

# Female mimicry in garter snakes: behavioural tactics of "she-males" and the males that court them

Richard Shine, David O'Connor, and Robert T. Mason

**Abstract:** Red-sided garter snakes (*Thamnophis sirtalis parietalis*) in central Manitoba court and mate in early spring soon after emerging from communal overwintering dens. Some males ("she-males") produce female-like skin pheromones, and hence attract courtship from other males. Studies at a den near Inwood, Manitoba, support and extend results from work at other dens. She-males were males that had recently emerged from hibernation and had not yet regained full locomotor capacity or muscle strength. She-males resembled "he-males" rather than females in their antipredator responses, including the thermal threshold at which they fled from a simulated predator (a plastic crow) rather than remaining stationary and displaying. Males courting she-males were cooler than those courting females; nonetheless they were more likely to flee when we approached them. Compared with courting groups focussed on females, groups around she-males were smaller, consisted predominantly of smaller he-males, and were found over a more restricted time of day (early afternoon). Arena trials confirmed that she-males are disproportionately courted by small rather than large he-males, and clarified other aspects of she-male attractiveness and behaviour. She-males attracted more intense courtship when large females were absent. She-males courted less vigorously when large he-males were present, especially when they were vigorously courted themselves. Overall, our data reveal hitherto-unsuspected complexity in the behavioural tactics of reproducing garter snakes.

**Résumé :** Des Couleuvres rayées *Thamnophis sirtalis parietalis* du centre du Manitoba se courtisent et s'accouplent au début du printemps, peu après leur sortie des terriers d'hiver communaux. Certains mâles ("mâles féminins") produisent des phéromones semblables à celles de femelles et attirent donc d'autres mâles qui viennent les courtiser. Les résultats d'une étude menée près d'Inwood, Manitoba, confirment ceux d'études à d'autres terriers et apportent des informations supplémentaires. Les mâles féminins sont des mâles qui sortent d'hibernation et qui n'ont pas encore retrouvé toute leur capacité motrice ou leur force musculaire. Ces mâles ressemblent plus à de véritables mâles qu'à des femelles par leurs réactions anti-prédateurs, notamment le seuil thermique qui les fait fuir un prédateur simulé (une corneille de plastique) plutôt que de rester sur place ou de parader. Les mâles qui font la cour aux mâles féminins ont une température moins élevée que les mâles qui courtisent les femelles, mais ont plus tendance à fuir à notre approche. Comparativement aux groupes qui courtisent des femelles, les groupes autour de mâles féminins sont plus petits, formés surtout de petits mâles et ces groupes restent formés pendant une période plus restreinte de la journée (au début de l'après-midi). Des expériences en enceintes ont démontré que les mâles féminins sont courtisés par plus de petits mâles que de gros mâles et ont clarifié d'autres aspects du pouvoir d'attraction et du comportement des mâles féminins. Les mâles féminins s'attiraient des comportements de cour plus intenses en l'absence de femelles de grande taille. Les mâles féminins faisaient une cour moins intense en présence de gros mâles, particulièrement s'ils étaient eux-mêmes la cible de comportements de cour assidus. Dans l'ensemble, nos données mettent en lumière la complexité insoupçonnée des tactiques comportementales chez les Couleuvres rayées en période de reproduction.

[Traduit par la Rédaction]

## Introduction

Although recent years have seen a rapid growth in the numbers of studies devoted to mating systems of reptiles (e.g., Schuett and Gillingham 1989; Duvall et al. 1993; Luiselli 1996), we still know much less about the behavioural "tac-

tics" of reproducing reptiles than we do about those of birds or mammals (e.g., Bartholomew 1970; Clutton-Brock 1988; Andersson 1994). In part, the problem undoubtedly reflects logistical constraints: it is difficult or impossible to obtain detailed information on reproductive interactions of many kinds of reptiles. Snakes fall into this category. Most species are too widely dispersed during the mating season, and too difficult to observe at this time, for effective behavioural study (e.g., Seigel 1993). Thus, published information on the mating systems of snakes is derived primarily from a few "model" systems (Duvall et al. 1993).

