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Sexual conflict in the snake den

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Abstract Red-sided garter snakes (*Thamnophis sirtalis parietalis*) court and mate in spring, soon after they emerge from large communal overwintering dens in south-central Manitoba. Because of a massive bias in the operational sex ratio, every female attracts intense courtship from dozens to hundreds of males. We suggest that this courtship constitutes significant "harassment," because it delays the females' dispersal from the den and hence increases their vulnerability to predation. Small females may face the greatest costs, because they are less able to escape from amorous males (who court all females, even juvenile animals). Our measurements show that males are stronger and faster than females. Experimental trials confirm that the locomotor ability of females (especially small females) is greatly reduced by the weight of a courting male. Arena trials show that intense courtship stimulates females to attempt to escape. Remarkably, some females that are too small to produce offspring may nonetheless copulate. This precocious sexual receptivity may benefit juvenile females because copulation renders them unattractive to males, and thus allows them to escape more easily from the den. Female "tactics" to escape male harassment may explain other puzzling aspects of garter snake biology including size-assortative mating, temporal patterns in dispersal from the den, avoidance of communal dens by young-of-the-year snakes, and female mimicry. Hence, sexual conflict may have influenced important features of the mating system and behavioral ecology of these animals.

Keywords Female mimicry · Garter snake · Mating · Sexual harassment · *Thamnophis sirtalis*

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Introduction

Romantic views to the contrary, the natural world does not operate by rules that resemble the ethical structures advocated by humans. There are many examples of animals behaving in ways that superficially resemble human activities such as murder, incest, and rape (e.g., Trivers 1972; Wilson 1978; Gould 1984). For example, behavioral studies suggest that forcible insemination occurs in a diverse array of species (Ghiselin 1974; McKinney et al. 1983; West-Eberhard 1987; Olsson 1995). Notions of sexual harassment and forcible insemination are difficult to apply to non-human species, because the concepts involve a judgment about whether the female is a "voluntary" participant in the process (e.g., Hrdy 1986; McLain and Pratt 1999). Nonetheless, there is strong theoretical and empirical support for the notion that sexual coercion and harassment occur in natural populations (e.g., Smuts and Smuts 1993; Clutton-Brock and Parker 1995; McLain and Pratt 1999). The "costs" that females experience from such harassment may involve increased energy expenditure (e.g., Watson et al. 1998), reduced time for feeding (e.g., Rowe et al. 1996), or reduced quality of food (e.g., Stone 1995). Such "costs" may be substantial: for example, a 50% reduction in female fecundity in one insect species (McLain and Pratt 1999).

Although demonstrating that an insemination is forcible rather than involving an element of female cooperation is difficult (Hrdy 1986; Allen and Simmons 1996), some cases are unequivocal (e.g., where the female is killed: LeBouef and Mesnick 1990). Forcible copulations may impose significant selection on male attributes (Ghiselin 1974; Berry and Shine 1980; Thornhill 1980; Brooks and Jennions 1999). Evolutionary biologists have generally interpreted forcible copulations as a mechanism for enhancing male reproductive success, but some cases are difficult to reconcile with this hypothesis. For example, forcible insemination may occur at a time of year when females are unlikely to conceive (e.g., McKinney et al. 1983) or involve partners that are incapable of conceiving (e.g., juvenile females, males, heterospecific females: Trivers 1976; Hardy 1998; McLain and Pratt 1999). To understand the phenomenon of forcible copulations unrelated to conception, we need to clarify the nature of the interaction between the sexes, and the consequences of copulation for each sex.

