

RESEARCH ARTICLE

Factors Increasing Snake Detection and Perceived Threat in Captive Rhesus Macaques (*Macaca mulatta*)STEPHANIE F. ETTING^{1*}, LYNNE A. ISBELL^{1,2}, AND MARK N. GROTE¹¹Department of Anthropology, University of California, Davis, California²Graduate Group in Animal Behavior, University of California, Davis, California

The primary predators of primates are all ambush hunters, and yet felids, raptors, and snakes differ in aspects of their ecology that affect the evasive strategies of their primate prey. Felids and raptors can traverse long distances quickly, thus the urgency of threat they present increases as they come closer in proximity to primates. In contrast, snakes do not move rapidly over long distances, and so primates may be reasonably safe even at close distances provided snakes can be detected and monitored. We investigated the ability of captive rhesus macaques (*Macaca mulatta*) to detect snakes at distances ranging from 15 to 1.5 m. We also examined variation in intensity of perceived threat by applying a Hidden Markov Model to infer changes in underlying state from observable behaviors, that is, increased attention and mobbing. We found that the macaques often failed to detect snake models but that closer proximity improved snake detection, which is necessary before threat can be perceived. We also found that having only one individual in fairly close proximity (≤ 7.5 m) was sufficient to alert the rest of the group and so the chances of detection did not increase with increasing group size. Finally, we found that when the snakes were perceived, they did not elicit greater intensity of response with closer proximity. These results provide evidence that the threat from snakes is greatest when they are in proximity to primates but are unseen. When snakes are seen, however, distance appears not to affect primates' perceived risk, in contrast to their perceived risk from raptors and felids. *Am. J. Primatol.* 76:135–145, 2014. © 2013 Wiley Periodicals, Inc.

Key words: anti-predator behavior; mobbing; snakes; primates; Hidden Markov Model

INTRODUCTION

Predation has long been considered an important source of selection on primates [Alexander, 1974; Anderson, 1986; Isbell, 1994; Stanford, 2002; van Schaik, 1983]. The most common predators of primates are felids, raptors, and snakes. Felids and raptors are thought to have greater impact on primate populations than snakes [Ferrari & Beltrao-Mendes, 2011; Hart, 2007]. Based on biogeographical, fossil, and molecular evidence, however, snakes were likely the first of these predator classes to evolve, and the only one with a geographic range fully overlapping that of primates today [Greene, 1997; Isbell, 2006, 2009].

All three types of predators are largely ambush hunters, depending on surprise to kill their prey [Shine et al., 1999; Shultz, 2001; Zuberbühler & Jenny, 2002]. As a result, early detection is key for primates, as their predators will often give up their hunt and move on once they are detected [Cordeiro, 2003; Eason, 1989; Gursky, 2006; Hayward et al., 2006; Ross, 1993; Zuberbühler et al., 1999]. The most effective detection distance for these predators may differ, however, due to differences in hunting style

and ranging behavior. Felids and raptors hunt largely by sight, can move rapidly over long distances, and range widely [Brockman, 2003; Cordeiro, 2003; Eason, 1989; Hayward et al., 2006; Peres, 1990; Ross, 1993; Shultz, 2001; Zuberbühler et al., 1999], all characteristics that make it advantageous to detect these predators from as far away as possible. Bonnet macaques (*Macaca radiata*) detect and respond (by alarm-calling and fleeing) to leopard models from approximately 25 m away [Coss et al., 2005], and perched raptor models elicit responses from Geoffroy's marmosets (*Callitrix geoffroyi*) at 8–16 m away

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[Caine, 1998]. However, as ambush predators often rely on stealth and camouflage, primates may not always detect them. Tufted capuchin monkeys (*Cebus apella*) detected stationary ocelot models and perched hawk-eagle models only 50% of the time when they were 2 and 4 m away, respectively [Janson, 2007]. When movement was added to the models, the capuchins' 50% detection rate improved to 8 m for the ocelot and 12 m for the hawk-eagle.

It has also long been thought that primates improve predator detection by living in larger groups. Larger groups may detect predators more quickly or more reliably by having "more eyes" engaged in vigilance [Pulliam, 1973], although empirical evidence in primates is mixed [Boinski et al., 2003; Garber & Bicca-Marques, 2002; Treves, 2000; van Schaik et al., 1983].

Snakes differ from felids and raptors in that they rely on short distance infrared imaging to detect prey [Grace & Matsushita, 2007], are fast-moving only over short distances [Young, 2010], and often lie still in the same location for days, waiting to ambush their prey [Greene, 1997]. Because of their unique behavioral ecology and morphology, snakes may be the most difficult of the three types of predators to detect. For example, only 13% of wild brown mouse lemurs (*Microcebus rufus*) responded fearfully to a stationary snake model. When movement was added, however, the percentage of lemurs responding increased to 44% [Deppe, 2006].

