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Predatory Attacks to the Head vs. Body Modify Behavioral Responses of Garter Snakes

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Abstract

An animal's response to predatory attack may depend upon which part of its body is the focus of that attack, because of differential vulnerability to injury. Many avian and mammalian predators direct attacks preferentially toward the prey's head, so simulated attacks that do not have this focus may elicit non-natural responses. We 'pecked' 152 free-ranging adult male garter snakes (*Thamnophis sirtalis parietalis*) in Manitoba either on the head or the midbody, and recorded their responses. The snakes' antipredator tactics were affected not only by body size (larger snakes performed threat displays more often) and body temperature (hotter snakes were more likely to flee), but also by location of the attack. Pecks to the head generally resulted in snakes coiling and hiding their heads, often simultaneously elevating and wriggling their tails in an apparent distraction display. In contrast, pecks to the midbody stimulated either escape responses, or (in snakes that did not flee) open-mouthed threat displays. More generally, antipredator tactics may respond in flexible ways to details of the predator–prey encounter (including attributes of the habitat as well as the morphology and behavior of both participants) and hence, experimental studies need to carefully simulate such details. The part of the body under attack may be an important factor in this respect.

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Introduction

Predation is a major cause of death and injury in natural populations of many animal species, and Darwinian theory thus suggests that there should be strong selection on antipredator tactics (e.g. Vermeij 1982; Lima & Dill 1990; Magnhagen 1991; Lima 1998). Empirical studies show that there is indeed a considerable diversity in antipredator behaviors, and that a single animal is often

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capable of manifesting several alternative responses to attack by a predator. Thus, there is a strong facultative component in antipredator responses, with the prey animal's behavior presumably optimized by natural selection such as to minimize the probability of mortality or serious injury resulting from the attack (e.g. Curio 1976; Greene 1988).

Antipredator tactics depend upon a range of factors that influence the relative success of different potential responses. For example, the optimal antipredator response may depend upon attributes of the predator (such as its species and size: Lopez & Martin 2001; Persons & Rypstra 2001; Van Buskirk 2001; Bealor & Krekorian 2002), of the habitat where the encounter occurs (such as distance to refugia: Duvall et al. 1990; Smith 1997; Labra & Leonard 1999), the social context of the encounter (such as presence of offspring: Clutton-Brock 1991) or of the prey animal itself (such as age, body size, sex, and capacity to flee or retaliate: Keogh & DeSerto 1994; Passek & Gillingham 1997; Fox et al. 1998; Brown et al. 2001; Hanson & Coss 2001; Mori & Burghardt 2001; Williams et al. 2001; Head et al. 2002). Another potentially important factor that has attracted less scientific attention is the exact form of attack, and especially the specific part of the body that is the focus of the predator's attentions (Brodie 1977; Ducey et al. 1993). Some parts of the body are much more vulnerable than others, with the head (especially the eyes) often the most vulnerable part of the body (Curio 1976; Smith 1976). Presumably for this reason, some prey taxa display complex behaviors that function to distract the predator's attack away from the (vulnerable) head to the (less vulnerable) tail or midbody (Arnold & Bennett 1984; Greene 1988). Although this phenomenon has been described in several species, there are few quantitative data on the way in which antipredator responses are influenced by the bodily focus of predator attack, nor on the ways in which this factor might interact with other influences on antipredator responses (above).

Small, non-venomous garter snakes (genus *Thamnophis*) are widespread in North America, are preyed upon by a diverse array of birds, mammals and reptiles, and display a complex repertoire of antipredator responses (Arnold & Bennett 1984; Herzog & Bailey 1987; Brodie 1989; Herzog et al. 1989, 1992; Herzog & Schwarz 1990; Rossman et al. 1996; Passek & Gillingham 1997; Shine et al. 2000, 2003). These studies have shown that the responses of garter snakes are influenced by a variety of intrinsic and extrinsic factors. For example, whether a snake flees from the attack, relies on crypsis, or mounts some kind of defense (display or retaliation) depends upon multiple aspects of its phenotype (e.g. age, body size, sex, and color) as well as its physiological state (fatigue, recent feeding, body temperature, reproductive condition). Plausibly, the focus of attack might also influence antipredator responses. In particular, many avian and mammalian predators direct their attacks to the head of a prey item (e.g. Curio 1976; Smith 1976); this may be especially true for attacks on snakes (Jackson 1979). Do garter snakes respond differently depending on the benefits and costs of the responses (threat, attack, flee, protective hiding, distraction display, and crypsis) as a function of the site of attack? For example, if the benefit of protecting the head is more than the cost of remaining stationary and risking further injury to the body, then the adaptive response to an attack on the head would be to adopt a defensive head-hide posture. Similarly, if the opposite were true (the cost of injury to the body outweighed any benefit of protecting the head), the adaptive response to an attack on the head would be to adopt an alternate strategy, such as flee.

