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Rhesus Macaques (*Macaca mulatta*) Use Posture to Assess Level of Threat From Snakes

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Abstract

Once prey animals have detected predators, they must make decisions about how to respond based on a cost-benefit analysis of their risk level. The threat sensitivity hypothesis predicts that prey animals match their response to the level of risk, with high-risk predator encounters eliciting stronger evasive responses than low-risk encounters. Primates are known prey of snakes, yet they vary their responses toward snakes. We predicted that primates match their response to the threat level from snakes by assessing posture, with striking postures indicating greater risk than coiled postures and coiled postures indicating greater risk than extended sinusoidal postures. We tested this prediction in a series of experimental trials in which captive rhesus macaques (*Macaca mulatta*) were exposed to snake models in those postures. Results supported the predictions: macaques responded more strongly to a snake model in a striking posture than in a coiled posture and more to a snake model in a coiled posture than to an extended sinusoidal snake model. We also examined responses of macaques to a partially exposed snake model to mimic the condition of incomplete information, as snakes are often occluded by vegetation. The occluded snake model evoked a response comparable to that of the striking snake. These findings support the threat sensitivity hypothesis. Rhesus macaques use the posture of snakes as a cue in threat assessment, responding more intensely as threat increases, and they also behave as if risk is elevated when their information about snakes is incomplete.

Introduction

When prey animals detect their predators, they must make decisions about how to respond. Among their choices are fleeing, approaching to mob or harass the predator, or simply monitoring it from a distance (Curio 1978; Caro 2005). The threat sensitivity hypothesis predicts that prey should match their response to their predation risk, with high-risk predator encounters eliciting stronger evasive responses than low-risk encounters (Helfman 1989). Prey animals may assess their level of risk based on a variety of factors, such as distance to refuge, their ability to defend themselves, and cues from the predators themselves (Stankowich & Blumstein 2005; Stankowich & Coss 2006).

Cues from predators that prey may use in risk assessment include size, speed, style of the predator's approach, and the predator's body condition (Stankowich & Blumstein 2005). For example, California ground squirrels (*Spermophilus beecheyi*) aggressively bite and attack the heads of smaller snake models, but more cautiously attack the tails of larger snake models (Mitrovich & Cotroneo 2006). Striped plateau lizards (*Sceloporus virgatus*) and Yarrow's spiny lizards (*S. jarrovii*) are more likely to flee from large animal models than from small models (Cooper & Stankowich 2010). Models of flying sparrow hawks (*Accipiter nisus*) elicit greater flight distances, increased vigilance, and decreased feeding in red knots (*Calidris canutus*) compared with perching models (Mathot et al. 2009). Columbian black-tailed deer (*Odocoileus hemionus* *columbianus*) flee at greater distances and show longer escape bouts when approached by humans using faster, more direct movement (Stankowich & Coss 2006, 2007). Captive cotton-top tamarins (*Saguinus oedipus*) alarm call more to moving animals (predatory snakes and non-predatory rats) than to live but non-moving snakes (Hayes and Snowdon 1990). Kangaroo rats (*Dipodomys deserti* and *D. ingens*) harass live, moving snakes more than static snake models (Randall & Boltas King 2001). These latter two examples suggest that when predators hunt using ambush methods involving concealment and surprise, as snakes often do, movement may be key to their detection or assessment of increased threat.

Alternative cues for assessing risk from ambush predators, such as snakes, include body temperature and posture. By provoking Pacific rattlesnakes (*Crotalus viridis oreganus*) to rattle their tails, California ground squirrels gain information about the temperature of snakes and thus the likelihood of attack through the rate, amplitude, and latency to rattle (Rowe & Owings 1996). Snakes in striking pose present an immediate threat and snakes in coiled posture present a less immediate threat than striking snakes, but more than snakes in a sinusoidal posture (Arnold & Bennett 1984; Greene 1988). California ground squirrels approach snakes in a sinusoidal posture more closely than snakes in a coiled posture (Coss & Biardi 1997), suggesting that they perceive the coiled posture as riskier. Similarly, human children detect snakes in striking pose significantly faster than snakes in resting pose when both are presented against a background of flowers (Masataka et al. 2010).

