ Lynne A. Isbell
laisbell@ucdavis.edu

1 Department of Anthropology, University of California, One Shields Ave., Davis, CA 95616, USA

2 Animal Behavior Graduate Group, University of California, Davis, USA

3 Mpala Research Centre, Nanyuki, Kenya

4 Kenya Wildlife Service, Nairobi, Kenya

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Kawai 2009; LoBue and DeLoache 2010; LoBue et al. 2010; Masataka et al. 2010; Öhman et al. 2001, 2012; Soares 2012; Penkunas and Coss 2013a, b; Soares and Esteves 2013; Soares et al. 2014; Yorzinski et al. 2014; Thrasher and LoBue 2016; Kawai and Koda 2016).

Recent electrophysiological and neurophysiological findings are increasing our understanding of the mechanisms for rapid visual detection of and attention to snakes. For instance, snakes evoked stronger early attention-related brain potentials than other natural stimuli, including spiders, birds, crocodiles, and turtles (He et al. 2014; van Strien et al. 2014a, b). Such signals are thought to reflect automatic visual attention to salient stimuli (Schupp et al. 2003, 2006; van Strien et al. 2014a, b). In addition, compared to conspecific faces, snakes evoked earlier gamma oscillations in pulvinar neurons (Le et al. 2016). The pulvinar is a visual nucleus, which, along with the superior colliculus, forms part of the subcortical visual system. This visual system exists in all primates and appears to be responsible for rapid, non-conscious vision (reviewed in Isbell 2009). Gamma oscillations are very fast brain waves that have been linked to heightened awareness or conscious recognition of visual stimuli (Fisch et al. 2009), and may facilitate bottom-up processing that activates the cortical visual system to hold attention (Le et al. 2016). Consistent with the interpretation that the subcortical visual system functions to detect salient stimuli rapidly and automatically, in Japanese macaques (*Macaca fuscata*), neurons in the pulvinar responded more strongly and quickly to images of snakes than to images of faces of monkeys, hands of monkeys, and simple geometric shapes, and more strongly to snakes in striking postures than in non-striking postures (Le et al. 2013, 2014). These nuclei also respond strongly to snakes presented in both foveal and peripheral visual fields in humans (Almeida et al. 2015).

Thus, findings from multiple approaches are consistent in suggesting that some parts of primate visual systems are preferentially attuned to snakes. This preference becomes even more pronounced in environments that can be described as visually heterogeneous, complex, or cluttered, with multiple potential distractors, i.e., conditions under which snakes are often found in nature (Öhman et al. 2012; Soares 2012; Soares and Esteves 2013; Soares et al. 2014).

Several characteristics of snakes could serve individually or in combination as evocative visual cues, including their curvilinear shape, limblessness, head shape (especially for vipers), coloration, and scales. Although it would be expedient for primates to use all possible cues to detect snakes, cluttered environments likely make detection more difficult because not all cues may be available. Recent studies provide evidence that the snake's curvilinear body shape is an important visual cue (LoBue and DeLoache 2011; van Strien et al. 2016). Snakes can, however, modify their body shape to some extent (Arnold and Bennett 1984), and they can reduce the reliability of shape cues further by remaining motionless and obscured among layers of vegetation for long periods of time. Terrestrial snakes that are ambush predators, for example, are well known for being difficult to see in visually complex environments that break up the visual coherence of their bodies.

Van Strien et al. (2016) suggested that although the curvilinear body shape of snakes may be a factor in their detection, other important visual cues, such as coloration, are likely to exist because snakes evoked a stronger visual response than worms, which are also curvilinear. Children detect colored snakes faster than grayscale snakes (Hayakawa et al. 2011), suggesting that color may indeed be another important cue. Since coloration is highly variable among snakes, however, sometimes even within a species (Greene 1997), it would seem less reliable than other cues. Furthermore, not all primates can distinguish the full spectrum of colors that snakes can exhibit (Jacobs 2009).

White-faced capuchins (*Cebus capucinus*) responded more strongly to coiled snake models that were colored and scaled than white and non-scaled (Meno et al. 2013), suggesting that scales may also be important. Captive common marmosets (*Callithrix jacchus*) spent more time visually attending to both curvilinear and triangular shapes with patterns, including scales, than to similar shapes that were smooth (Wombolt and Caine 2016). Young children also appear sensitive to snake scales. Coss (2003) showed that prior to handling plastic jars in day-care facilities, 7–15 month-old infants and toddlers carefully poked a jar displaying a python scale pattern at a reliably higher frequency than jars displaying no pattern or a plaid print. The plaid print was composed of a combination of larger and smaller squares whereas scales on snakeskins are more uniform in size. Although these studies suggest that snake scales may be an important visual cue for holding attention, to date, no studies have examined scales as a visual cue for snake detection.