In this paper, we deal with a study organism that appears to be an unlikely candidate for forcible insemination. The elongate and flexible bodies of snakes make it impossible for a male to copulate with a resisting female (Devine 1984). Nonetheless, a courting male might be able to harass a female to such a degree that she accepts copulation. Our study was stimulated by observations of courtship and mating at communal dens of red-sided garter snakes in Manitoba. All females are courted intensely by males, with very large numbers of suitors (sometimes in the hundreds) clustering in a "mating ball" around the female (Gregory 1974; Gregory and Stewart 1975). Females are occasionally killed (crushed) by these courting males (Shine et al. 1999, 2000c). More commonly, the females' attempts to disperse from the den are hindered, especially where egress requires them to move up steep inclines. Writhing balls of snakes with a female at the center often fall back down the slope, forcing the female to recommence her dispersal efforts from the beginning (personal observation). The largest females are able to escape, but small females may be virtually unable to move.

Does courtship by these hordes of amorous males constitute a significant "cost" to a female garter snake? That is, are females genuinely disadvantaged (e.g., in energy expenditure, exposure to predation) by courtship and, if so, do they modify their behavioral "tactics" to reduce such costs? Do males actually obtain copulations by stressing the female rather than by inducing receptivity in the co-operative fashion that is generally assumed? Although intuition suggests that the males are harassing the females in this situation, the hypothesis is difficult to test in any objective fashion. We nonetheless attempt to do so, by focussing on some of the assumptions and predictions inherent in the "harassment" hypothesis. In particular, we gathered data on the ways in which a female's body size influences her attractiveness to males, her response to courtship, her behavioral "tactics" (e.g., times of emergence, probability of mating), and her ability to mate and/or to escape from courting males (e.g., by superior strength or speed).

Methods

Study species and area

In the Interlake region of south-central Manitoba, red-sided garter snakes (*Thamnophis sirtalis parietalis*) overwinter in limestone sinkholes. Some of the dens contain many thousands of these small colubrid snakes (Gregory 1974; Gregory and Stewart 1975). They mate soon after spring emergence, before dispersing to surrounding areas. Young-of-the-year snakes do not use these communal dens, and presumably hibernate in smaller groups in other places (Gregory 1974, 1977; Gregory and Stewart 1975). Although each den contains approximately equal numbers of adult males and females, the operational sex ratio during the mating season in spring is heavily male biased (often >100:1; Gregory 1974; unpublished data). This bias results from sex differences in emergence patterns: females disperse soon after emerging, whereas males remain for much longer in the vicinity of the den (Gregory 1974; Sexton and Bramble 1994). Because of this highly skewed sex ratio, emerging females are exposed to intense courtship. The location of females can often be ascertained by finding a mass of hundreds of males, and searching within this "mating ball" to reveal a female at its center.

Most of the data in this paper derive from studies in May 1999 at a snake den in a gravel quarry 1.5 km north of the town of Inwood, Manitoba, 0.5 km east of Highway 17 (50°31.58′ N 97°29.71′ W). This den is approximately 30 km south of the Narcisse dens that have been the focus of most previous research on this system. Because the reproductive status of females cannot be determined during the mating season in early spring, we needed to maintain a sample of females in captivity until we could make this determination. Thus, we collected females from the Inwood den and maintained them in captivity at Oregon State University until they gave birth during summer. All of these females were measured and weighed at the time of capture, so our data on body sizes of the captive snakes are not confounded by growth subsequent to their collection. Apart from these animals, all data in the present paper are based on measurements made in the field. To ensure statistical independence, each snake was used for only one segment of the study and then released.

General methods

To characterize body size distributions of reproducing snakes, we collected, measured (snout-vent length, SVL), and weighed snakes that were being courted, or were mating. Snakes were measured by being stretched out beside a metal ruler, and were weighed with an electronic balance. Regular sampling of all snakes around the den also allowed us to compare the attributes of these samples to prevailing weather conditions. Weather data were obtained for the town of Lundar, 25 km west of Inwood (Environment Canada).