Snakes also differ from felids and raptors in the response they elicit from primates once detected. Responses toward predators include alarm-calling, fleeing, and mobbing. Mobbing involves several animals gathering around a predator and is often accompanied by alarm-calling [Crofoot, 2012; Curio, 1978]. Raptors and felids most often elicit alarm-calling and fleeing to safety, and when they are mobbed, typically only adult males participate [Arlet & Isbell, 2009; Busse, 1980; Eckardt & Zuberbuhler, 2004; Gautier-Hion & Tutin, 1988; Leland & Struhaker, 1993; Lloyd et al., 2006; Matsuda et al., 2008; Ross, 1993]. The response to snakes more often includes alarm-calling and mobbing by all age/sex classes, but importantly, not fleeing [Chapman, 1986; Gursky, 2002, 2005; Perry et al., 2003; Schülke, 2001; Srivastava, 1991; Tello et al., 2002; van Schaik & Mitraseta, 1990]. This suggests that mobbing of snakes may be less risky than mobbing of felids and raptors. Given the apparent difficulty with which snakes are detected, it may even be advantageous to stay near snakes to keep them in sight. At least some primate alarm calls are outside the auditory range of snakes [Coss et al., 2007], and one function of alarm calls toward snakes may be to attract conspecifics to the location of the snake [Wheeler, 2008]. Alarm calls of spectral tarsiers (*Tarsius spectrum*) toward snakes attract males even across territorial boundaries to join in alarm-calling and mobbing [Gursky, 2006].

Alarm-calling and mobbing suggest that many primates become agitated or aroused when they detect snakes, but their perceived level of risk is difficult to assess. Some primates have alarm calls that are urgency-based, and become noisier depending on the apparent level of threat, for example, macaques and baboons, *Papio* spp. [Coss et al., 2007; Fischer & Hammerschmidt, 2001a,b; Fischer et al., 2001]. Vervets (*Chlorocebus pygerythrus*) are well known for their functionally referential alarm-calling [Seyfarth et al., 1980a] but within a predator type, alarm calls may also suggest a perception by the monkeys of elevated threat. For example, when a resting leopard begins to move, vervet alarm-call bouts become more frequent (L.A. Isbell, personal observation). A felid or a raptor may be perceived as more dangerous when it is closer [Blumstein & Armitage, 1997; Coss et al., 2007; Wheeler, 2010] but is that also the case with snakes? Attraction rather than flight in the presence of snakes suggests that once snakes are detected, their perceived threat may not increase with closer proximity as is the case with felids and raptors. We tested whether perceived risk changes with proximity to snakes with captive rhesus macaques (*Macaca mulatta*). In the wild, rhesus macaques co-occur with potentially deadly pythons (*Python* spp.), cobras (*Naja* spp.), and kraits (*Bungarus* spp.) [Greene, 1997], and captive rhesus macaques are known to react with alarm calls and increased vigilance when they encounter snakes and snake models [Amaral, 2002; Cook & Mineka, 1989; Mineka et al., 1980].

Our main goals were thus to determine how often and at what distances rhesus macaques in captivity detect snakes and to estimate levels of perceived risk at different distances. We assessed the latter by employing a Hidden Markov Model (HMM) that uses observable behaviors to infer latent motivational states [Schliehe-Diecks et al., 2012].

METHODS

Study Site and Subjects

We conducted experiments with six groups ($N = 38\text{--}156$) of rhesus macaques at the California National Primate Research Center (CNPRC), Davis, CA, in which we presented three stimuli (snake model, rope, and stuffed toy bear) to the groups at decreasing distances. All study groups were housed in $30.5 \times 62 \times 2.5$ m enclosures ($W \times L \times H$). All enclosures contain A-frame houses, hanging plastic barrels, perches, and swings. The rhesus macaques were fed monkey chow, and also received supplementary fruits, vegetables, seeds, and nuts. The enclosures are constructed with chain-link fencing, which does not create visual or physical barriers separating snakes from the macaques, as live gopher snakes (*Pituophis catenifer*) have been observed entering the

enclosures [Isbell, 2009]. When this happens, nearly the entire group gathers around the snake at the same time. Thus, we assume that the majority of monkeys have had at least some exposure to live snakes.

