

# Effects of sex, body size, temperature, and location on the antipredator tactics of free-ranging gartersnakes (*Thamnophis sirtalis*, Colubridae)

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Gartersnakes (*Thamnophis sirtalis parietalis*) in southern Manitoba are subject to intense predation (primarily by crows) during their spring breeding season. The huge numbers of snakes provide a unique opportunity to quantify behavioral traits. We simulated predator attacks by “pecking” more than 500 free-ranging snakes, to explore the determinants of snake response. Snakes responded to a human finger in the same way as they did to a more realistic stimulus (a model crow). A snake’s response to attack depended on several factors, which interacted in complex ways. The primary influences on response were body temperature (warmer snakes tended to flee, whereas colder snakes remained cryptic or flattened and/or gaped and struck) and sex (males were more likely to flee). Responses also depended on microhabitat (i.e., inside the winter den versus in adjacent grassland) and on the snake’s prior activity (e.g., courting snakes often ignored our close approach). These factors interacted in significant ways; for example, snakes outside the den were smaller and warmer than those inside, male snakes were smaller and warmer than females, and mean body temperatures were higher in larger snakes within each sex. Thus, a snake’s body size and its location affected its defensive response indirectly (via their influence on body temperature). Our results differ from those of previous studies and suggest that antipredator responses in these animals depend in a flexible and complex way upon biotic and abiotic variables. Interactions among these variables also must be considered before we can identify underlying causal processes. *Key words*: display, predation, snakes, temperature, *Thamnophis sirtalis parietalis*. [*Behav Ecol* 11:239–245 (2000)]

Predation is an important influence on survival rates for many kinds of animals, and a diverse array of morphological and behavioral traits have evolved in response to this selection pressure (e.g., Lima and Dill, 1990; Vermeij, 1982). Indeed, the interplay between prey and predator is a central theme of behavioral ecology. The ways in which potential prey items respond to a perceived threat of predation can have substantial implications not only for the vulnerability of individuals, but also for overall patterns of habitat use and demography (e.g., Lima, 1998; Sinclair and Arcese, 1995). Unfortunately, there are formidable logistical obstacles to quantifying organismal responses to predator attack for many species in their natural habitats. Not only does the prey animal’s response depend on factors such as its sex, size, locomotor ability, and habitat (e.g., Lima, 1998), but these latter factors are intercorrelated in complex ways. For example, sex differences in response to predator approach might be secondary consequences of sex differences in body size or location, rather than intrinsically gender-specific responses. To disentangle such complexities, many authors have taken the study system into the laboratory, where it is feasible to control such confounding influences. Nonetheless, much is lost in this process of simplification. If we are to understand why animals behave as they do in the field, we need to appreciate not only the ways in which multiple factors influence the organism’s response to a predator, but also the ways in which those factors interact with each other.

Snakes are ideal models to investigate these questions be-

cause they have the most elaborate antipredator mechanisms yet described among reptiles (Greene, 1988). Snakes have been used to investigate the ways in which antipredator responses are influenced by genetic factors (e.g., Brodie, 1989) as well as environmental cues (e.g., temperature and feeding: Brodie and Russell, 1999; Herzog and Bailey, 1987). For ectothermic species, body temperature may be one of the most important influences on antipredator behavior because temperature will determine the animal’s ability to detect, repel, or escape the predator. Body size is important for the same reasons, and habitat (especially proximity to a secure retreat) may also influence an animal’s response to a predatory attack (e.g., Duvall et al., 1985). Finally, sex differences in antipredator behavior are widespread in animals (e.g., Clutton-Brock, 1991; Fitch, 1999). We investigated the role of these four variables as potential determinants of the response of free-ranging gartersnakes to simulated predator attack. We also explored the relationship of these variables to each other.

The massive aggregations of red-sided gartersnakes (*Thamnophis sirtalis parietalis*) that occur in springtime in southern Manitoba, Canada, as the snakes emerge from their overwinter dens, constitute an ideal study system. This study system confers three major advantages. First, the extraordinary abundance of the snakes enabled us to obtain independent measures on a large number of animals in a short time. We could thus avoid the significant artifacts that are likely to arise if the same study animals are used more than once (because repeatabilities for antipredator behavior are typically high; Arnold and Bennett, 1984; Brodie, 1989; Brodie and Russell, 1999; Garland, 1988). Second, the snakes concentrate on courtship and dispersal at this time of year. They do not feed, and the females are not pregnant (Gregory and Stewart, 1975), thereby eliminating two sources of variation that might