To quantify the minimum body size at which females are capable of copulating, we gathered data on the size of male hemipenes and females' cloacal vestibule that contains the hemipenis during mating. The crucial dimension in this respect is width, since excessive length of the hemipenis presumably would not preclude effective copulation. We measured hemipenile sizes from a sample of dead male snakes collected after they suffocated in a Narcisse den in 1997 (Shine et al. 1999). Hemipenes were manually everted from these animals, and measured with vernier calipers. To quantify the internal dimensions of cloacal vestibules, we filled the cloacas of dead (predator-killed) females with fluid rapid-drying silicone (Dow-Corning). This method was developed by Guinea (1986) to quantify cloacal volumes of sea-snakes. The plugs were allowed to dry for 2 days before removal and measuring.

A female's ability to escape harassment should depend upon her speed and strength relative to that of males. Because such abilities are influenced by body size, we measured locomotor abilities of 12 females from each of three size classes: small (SVL <45 cm), medium (SVL 45–55 cm). and large (SVL >55 cm), as well as 12 large (SVL >50 cm) and 12 small (SVL <40 cm) males. The snakes were filmed with a videocamera as they crawled down a wooden runway 160 cm long by 30 cm wide, with walls of 15 cm. The runway was marked at 20-cm intervals. Body temperatures were recorded immediately after the trials, averaged 22.2°C (SD=3.2°C), and did not differ among the four groups of snakes (one-factor ANOVA, $F_{3,54}$=0.78, P=0.51). To estimate the females' ability to disperse from the den while being courted, we taped a dead male snake to the dorsal surface of the female approximately halfway between her head and vent. The same male (intermediate sized, 39.6 cm SVL, 21.7 g; found dead near the den) was used in all trials. Half the females were run with no male on their backs and then immediately run with the male attached.

The other half were first run with the male attached and then without. From the videos, we recorded the time from when the snake's snout crossed the forward edge of the start line to when it crossed the finish line, 120 cm away. To encourage the snakes to move as fast as possible, they were tapped on the tail with a finger as they moved along the runway.

To quantify muscular strength, we used a modified version of a protocol first developed by Schwaner and Sarre (1988). 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 tail, simultaneously prodding the snake's tailbase to stimulate contraction. The force exerted by the snake, as it pulled its tail back towards its head, was read from the spring balance.

If females attempt to avoid courtship by males, we expect that females courted by a larger number of males would spend more time moving about in an attempt to escape. To test this idea experimentally, we set up arenas (1.1×1.2 m, 90 cm high) of nylon material adjacent to the den. Each arena contained either 6 or 12 males (selected such that mean male body size remained consistent across all trials) plus one female-mimic ("she-male": Mason and Crews 1985, 1986; Shine et al. 2000a), and three females (one small, one medium, one large; size categories as above). Females of all sizes had their cloacas taped shut to prevent mating during the trials. At 10-min intervals for 60 min, we recorded whether or not each of the females was moving about the arena or remaining still. The behavior of she-males during these trials has been analyzed in a separate paper (Shine et al., in press b) and will not be discussed here.

Results

Body sizes of females versus reproductive status

Courted females

Males courted the entire size range of females that were found near the den, including the smallest female we found (28.8 cm SVL, 8.4 g).

Mated females

Females <43 cm SVL were never recorded to copulate (Fig. 1). The proportion of females above this size that copulated was high (Fig. 2). These data undoubtedly underestimate the real incidence of mating, because many of the females we recorded as "unmated" would presumably have mated at some later time.

Gravid females

The minimum body size at which females begin producing offspring can be determined from data on 67 females captured at Inwood in May 1999 and brought back to Oregon to give birth. The smallest reproductive female was 49.9 cm SVL; most (36 of 45) females above this size produced offspring, but all 22 females below this size did not.