Procedure

It is unclear how close snakes must be in order for primates to detect them. Most experimental work using snake models usually involves presenting the models at very close distances to primates, for example, less than 1 m [Clara et al., 2008; Hankerson & Caine, 2004; Ramakrishnan et al., 2005; Vitale et al., 1991], less than 2 m [Barros et al., 2002; Gursky, 2003], or at 2 m [Hollis-Brown, 2005]. Since the maximum distance at which primates can detect snakes is unknown, we arbitrarily began testing for behavioral responses at 15 m and continued testing at decrements of 1.5 m, ending at 1.5 m from the enclosure fenceline. We recorded the following behaviors (following Caine, 1998): (1) the number of animals in the area of the enclosure that afforded the best view of the stimulus (BVA), (2) the number of those animals gazing in the direction of a model snake, and as controls, a rope, and a stuffed toy bear, and (3) the number of alarm calls. We assume that changes in these components reflect changes in arousal or responsiveness by the animals and are thus indicative of differences in perceived threat. We operationally defined animals as exhibiting the greatest response and thus greatest perceived threat when the number of animals in the BVA, the number of animals in the BVA gazing toward the stimuli, and the number of alarm calls increased significantly compared to all other distances. The BVA was determined before the start of the study. For each enclosure, the chosen area had to be one not used for feeding or sleeping (activities that tend to aggregate animals) and that did not permit neighboring groups to potentially see the snake and thus attract the attention of the experimental group. The BVA was 7.5 m along the fenceline, 2.5 m high (the maximum height of the enclosure), and 2.5 m into the enclosure, marked by support poles.

The snake model was a 94-cm hard-foam replica of a cottonmouth snake in a sinusoidal posture (WASCO Wildlife Artist Supply Co.). The model was painted with olive green and brown craft paint mixed to produce a greenish-brown snake lacking any distinguishing markings except the scale pattern of the model. The eyes were painted black, and the entire model was coated in shiny, clear paint. The rope was selected because it was similar in shape to the sinusoidal snake model, but lacked the scale pattern typical of snakes. The stuffed bear was selected because it differed both in shape and pattern from the snake and the rope, but was similar in size and color. All were novel objects at the beginning of

the experiment, but only the snake model was predicted to generate high levels of arousal. We chose these other objects to test the alternative prediction that novelty alone is sufficient to elicit an increased response.

For each trial, one of us (SFE) placed one of the three stimuli in front of the enclosures, keeping it covered with a white fabric (approximately 60 × 90 cm) for 10 min while baseline data on foraging, feeding, and grooming behavior were collected. The stimulus was then uncovered for 10 min during the experimental phase. Finally, the stimulus was recovered and the animals were observed for an additional 10 min. Thus, each trial lasted 30 min. On occasion, human activity (e.g., animal managers entering enclosures) interrupted the trial. In such cases, SFE halted observations until at least half the animals in the group returned to pre-disturbance foraging, feeding, and grooming behaviors. Each of the three stimuli was presented to the animals at the same distance in decrements of 1.5 m, beginning at 15 m, and ending at 1.5 m from the enclosures. At each distance, only one 30-min trial using one stimulus was presented each day. Once all three stimuli were presented at a given distance, the presentations were moved closer to the fenceline. The substrates on which the stimuli were presented were dirt and grass. The order of presentation of the three stimuli was systematically randomized for each distance, such that the order of presentation of the stimuli was balanced across groups. To minimize the potential for habituation or stress to the animals, subjects were tested no more than 3 days per week, with at least 48 hr separating trials.

Once every minute during each of the 30-min trials, SFE scanned the BVA for as long as it took to count all animals in the BVA and record how many were gazing at the stimulus. This experimental design resulted in 30 observations per trial × 3 stimuli per distance × 10 distances per group, resulting in a total of 900 observations per group. All alarm calls during any given observation minute were recorded on a voice recorder and later counted. Each distinct vocalization was scored as one alarm call.

This experimental protocol received IACUC approval from the University of California, Davis (no. 13193), and adhered to the American Society of Primatologists' principles for the ethical treatment of primates.

Statistical Analyses

One group (NC 15) was partially disbanded in the early part of the study and thus only the latter portions of their trials, conducted after the group re-stabilized, were analyzed.

We used the Mann–Whitney *U*-test to compare the distances at which trials with and without alarm

calls occurred, with the expectation that alarm calls would be more likely when the snake was closer. We calculated Spearman rank correlations to determine whether the latency to alarm call decreased with proximity to the snake. Both of these calculations test the prediction that snakes are more reliably and quickly detected when they are closer. Since alarm calls were the clearest indication that the monkeys detected the snake, for some tests we compared only those trials with and without alarm calls to the snake model within 7.5 m of the fenceline, as 7.5 m was the farthest distance to the snake model at which alarm calls were given (see Results Section). Because alarm calls invariably attracted other animals to the BVA, however, we compared the total numbers of animals in the BVA in the minute before alarm calls were given to the mean number of animals in the BVA during the 10-min stimulus presentation period for trials without alarm calls. We did the same for numbers of animals in the BVA who gazed toward the stimulus. Significance levels for these non-parametric tests were obtained by permutation using the boot package in R (v. 2.9.0, The R Foundation for Statistical Computing, available online at: <http://www.r-project.org>).