Here, we examine the responses of rhesus macaques (*Macaca mulatta*) to snake models in different postures. Rhesus macaques are widely distributed from western India to eastern China to northern Vietnam (Fooden 1982; Abegg & Thierry 2002). They coexist with a wide range of deadly snakes, including pythons (*Python* spp.), cobras (*Naja* spp.), and kraits (*Bungarus* spp.) (Greene 1997). Strong reactions by rhesus macaques toward live and model snakes in captivity are well documented (Mineka et al. 1980; Cook & Mineka 1989; Amaral 2002; Etting et al. 2014). We tested specifically whether rhesus macaques are able to use snake posture to assess level of threat by presenting captive, group-housed macaques with models of a striking snake, a coiled snake, and a sinusoidal snake. We predicted that they would respond more strongly to the striking snake than to the coiled snake, and more strongly to the coiled snake than to the extended, sinusoidal snakes. We also compared their responses to snakes in these postures to a partially exposed snake. The addition of the partially exposed snake presents a scenario that is common in nature, when snakes are occluded by vegetation. In such cases, cues from the snake's posture incompletely signal its intent at best. We wanted to understand how incomplete information affects the primates' perceived level of threat.

Methods

Study Animals and Site

We tested rhesus macaques in twelve groups ranging in size from 55 to 179 individuals that were housed in 0.2-ha enclosures at the California National Primate Research Center (CNPRC), Davis, CA. All enclosures contain A-frame houses, hanging plastic barrels, perches, and swings enclosures but vary in ground substrate, ranging from predominantly gravel/dirt to primarily grass. The enclosures are constructed with chain-link fencing, which does not provide a visual barrier for the macaques or a physical barrier to native snakes, as live gopher snakes (*Pituophis catenifer*) have been observed in and around the enclosures (Isbell 2009). Because snakes do occur in the area, the monkeys are assumed to have had some exposure to snakes.

Procedure

We tested the monkeys using models of snakes under four different snake-threat conditions: a striking cottonmouth, a coiled copperhead, a sinusoidal copperhead, and a partially exposed cottonmouth (a length of approx. 15 cm) (WASCO Wildlife Artist Supply, Monroe, GA; Fig. 1). We controlled for snake body size by choosing similarly sized snake models. The snake models ranged in length from 91 to 94 cm fully extended. All models were painted the same color, a mix of olive green and brown acrylic craft paint and covered with a clear coat of paint. The interior of the striking snake model's mouth was painted pale pink, and the eyes of all models were painted black. We did not include a non-snake control because previous research has shown that rhesus macaques do not show heightened interest to non-snake stimuli (Etting et al. 2014).

The snake models were presented 1.5 m from the fence as previous research has shown that rhesus macaques are clearly able to recognize snakes from this distance (Etting et al. 2014). Prior to the start of each trial, a fully covered snake model was placed at 1.5 m from the enclosure fence by SFE. Each experi-