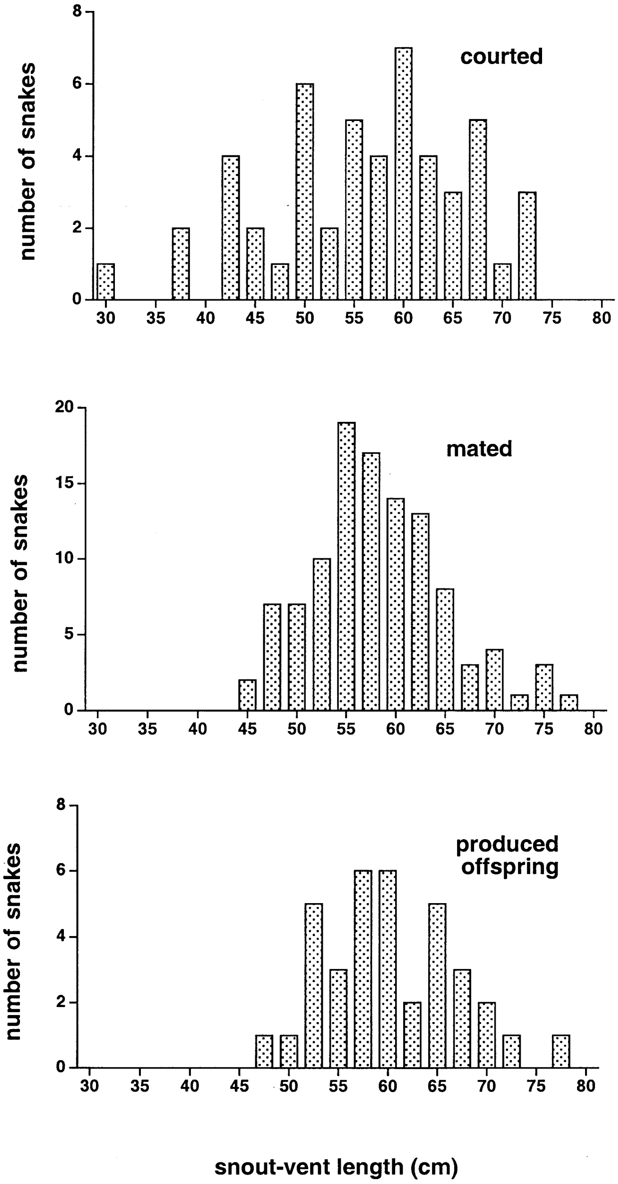

Fig. 1a–c Frequency distributions of body sizes (snout-vent lengths, SVLs) of female red-sided garter snakes. **a** Females that were being actively courted. **b** Mating females. **c** Females that were maintained in captivity after mating, and later produced offspring

Figure 1 thus reveals substantial differences in the minimum body sizes at which female snakes were courted, mated, or were found gravid. All females were courted regardless of body size. The proportion that produced offspring increased with maternal size, with most females not reproducing until they attained >50 cm SVL (Fig. 2). In contrast, most females mated in every size class >42.5 cm. The strongest comparison comes in the size range from 42.5 to 50 cm SVL (Fig. 2). Mating occurred in at least 16 of 29 snakes (64%) whereas only 1 of 10 captive animals within this range of SVLs was gravid (10%; χ^2=4.51, 1 *df*, *P*<0.04). The disparities in body size between the three classes are much greater when calculated on the basis of body mass rather than SVL. The smallest courted snake weighed 8.4 g, the smallest mated animal weighed 14.2 g, and the smallest gravid snake weighed 45.6 g.