One such situation that is particularly amenable to study occurs in south-central Manitoba, where red-sided garter snakes (*Thamnophis sirtalis parietalis*) gather in enormous numbers at overwintering dens and mate as they emerge and

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disperse the following spring. Research on this system has generated many interesting results (e.g., Gregory and Stewart 1975; Whittier et al. 1985; Krohmer et al. 1987). Perhaps the most remarkable discovery involves female mimicry. Some male garter snakes ("she-males") produce female-like skin lipids (pheromones), thereby attracting courtship from other males (Mason and Crews 1985). Recent studies have confirmed these reports, and have suggested that she-maleness is a transitory phase. Most or all males appear to pass through a she-male phase on their emergence from hibernation, but revert to he-maleness after they recover full locomotor capacity (Shine et al. 2000a).

In the present paper we describe additional facets of the biology of she-males, based on studies at a den 30 km from those used in most previous research on this topic. First, we quantify and compare phenotypic traits of she-males and he-males, to examine the generality of conclusions from previous work. Second, we look in more detail at the circumstances in which she-males attract courtship, and at the phenotypes of males that court these individuals. Third, we examine the tactics of she-males in terms of the situations in which they engage in courtship. To clarify these issues we use a combination of descriptive and experimental studies.

## Materials and methods

### Study species and area

Red-sided garter snakes are small (in our study population, adult males average 45 cm snout-vent length (SVL) and 25 g body mass) non-venomous colubrid snakes that are widely distributed across eastern North America (Rossman et al. 1996). These snakes overwinter in communal hibernacula over most of their range, but the sizes of these winter aggregations vary geographically. In the Interlake region of central Manitoba, some dens contain >20 000 snakes (R.T. Mason, unpublished data). Courtship and mating occur near the den throughout the month-long period of spring emergence, with males remaining close to the den and intercepting recently emerged females as they disperse towards their summer habitat (e.g., Gregory 1974, 1977). Because each female is simultaneously courted by several males, she is typically surrounded by a "mating ball" of suitors (Hawley and Aleksuk 1975).

The primary mechanism for sex recognition involves lipids in the skin (Mason et al. 1987; Mason 1993). Some males produce female-like skin lipids (she-males) and are actively courted by other males (Mason and Crews 1985). This courtship does not result in copulation, except in occasional circumstances (Pfrender et al. 2000). Recent studies suggest that most or all males pass through a relatively brief she-male phase soon after emergence from the den; they then revert to "he-male" status (Shine et al. 2000a). Both males and females take some days to recover locomotor performance after the long period of winter inactivity. The she-maleness phase occurs at this time, with the result that she-males are relatively slow and less adept at obtaining matings than are other males (Shine et al. 2000a).

Most previous studies on the mating system of the Manitoba garter snakes were focussed on three large dens in the Narcisse Community Pasture (e.g., Mason and Crews 1985; Whittier et al. 1985; Shine et al. 2000a, 2000b, 2000c). To clarify whether the same phenomena occur in other populations, we studied a population of *T. s. parietalis* at a den 30 km south of the Narcisse dens. This den was in a gravel quarry 1.5 km north of the town of Inwood, 0.5 km east of Highway 17 (50°31.58'N, 97°29.71'W). This den was close to the site of previous studies by Gregory (1974, 1977) and Gregory and Stewart (1975).

### Methods

We gathered data at the Inwood den during May 1999. To quantify phenotypic traits of she-males, he-males, and females, we collected courting groups after identifying which snake was the target of courtship. The sex of snakes was determined by manual eversion of hemipenes, and we scored whether or not the animal was covered in soil (reflecting recent emergence from the den). Immediately after capturing the snakes we recorded cloacal temperatures of the target snake and a courting male and associated shaded ground and air (1 m above ground) temperatures. The entire group was then placed in a cloth bag for later measurement of body size.

For a subset of these groups, we also obtained data on antipredator responses at the time of collection. A plastic crow on the end of a 1.5-m stick was used to simulate a predator, and was brought down to "peck" at the centre of the courting ball. We then recorded how many of these snakes immediately fled (versus stayed and displayed (i.e., flattened the body and gaped); see Shine et al. 2000b). These data enabled us to compare antipredator responses of she-males, he-males, and females as a function of body temperature and group size.