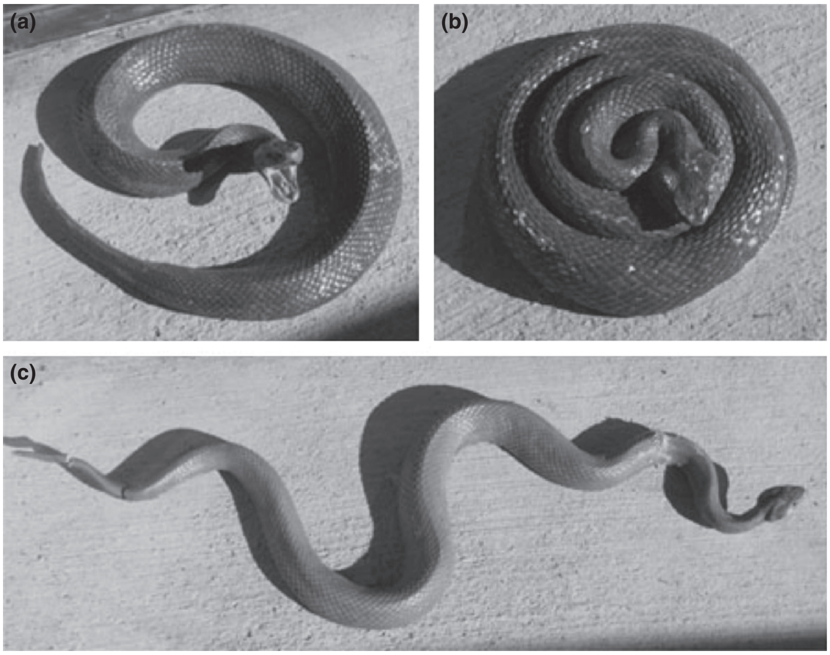

Fig. 1: Snake models used: (a) Striking snake model (also used for partially exposed snake condition), (b) Coiled snake model, and (c) Sinusoidal snake model.

mental trial consisted of a 2-min baseline period during which the snake model was covered by a tan-colored cloth (approx. 70 × 100 cm) that was attached to monofilament (approx. 4.5 m), followed by a 4-min experimental period during which the models were fully or partially exposed by pulling on the monofilament. In the partially exposed condition, the tan cloth was pulled back just enough to reveal an approx. 15 cm length of the body of the snake model. In this experimental condition, the head and tail of the snake model remained covered. A RICOH CX1 digital camera was used to take photographs at 30-s intervals throughout each 6-min trial. The photographs captured a 9 × 2.5 m area with the snake at the bottom center of the frame. From the photographs, the following postures of all macaques in the viewing area were scored: sitting/lying, quadrupedal, bipedal, and fence-clinging. Sitting/lying involved having the posterior or torso touching the ground. Quadrupedal involved having both feet and both hands on the ground. Bipedal involved having both feet on the ground, while the torso was elevated and the forelimbs were raised off the ground. Fence-clinging involved both feet and both hands grasping the fence. Bipedal and fence-clinging were considered active snake-monitoring positions indicating greater levels of interest in the model than sitting/lying and quadrupedal because they involved changes in posture or increased activity levels from the more common sitting/lying and quadrupedal positions, while the monkeys directed their attention to the model.

The order of presentation for the four snakes was systematically randomized for the 12 groups such that each was presented with the snake models in a different order. Each snake model was presented once per group. Trials were performed no more than once every 2 weeks for each group, and the location of presentation around the perimeter of the enclosure varied. These precautions were taken to minimize risk of habituation. In total, 48 trials were conducted.

This experimental protocol received IACUC approval from the University of California, Davis (no. 13193).

Data Analysis

Our goal was to determine whether or not variation in the number of animals in an active-monitoring position (bipedal and fence-clinging) was meaningfully associated with the snake's posture. Over repeated observations within a trial, these numbers may be serially correlated (as animals may remain in the posture for longer than a 30-s interval). Thus, a time series model was needed that incorporates dependence between successive counts. We used a moving-average model for count time series—one of a family of generalized auto regressive moving-average models described by Davis et al. (2003). Moving-average models account for serial correlation by involving residuals of past observations (differences between observed and predicted counts at times *t*-1, *t*-2, ...) in the prediction of the count at time *t*. Unlike in a Markov chain, a given data point in a moving-average model is dependent on the whole past series of data points within a trial. This is achieved by compounding the effects of each observation, with more recent observations typically having a greater influence on the current state than observations occurring farther back in the series.