We used the HMM to examine subtle variation in intensity of response based on the number of animals in the BVA, the number of animals gazing toward the object, and the number of alarm calls given. As the HMM is a relatively new statistical technique, we describe its attributes in detail. The HMM is a latent-state model. Latent-state models aim to relate changes in observed behavioral variables to corresponding changes in underlying unobservable states [Courvoisier et al., 2007; Lanza et al., 2005; Schmukle & Egloff, 2005]. In principle, these models enable the statistical detection of subtle shifts between levels of responsiveness to experimental stimuli. Among the latent-state models, HMMs are best suited to observations taken at regularly spaced, discrete time points, such as our instantaneous scan samples [Zucchini & Macdonald, 2009]. In order to identify the distance at which subjects were most aroused by the three kinds of stimuli, we quantified shifts in responsiveness by fitting HMMs to multivariate time series for the following variables: the number of animals in the BVA, the number of those animals gazing toward the stimulus, and the frequency of alarm-calling.

We adapted functions of the package Hidden-Markov (v.1.2-8; Harte, 2009), written in the statistical programming language R, to fit HMMs to the observations for each group of animals. Our analysis is “unsupervised,” as we make no a priori assumptions about how behaviors will vary across distances, experimental phases, or stimuli. This means that underlying states are inferred without specific reference to the experimental conditions in effect at any given time. Parameters of the HMMs are estimated

by an EM algorithm, a standard tool for missing-data problems [McLachlan & Krishnan, 1997]. Here, the missing data are the latent states. Computation with the EM algorithm depends on an expression for the “complete data” likelihood, which is given along with other technical details in the Appendix (online Supplementary Material).

We fitted HMMs separately to each group of animals, allowing for the possibility that different groups exhibit different numbers of latent states. By comparing a group’s behavior only to itself across all trials, we also control for any potential variation across groups in group size, history, personality, inherent excitability, etc. For each group, we used the Akaike Information Criterion (AIC) [Burnham & Anderson, 2002] to compare models differing in number of latent states, beginning with a two-state model. We considered successively larger numbers of latent states, evaluating the AIC after each addition of a state. AIC values decrease along the sequence of models, as long as additional latent states are supported by the observations; then AIC values increase as models become too complex. For each group, we chose the model with the smallest AIC (see Online Supplementary Material).

Each latent state can be characterized by the typical behaviors one might observe given the state: in the present case, the latent states are distinguished by differences in expected number of animals in the BVA, number of animals gazing toward the stimulus, and number of alarm calls per minute. The unsupervised analysis produces a most-probable latent state for each minute of observation, without applying meaning to or organizing the states in any fashion. The analyst must then decide if, and how, inferred shifts between latent states can be interpreted in light of experimental conditions.

RESULTS

Detection of the Snake Model

Distances at which alarm calls were given (mean: $3.6 \text{ m} \pm 1.1 \text{ SE}$) were significantly shorter than distances at which no alarm calls were given (mean: $8.3 \text{ m} \pm 0.61 \text{ SE}$; Mann–Whitney $U = 205.5$, $n_1 = 5$, $n_2 = 50$, $P = 0.008$, 1-tailed; Fig. 1a). In addition, the latency to alarm call was shorter with shorter distances (Spearman rank correlation test, $r_s = 0.95$, $n = 5$, $P = 0.035$, 1-tailed).

Alarm calls in the presence of the snake model occurred in only three of the six groups and only at 7.5 m or less. Alarm calls were not invariably given at all those distances, however. Animals in one enclosure (NC 14) gave alarm calls at 7.5, 3, and 1.5 m, animals in another (NC 8) gave alarm calls only at 4.5 m, and animals in the third (NC 15) gave alarm calls only at 1.5 m. The gap in alarm-calling at 6.0 and 4.5 m in NC 14 can be explained by the absence of