The only quantitative examination of this possibility was a study by Arnold & Bennett (1984), using captive-born neonatal *Thamnophis radix* that they exercised to exhaustion prior to simulating predator attacks in various ways. Snakes tapped on the head rather than the tail adopted more defensive postures (including forming a compact ball with the head hidden) whereas tail-tapping generally evoked more offensive tactics (striking etc.). However, it is not clear how to extrapolate these results to the field situation. First, the neonatal snakes were exhausted and thus, unable to use their primary antipredator tactic (escape). Secondly, captivity can modify antipredator responses (Fitch 1965; Greene 1988), as can many other variables that differ between the laboratory and the field (see above). Thirdly, the experimental design of Arnold & Bennett (1984) confounded testing order with stimulus type. Thus, we conducted an experimental study on free-ranging snakes to evaluate the influence of attacks directed to the head rather than the body.

Methods

Study Species and Area

Red-sided garter snakes (*T. sirtalis parietalis*) are small (to 1 m total length) snakes that extend northwards into severely cold regions of central Canada (Rossman et al. 1996). In south-central Manitoba, Canada, these animals overwinter in large communal dens containing many thousands of snakes (Gregory 1974; Gregory & Stewart 1975; Shine & Mason 2004). Males remain close to the den for about 2 wk, intercepting and courting newly emerged females (Shine et al. 2001a), and the snakes are subject to high rates of predation by crows at this time (*Corvus brachyrhynchos*: Shine et al. 2001b). Inspection of dead and dying snakes in this area suggested that approximately one-third of the animals had been pecked in the head prior to having their livers removed by crows; in the remaining animals we could find no evidence of head injuries (R. Shine, unpubl. data). However, it is difficult to detect head injuries in dead snakes, so we set out plasticine models of garter snakes in the field and recorded locations of crow pecks. Three of the nine models bore evidence of crow attack, and all of these attacks were to the head. Previous studies on the same population have shown that Manitoba garter snakes display complex antipredator repertoires, influenced by sex, body size, reproductive state and body temperature (Shine et al. 2000, 2003). This work also showed that responses by the snakes to being ‘pecked’ by a human finger were very similar to those after being ‘pecked’ by a realistic model of a crow (Shine et al. 2000), greatly facilitating experimental study. In previous studies of this population, all snakes were ‘pecked’ in the midbody.

Experimental Design

We scored antipredator responses of snakes from 12 to 16 May 2002 during the spring mating period, at a communal den containing approx. 10 000 garter snakes (data from a census conducted in May 2003), 1.5 km N of the town of Inwood, 250 m E of Highway 17 in central southern Manitoba (50°31.58′N, 97°29.71′W). To remove potentially confounding variables, we conducted all trials between 09:00 and 10:00 h, restricted our attention to adult male snakes, and conducted all trials in the same open area (a gravel road bisecting the main emergence areas within the den). The weather was fine and sunny throughout this study. Thus, all snakes tested were active on an open area 2–3 m from the nearest cover. There were consistently 50–100 snakes moving through this area at any one time. We selected a snake that was crossing this open area approx. 3 m from us, and then one of us (TL) approached it directly and tapped it with a finger 10 times (taking approx. 4 s) on either the top of the head or dorsally on the midbody. We then scored the animal's response over the ensuing 30 s, with respect to whether it attempted to flee, or remained immobile, or engaged in an open-mouth threat display ('gape'), or hid its head beneath the body coils, and/or elevated and wriggled its tail-tip (see Fig. 1). Every snake was tapped 10 times, even if it responded before the completion of the 10 taps. The snake was then picked up and its cloacal temperature taken with a quick-registering electronic thermometer (Comark KM45: Comark Ltd., Hertfordshire, UK), and its snout-vent length (SVL) was recorded before release. Order of testing (tapping on head vs. body) was alternated. The large number of snakes active at the den means that the probability of retesting any single individual was trivially small.