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**Figure 1**  
Antipredator display by a female red-sided gartersnake, *Thamnophis sirtalis parietalis*. Note the combination of body flattening and mouth gaping.

otherwise influence antipredator tactics (Duvall et al., 1985; Herzog and Bailey, 1987). Third, both direct and indirect evidence suggests that these snakes experience strong selection for effective antipredator responses. The direct evidence comes from the high levels of predation in our study population (see below). The indirect evidence comes from intraspecific geographic variation in color patterns across the range of this species. The snakes in our study population display bright red lateral patches, unlike most other subspecies of *Thamnophis sirtalis* (Rossman et al., 1996). These blotches are normally hidden by overlapping scales and thus are evident only during antipredator displays (see Figure 1). The evolution of this conspicuous display coloration within *T. sirtalis* suggests that antipredator displays may have been a target of significant selection in this species.

## METHODS

### Study species and study area

Red-sided gartersnakes are slender, surface-active, nonvenomous natricine colubrids. In our population, adult females attain much larger sizes [mean 55–60 cm snout-vent length (SVL), 70–80 g] than do adult males (mean 45–50 cm SVL, 30–40 g). We studied this species near the northern limit of its range in Manitoba at three large communal dens within the Chatfield Community Pasture 100 km north of Winnipeg. At least 50,000 snakes overwinter in these dens every year, dispersing into the surrounding muskeg swampland during summer (Gregory, 1977; Gregory and Stewart, 1975; Mason and Crews, 1985). We studied the snakes during spring (May 1997 and 1998), at which time the snakes were in the process of emerging from the den and mating. Thus, we encountered snakes either inside the dens (rock-lined sinkholes approximately 20 m long, 3 m wide, and 2 m deep), as they emerged from underground cavities, or in the mosaic grassland–aspen woodland habitat surrounding the den. Courting and mating activity occurred primarily outside the den, probably because of low temperatures in the deeply shaded den area (see below).

The snakes were exposed to heavy predation during the course of our study. We recorded 590 predator-killed snakes at or near the dens over a 10-day period (8–17 May 1997),

mostly due to attacks by American crows (*Corvus brachyrhynchos*). The crows inflicted injuries of several kinds, usually involving removal of the snake's liver. Crow attacks occurred at all times of the day, but the temporal distribution of fresh kills indicates that predation was concentrated in the early morning and late evening, perhaps because humans were absent from the den area at those times. Crows fled at our approach, so we were not able to observe predation as it occurred. The predator-killed snakes included both males ( $n = 433$ ) and females ( $n = 157$ ), comprising a wide size range in each case (males, 30.2–55.0 cm SVL; females, 31.0–73.3 cm). Hence, all size classes of both sexes were vulnerable to predation at this time.

### Experimental techniques

Our aim was to simulate crow attack using humans rather than crows as the actual stimulus. In using a human finger as the predatory stimulus, we follow most previous analyses of defensive responses by snakes. Experimental work provides a justification for this logistically convenient technique: the exact form of the predatory stimulus appears to be unimportant in determining the snakes' response; the human hand elicits the same kinds of responses as a realistic model of the predator (Herzog et al., 1989; Scudder and Chiszar, 1977). Movement and elevation, rather than the exact shape of the stimulus object, are the prime determinants of the snake's response (Herzog et al., 1989). Our technique has the additional advantage of avoiding ethical difficulties involved with the use of live nonhuman predators. However, to test whether responses to humans were similar to those to crows, we also quantified snake responses to a model crow (see below).

We carried out three types of trials. In the first, the observer approached the snake to a distance of approximately 1 m, then "pecked" the snake in the midbody region with an outstretched finger. The peck was repeated five times, with a 1-s pause between pecks. The snake was then picked up by the midbody, and its response at the time it was seized was scored into one of four categories: (1) flee, without any defensive display; (2) remain still, without any overt reaction to the stimulus; (3) flatten the body (i.e., obvious dorsoventral compression); and (4) flatten the body and strike open-mouthed. The

strike display [equivalent to Hailey and Davies's (1986) "viprine display") was highly stereotyped and performed slowly. The strike was launched toward the stimulus on some occasions, but the snakes often simply waved their heads in the air with the mouth gaped widely open (see Figure 1). These trials were carried out on 18 and 19 May 1997, in cloudy conditions with air temperatures around 2°–10°C. After the antipredator response was described, we measured the snake's body temperature with a quick-registering cloacal thermometer, and then recorded its sex, SVL, and mass. All snakes were released at the site of capture after completion of the trials.