It seems reasonable to expect that primates would take advantage of scales to detect snakes. Anthropoid visual acuity is the best among mammals (Ross 2000; Kirk and Kay 2004), and on a neurobiological level, neurons in the pulvinar and other visual structures have been found to respond preferentially to diamond-shaped or checkerboard stimuli (Okusa et al. 2000; Kastner et al. 2004; Villeneuve et al. 2005), patterns that are reminiscent of snake scales (Isbell 2009). Scales are also small enough to be visible even when snakes are mostly hidden and are universal in snakes but are otherwise rare in nature (Coss 2003; Isbell 2009).

Here we report the findings of a field experiment on free-ranging vervets (*Chlorocebus pygerythrus*) designed to answer the following questions: (1) are scales alone

sufficient as cues for detecting snakes, (2) are primates slower to detect snakes in more visually complex environments, and (3) does the detection of a perceived snake in a given location result in the association of that location with a snake, as evidenced by behavioral indications of greater wariness or vigilance for snakes there in the future? Vervets are eaten by pythons (*Python* spp.) and often respond to snakes by gathering around them, vocalizing with a snake-specific alarm call, and staring or peering at them for extended periods of time while either quadrupedal or standing bipedally (Struhsaker [1967]; Seyfarth et al. [1980]). Their obvious behavioral responses to snakes make them an ideal species with which to ask these questions.

Methods

Study site and subjects

We conducted the experiment on four groups that consisted of a total of 82 vervets (Table 1) living in and around Mpala Research Centre on the Laikipia Plateau in central Kenya (0.29°N, 33.90°E). This area is a semi-arid savannah-woodland/bushland dominated by *Acacia etbaica*, *A. mellifera*, *A. brevispica*, and *Boscia angustifolia*, and along the Ewaso Nyiro River, *A. xanthophloea*. Three vervet study groups lived along the Ewaso Nyiro R. and one lived near the Research Centre away from the river. Snakes occurring in the area include puff adders (*Bitis arietans*) and red and Ashe's spitting cobras (*Naja pallida* and *N. ashei*) (Wüster and Broadley [2007]; S. Spawls, pers. comm.; LAI, pers. obs.). Rock pythons (*P. sebae*) have not been confirmed at Mpala, but are known to occur elsewhere in Laikipia (LAI, unpub. data).

Experimental design and data collection

We conducted four treatments on each group. All treatments were filmed with a Canon EOS Rebel T3i/EOS 600D digital camera on foot or from a vehicle, depending on the vervets' degree of habituation to humans, from 12 to 17 m away, with durations ranging from 80 to 768 s. For all treatments we placed on the ground two green hand towels separated by a gap of 2.5–2.7 cm. The towels were connected to each other with thread sewn into them in two

places to keep the gap consistent across treatments. We attracted monkeys to the towels by sprinkling dried maize on and around the towels and in the surrounding area to minimize aggression. The first treatment involved presenting just towels to establish whether monkeys were attracted to them as novel objects and to provide a baseline for subsequent behavior. In the second treatment we placed a cured, 90 cm-long gopher snake (*Pituophis catenifer*) skin from a road-killed snake under the two towels, with a middle section of the skin exposed in the gap (Fig. 1a). The skin was tied with brown thread around a cylindrical piece of quilt batting to simulate the shape of a live snake. Since gopher snakes are native to North America, all subjects were naïve to their specific color pattern. In the third treatment we placed the two towels on the ground without the snakeskin to determine if the monkeys were more wary in that location 1–2 days later. Finally, in the fourth treatment we flattened a middle section of the snakeskin and placed it in the gap (Fig. 1b) to determine if the monkeys could detect the snakeskin in the absence of its small transverse curves, and if their one experience with the snakeskin under the towels enabled them to detect the snakeskin more quickly after that experience, even without the curves.