To quantify muscular strength we used a modified version of a protocol first developed by Schwaner and Sarre (1990). We held a snake by the back of the neck against a table, stretched out its body, and clipped the end of a spring balance (Pesola 300 g) midway along the tail. We then released the snake's tail, simultaneously prodding the base of the tail to stimulate contraction. The force exerted by the snake as it pulled its tail back towards its head was read from the spring balance.

Open-topped nylon arenas (1.1 × 1.1 m, 0.9 m high) were set up adjacent to the den so that we could control the sizes and numbers of interacting snakes. Each arena contained one she-male (recognised as such by virtue of being courted in the den area immediately prior to the trials) plus he-males and females. The numbers and sizes of he-males and females varied among trials. We classified males into two size classes (<40 or >50 cm) each constituting one extreme of the natural distribution of sizes of courting males. Females were grouped into three size classes (<45, 45–55, and >55 cm SVL), and all had their cloaca taped shut to prevent mating during the trials.

In most trials we used 12 he-males and 3 females plus the she-male. In some trials 6 large plus 6 small he-males were used, and in others either 12 large or 12 small he-males were used. The she-males varied in size, covering the full range of male body sizes. One female of each size class (a total of three per arena) was used in most trials, but some trials included only one size class (three small females per arena). In a few trials, the number of he-males per arena was reduced from 12 to 6.

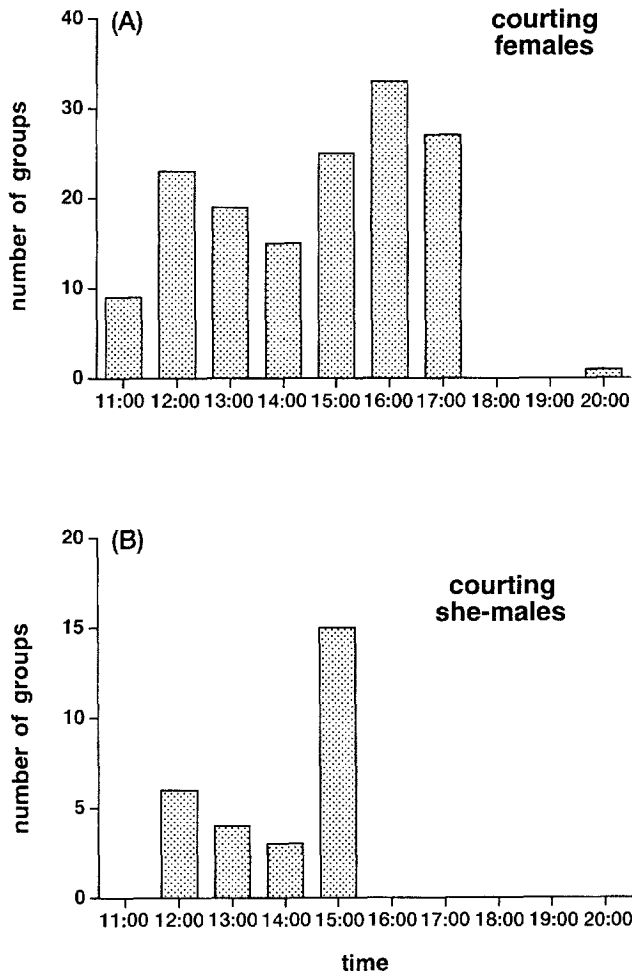
Using these various combinations of animals, we performed a series of trials whereby we quantified snake behaviour at 10-min intervals for 60 min. At each of these times we scored the she-male's courtship behaviour (e.g., was it courting, and if so, which female?) as well as the numbers and sizes of males courting it. Courtship was scored as occurring only when a male's body was aligned with that of the "target" snake with his chin firmly adpressed to it (e.g., Whittier et al. 1985).