The second group of trials was conducted over a longer period (12–18 May 1997) and over a wider range of weather conditions (air temperatures 2–15°C). The range of body sizes of snakes used was almost identical to that in the first trial (36–60 cm SVL), but the snakes in courting groups were warmer than the solitary animals used in the first trials (means of 12.9° versus 9.3°C; maximum temperature approximately 19°C in both trials, but minima lower in the solitary-snake trials). In this second set of trials, we targeted groups of snakes that were actively engaged in courtship behavior (i.e., "mating balls"; Mason and Crews, 1985). Two observers approached the group to within a meter, and then suddenly moved their hands 20 cm above the snakes to simulate a crow's wings. This brief (<2 s) stimulus generally induced a proportion of the group to flee, whereas others remained, apparently unaware of the observers' presence (i.e., they continued courtship activity). We then captured both sets of snakes (i.e., those that fled and those that remained) and recorded the body temperature, sex, and SVL of snakes in each of these two groups.

The third set of trials (in May 1998) was designed to compare the snakes' response to a human and to a more accurate simulation of a natural predator. We used a commercially produced crow decoy (as used by hunters to attract crows). The model crow closely simulated a real crow in size (41 cm total length), shape, and color. We attached the plastic crow to a 2-m wooden dowel and pecked snakes with either the crow's bill or with a finger. Half of the snakes were first pecked with the crow and then (after a 30-s delay) with the finger. The other half were pecked by finger first, and then by the crow. As in the first set of trials, we recorded the snakes' response, sex, body size, and body temperature.

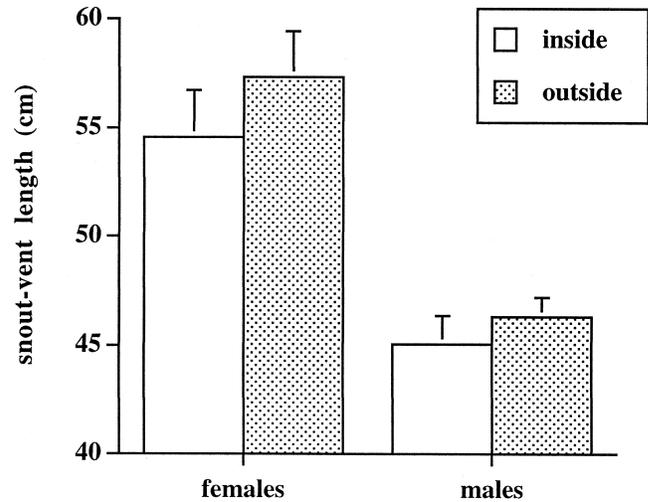
We tested data sets for normality and equality of variances before analysis. We relied on nonparametric contingency-table tests for most analyses. In these cases the chi-square calculations were based on raw numbers, although we report proportions to facilitate explanation of trends.

## RESULTS

### Sex, body temperature, body size, and location

Because sex, body temperature, body size, and location are plausibly associated with variation in antipredator behavior by the snakes, we first describe patterns of intercorrelation between these four factors. These patterns proved to be complex.

Contingency table analysis showed that the sex ratio was not significantly different between samples of snakes collected inside versus outside the den ( $\chi^2 = 2.16$ , 1 df,  $p = .14$ ). However, a two-factor ANOVA with sex and location (inside versus outside the den) as factors and ln SVL as the dependent variable showed that females were larger than males ( $F_{1,234} = 157.49$ ,  $p < .0001$ ) and that snakes outside the den were larger than those inside ( $F_{1,234} = 5.21$ ,  $p < .025$ ; see Figure 2). The interaction term between sex and location was not significant ( $F_{1,234} = 0.42$ ,  $p = .52$ ), indicating that the magnitude of sexual size dimorphism was similar inside versus outside the den



**Figure 2**  
Body lengths of male and female gartersnakes collected inside the overwintering den (inside) or in the surrounding grasslands (outside). Sample sizes were as follows: females inside, 30; females outside, 49; males inside, 44; males outside, 115.

(despite the difference in mean body sizes in the two locations).

To clarify the ways in which sex, size, and location might influence a snake's body temperature, we carried out a two-factor analysis of covariance. The factors were sex and location (inside versus outside den), the covariate was body size (ln SVL), and the dependent variable was body temperature. This analysis revealed no significant heterogeneity in slopes (i.e., all interaction terms had  $p > .10$ ), but body temperatures increased significantly with body size (covariate  $F_{1,234} = 17.95$ ,  $p < .0001$ ), and the intercepts of these regressions differed significantly as a function of both sex (males were warmer than females:  $F_{1,234} = 15.50$ ,  $p < .0001$ ) and location (snakes outside the den were warmer:  $F_{1,234} = 152.55$ ,  $p < .0001$ ).