Although accounting for serial correlation is essential, our basic questions were about the effects of snake posture on macaque positional behavior. These effects were included in the model along with group-specific effects and moving-average terms as follows: Suppose $y(t)$ is the number of animals performing the behavior of interest at time t of a given trial. We assume that $y(t)$ has a negative binomial distribution with mean μ_t and dispersion parameter alpha (the negative binomial distribution accommodates a larger variance to mean ratio than expected for Poisson counts). The model for the mean then has the form

$$\log(\mu_t) = \text{Treatment}_t + \text{Group} + Z_t$$

where Treatment_t is the experimental condition in effect at time t (i.e., baseline/covered condition or a condition in which any one of the four snake models is exposed), Group is a group-specific effect, and Z_t incorporates serial correlation effects. Specifically,

$$Z_t = \theta_1 e_{t-1} + \theta_2 e_{t-2} + \ldots + \theta_q e_{t-q}$$

where the θ_s are coefficients of the moving-average process and e_{t-i} is a normalized residual for the ith observation before time t. Adding in the group-specific effect allows us to simultaneously control for variation in both group size and baseline group arousal level by comparing each group's experimental treatment to its baseline.

To determine whether rhesus macaques respond to postural cues of snakes, we contrasted the coefficients produced by the model for bipedal and fence-clinging in the following conditions: striking, coiled, sinusoidal, partially exposed, and covered, the latter serving as the baseline comparison for the experimental conditions. Specifically, we predicted that the striking snake would evoke a greater response than the coiled snake and that the coiled snake would evoke a greater response than the sinusoidal snake. These contrasts were analyzed using a one-tailed test. Because we were unsure how a partially exposed snake would fit into this ranking, responses toward the partially exposed snake were compared with the other snake models using a two-tailed test. Thus, we analyzed the following six contrasts: (1) striking vs. coiled, (2) coiled vs. sinusoidal, (3) sinusoidal vs. covered, (4) partially exposed vs. striking, (5) partially exposed vs. coiled, and (6) partially exposed vs. sinusoidal. Separate analyses were performed for bipedal and fence-clinging.

The data were analyzed using R-language routines (version 2.12.2, The R Foundation for Statistical Computing, http://www.r-project.org) developed by William Dunsmuir, described in Davis et al. (2003) and in a University of New South Wales technical report available on request (Dunsmuir 2010). We made straightforward modifications to the routines to accommodate the structure of our dataset, which consists of four independent trials for each of 12 groups.

Results

We selected a lag-2 moving-average model for bipedal and a lag-4 model for fence-clinging. Thus the expression for $Z(t)$ included residuals $e(t\text{-}1)$, $e(t\text{-}2)$ for bipedal and $e(t\text{-}1)$, ... $e(t\text{-}4)$ for fence-clinging. The coefficients of additional lags were not significant at level 0.05, suggesting that the selected models adequately accounted for serial correlation between successive counts. The shorter lag for bipedal is reasonable from a biomechanical perspective, as transitions into and out of this posture by individuals are likely to occur more quickly than for fence-clinging. The fit of the models to the observations was quite adequate, based on examination of the residual plots (not shown).

The coefficients produced by the models showed trends consistent with our experimental predictions for both bipedal and fence-clinging conditions. These coefficients, and their standard errors, are shown in Fig. 2.

Directionality of the contrasts between coefficients, as indicated by positive or negative contrast values, for the number of animals standing bipedally indicates that the rhesus macaques were bipedal more for the striking snake than the coiled snake condition, more for the coiled snake than for the sinusoidal snake, and more for the partially exposed snake than the striking snake condition. The magnitudes of the contrasts indicate very little difference in response among the partially exposed, striking, and coiled snake conditions (Fig. 2a). Of these contrasts, the coiled vs. sinusoidal contrast ($p = 0.05$) was statistically significant. The contrast from this comparison indicates the average number of animals bipedal was $e^{0.44} = 1.6$ times greater in the coiled condition relative to the sinusoidal condition (Table 1).