We defined "location" as the two towels, with the expectation that they would provide obvious landmarks that vervets could use in remembering where they saw the snakeskin. To test this expectation, for one group we conducted the second two treatments in a different spatial location from the first two. In the event that this expectation was not met and the vervets used other landmarks, we placed the towels in the same place for all four treatments for the other groups. Wherever we placed the towels, the extent and complexity of ground cover differed by group, which we visually assessed as having no, sparse, more (Figs. 1a, 2a), or most ground cover (Figs. 1b, 2b). "No" ground cover was defined as bare ground. "Sparse" ground cover had less than 20 % ground vegetation and was less than 5 cm tall. "More" ground cover had 20–70 % ground vegetation that was less than 5 cm tall and mainly a monoculture of rhizomatous, closely cropped, *Cynodon* sp. "Most" ground cover had 20–70 % ground vegetation with a mixture of vertically heterogeneous forbs and grasses 5–15 cm tall. We limited treatments to one per day per group (Table 2).

Table 1 Age/sex compositions of vervet study groups in Laikipia, Kenya

Group	Adult males	Adult females	Subadults and juveniles	Infants	Total
HP	11	9	14	6	40
CT	1	2	3	0	6
BR	3	4	7	1	15
FG	4	5	12	1	21

Fig. 1 a Presentation of the snakeskin with ground substrate rated as having "more" ground cover. b Presentation of the flat snakeskin with ground substrate rated as having "most" ground cover

For all 16 videos, we each scored (1) the time of arrival of the first animal to approach to 1 m of the towels, (2) the time of arrival of the first animal, if any, to detect the snakeskin or to look at or near the towels in the absence of the snakeskin, (3) the time of the response, if any, and (4) the behavioral response, which, if one occurred, was either "staring/peering at" (done quadrupedally) or "bipedal standing". The videos were also scored by four assistants who were blind to the purpose of the study and the treatment conditions but were instructed to score all of the above. We trained them to identify responses by showing them photographs of staring/peering at and bipedal standing (Fig. 2a, b).

We measured latency to respond based on the difference in seconds from when the scorer estimated that the first responder approached to within 1 m of the towels to when it stared/peered at or stood bipedally. Limiting the analyses to the first responder avoided a potential bias that could arise if monkeys use social cues to help detect snakes. There were no replications of the same treatment with the same group because responses could potentially affect behavior in future replicates by, for example, increasing vigilance. We calculated from the scores of all observers the median latencies for the first animal to arrive in the baseline treatment, and for the
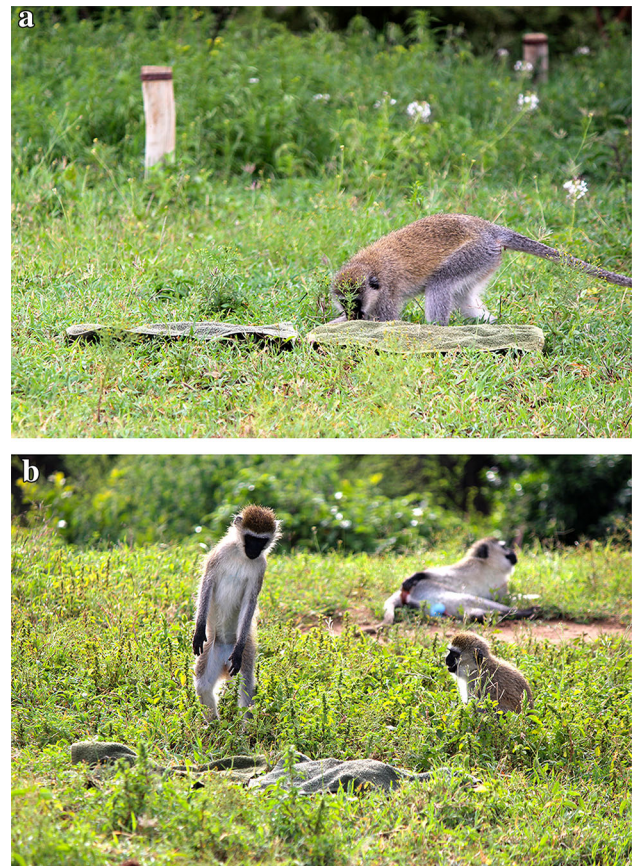

Fig. 2 a An example of staring/peering at while orienting to the snakeskin, a behavior that indicates snakeskin detection. b Standing bipedally while orienting to the snakeskin, a behavior that indicates snakeskin detection

other treatments, the median latencies for the first responders to stare/peer at or stand bipedally, and their corresponding median absolute deviations (MAD).