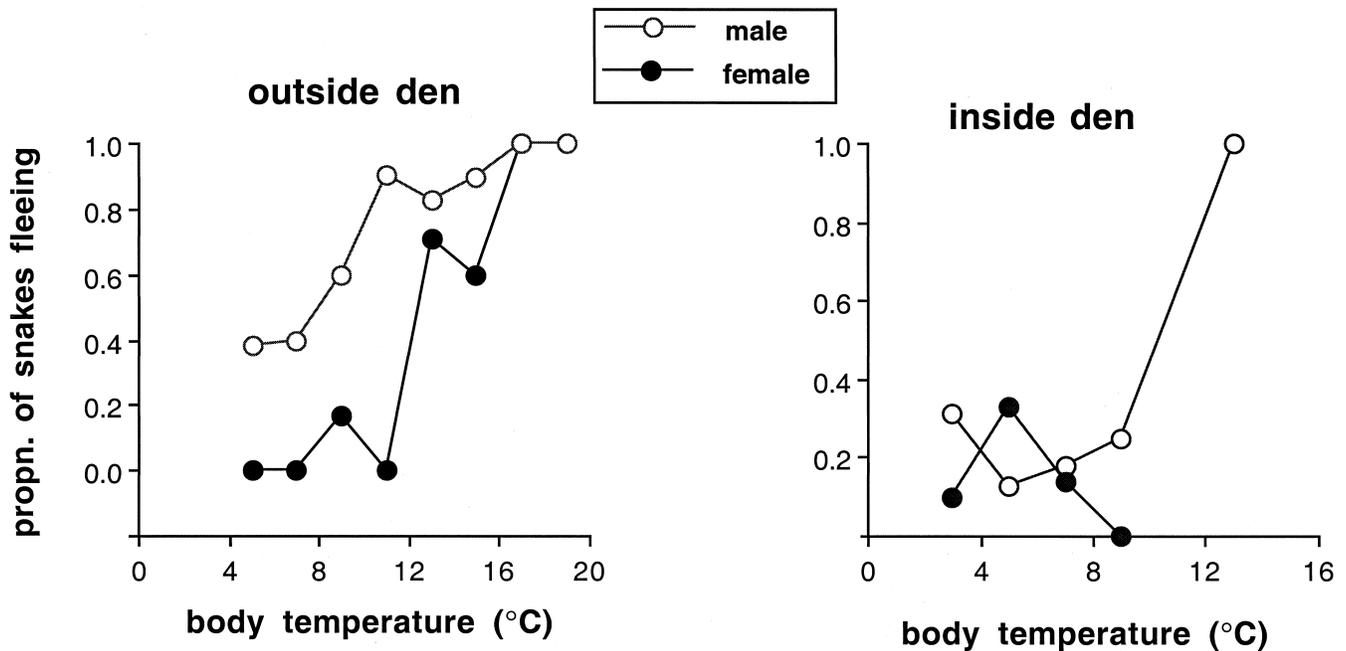
The end result of these relationships is that a snake's body temperature depends on its size, its sex, and its location. In turn, size depends on both sex and location. Thus, the distribution of four traits (sex, size, temperature, location) that might potentially affect a gartersnake's antipredator behavior are themselves intercorrelated in complex ways. We now turn to the ways in which these four traits modify snake responses.

### Antipredator responses

We obtained data on the antipredator responses of 238 snakes (159 males, 79 females) from the first set of trials, 293 snakes (263 males, 30 females) from the second set, and 55 snakes (33 males, 22 females) from the third. We analyzed these three data sets separately because of the different stimuli we provided to the snakes in each case.