## Results

### Frequency and circumstances of courtship of she-males

We recorded a total of 252 courting groups at the Inwood den, 43 of which (17%) were focussed on males (she-males) rather than females. The number of males per group was considerably lower around she-males than around females (means 1.44 vs. 4.39;  $F_{[1,130]} = 10.54$ ,  $P < 0.002$ ). She-male groups were found primarily in the early afternoon, whereas female-focussed courtship was recorded over a broader time

**Fig. 1.** Distributions of courting groups of red-sided garter snakes (*Thamnophis sirtalis parietalis*) with respect to time of day. Groups courting females were found over a protracted period (A), whereas groups courting female-mimic males (she-males) were generally found in the early afternoon (B). See the text for a statistical comparison of these distributions.



period. The day was divided into eight 1-h periods and the numbers of groups focussed on she-males versus females differed significantly among time periods ( $\chi^2 = 27.90$ , 6 df,  $P < 0.0001$ ; see Fig. 1). Males courting she-males were slightly cooler, on average, than males courting females (means of 16.9 vs. 18.8°C;  $F_{[1,224]} = 3.94$ ,  $P < 0.05$ ). This difference was due to the temporal separation of courting times: when analysis was restricted to groups encountered between 12:00 and 16:00 the thermal difference between males in the two kinds of groups was no longer significant ( $F_{[1,104]} = 0.86$ ,  $P = 0.36$ ).

#### Antipredator responses of she-males and their suitors

The percentage of he-males that fled from the predator (plastic crow) was higher for the snakes courting she-males than for those courting females (94.3 vs. 84.7%: using arcsine-transformed values to normalise variances,  $F_{[1,129]} = 4.70$ ,  $P < 0.04$ ). As in previous studies (Shine et al. 2000a), in groups with a higher mean body temperature, a higher percentage of snakes fled than remained (mean he-male temper-

ature against percentage of the group fleeing: Spearman's rank correlation,  $r_s = 0.55$ ,  $n = 131$ ,  $P < 0.001$ ). The percentage of he-males from larger groups that fled from the stimulus was higher than the percentage from smaller ones (group size versus percentage fleeing,  $r_s = 0.21$ ,  $n = 131$ ,  $P < 0.04$ ).

The antipredator response of the target snake also varied as a consequence of its sex, body temperature, and group size. This result can be seen from log-likelihood ratio tests from a logistic regression with target snake response as the dependent variable. Snakes were more likely to flee than display if they were she-males rather than females ( $\chi^2 = 14.49$ , 1 df,  $P < 0.0001$ ), and if they were warmer rather than cooler ( $\chi^2 = 19.06$ , 1 df,  $P < 0.0001$ ). The number of males in the courting group did not affect whether or not the target snake fled ( $\chi^2 = 0.37$ , 1 df,  $P = 0.55$ ). However, of those snakes that did not flee, whether they remained still or actively displayed was affected by the number of courting males ( $\chi^2 = 4.85$ , 1 df,  $P < 0.03$ ). Target snakes courted by a larger number of males were more likely to display than remain stationary.

#### Phenotypic attributes of she-males and their suitors

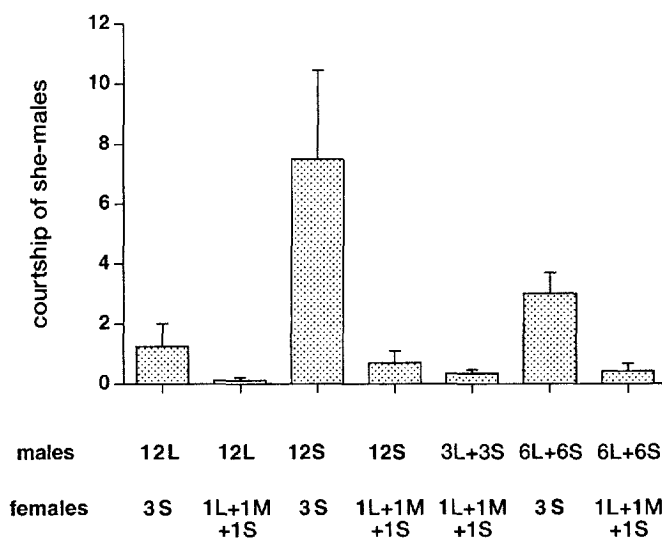
She-males did not differ from he-males in mean body size. The strongest test of such a difference comes from paired  $t$  tests comparing she-males with the he-males that were found courting them. Our analyses detected no significant differences between the two groups of males in either body length (means 43.1 vs. 43.2 cm SVL;  $t = 0.05$ , 42 df,  $P = 0.96$ ) or body mass (means 23.8 g for both groups;  $t = 0.05$ , 42 df,  $P = 0.96$ ). However, both of these groups were slightly smaller (on average) than males that were found courting females. The difference was statistically significant with respect to mean mass of the courting males (males courting she-males vs. females, 23.8 vs. 26.9 g;  $F_{[1,359]} = 3.97$ ,  $P < 0.05$ ) but not to their SVL (43.2 vs. 44.6 cm;  $F_{[1,376]} = 3.64$ ,  $P = 0.057$ ).