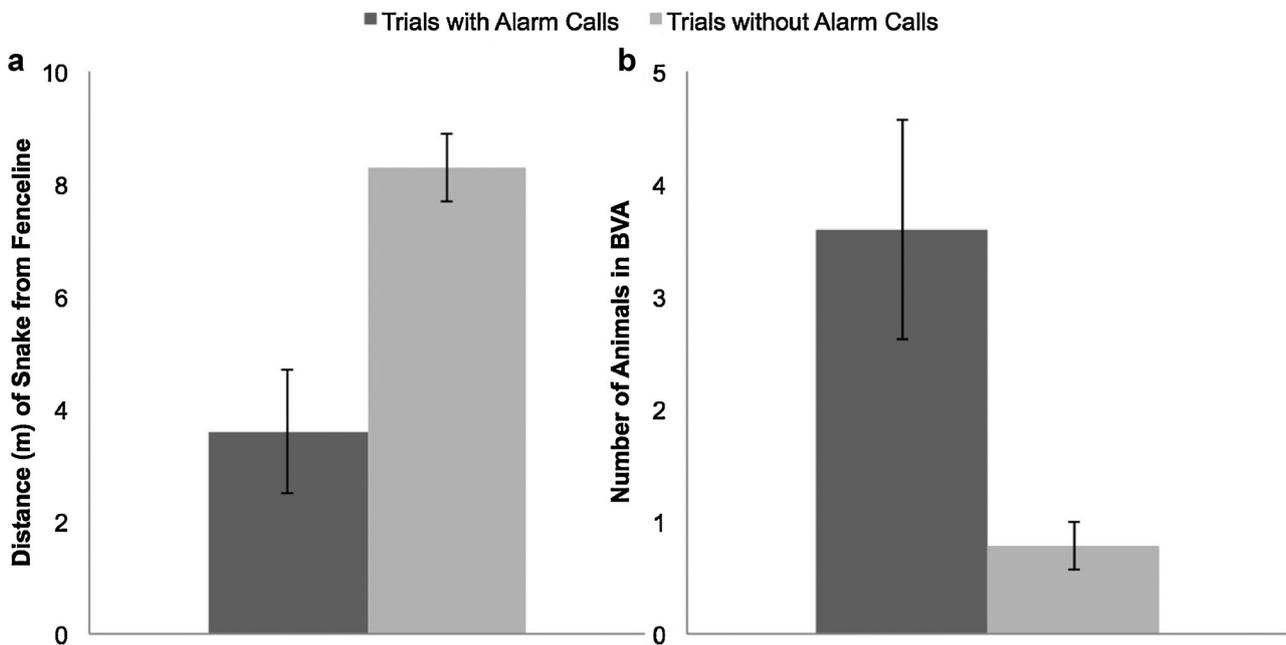


Fig. 1. When the snake model was exposed, (a) the mean distance of snake models from the fenceline in trials in which alarm calls were given compared to mean distance of snake models from the fenceline in trials in which no alarm calls were given and (b) the total number of animals in the BVA that gazed toward the snake in the minute before the first alarm calls were given in trials compared to the mean number of animals in the BVA for the 10-min period in trials without alarm calls. Error bars are ± 1 SE.

animals in the BVA during those trials. However, in NC 15, there were animals (1, 3, and 5) in the BVA in the three trials at 7.5 m or less when no alarm calls were given. Similarly, in NC 8, 1 and 3 individuals were in the BVA in the two trials at 7.5 m or less when no alarm calls were given. The low percentage of trials in which alarm calls were given at “detectable” distances even when animals were in the BVA suggests that the monkeys often failed to detect the snake even when they were close enough to see it. However, it is possible that using alarm calls to identify detection is too conservative. When we examined whether gazing increased with decreasing distance to the snake in the 16 trials without alarm calls, we found a significant correlation ($r_s = -0.78$, $P = 0.001$, $n = 16$, 1-tailed), although the numbers of animals gazing were still always very low (range of means: 0–0.6).

There were significantly more animals in the BVA in the minute before trials with alarm calls (3.6 ± 0.98) than there were, on average, for the entire 10-min period in trials without alarm calls (0.78 ± 0.21 ; $U = 20.5$, $n_1 = 5$, $n_2 = 25$, $P = 0.012$, 2-tailed; Fig. 1b). There were not, however, significantly more animals in the BVA gazing toward the snake in the minute before the first alarm calls were given (0.20 ± 0.2) than there were when no alarm calls were given (0.11 ± 0.04 ; $U = 46$, $n_1 = 5$, $n_2 = 16$, $P = 0.618$, 2-tailed). These results suggest that having more animals within fairly close proximity increases the chance that at least one animal will

sound an alarm but having greater numbers nearby does not increase detectability. Similarly, larger group size did not appear to improve snake detection. Groups ranged in size from 38 (NC 15) to approximately 100 (NC 14 and 16) to approximately 170 (NC 8, 10, and 18). Groups that detected the snake model were small (NC 15), mid-sized (NC 14), and large (NC 8). Despite large differences in group size, these groups had similar numbers of animals (range: 1–6, mode: 4) in the BVA immediately preceding detection.