Data were analyzed using Statview 5.0 and JMP 5.01 (SAS Institute 1998, 2002). Contingency table tests were conducted to examine patterns of association among responses, and logistic regression was used to identify influences on specific responses. One-factor ANOVA was used to compare temperatures and body sizes among snakes in different response categories. All test results reported are two-tailed.

Results

We obtained data on 152 active snakes, with SVLs from 26.2 to 56.7 cm and body temperatures from 2.7 to 29.2°C. Of these, only two snakes showed no overt response (i.e. relied on crypsis, remaining immobile) and another 90 fled from our attack. The remaining 60 animals did not flee, but instead either exhibited an open-mouth threat display ('gape', N = 16) or hid their heads beneath body coils ('hide head', N = 44). Within this latter group, eight animals elevated the tail-tip and twitched it slowly in the air ('tail-twitch').

Contingency-table analyses on these data show significantly non-random associations among the various behaviors. In particular, snakes that fled never displayed or hid their heads either prior to or during their attempt to escape whereas these behaviors were common from snakes that did not flee (comparing fleeing vs. non-fleeing snakes, for gape, $\chi^2_1 = 87.00$, 1 df, $p < 0.0001$; for

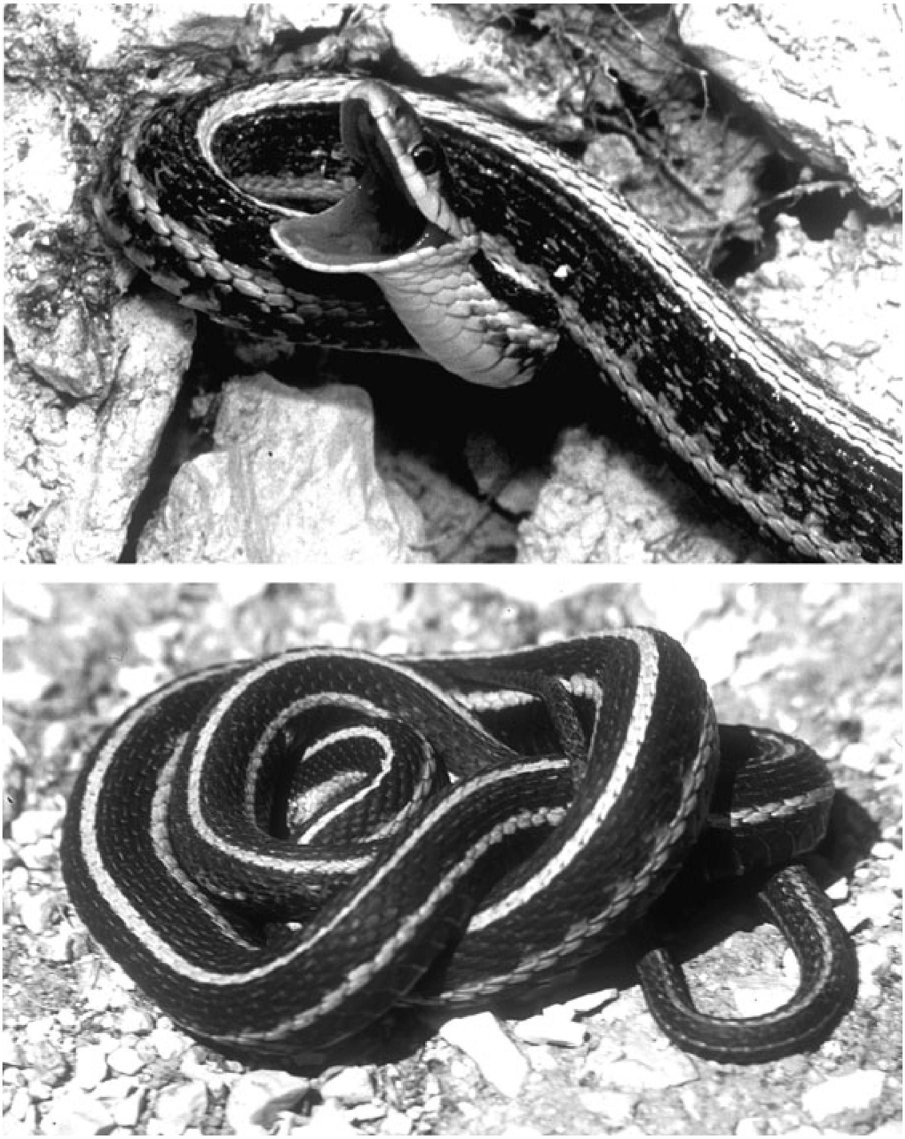

Fig. 1: Antipredator behavior of garter snakes (*Thamnophis sirtalis*) at a communal den in Manitoba. Upper photograph shows a threat display ('gape') and lower photograph shows a snake coiling its body, hiding its head, and elevating and wriggling its tail ('head-hide' and 'tail-twitch')

head-hide, $\chi^2_1 = 122.93$, $p < 0.0001$). Although tail-twitching was seen only in head-hiding rather than gaping snakes, low sample sizes meant that this association did not attain statistical significance ($\chi^2_1 = 1.97$, $p = 0.16$).

We conducted multiple logistic regressions for each of three dependent variables (for all snakes, whether or not the animal fled from us; for stationary snakes, whether they gaped or hid their heads; and for head-hiding snakes, whether or not they elevated and twitched their tailtips). In each case, the independent variables entered into the analysis were the snake's SVL and body temperature, and whether it was tapped on the head or midbody. These regressions showed that a snake was more likely to flee from our approach if it was hotter (likelihood ratio test, $\chi^2_2 = 65.56$, $p < 0.0001$; see Fig. 2) and if it was tapped on the midbody rather than the head ($\chi^2_2 = 34.04$, $p < 0.0001$; see Fig. 3).