#### Solitary snake trials

First we consider overall responses from the first set of trials (those in which the snakes were pecked by a finger). Logistic regression offers a powerful approach to detecting influences on categorical response variables such as those exhibited by the snakes. Our first analysis used "flee versus remain" as the dichotomous dependent variable. The snake's sex, body temperature, size (ln SVL), and location (inside versus outside den) were entered as independent variables. Log-likelihood ratio tests showed that the snake's decision (i.e., whether or not to flee from the predatory stimulus) depended on its body



**Figure 3**

Antipredator responses in female and male gartersnakes as a function of body temperature and location. These graphs show the proportion of snakes that attempted to flee from the “pecking” stimulus, calculated over each 2°C category of body temperature. Sample sizes for each group outside den females 6, 10, 12, 5, 7, 5, 4; males 8, 156, 30, 20, 17, 19, 3, 3; inside den females 10, 12, 7, 1; males 13, 15, 11, 4, 1. See text for statistical analyses.

temperature ( $\chi^2 = 35.48$ , 1 df,  $p < .0001$ ) and sex ( $\chi^2 = 8.04$ , 1 df,  $p < .005$ ), but not its body size ( $\chi^2 = 0.21$ , 1 df,  $p = .65$ ) or location ( $\chi^2 = 0.04$ , 1 df,  $p = .85$ ). Male snakes were more likely to flee than females, especially if they were warm.

Given that a snake does not flee, what factors determine whether it remains still, flattens, or strikes? We used logistic regression with the same independent variables as above, but restricted to the subset of animals that did not flee from our approach and with the dependent variable being “remain still, flatten, or strike”. The responses of these animals were affected by location ( $\chi^2 = 7.28$ , 2 df,  $p < .03$ ; 62% of snakes inside the den struck at the stimulus, versus 40% of snakes encountered outside the den), but not any of the other factors (all  $p > .50$ ).

In combination with these analyses, a more detailed inspection of patterns within the data set indicates that a snake’s response to a predatory attack depends on the following factors:

1. **Body temperature.** At body temperatures  $>12^\circ\text{C}$ , the snakes generally fled from our attack. Cooler snakes usually either remained still or launched a defensive display (Figure 3).

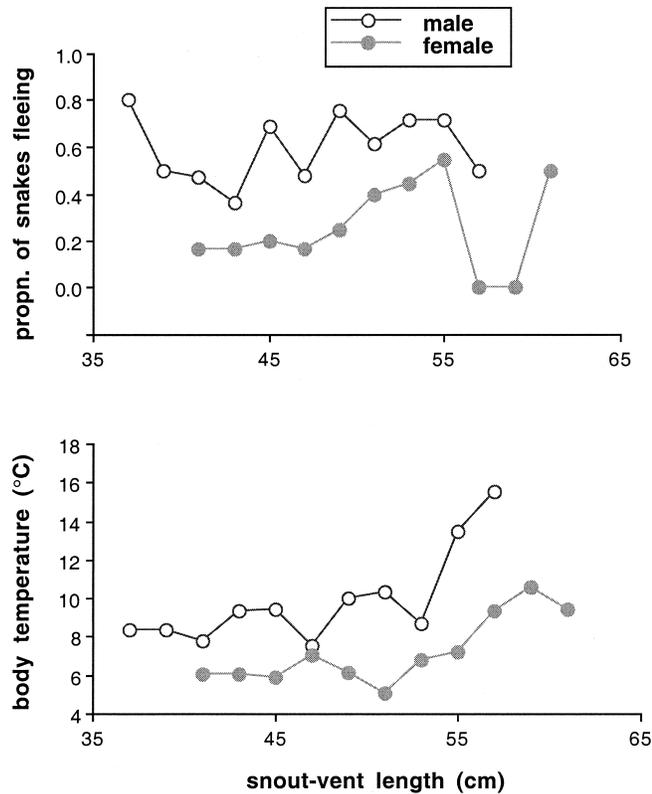
2. **Sex.** The above pattern was evident in both males and females, but the threshold level for fleeing was lower in males. Many males attempted to flee even at very low body temperatures, whereas females did not (Figure 3). Even when analysis was restricted to snakes at body temperatures close to the threshold for flight ( $8^\circ\text{--}12^\circ\text{C}$ ), contingency table analysis confirmed that the sex difference in the propensity for flight was statistically significant ( $\chi^2 = 11.25$ , 1 df,  $p < .003$ ; 10% of 30 females fled versus 59% of 92 males).

Although a snake’s sex and its body temperature influenced the probability that it stayed rather than attempted to flee, these factors did not affect its response if it stayed. Approximately 23% of the sedentary snakes did not show any overt response to the stimulus, whereas 27% flattened without strik-

ing, and 50% showed both flattening and striking. These proportions were similar in males versus females (24 versus 22%; 27 versus 27%; 49 versus 51%;  $\chi^2 = 0.06$ , 2 df,  $p = .97$ ), whereas the sex difference in the proportion of snakes that fled from our approach was highly significant (58 versus 25%;  $\chi^2 = 21.15$ , 1 df,  $p < .0001$ ). Similarly, mean body temperatures did not differ significantly among the response categories that did not involve attempts to flee (means =  $7.1^\circ\text{C}$  for “remained still,”  $7.3^\circ\text{C}$  for “flattened,”  $6.8^\circ\text{C}$  for “struck”; two-factor ANOVA with sex and response category as factors, body temperature as dependent variable: effect of sex,  $F_{1,120} = 0.14$ ,  $p = .71$ ; effect of response category,  $F_{2,122} = 0.29$ ,  $p = .75$ ; interaction,  $F_{2,120} = 0.15$ ,  $p = .86$ ).