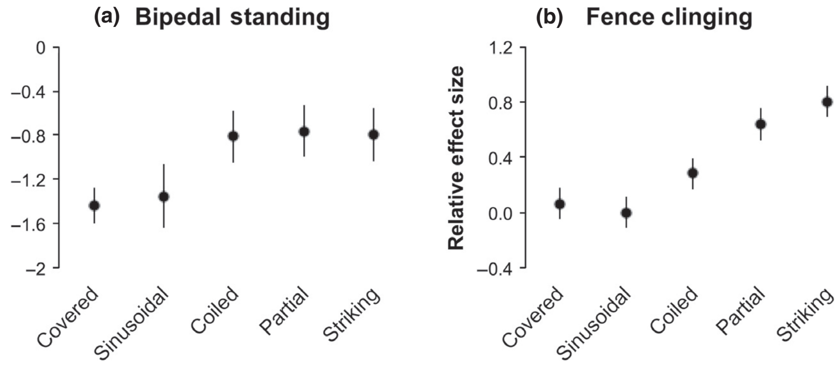

Fig. 2: Estimates and one-standard-error intervals of relative effect sizes ['Treatments' in the equation for log (μ_t)] in models for (a) standing bipedally and (b) fence clinging. *X*-axis shows experimental conditions: Covered snake model, Sinusoidal snake model, Coiled snake model, Partially exposed snake model, and Striking snake model.

Table 1: Contrast coefficients, standard errors, and uncorrected p-values for the six contrasted conditions. Individually significant p-values are in bold

	Fence clinging			Bipedal standing		
Contrast	Coefficient	SE	p-value	Coefficient	SE	p-value
Sinusoidal vs. covered	0.02	0.20	0.45	0.01	0.24	0.34
Coiled vs. sinusoidal	0.26	0.24	0.14	0.44	0.27	**0.05**
Striking vs. coiled	0.47	0.22	**0.02**	−0.09	0.25	0.63
Partial vs. sinusoidal	0.65	0.23	**0.01**	0.44	0.27	0.11
Partial vs. coiled	0.39	0.22	0.08	−0.01	0.25	0.98
Partial vs. striking	−0.08	0.21	0.71	0.08	0.25	0.76

The signs of the contrasts for the number of animals fence-clinging during presentation of each of the snake models indicate that more animals were fence-clinging during the striking snake condition than the partially exposed and coiled snake conditions, more in the partially exposed snake condition than the coiled snake condition, and more in the coiled snake condition than the sinusoidal snake condition (Fig. 2b). Of these contrasts, the striking vs. coiled ($p = 0.02$) and partially exposed vs. sinusoidal contrasts ($p = 0.005$) were statistically significant (Table 1). The coefficients of these contrasts indicate that the average number of animals clinging to the fence when the snake was in striking pose was $e^{0.47} = 1.6$ times greater than the average number of animals fence-clinging when the snake was in coiled pose, and the average number of animals fence-clinging when the snake was partially exposed was $e^{0.65} = 1.9$ times greater than the average number of animals fence-clinging when the snake was in sinusoidal pose. Mean total animals in the viewing area and mean proportions of responding animals standing bipedally and fence-clinging for each of the four experimental conditions are provided for each group in the online supplementary materials (Table S1).

Discussion

The experiment presented here was designed to test whether rhesus macaques use postural cues of snakes to assess their threat level. We presented captive monkeys with snake models in striking pose, coiled pose, and sinusoidal pose, each of which represent different levels of offensive/defensive behavior in snakes. Snakes that are about to strike are more dangerous than those in coiled pose, and sinusoidal snakes are the least dangerous of the three because their ability to strike from this position is more constrained (Arnold & Bennett 1984; Greene 1988). We also included a partially exposed snake as an additional condition to obscure postural cues. We evaluated the monkey responses bipedal and fence-clinging because they reflect greater interest or fear than sitting/lying and quadrupedal, and we found that the monkeys increased fence-clinging in response to the striking snake compared with the coiled snake and in response to the partially exposed snake compared with the sinusoidal snake. We also found a consistent trend of more animals standing bipedally and fence-clinging in the presence of the striking and partially exposed snakes than the coiled snake, and fewer responding in those ways to the sinusoidal snake. Our results indicate that rhesus macaques are able to use snake posture as a cue in evaluating the threat level presented by snakes. Our results thus also support the threat sensitivity hypothesis, which posits that animals can recognize different levels of threat from predators and will match their responses accordingly (Helfman 1989).