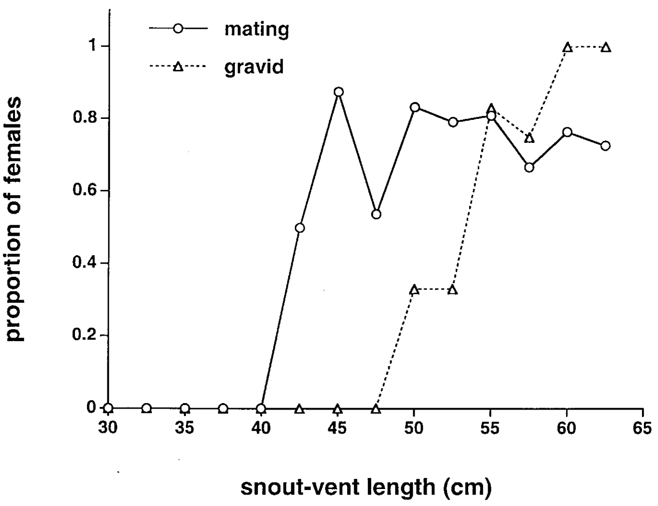

Fig. 2 The proportion of female garter snakes recorded to mate or to produce offspring, as a function of female body size (SVL). See text for statistical tests

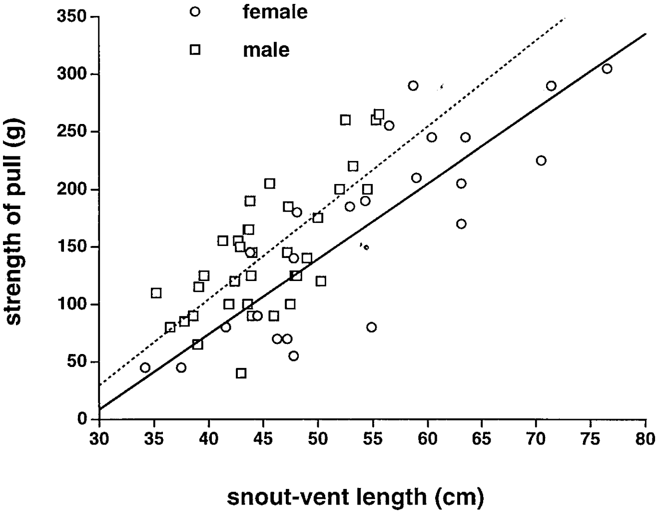

Fig. 3 Muscular strength of male and female garter snakes, as measured by the snake's ability to pull back against a spring balance. See text for statistical tests

The conclusion that juvenile females copulate is the most surprising result from our study, and warrants careful scrutiny. The crucial evidence is the minimum body sizes at copulation versus at reproduction (i.e., offspring production). Sizes of copulating snakes are straightforward to measure, and the smallest size at mating from our study (43 cm SVL) is similar to those reported from previous studies on the same species (45 cm: Hawley and Aleksiuk 1976; Whittier et al. 1985). The size at which females first begin producing offspring is more difficult to assess, because we cannot determine a female's reproductive status until several weeks after she has mated. Therefore, captivity may modify female reproductive "decisions." Nonetheless, data on body sizes of reproducing females in the field fit well with the data from our captives. Previous estimates of the minimum size at parturition in Manitoba garter snakes are consistent with (or exceed) our own (e.g., 55 cm SVL: Whittier et al. 1985). Gregory (1977) also reported a minimum SVL of 53 cm for a female giving birth (his Fig. 12). Gregory's dissections suggested that females as small as 45 cm SVL (approximately the size threshold for mating – see above) were potentially reproductive (his Table 2), but the proportion of animals reproducing at this size was very low. P.T. Gregory has generously provided his original data on body sizes and reproductive status of females captured during summer in areas adjacent to the dens (70 in 1971, 93 in 1972); we also have data on 29 females captured from their summer ranges in 1998. The size distributions of gravid snakes in these summer samples were almost identical to those of the reproducing captive females we collected from Inwood in 1999 (e.g., 53 of 57 snakes <50 cm were not gravid in the summer samples). We thus conclude that females copulate at body sizes smaller than those at which they produce offspring.