3. **Location.** Whether snakes were inside or outside the den had a substantial effect on their antipredator behavior, but this was largely an indirect consequence of the thermal environment. The proportion of snakes that fled from our approach was much higher for snakes outside the den than for those inside (59% versus 21%;  $\chi^2 = 26.43$ , 1 df,  $p < .0001$ ). However, the logistic regression showed that once this thermal effect was factored out of the analysis, location exerted little effect on snake response. The only significant effect that we detected was that snakes inside the den were more likely to strike at us than were those outside.

4. **Body size.** A snake’s size might affect its body temperature (due to thermal inertia) or its ability to flee (i.e., locomotor speed) or display effectively (i.e., be sufficiently intimidating). However, we did not detect any relationship between size and behavior (Figure 4; note nonsignificant size effect in the logistic regressions). Larger snakes had higher body temperatures within each sex, but males (the smaller sex) were consistently warmer than females (Figure 4). To determine whether the sex difference in the proportions of snakes fleeing from our approach was simply due to a body size difference between the sexes, we compared the responses of males with those of females over the same range of body sizes (i.e.,



**Figure 4**  
The effect of sex and body size on antipredator responses of gartersnakes (proportion of snakes attempting to flee, upper graph) and body temperature (lower graph). Each data point is based on the mean value for the dependent variable over a 2-cm snout-vent length category. Sample sizes, left to right: females 10, 7, 8, 7, 7, 5, 10, 11, 21, 10, 7; males 12, 31, 58, 64, 61, 61, 70, 30, 17, 12, 5. See text for statistical analyses.

<61 cm SVL). Over this common size range, males were more likely to flee than were females ( $\chi^2 = 7.15$ , 1 df,  $p < .008$ ). Thus, the behavioral difference between the sexes is not simply an indirect effect of sexual size dimorphism.

Because the size-related shift in mean body temperature was relatively subtle (Figure 4), it had only a minor effect on defensive responses. For example, snakes inside the den were significantly larger than those outside the den (Figure 2), and hence would tend to be warmer for this reason (Figure 4). However, the magnitude of the thermal difference inside versus outside the den was so great that it overwhelmed the size effect. Thus, the proportion of snakes fleeing from our approach was more than twice as high outside the den as inside (see above and Figure 3), with the spatial effect on body temperatures completely overriding the more subtle size-related effect.

#### Response to model of a crow

We now consider the set of trials in which we compared the snakes' response to a finger with their response to a plastic crow (a more realistic simulation of the actual predator). The clear result was that the snakes responded in similar ways to the two stimuli. In 43 of the 55 cases (78%), the snake responded identically to the finger versus the plastic crow (9 snakes gaped to both stimuli, 8 flattened, 3 remained still, 22 fled). Interest thus focuses on the remaining 13 cases. Analysis reveals no consistent difference in response to the two kinds of stimuli. For example, the number of times a snake fled

from the crow but flattened in response to the finger was exactly the same as the number of times that the snake fled from the finger but flattened in response to the crow (two in each case). To test the statistical significance of minor differences between these two data sets, we compared the observed frequencies of responses to those expected under two null models. The data deviated markedly from the patterns expected if a snake's response to one type of stimulus was completely independent of its response to the other stimulus ( $\chi^2 = 26.69$ , 9 df,  $p < .01$ ), but did not differ significantly from the patterns expected if responses to the two stimuli were identical ( $\chi^2 = 4.75$ , 9 df,  $p = .85$ ). Also, if analysis is restricted to responses to the plastic crow only, we see the same patterns as for the trials using the human finger as the stimulus (above). For example, the proportion of snakes that fled in response to the crow was much higher for snakes with body temperatures  $>15^\circ\text{C}$  than for snakes below that temperature ( $\chi^2 = 54.5$ , 1 df,  $p < .0001$ ).