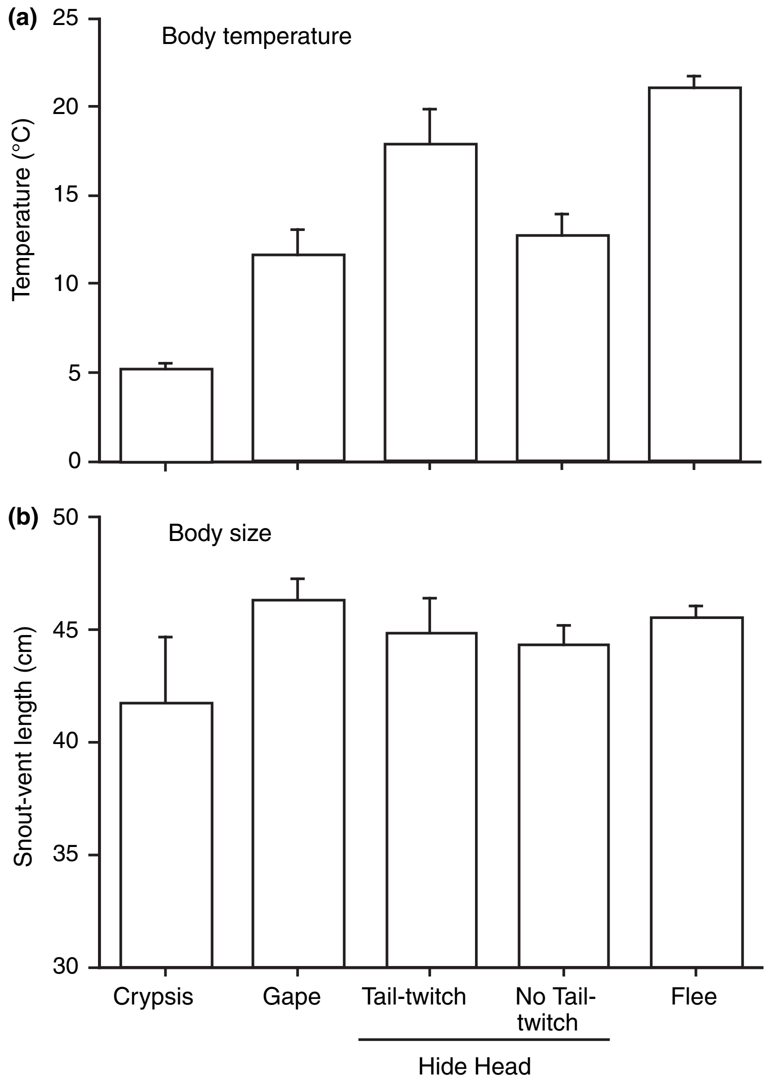

Fig. 2: $\bar{x} \pm$ SE body (a) temperatures and (b) snout-vent lengths of garter snakes (*Thamnophis sirtalis*) exhibiting different antipredator responses. Data are combined for snakes 'pecked' either on the head or midbody. Sample sizes (left to right) are 2, 16, 8, 35, and 90 snakes

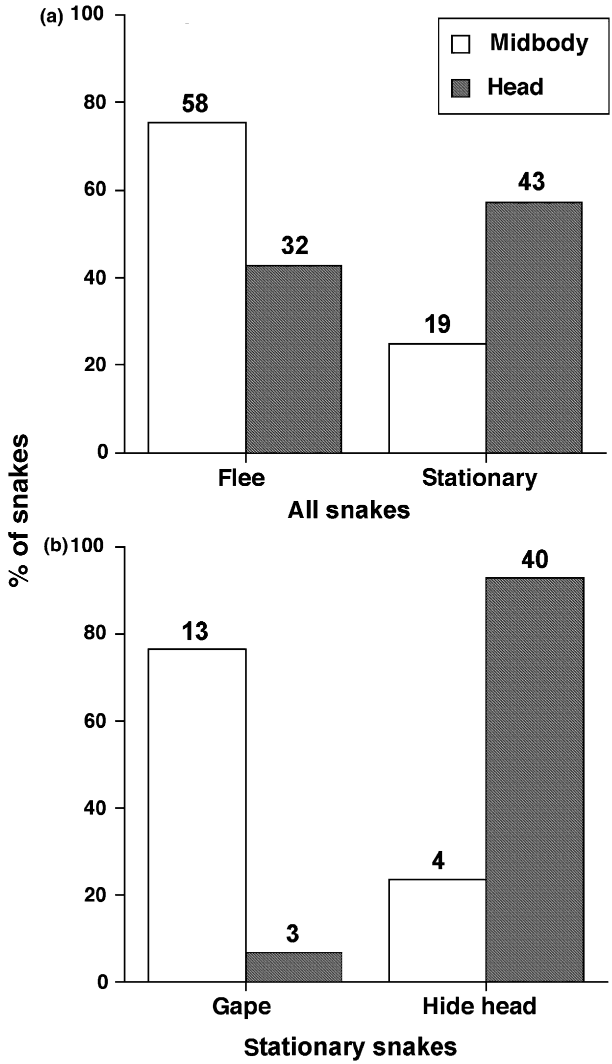

Fig. 3: Percentages of free-ranging garter snakes (*Thamnophis sirtalis*) exhibiting alternative responses to being 'pecked' on either the head or midbody. The graph shows different subsets of data. (a) The percentages of snakes (N = 152 snakes total) that fled or remained stationary. (b) The percentages of animals exhibiting gape or hide-head responses, based only on the 60 animals that did not flee (because no animals that fled showed either gaping or head-hiding). Numbers above each bar represent individual n values

The animal's body size did not affect this response ($\chi^2_2 = 1.69$, $p = 0.43$; see Fig. 2). There was no significant interaction between these factors ($p > 0.35$). Snakes that did not flee were more likely to gape (rather than hide their head) if they were tapped on the midbody not the head ($\chi^2_1 = 27.13$, $p < 0.0001$; see Fig. 3), and if they were relatively large ($\chi^2_1 = 3.85$, $p < 0.05$; Fig. 2). The animal's body temperature did not affect this response ($\chi^2_1 = 0.59$, $p = 0.44$). There was no significant interaction between these factors ($p > 0.23$). Lastly, snakes that hid their heads were more likely to elevate and twitch their tails if they were warmer ($\chi^2_1 = 4.77$, $p < 0.03$), but this probability was not influenced by either their body size ($\chi^2_1 = 0.67$, $p = 0.41$) or where they had been tapped ($\chi^2_1 = 0.55$, $p = 0.46$; interactions, $p > 0.96$). We note, however, that low sample sizes in these latter tests make them relatively weak.