Intensity of Response

For the models presented here, the latent states can be ordered consistently to reflect increasing levels of responsiveness, agitation, or arousal indicative of greater perceived risk. For example, in a six-state model, the latent states range from a state characterized by minimal response (represented by few or no animals in the BVA, few or no animals gazing toward the stimulus, and few or no alarm calls) to a state reflecting the highest level of agitation exhibited by the group (represented by a significant increase in the number of animals in the BVA, the number gazing at the stimulus, and the number of alarm calls). Each underlying state is characterized by a mean value for each of the three behaviors, an example of which is shown in Table I. In graphical displays of fitted models, we label the minimal response state “1,” and successively stronger

TABLE I. Hidden Markov Model Parameter Estimates for Rhesus Macaque Group NC 14^a

Behavior	State					
	1	2	3	4	5	6
Mean number of animals in the BVA	0.01	0.9	2.6	5.9	11.9	24.4
Mean number of animals in BVA gazing toward the stimulus	0	0	0.1	0.1	1.2	3.7
Mean number of alarm calls	0	0	0	0	0.1	4.3

^aThese parameter estimates are for the same data and model presented in Figure 2.

response states “2,” “3” and so on. These underlying states are graphically represented by progressively darker bars as agitation increases, placed underneath the graphs. Figure 2 provides an example from one group (NC 14); graphs for all other groups are available in the online supplementary materials. By overlaying the graphical displays of the data and the fitted HMM with the experimental design (distance of presented stimuli, model presented, and phase of experiment), we determined the distance at which each group was most aroused when each of the objects was exposed.

Groups differed in the intensity of their responsiveness to the snake model. Three of the six groups (NC 10, 16, and 18) responded weakly or not at all (Table II). A two-variable model (including only changes in numbers of animals in the BVA and the number of animals gazing toward the stimuli because there were no alarm calls) indicated that NC 18 had very few animals in the BVA during the snake trials. Similarly, NC 16 showed mild arousal toward the bear and the rope, with more animals in the BVA, on average, than when the snake was presented (Fig. S4). Thus, animals in these enclosures may not have seen the snake. It is unlikely that lower use of the BVA by these groups when the snake model was presented was due to experimental conditions, as the animals in these groups never showed any distress over any of the trials or experimental procedures.

One group (NC 10) was more reactive to the rope and bear than to the snake. The snake model elicited a moderate response at the closest distance (1.5 m) but only *after* it was covered up (Fig. S2). This group alarm-called in more trials with all stimuli than any other group and appeared to be more reactive in general compared to other groups. It has a history of social instability (B.A. Beisner, personal communication), which may have increased tension and reactivity.

Three groups (NC 8, 14, and 15) responded very strongly to the snake model. These groups also

reacted strongly to the rope when it was presented after the snake model at the same distance, but not when the rope was presented before the snake model (Fig. 2 and Supplementary Materials).

Responsiveness Relative to Proximity of the Snake

The three groups that responded strongly to the snake reacted at varying distances from the boundary of the enclosure: 7.5, 3, and 1.5 m (NC 14), 4.5 m (NC 8), and 1.5 m (NC 15) (Table III). When the snake was detected at 7.5 m, the group was alerted to the snake model by alarm calls from the only animal in the BVA (Fig. 2). This individual was sitting at the edge of the BVA farthest from the snake model, approximately 2.5 m from the fenceline (thus, 10 m from the snake model), and on a perch approximately 2 m off the ground. All other strong responses were generated by animals at or near the enclosure’s fenceline on the ground.

DISCUSSION

Factors That Improve Snake Detection

In this study, even within the identified range of detection distances (≤ 7.5 m), the macaques failed to detect the snake more often than they saw it. The monkeys improved snake detection by being physically closer to the snakes. Although living in larger groups is often viewed as beneficial for detecting predators earlier or from farther away [Ebensperger & Wallem, 2002; van Schaik & van Hooff, 1983; van Schaik et al., 1983], we found that what mattered more for detecting snakes in our study was having at least one individual near the snake. Increasing the number of group members near the snake may increase the chances that at least one will see it, but there may not be a correspondence between detection and absolute numbers in the group. On the other hand, relative numbers, and especially numbers of relatives, might be important factors in determining whether or not an animal will alarm-call. We found that there were more animals in the BVA just before alarm calls were given even though there were not more animals gazing toward the snake. Macaques preferentially associate with kin and the macaques in our study have large matriline. Our results are consistent with the idea that alarm-calling occurs more often around kin [Cheney & Seyfarth, 1985].

In our study, the farthest distance at which the snake was detected was at 7.5 m when a monkey was elevated on a perch. A common practice among terrestrial and semi-terrestrial primates is to stand bipedally on the ground when they have detected a snake [Cheney & Seyfarth, 1990; Hollis-Brown, 2005; Ramakrishnan et al., 2005; Seyfarth et al., 1980b]. Standing bipedally reduces visual obstructions such