Strength and speed as a function of sex and body size

Muscular strength (ability to pull against the spring balance) increased with body size in both sexes, but was generally higher in males than in females at the same body length (Fig. 3). One-factor ANCOVA was used to test these results, with sex as the factor, SVL as the covariate, and strength as the dependent variable. Strength increased with SVL ($F_{1,55}$=81.05, P<0.0001), at similar rates in the two sexes (interaction $F_{1,55}$=0.40, P=0.53). At the same SVL, males were considerably stronger than females ($F_{1,56}$=9.02, P<0.005). Because females attain larger body sizes than males, however, the largest females were as strong as any males (Fig. 3).

Similar patterns were seen from our trials of locomotor speed. Males were faster than females (one-factor ANOVA, $F_{1,56}$=22.85, P<0.0001), with no difference in mean locomotor speeds between large versus small males ($F_{1,22}$=0.01, P=0.95). Repeated-measures ANCOVA (with female body size as the covariate and with/without male as the repeated measure, as per Fig. 4) revealed a significant effect of the burden on female locomotor speed ($F_{1,33}$=14.20, P<0.001). Furthermore, a female's body size affected not only her absolute speed ($F_{1,33}$ =7.64, P<0.01) but also the degree to which she was slowed by the attached male (interaction $F_{1,33}$=5.32, P<0.03). When a dead male was taped to the female, her locomotor speed decreased by an average of 21% in large females, 34% in medium-sized females, and 56% in small females (Fig. 4). That is, small females were not only the slowest animals, but were less capable than larger conspecifics of carrying an additional burden.

Male body size relative to female body size

We examined two facets of the relationship between male and female body sizes.

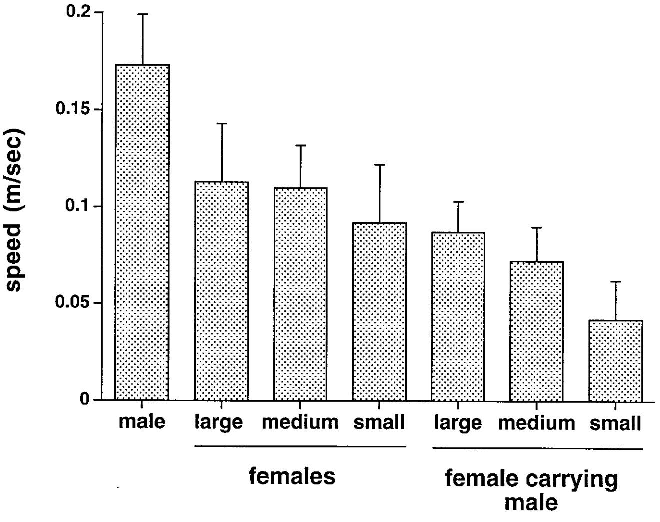

Fig. 4 Locomotor speeds of garter snakes on a wooden runway. Speeds were measured while the snakes were unencumbered (males and females) and female speeds were also measured when the female was carrying a dead male snake attached to her dorsal surface. Mean±2 SE. See text for statistical tests

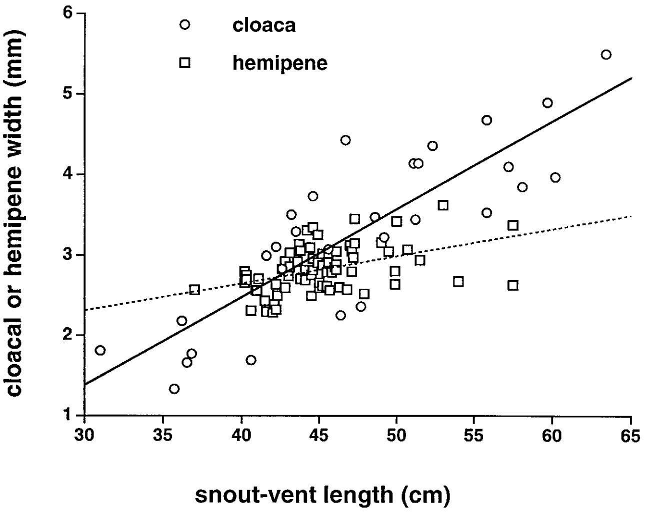

Fig. 5 Sizes of reproductive structures of male and female garter snakes in relation to the snake's overall body size (SVL) [*dotted line* and *squares* widths of male hemipenes (means of right and left), *solid line* and *circles* width of the female cloacal vestibule]