Results

First treatment: baseline

The baseline treatments were filmed for 130–442 s. The first animal's median arrival at the towels ranged from 0–120 s, depending on the group (MAD 0–3). No animals in any group stared/peered at the towels or stood bipedally while orienting toward the towels.

Second treatment: snakeskin

The second treatments were filmed for 80–446 s. All groups detected the snakeskin as evidenced by staring/peering at it (two groups) or standing bipedally (two groups). The first responder's median latency to respond ranged from 10–39 s

Table 2 Treatment schedule for each vervet study group

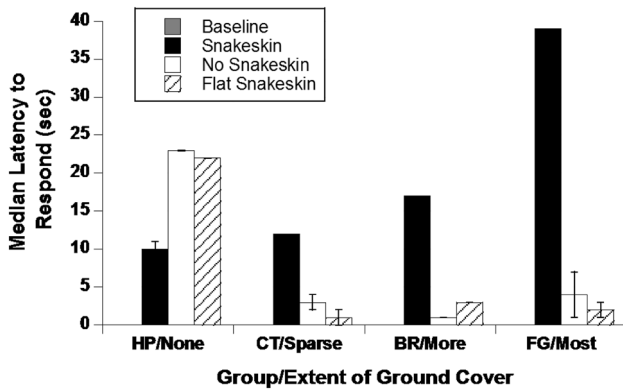| Group	Baseline (no snakeskin)	Snakeskin	No snakeskin	Flat snakeskin
HP	Day 0	Day 1	Day 2	Day 5
CT	Day 0	Day 1	Day 2	Day 3
BR	Day 0	Day 1	Day 3	Day 4
FG	Day 0	Day 1	Day 3	Day 4

Fig. 3 Median latencies to detect snakeskins or to stare/peer at towels by group, treatment, and extent of ground cover. *Error bars* represent median absolute deviations. See text for definitions of extent of ground cover. Abbreviations: *HP* Hippo Pool group, *CT* Centre group, *BR* Bridge group, *FG* Fig group

Fig. 4 Age/sex differences in first to arrive ($n = 16$ treatments) and first to detect the snakeskins or to stare/peer at or stand bipedally while orienting toward the towels in the absence of the snakeskin ($n = 12$ treatments). Adult males and adult females differed significantly as first arrivers vs. first responders

(MAD 0–1), and the latency to respond was longer as ground cover became more complex (Fig. 3). In the minute after the first responder detected the snakeskin, the maximum number of animals present at the towels per group ranged from 4 to 6 and 1 to 5 individuals, including the first responder, exhibited behaviors indicating detection.

Third treatment: no snakeskin

The third treatments were filmed for 194–768 s. As with the baseline treatments, no snakeskin was placed under the towels. The first responder's median latency to stare/peer at the towels (two groups) or stand bipedally (two groups) while orienting toward the towels ranged from 1 to 23 s (MAD 0–3). Three of the four groups had shorter median latencies to respond with the towels alone than with the snakeskin (Fig. 3).

Fourth treatment: flat snakeskin

These treatments were filmed for 349–646 s. Despite the unnatural shape of the snakeskin, all four groups detected it. The first responder's median latency to detection ranged from 1 to 22 s (MAD 0–1). Two groups stared/peered at and two groups stood bipedally. Three of the four groups responded more quickly than during their first exposure to the snakeskin (Fig. 3).
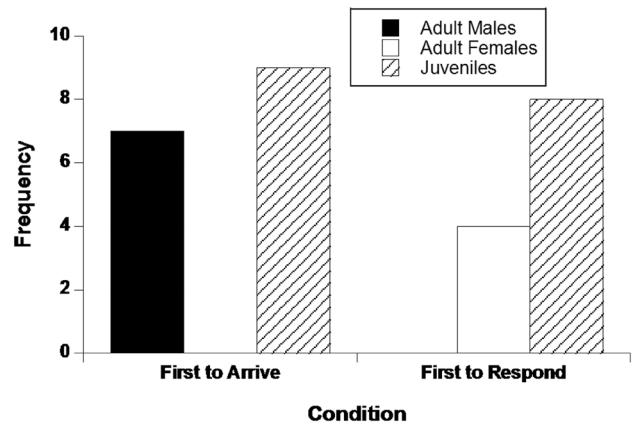
Age/sex differences in response