#### Courting group trials

For the trials in which we frightened (but did not "peck") courting groups, we never recorded any cases of flattening or striking; instead, an average of 28% of the snakes in the group attempted to flee, whereas the remainder continued courting. There was a strong sex bias in the results, with only 1 of 27 females fleeing (4%) compared to 81 of 263 males (31%;  $\chi^2 = 7.58$ , 1 df,  $p < .006$ ). The proportion of males that fled from our approach was strongly related to mean body temperature of snakes in the courting group: more snakes fled from warmer groups (mean body temperature versus proportion that fled:  $r = -.48$ ,  $n = 36$ ,  $p < .004$ ). Analysis did not reveal any determinants of "stay versus flee" within the males of each group. Because both mean body sizes and mean body temperatures differed among courting groups, we used a two-factor nested ANOVA (with group number and "stay versus flee" nested within group number as the factors) to investigate such effects. Male snakes that fled from us did not differ from those that stayed in terms of body sizes ( $F_{25,35} = 0.58$ ,  $p = .92$ ) or body temperatures (for males only,  $F_{25,35} = 0.16$ ,  $p > .99$ ).

## DISCUSSION

Our data paint a complex picture of the determinants of antipredator responses in free-ranging gartersnakes. The tactic used by a snake in response to our simulated attack depended on a series of factors (such as body temperature, sex, location, and prior activity) and, just as importantly, these factors showed strong relationships with each other (for example, body temperatures were a function of sex, body size, and location). Although the stimulus we used was an artificial one, the similar responses to the human hand versus a model crow suggest that we are measuring a biologically meaningful response. The end result is that antipredator responses of these small snakes provide a useful model system in which to clarify the ways an ectotherm's behavioral decisions are influenced by abiotic and biotic variables.

The published literature on antipredator responses of snakes contains many apparent inconsistencies, most notably in terms of the effect of body temperature on defensive responses. Some of these inconsistencies undoubtedly result from real interspecific differences (Scudder and Burghardt, 1983); for example, May et al.'s (1996) extensive field study clearly showed that pigmy rattlesnakes (*Sistrurus miliarius*) are more likely to strike defensively when they are hot rather than when they are cold. This pattern is the opposite to that shown by our gartersnakes and may reflect different defensive capabilities of the two taxa (cf. McLean and Godin, 1989; but

see also Duvall et al., 1985). However, much of the published literature on antipredator tactics in snakes has been based on natricine colubrids, especially gartersnakes.

Early reports noted (without quantification) that colder gartersnakes were more likely to display rather than to flee (Costanzo, 1986; Fitch, 1965; Heckrotte, 1967). Some of the extensive laboratory studies on captive gartersnakes supported these early reports (Arnold and Bennett, 1984), but others found the reverse pattern, whereby warmer snakes display more often than cold snakes (Schieffelin and de Quieroz, 1991; and see Keogh and DeSerto, 1994, for a similar result on other small colubrid species). Our study strongly corroborates the early reports: colder gartersnakes were more likely to display rather than to flee, as has been reported also in a variety of lizard species (e.g., Hertz et al., 1982). A recent field study on *Thamnophis sirtalis*, similar to our own, also concluded that colder snakes are less likely to flee (Passek and Gillingham, 1997). Remarkably, however, the threshold temperatures for flight recorded by these authors (working on a Michigan population during May and June) were much higher than those we measured in the Manitoba snakes; for example, they reported mean body temperatures of 30.7°C for fleeing snakes and 27.4°C for snakes that did not flee. Thus, although the general pattern is the same, the thermal ranges at which these responses were recorded were dramatically different (see Figure 3).

Other aspects of our results also provide a strong contrast to previous studies. Part of the reason may relate to interspecific (or even intraspecific or ontogenetic) differences in responses, but we suspect that results from laboratory studies may sometimes give an unreliable indication of the behavioral responses of free-ranging snakes. Even brief captivity can substantially affect defensive responses of snakes (e.g., Fitch, 1975; Platt, 1969). Such captivity-induced modifications to defensive responses accord well with one of the main conclusions from our own study: these behaviors show considerable flexibility in response to several variables.

What is the biological significance of the diversity we documented in antipredator responses of red-sided gartersnakes? Optimality models suggest that an organism should adopt the antipredator tactic most likely to maximize its chances of surviving the encounter without injury (Vermeij, 1982). Some of the patterns we observed are easily interpretable in this light, but the adaptive advantage of others (if any) remains obscure. The most straightforward case is the consistent trend for warmer snakes to flee from our approach, whereas colder snakes remained sedentary (e.g., Figure 3). Higher body temperatures enhance locomotor ability in gartersnakes (Heckrotte, 1967; Scribner and Weatherhead, 1995), as in other ectotherms (Huey and Slatkin, 1976), and a snake is presumably more likely to escape if it can move rapidly. Because gartersnakes are nonvenomous and relatively small, even the largest snake may pose little threat to a predator such as a crow. This is especially true when the snake is cold (and hence, less able to launch accurate strikes), as is generally the case with displaying snakes. Perhaps for this reason, body size had little effect on the snake's probability of launching an offensive display (Figure 4).