(1) Because large females are stronger than small males (see above), they should be better able to resist harassment (e.g., Crean and Gilburn 1998). Hence, if copulation reflects successful harassment, we expect that large females will mate primarily with large rather than small males. Analysis of the sizes of copulating snakes confirms a highly significant trend to size-assortative mating (male vs female SVL, n=109, r^2=0. 09, P<0.0001; see Shine et al. 2000b for further discussion).

(2) Both cloacal and hemipenis sizes increase with body size, but at very different rates (Fig. 5). This difference in slopes can be shown with a one-factor heterogeneity of slopes test (sex as the factor, SVL as the covariate, and genital size as the dependent variable: $F_{1,99}$=27.61, P<0.0001). Females <45 cm SVL are physically incapable of mating with most males, whereas females beyond this size can mate with almost any male (Fig. 5).

Female body size versus weather conditions at emergence

If small females are disadvantaged by intense courtship, they may benefit by emerging and dispersing from the dens during unusually cool weather, when they attract less courtship. This hypothesis predicts that females too small to copulate (<45 cm SVL) should emerge primarily on days with low ambient temperatures. To test this prediction, we obtained data on minimum ambient temperature for each day during May 1997 from a nearby town (see above) and sampled snakes around the den twice each day (mid-morning and mid-afternoon). In keeping with our prediction, small females constituted a higher proportion of snakes found emerging and dispersing from the den on cooler days (minimum temperature vs proportion of all snakes consisting of females <45 cm SVL: n=10 days, mean of 82.3 snakes per day, r^2=0.73, P=0.0015).

Effects of courtship on females

Field observations suggest that females attempt to escape from intense courtship and (especially in the case of large females) often succeed in doing so. The trials in outdoor arenas allowed us to test this proposition experimentally, by comparing the behavior of females of various size classes when exposed to different levels of courtship. We used a two-factor ANOVA to analyze these data, with female size class and number of males per arena as the factors, and female activity (proportion of time active) as the dependent variable. All females were courted continuously throughout the trials, but at different intensities depending on the operational sex ratio within the arena. Figure 6 shows that the proportion of time females spent moving was related to body size, with larger females more active overall ($F_{2,147}$=8.75, P<0.0003). Female activity level was also affected by the number of males in the arena: females exposed to no males or only 6 males were similar in this respect, and less active than females exposed to courtship from 12 males ($F_{2,147}$=13.33, P<0.0001; post hoc Fisher's PLSD tests confirm that females were more active in the 12-male treatment than in the other two). Although the increased activity in 12-male trials was seen in all female size classes, the proportional increase was greater in small females (e.g., comparing 6- vs 12-male trials, increases of 50% for large females, 75% for medium females, and 350% for small females; Fig. 6).

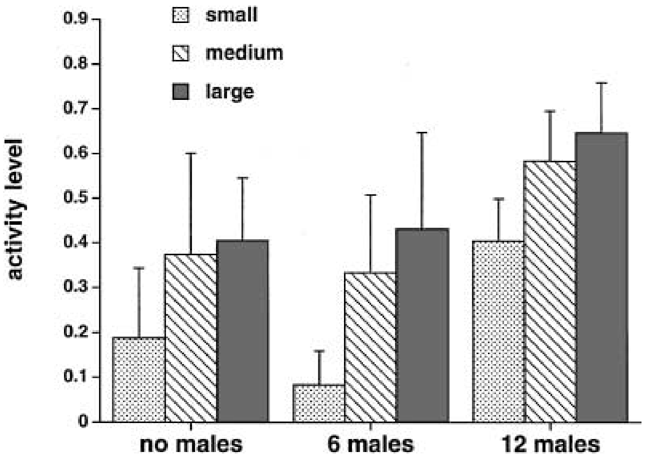

Fig. 6 Activity levels (proportion of sampling occasions when the animal was moving rather than stationary) of female garter snakes in outdoor arena trials. The females were grouped into three size classes: small (SVL <45 cm), medium (SVL 45 to 55 cm), and large (SVL >55 cm). The arenas contained no, 6, or 12 males. Mean±2 SE. See text for statistical tests