Although not predicted, it became apparent during the study that there were obvious age/sex differences in response to the snakeskins or towels (Fisher's Exact Probability test: $p = 0.003$, 2-tailed). Adult males were the first to arrive in seven of 16 treatments, but they were never the first to respond, whereas adult females never arrived first, but were the first to respond in four of the 12 treatments with responses (Fisher's Exact Probability test: $p = 0.003$, 2-tailed; Fig. 4). Juveniles (of undetermined sex) arrived first in nine of 16 treatments and were the first to respond in eight of the 12 treatments with responses. There was no significant difference in behavior between adult females and juveniles (Fisher's Exact Probability test: $p = 0.10$, 2-tailed) or between adult males and juveniles (Fisher's Exact Probability test: $p = 0.54$, 2-tailed).

Discussion

Snakes can be difficult to see in nature because their coloration can camouflage them, and they are often obscured by vegetation, with only parts of their bodies revealed. Nonetheless, within less than a minute after arriving, the first responders in all groups behaved as if they perceived

the object under the towels to be a snake ("snakeskin" in Fig. 3). After only one encounter with the snakeskin, three of the four groups became more vigilant around the towels even when no snakeskin was present, and they responded more quickly to the unnaturally shaped, flat snakeskin than during their first encounter with the snakeskin.

One group differed from the others after the initial exposure to the snakeskin. In this group, individuals near the towels in one treatment were not always the same as those near the towels in another treatment, likely because the group was nearly twice the size of the next largest group, and its members had a large glade in which to feed, and so were more dispersed during the treatments. In the three smaller groups, the same individuals routinely fed on the maize in a more compressed area, and all individuals exposed to the initial snakeskin treatment were also involved in the other treatments. Because of these differences, the only treatments from the largest group that are strictly comparable to those from the other groups are the baseline and initial snakeskin treatments.

Scales are the smallest reliable visual cue for snake detection

In making only 2.5–2.7 cm of snakeskin visible to the monkeys, we limited the potential cues for snake detection to a small section of the gopher snake's tubular body shape, a small section of its coloration, and a small section of its scale pattern. The vervets' detection of the flat snakeskin shows that even small curves are not essential for snake detection, especially when animals are already vigilant. Similarly, because the vervets reacted to the snakeskin even though gopher snakes do not occur in Africa, coloration and experience with particular snake species do not appear to be essential cues. Scales thus appear to be the most likely visual cue for snake detection. Scales should also be a highly reliable cue because they are universal in snakes.

The ability to detect snakes using only their scales would clearly be beneficial, especially when vegetation obscures large portions of the snakes' bodies. It might then be hypothesized that snakes, particularly those that rely on camouflage, faced selection to evolve color patterns that help to visually distract from scales or disrupt scale patterns. Many snakes have repetitive color patterns that are larger than individual scales, e.g., blotches, which may help to draw attention away from scale edges. Other snakes have color transitions that are independent of scale edges, and thus visually disrupt scale patterns. Black-tailed rattlesnakes (*Crotalus molossus*) are an exception. In this species, each scale expresses only one of several colors, and this appears to accentuate their identities as scales (H. W. Greene, pers. comm.). Future research might explore this idea further.

Responses relative to differences in ground cover

More heterogeneous, complex substrates should make remaining undetected easier for snakes, and, as expected, latency to detect the snakeskin in the initial treatment increased as ground cover became more extensive and complex, but the maximum latency was still under 1 min. Although snakes often blend into the background as they lie in vegetatively heterogeneous substrates, there is evidence suggesting that primates also have heightened visual sensitivity to snakes under such conditions. For example, humans are able to detect images of snakes more quickly or more accurately than other stimuli under conditions of high perceptual load (Soares 2012; Soares and Esteves 2013; Soares et al. 2014).

Acquiring a memory for the location of snakes

In all four groups, the monkeys paid no obvious attention to the towels before the snakeskin was presented to them. After the initial snakeskin treatment, individuals in all four groups persistently peered/stared at or stood bipedally near the towels in the absence of the snakeskin, and three of the four groups responded more quickly than during their initial exposure to the snakeskin. These same three groups were also quicker to detect the flat snakeskin after the initial snakeskin exposure, even after as many as 3 days.