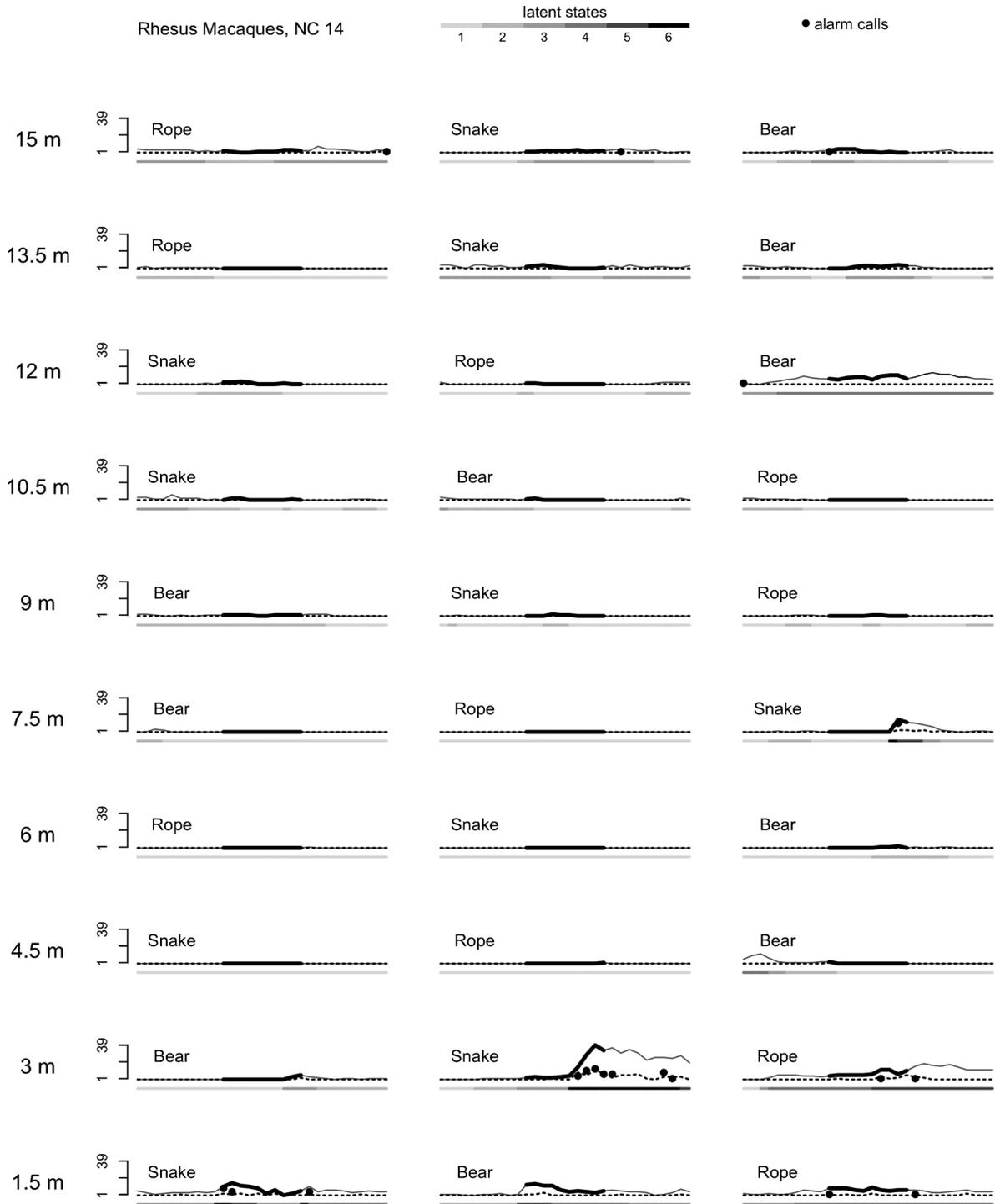


Fig. 2. Hidden Markov Model fitted to one rhesus macaque group. The X-axis reflects time. The Y-axis reflects the number of (1) animals in the BVA (solid line—gray segments represent pre/post-exposure period, black segment represents experimental phase of trial), (2) animals in BVA gazing toward the stimuli (dotted line), and (3) alarm calls (black dots). The most likely state at each time is indicated by a grayscale line beneath the graphs. Graphs are arranged in order of the experiment, with three trials per distance (one for each stimulus), displayed in order of presentation (horizontally left-to-right), and in decrements of 1.5 m (represented by vertical descent down the page).

as tall grasses, thus allowing animals to see better or farther [Enstam & Isbell, 2004]. Vervets stood bipedally more often in those parts of their home ranges that remained unburned after a wildfire [Jaffe

& Isbell, 2010]. Indeed, improved predator detection has been argued as one of the advantages to humans in being bipedal [Day, 1986]. However, some groups showed little response when they were close enough

TABLE II. Mean Numbers and Range of Animals in the BVA During the 10-Min Exposure Period for Each Stimulus and Group, Across All Distances

Group	Bear		Rope		Snake	
	Average #	Range	Average #	Range	Average #	Range
NC 8	2.4	0–27	1.4	0–15	2.3	0–39
NC 10	3.9	0–27	4.7	0–28	1.4	0–6
NC 14	2.1	0–13	1.5	0–11	2.7	0–39
NC 15	1.2	0–8	0.4	0–5	1.1	0–6
NC 16	1.3	0–12	2.3	0–28	0.3	0–2
NC 18	2.1	0–11	1.4	0–14	1.2	0–5

to detect the snake model and may have missed seeing it. In a recent study of chacma baboon (*Papio ursinus*) responses to snakes, Carter et al. [2012] found that 59% of all detections occurred within 2 m. Even at that close distance, however, in 8% of trials baboons still failed to see the snake when it was in the open and unoccluded by vegetation (A. Carter, personal communication).