She-males differed from he-males in other respects. Almost half of the she-males that we scored (21 of 43, or 49%) were covered with soil, suggesting recent emergence from the den. In contrast, only 5 of 232 courting males (a random sample of this group) were dirty (2%; comparing the two samples,  $\chi^2 = 94.61$ , 1 df,  $P < 0.001$ ). Our tests of muscular strength showed that the snakes' ability to pull against the spring balance (pull strength) increased with their body size, but that she-males were significantly weaker than he-males at the same length. These results are evident from a two-factor analysis of covariance (ANCOVA) with sex as the factor, SVL as the covariate, and ln-transformed pull strength as the dependent variable. Larger snakes pulled harder ( $F_{[1,53]} = 42.09$ ,  $P < 0.0001$ ). Pull strength increased with SVL at the same rate in she-males and he-males (interaction,  $F_{[1,53]} = 0.40$ ,  $P = 0.40$ ), but she-males were weaker than he-males of the same body size (overall means of raw data 92 vs. 144 g;  $F_{[1,54]} = 5.10$ ,  $P < 0.031$ ).

#### Arena trials: which snakes court she-males, and when?

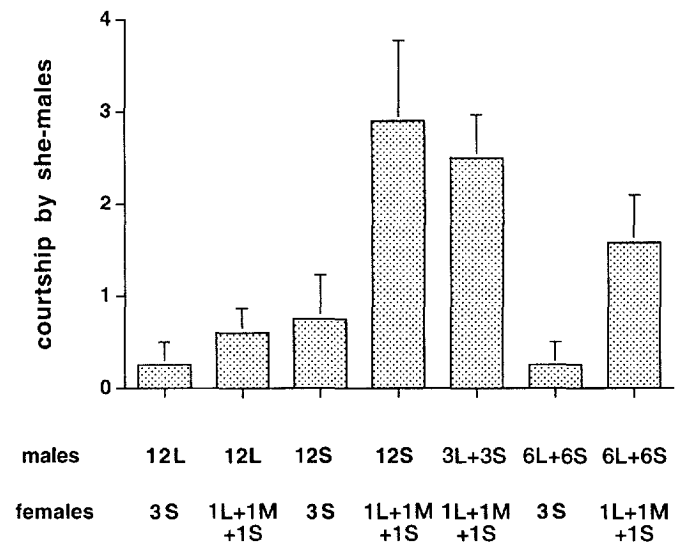
The amount of courtship directed to she-males differed substantially among arena trials, depending on the numbers and sizes of he-males and females present (one-factor ANOVA with trial type as the factor:  $F_{[6,49]} = 11.46$ ,  $P < 0.001$ ). Two strong trends were apparent. (1) Although the two size classes

**Fig. 2.** Amounts of courtship directed to she-males in arena trials with red-sided garter snakes. The courtship score reflects the numbers of males courting a she-male during trials with different combinations of males and females. Both sexes were sorted into predefined size classes (see the text). One she-male was present in each arena, together with one of the following combinations: (i) 12 large (L) males and 3 small (S) females,  $n = 4$  trials; (ii) 12 large males and 1 small, 1 medium-sized (M), and 1 large female,  $n = 10$  trials; (iii) 12 small males and 3 small females,  $n = 4$  trials; (iv) 12 small males and 1 small, 1 medium-sized, and 1 large female,  $n = 10$  trials; (v) 3 large and 3 small males and 1 small, 1 medium-sized, and 1 large female,  $n = 12$  trials; (vi) 6 large and 6 small males and 3 small females,  $n = 4$  trials; and (vii) 6 large and 6 small males and 1 small, 1 medium-sized, and 1 large female,  $n = 12$  trials. Error bars show 1 standard error on either side of the mean.