Discussion

Our results are interesting from two perspectives: what they tell us about antipredator tactics of garter snakes, and in the cautionary tale they provide for experimental studies of antipredator behavior. Below, we address each of these issues.

Our first main conclusion is that the behavioral responses of garter snakes to a simulated attack are even more complex than suggested by previous studies. The specific part of the body under attack (head vs. body) significantly influenced the snakes' responses, often to a substantial degree (Fig. 3). For example, >75% of snakes tapped at the midbody fled from us, and <25% of the remaining (stationary) animals hid their heads (Fig. 3). In contrast, <45% of snakes tapped on the head resorted to flight, and >90% of the remainder hid their heads beneath their coils (Fig. 3). Thus, predicting the way in which a snake from this population will respond to a natural predation event requires information not only on the habitat and the snake's morphology and physiological state (Shine et al. 2000, 2003), but also on the predator's behavior as well.

Such data are difficult to gather as the crows in Manitoba are very wary of people, and thus it is difficult to see predation directly. However, we and our collaborators have watched crow attacks four times at a close enough range to see detail. In each of these cases the crow hit the snake multiple times (more than 10, on two occasions), with some hits to the body and some to the head. We suspect that snakes that do not receive an effective peck to the head often escape, and hence the sample of dead snakes is biased toward those that receive head-shots.

The influences on antipredator tactics detected by our study are generally consistent with those reported by earlier work. These snakes seem to employ antipredator tactics suited to the conditions under which the encounter occurs. Thus, several authors have reported that garter snakes too cold for rapid locomotion rely on crypsis or bluff rather than attempting to escape (Fitch 1965; Heckrotte 1967; Arnold & Bennett 1984; Brodie & Russell 1999; Shine et al. 2000, 2003), the same pattern as in the present study. Similarly, offensive displays (ranging from bluff to biting) are likely to be more effective for larger than smaller animals, and indeed are performed more often by larger snakes (Fitch 1965; Shine et al. 2003; but see Shine et al. 2000). In the current study, larger snakes were more likely to gape.

In the same way, modifying antipredator responses based on the focus of the predator's attack makes adaptive sense. Heads (especially eyes) are the most vulnerable part of the body, and can be severely damaged by pecks from a crow-sized bird (Bonnet et al. 1999). Thus, if this benefit of shielding the head outweighs any cost of potential attack to the body, protecting the vulnerable head under coils formed by the body makes sense if the head is under direct attack, whereas escape may be the optimal response if pecks are directed to less sensitive body parts. Our second main conclusion is a cautionary tale about the methodology for experimental studies in this field. Experiments are necessary because descriptive data on natural predation events cannot enable us to tease apart complex behavioral feedbacks between predators and prey (e.g. Lima 1998). For example, a predator may change its attack strategy depending on attributes of the prey item, such as its location, behavior or body size (Curio 1976). Because these attributes also influence antipredator tactics of the prey, we might see significant correlations between such characteristics and predator attack modes (including the focus of attacks on head vs. body) even if there was no causal relationship between predator behavior and prey response. Because such correlations could obscure causal effects of predator attack tactics on prey behavior, experimental trials are needed to resolve the issue. Unfortunately, the flexibility evident in antipredator tactics means that simulated attacks that do not faithfully recreate the natural situation may engender non-natural responses. Data from the present study suggest that 'pecking' a garter snake midbody (as in previous studies on this population: Shine et al. 2000, 2003) may have stimulated responses different from those elicited by natural predators (crows), which often direct their initial attack to the snake's head rather than its body.

There is no easy solution to this problem. Clearly, we need observations (even if fragmentary) on natural predation events, so that we can incorporate as much detail as possible into our recreations of predation in experimental trials. Unfortunately, we can never mimic natural situations perfectly, especially in studies using vertebrate species as prey. Natural predators will usually strike the prey much harder, with more formidable weapons, than is ethically acceptable in experimental studies. The resulting injury may well modify prey behaviors in ways that are not elicited in simulated predation events. This does not mean that we cannot learn anything from such studies; many aspects of antipredator responses may be relatively unaffected by such details. However, it means that we should attempt to maximize the biological reality of the situations in which antipredator tactics are to be documented, and to pay special attention to the behavior of natural predators when simulating an attack.

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