In general, after the first exposure to the snakeskin, animals frequently scanned the ground near themselves and had slower, more deliberate footfalls when they were near the towels, especially in the two groups with the more complex ground cover. In the group with the most complex ground cover, a juvenile even climbed onto a dried pile of elephant dung while scanning the ground near the towels. All of these behaviors suggest that the initial exposure to the snakeskin facilitated memory encoding, storage, and retrieval, resulting in heightened awareness after discovering a "snake" under the towels only once before. This was also true for the group for which the towels were moved to a different spot, suggesting that after the snakeskin had been detected, the towels became associated with snakes, and they provided a relevant landmark for potential snake presence afterward.

Greater vigilance in or avoidance of an area where snake models have been seen has also been reported in captive Geoffroy's marmosets (*C. geoffroyi*) (Hankerson and Caine 2004) and in wild long-tailed macaques (*M. fascicularis*) (van Schaik and Mitrasetia 1990). Snakes can strike quickly (Kardong and Bels 1998; Whitaker et al. 2000; Young 2010; Penning et al. 2016), but otherwise move fast over only short distances, remain inactive for long periods of time, and show low daily spatial displacement (Greene 1997). Memory recall of where snakes had been seen

recently should thus be effective in decreasing predation or envenomation, and any behaviors that facilitate memory formation should have been favored evolutionarily.

Sex differences in snake detection

An unexpected finding was that adult males never responded first to the snakeskin despite having ample opportunity. Although males never detected the snakeskin first, they did stare/peer at or stand bipedally when they finally saw the snakeskin. Other studies are consistent with our finding of an age/sex difference in snake detection. Adult male vervets in Amboseli National Park, Kenya, gave snake alarm calls less often than other age/sex classes (Struhsaker 1967), but it was unlikely that they perceived snakes as a non-threat because they responded to snake alarm calls as often as other age/sex classes (Seyfarth et al. 1980).

This apparent sex difference in snake detection suggests hormonal involvement. Female mammals have an attentional bias toward objects and male mammals, toward movement, a sex difference influenced by androgens (Handa and McGivern 2015). Also influenced by sex hormones (Goel and Bale 2008) is a sex difference in anxiety or stress response, found in both rodents and humans (Palanza 2001). Interestingly, women detect snakes faster during the luteal phase of their hormonal cycles when anxiety is more common (Masataka and Shibasaki 2012). Anxiety and fear are common responses to snakes (Öhman 2009; Öhman et al. 2012).

Carter et al. (2012) found that chacma baboons (*Papio ursinus*) with the most frequent alarm responses to a taxidermied puff adder also visually monitored the snake longest, and that such responses were not positively correlated with approaching and handling novel foods. They concluded that the responses to the snake reflected anxiety, but that responses to the food reflected boldness. Thus, it is possible that in our study, detection of the snakeskin also reflected anxiety, which is expected to be expressed more in females than males, whereas the maize may have attracted bolder individuals, i.e., those who were first to arrive. Adult males and juveniles were always the first to arrive. Alternatively, adult males could have simply been more focused on the maize than adult females, although this would not explain a similar sex bias toward snake detection in non-provisioned vervets in Amboseli. It is also not likely that females were more sensitive to the snakeskin to protect their infants better. No female first responders had clinging infants and, because it was the beginning of the birth season, the youngest previous offspring would have been approximately 1 year old and considered juveniles. Perhaps adult females were more sensitive to the snakeskin because they had juvenile offspring nearby, but

juveniles themselves were also excellent first responders, suggesting no deficit in their ability to detect snakes.

Future directions

To extend this line of exploration, a future study might expose primates to a flat or normal piece of snakeskin without scales first to learn how quickly they detect it and respond with typical behavior. Our prediction is that they would not respond. There are many small, flat or tubular objects in the natural world that have no scales, and primates cannot afford to be reactive to all of them. Another study might explore the association between landmarks and location in greater depth by, for example, using one occluding agent in the first exposure trial and a different one in the second trial while removing all other obvious landmarks. If landmarks are required for remembering the spatial location of snakes, then the second occluding agent should elicit little vigilance. If landmarks are unimportant, then vigilance should be observed.

Although limited by a small sample size, this study helps to increase our understanding of the arsenal of tools primates use in dealing with snakes. Such tools include rapid visual detection of mostly occluded snakes using scales as a basic visual cue, continued attention to them once detected, memory construction of their location, likely via landmarks, memory recall of snakes seen earlier in those locations with the same landmarks, and heightened alertness in those same locations in the days following their detection. All of these behaviors add to our growing recognition of a long and important evolutionary relationship between snakes and primates.

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