of he-males were present in equal numbers in each trial, she-males were courted more often by small he-males (53 records overall) than by large he-males (11 records). This strong bias (83% courtship by small males) allows rejection of the null hypothesis of equal intensity of courtship by each size class of he-males ( $\chi^2 = 25.81$ , 1 df,  $P < 0.001$ ). The same effect is obvious in the comparisons among trials (Fig. 2). More courtship of she-males occurred in trials with small he-males than in trials involving large he-males, regardless of whether the three females in the arena were all the same size (small) or of three different sizes (Fig. 2). Trials with a mixed size distribution of he-males (six large plus six small) generally produced levels of courtship of she-males that were intermediate between those seen in trials with either all small or all large he-males (Fig. 2). Post-hoc (Fisher's PLSD) tests showed that all these differences were statistically significant ( $P < 0.05$ ). (2) She-males were courted less frequently in trials in which large as well as small females were available in the arena. This difference is evident (and statistically significant by post-hoc tests) in comparisons involving trials with large males only, small he-males only, and mixed sizes (six large, six small). In each case, she-males attracted considerable courtship when the only females in the arena were small, but were courted less frequently when the trial included females of three different body sizes (Fig. 2).

**Fig. 3.** Frequency of courtship by she-male red-sided garter snakes during outdoor arena trials with different combinations of males and females. See Fig. 2 for details of combinations and sample sizes. Error bars show 1 standard error on either side of the mean.



**Arena trials: which snakes do she-males court, and when?**

The arena trials also allow us to evaluate factors influencing the she-males' own courtship behaviour. Four results were evident. (1) She-males selectively courted large rather than small females, but were no different in this respect than he-males in the same trials. In total, she-males directed 4 courtship attempts to small females, 40 to medium-sized females, and 40 to large females (i.e., proportions of 0.05:0.48:0.48), whereas the corresponding numbers for he-males were 87, 470, and 725 (0.07:0.37:0.57). Contingency-table analysis reveals no significant difference between these two distributions ( $\chi^2 = 4.15$ , 2 df,  $P = 0.13$ ). (2) She-males courted more frequently if the arena contained large females as well as small ones. This result is evident in a series of comparisons involving trials with large he-males only, trials with small he-males only, and trials with large as well as small males (Fig. 3;  $F_{[6,49]} = 3.08$ ,  $P < 0.015$ ; in all relevant post-hoc comparisons  $P < 0.05$ ). (3) The presence of large he-males in an arena suppressed courtship by she-males. This result emerges from a comparison of she-male courtship frequency both in trials with three small females and in trials with females of three different body sizes. In both cases, she-males courted frequently in "small-male" trials but not in "large-male" trials (Fig. 3; in post-hoc tests  $P < 0.05$ ). (4) She-males courted less vigorously in trials when they were themselves attracting substantial courtship (courtship of she-males versus by she-males,  $n = 56$ , Spearman's rank correlation,  $r_s = -0.16$ ,  $P < 0.005$ ).

**Discussion**

Our data support and extend the results of previous studies of this system and reveal a surprising degree of complexity in the behavioural tactics of reproducing snakes. Within

the superficially chaotic mating balls of snakes around a den, several deterministic processes are at work. Some of the most remarkable of these involve the behaviour of female mimics (she-males) and their suitors.

First, we note that the results of our studies at the Inwood den offer strong support for earlier work at the Narcisse dens. For example, a snake's antipredator tactics (i.e., whether it flees, remains still, or displays to the predator) depend upon its sex and body temperature (Shine et al. 2000*b*). These effects plausibly reflect the snake's locomotor ability: colder snakes may display because they are less able to flee, and females may display because they are slower than males at this time of year (Shine et al. 2000*b*). According to this hypothesis, we might expect she-males to resemble females rather than he-males in antipredator behaviour because she-males are relatively weak (this paper) and slow (Shine et al. 2000*a*). However, our data do not support this prediction: she-males generally resembled other males rather than females in their response to attack by a predator.