One of the most interesting results from our study is the clear sex difference in defensive tactics. Previous studies have often reported sex differences in antipredator responses, but high levels of aggressive antipredator display by females are typically associated with protection of offspring (e.g., in several taxa of mammalian carnivores and ungulates). This factor is irrelevant to gartersnakes, which show no postpartum care of offspring (Rossman et al., 1996). Higher levels of antipredator displays in males than in females have been reported in two snake species (Scudder and Burghardt, 1983; Zinner,

1985), but a recent report noted (without quantification) that female red-sided gartersnakes are more likely than conspecific males to display and to bite when handled (Fitch, 1999). This latter report is consistent with our own data. An earlier study of neonatal *Thamnophis sirtalis* reported no sex difference in levels of display (Scudder and Burghardt, 1983). Aggression is more closely linked to body temperature in gravid female rattlesnakes than in nongravid females or males but is no more common overall in one sex than the other (Goode and Duvall, 1988). Similarly, Scribner and Weatherhead (1995) reported that antipredator responses did not differ between the sexes in three species of natricine colubrids (including *T. sirtalis*). In their field study of *T. sirtalis*, Passek and Gillingham (1997) did not examine sex differences in antipredator behavior.

In our study, female snakes engaged in a higher proportion of aggressive displays than did males, but this sex difference disappeared if attention was restricted to the subset of snakes that did not flee from the observer. That is, males and females that did not flee were equally likely to remain still, to flatten, or to flatten and strike. The sex difference lies in the fact that a high proportion of males fled from the observer, whereas fewer females adopted this tactic. Why were males more likely to flee? Male and female gartersnakes in our population differ in at least three factors—body size, thermal ecology, and emergence patterns—that might favor a sex divergence in antipredator tactics. We evaluate these possibilities below.

First, sex differences in body size per se cannot explain the behavioral difference, because size had little effect on response patterns within each sex (Figure 4).

Second, body temperature clearly plays a role. One reason that males fled so often is that they were warmer than females, despite a trend for mean body temperatures to increase rather than decrease with body size within each sex (Figures 3 and 4). Nonetheless, thermal factors cannot explain all of the sex difference in antipredator behavior. Even when snake response was plotted as a function of body temperature, the sexes followed different trajectories (Figure 3).

Third, males remain near the dens for some weeks during the mating period, whereas females tend to disperse toward summer habitats soon after emergence (Gregory and Stewart, 1975). Many of the females that we tested were thus newly emerged and had not attained full locomotor ability since emerging from their long overwinter dormancy. Trials of locomotor ability show that females are substantially slower (and thus less well-suited to relying on speed to escape predation; Shine et al., unpublished data). This sex bias in locomotor ability provides a plausible adaptive basis for the sex difference we observed in defensive behavior.

More generally, antipredator responses in free-ranging snakes may offer an unusually powerful opportunity to test adaptationist (optimality) models on behavioral decisions. In combination with previous studies, our work suggests that gartersnakes modify their antipredator behavior in response to a complex suite of traits, with a strong focus on factors that influence the snake's ability to successfully flee from a predator. Thus, snakes are more likely to display rather than to flee if their locomotor ability is compromised by factors such as low body temperature (see above), fatigue (Arnold and Bennett, 1984), poor condition (Andren, 1982), pregnancy (Goode and Duvall, 1988), or a recent meal (Herzog and Bailey, 1987), or if the effectiveness of escape is influenced by the proximity of shelter or conspecifics (Duvall et al., 1985; and see above). This hypothesis is potentially testable by experimental manipulation and by taking advantage of the wide range of locomotor abilities often present within a single population (e.g., Arnold and Bennett, 1984; Garland, 1988). This range may be further increased by experimental manipula-

tions early in ontogeny (e.g., Shine, 1995; Sinervo and Huey, 1990). Correlational evidence is consistent with the hypothesis that antipredator responses in gartersnakes are fine-tuned by natural selection in such a way as to maximize an individual's probability of surviving such an encounter, but we will need additional data, both on predator behavior and prey responses, before we can fully understand the dynamics of that interaction.

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