Observational research on animals can be challenging when behaviors of interest, such as underlying emotional states, cannot be measured directly; but latent-state models such as HMMs enable us to infer emotional or other behavioral states that are represented by subtle changes in measurable variables. The HMMs revealed considerable group-level variation in intensity of response among rhesus macaques. By employing HMMs to analyze observable behaviors that reflect underlying changes in perceived risk, we were able to identify group-level variation in intensity of response. The groups that showed strong responses indicating elevated perceived risk toward the snake, but not the rope or bear, suggest that novelty per se did not increase arousal.

The numbers of latent states for the HMMs (S_Table in osm), which reflect variation in intensity of perceived threat, also varied among groups. We believe there are two primary reasons for the

variation in number of latent states. First, the number of states depends on the richness of behaviors displayed by the group. Thus, a less responsive group that did not vary much across scans (e.g., in number of animals in the BVA or frequency of alarm calls) would be represented by an HMM with fewer underlying states, compared to a more responsive group that exhibited more variation in behavior. Group history is one potential factor that could contribute to group-level differences in responsiveness. For instance, one of the study groups was highly reactive toward all stimuli, perhaps because tensions were already high as a result of their history of social instability. Clara et al. [2008] also found group-level differences in the responses of common marmosets (*C. jacchus*) to snake models, which they attributed to differences in rearing history. Differences in group size give a second reason for variation in the number of underlying states across groups. Larger groups have the potential for greater behavioral variation, and therefore a greater number of underlying states, simply because there are more animals that can perform a behavior at any given time. These two explanations are not necessarily connected, however, as the largest group (NC 18) showed fewer latent states than a much smaller group (NC 14) because it was generally less responsive toward the stimuli.

TABLE III. Summary of Responses by All Rhesus Macaque Groups to All Presented Stimuli

Group	Stimulus		
	Rope	Bear	Snake
NC 8	No response	1.5 m	4.5 m
NC 10	4.5 m	3 m	1.5 m (only after snake was covered up)
NC 14 ^a	No response	No response	7.5 and 3 m, weak response at 1.5 m
NC 15	No response	No response	1.5 m
NC 16	4.5 m	4.5 m	No response
NC 18	1.5 m	1.5 m	No response

^aGraph for this cage is presented in Figure 2.

Why Are Primates Attracted to Snakes?

Increased agitation in rhesus macaques was best identified by increased numbers of animals in the BVA, increased numbers of animals gazing at the object, and increased numbers of alarm calls. In contrast, Caine [1998] found that in the presence of owls, increased agitation in marmosets could be identified without including alarm calls. Alarm calls seem to be a key component in eliciting snake mobbing, however. In all trials with heightened arousal toward the snake model, at least one alarm call was heard within the first minute or two of the heightened response. Indeed, Meno et al. [2013] found that snake mobbing also co-occurred with alarm calls in capuchin monkeys (*C. capucinus*).

Alarm-calling and mobbing may draw conspecifics into closer proximity with snakes specifically to help them monitor snakes' movements and their locations on subsequent days. Consistent with this view is our finding that groups increased their response to the rope, a snake-like object, in the days after reacting to the snake model, but only when the rope was presented at the same distance (see Supplementary Figures). Their memory of seeing a snake at that location days earlier may have contributed to their stronger reaction to the rope. Vervets in the wild also appear to be more sensitive, at least over a period of several days, to the potential presence of a snake in a given location after they have associated that location with snakes. They were observed to stand bipedally and scan the ground in areas where, days prior, experimenters played recordings of snake alarm calls given by vervets [Cheney & Seyfarth, 1990]. Marmosets also seem to use memory to monitor or avoid locations where snakes were seen previously [Hankerson & Caine, 2004; Tello et al., 2002].

We suggest that the threat from snakes is different from that of raptors and felids, in that it is minimal once primates know where the snake is and can keep it in sight. Indeed, at times the monkeys in our study appeared more agitated after they saw the snake covered up. On several occasions they placed their heads on the ground in attempts to peer under the cloth after the snake model had been re-covered. Fruitful research for the future might explore cognitive abilities involved in snake monitoring.

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