Much of the literature on risk assessment by prey is based on flight responses toward pursuit or coursing predators (Stankowich & Blumstein 2005), but different strategies may be employed in response to ambush predators. Ambush hunters are far less dangerous once they are detected and can be monitored, and monitoring predators provides further information for prey through the predator's behavior. The research presented here shows that macaques are sensitive to the level of threat presented by snakes via the snake's posture. Posture reveals important information about the snake's current state, and by using this information, prey animals can adjust their behavior to reduce both the risk of predation and the potential costs of over-reacting when the risk is minimal.

Ample evidence indicates that humans and other primates are able to detect snakes faster than other, more innocuous objects (Öhman et al. 2001; Shibasaki & Kawai 2009; Le et al. 2013). In humans, the coiled shape of snakes has been implicated as a strong cue for fast detection of snakes. Both adults and children detect coiled objects, including snakes, faster than they detect flowers, but they do not detect non-coiled snakes faster than flowers (LoBue & DeLoache 2011). This is consistent with our findings in that coiled snakes present a greater threat than non-coiled snakes. In our case, however, coiling was not necessary to elicit a strong reaction; the monkeys responded even when the snake's body was only partially exposed and gently curving at most. The strong reaction of rhesus macaques toward the partially exposed snake suggests that they perceive it to be as threatening as the striking snake, perhaps because their information about the snake is incomplete. As snakes primarily rely on ambush hunting, they are expected to pose a lesser threat once they are detected. Furthermore, snakes, unlike pursuit or cursorial predators, do not move over great distances and may be easily monitored without significant cost to baseline activities such as feeding, grooming (SF Etting & LA Isbell, unpub. data). If the intention of the snake (e.g. on the offensive or not) can be inferred through monitoring its movements, this would also provide potential prey with information about how dangerous the snake is to them at present. The importance of being able to monitor snakes is supported by observations that in the presence of covered model snakes, rhesus macaques would sometimes lie down on the ground and attempt to peer under the cloth to see the snake (Etting et al. 2014).

Another cue that could be used to detect snakes quickly, especially those that are only partially visible, is their characteristic pattern of scales, otherwise uncommon in nature. Capuchins react more strongly to coiled, colored snake models with scales than those of coiled, white snake models without scales (Meno et al. 2013). Both rhesus macaques and titi monkeys (*Callicebus moloch*) respond more strongly to colored elongated objects with scale patterns than similarly colored elongated objects without scales (SF Etting & LA Isbell, unpub. data). Indeed, this may be facilitated by neurons in the visual systems of primates that are particularly responsive to diamond-shaped, plaid, or checkerboard stimuli (Okusa et al. 2000; Casanova et al. 2001; Kastner et al. 2004). Research to investigate the possibility that primates cue in on snakes by their scales, specifically, would be valuable. Such an ability might help to explain why even harmless snakes can elicit a strong response. Humans often do not distinguish between dangerous and harmless snakes. In Santa Rosa National Park, Costa Rica, capuchin monkeys, also known for their intelligence, respond to harmless Indigo snakes (*Drymarchon corais*) with mobbing, vigilance, and alarm calls (Rose et al. 2003).

Unusually, wild bonnet macaques (*M. radiata*) have been argued to distinguish between constricting and venomous snakes (Ramakrishnan et al. 2005). In a series of field experiments, a cobra model in a raised posture displaying eyespots elicited a startle response from the macaques, whereas constrictor models (a python in an extended posture and a rat snake in a coiled posture) evoked bipedal standing and monitoring. In addition, alarm calls were given toward the python but not the other snake models. Our findings that macaques are sensitive to snake posture suggest, however, that posture may have confounded their results. On the other hand, Texas horned lizards (*Phrynosoma cornutum*) are able to distinguish venomous snakes that ambush from non-venomous pursuit snakes and respond in different ways as the snakes approach (Sherbrooke 2008). More research is needed to distinguish between subjugation style and posture of snakes as an assessment of risk.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: For each group, mean total animals in the viewing area (responding animals) and mean proportions of responding animals standing bipedally and fence-clinging for each of the four experimental conditions.