Although in initial work on she-males these animals were viewed as a discrete subset of males pursuing an alternative mating tactic (Mason and Crews 1985), authors of recent studies have proposed a different interpretation. She-maleness is seen as a transitory (condition-dependent?) phenomenon exhibited by males in the period immediately following their initial emergence from the den (Shine et al. 2000*a*). Our data from the Inwood den offer strong support for this hypothesis. She-males were similar in body size to he-males, as would be expected if they were the same group of animals at different stages post emergence. She-males were often covered in soil, indicating that they had emerged from the den only recently. Also, she-males were weaker than he-males, in keeping with the idea that the she-males were recent emergers that had not yet regained full muscular strength.

Our study provides the first detailed comparison of males that were found courting she-males with those courting females. Again, however, our results are readily interpretable in the light of previous work. Arena trials and field observations both revealed that she-males attract less vigorous courtship than do unmated females (Mason and Crews 1985; Shine et al. 2000*b*). This lower attractiveness may explain why smaller numbers of males courted she-males than females (i.e., a lower group size). The lower vigour of courtship of she-males may also explain why a higher proportion of males in she-male groups than in female-focussed groups fled as we approached. This result is otherwise paradoxical, given that (i) warmer snakes are generally more likely to flee, and she-male-centred groups were actually cooler than female-courting groups; and (ii) snakes in larger groups were more likely to flee, and she-male-centred groups were smaller than female-courting groups.

In both the field and the arena trials, she-males attracted disproportionate courtship from small rather than large males. The simplest explanation for this phenomenon involves a general pattern of size-assortative courtship within Manitoba garter snakes. Small males devote much of their time to courting small females, whereas larger males court larger females (R. Shine and R.T. Mason, unpublished data). In consequence, there is strongly size-assortative mating within this system (Joy and Crews 1988; Shine et al. 2000*c*; R. Shine and R.T. Mason, unpublished data). Because of the

marked disparity in mean body sizes of males and females within this species, she-males resemble small rather than large females. Hence, small males court she-males as well as small females, whereas larger males tend to ignore both of these targets in favour of larger females.

Another strong result from the arena trials was that adding large and medium-sized (rather than small) females substantially increased the she-male's own courtship activity but decreased the amount of courtship directed to the she-male. Despite the tendency towards size-assortative courtship (above), larger females attract more courtship overall, and not just from larger males (see above; and also see Hawley and Aleksasuk 1975; Gartska et al. 1982; R. Shine et al., unpublished data). Thus, arena trials that included larger females generally involved more active courtship, by the she-male as well as the he-males. Under these circumstances, males devoted most of their efforts to courting the large females rather than the smaller females or she-males.

Although size-assortative courtship can explain why she-males attracted less attention in trials with large males, it does not explain why the she-males' own courtship behaviour was also modified under these circumstances. The data from arena trials show a clear suppression of she-male courtship in the presence of large males (Fig. 3). A she-male subjected to vigorous courtship may be stressed and thus unwilling to engage in courtship himself. Such a facultative reduction may also enhance she-male fitness. In mating trials, physical strength is important in determining the outcome. Larger males consistently outcompete their smaller rivals (Shine et al. 2000*c*; contra Joy and Crews 1988), and she-males are rarely able to obtain matings even when in competition with same-sized he-males (Shine et al. 2000*a*). Given the high energy costs of courtship (R. Shine and R.T. Mason, unpublished data), a she-male that vigorously courted in a "large-male" trial would pay a high cost but would be unlikely to obtain a mating. Under these circumstances, the tactic that is observed, i.e., forgoing courtship when larger rivals are present, may well enhance the she-male's eventual reproductive success over the entire mating season. The negative correlation between intensity of courtship of the she-male versus by the she-male suggests that she-males may use the amount of courtship they experience themselves to evaluate the intensity of rivalry.

Similar assessment tactics may well be widespread, whereby males evaluate relative costs and benefits before engaging in reproductive activity. As is the case with the Manitoba she-males, such evaluations may involve such factors as the number and size of rival males and the availability of large (and hence fecund; Gregory 1977) females. Although such tactics have not previously been documented in reptiles, the dearth of examples probably reflects logistical difficulties rather than a real scarcity of such complex behaviours (e.g., Bagemihl 1999). Bizarre phenomena such as female mimicry may be only the tip of the iceberg in this respect.

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