Discussion

We suggest that female garter snakes experience a "cost" in being physically buffeted by males during courtship, and hindered from dispersing from the den. The alternative view would be that female garter snakes do not experience significant "costs" from male attention, and that the interaction between the two sexes is simply one that ensures that females obtain sperm that they will need for the production of offspring. For example, females resisting copulatory attempts may thereby tend to mate with larger more vigorous partners, with a consequently enhanced viability of their progeny (e.g., Allen and Simmons 1996). Below, we examine questions that arise from our study, in terms of the sequence of behaviors involved in mating.

Why do males court juvenile females?

Given the relatively brief mating season, we might expect males to be highly selective and only court females large enough to produce offspring. This is clearly not the case. Males court all females in the general vicinity of the den, although they devote more vigorous courtship to larger females (e.g., Aleksiuk and Gregory 1974; Gartska et al. 1982). This unexpected finding may reflect the difficulties faced by males. The few adult females that emerge are often covered by hordes of competing males, so that males may be under strong selection to detect and respond to any snake that bears even a slight resemblance to a reproductive female. This argument also fits well with the existence of female-mimics at the Manitoba dens. Male snakes that produce female-like skin lipids ("she-males") attract considerable courtship from other males (Mason and Crews 1985, 1986; Shine et al. 2000a).

Does courtship entail a "cost" to females?

A few females are actually killed (suffocated) under piles of courting males, but this occurs rarely (Shine et al. 1999, and unpublished data). More often, females are simply delayed in their attempts to leave the den and its vicinity. Although such a delay may only involve a day or two, it may nonetheless considerably increase female vulnerability to predation. Crows kill many snakes around the den, and disproportionately take females rather than males, and small rather than large individuals (Shine et al., unpublished data). These biases may partly reflect the tendency of small females to disperse in unusually cool weather, when they are less able to escape from the predator.

Can males obtain copulations by harassment?

Given their elongate and flexible bodies, it would seem unlikely that a male snake could force a female to copulate (Devine 1984). Indeed, a review by Gillingham (1987, p. 191) concluded that "although some authors have speculated that copulatory adjustment is brought about by the male ... with little or no female participation ..., it is now well established that female cloacal gaping is necessary for intromission". However, examples of male-male copulation, and copulations with dead or dying females, challenge the generality of this assertion (Hardy 1998). Male garter snakes cannot copulate if females actively resist their attempts, but they can do so if the female does not resist. Arena trials confirm that females sometimes refuse to copulate despite prolonged vigorous courtship by many males. However, this is not the same as saying that active female co-operation is necessary for intromission (above). Male garter snakes frequently copulate with dead females, dying females, and injured (usually by crow pecks) females. We have observed literally hundreds of such copulations: very obviously, these do not involve active co-operation from the female. We also recorded one case of copulation with a female-mimic (Pfrender et al., in press). As noted above, matings with dead and dying females (sometimes of species different from the male) have also been reported in captive snakes of other species (Klauber 1956; Hardy 1998).

Actively courting male garter snakes align their bodies with that of the female, and powerfully contract their lateral musculature to generate caudocephalic waves that push strongly against her body (e.g., Whittier et al. 1985). Given that the male is stronger and faster than the female, and generally also warmer (Shine et al. 2000c), he may be able to induce substantial stress by vigorous courtship. Males twist their tails underneath the female's tail and lift it up; intromission occurs when the female's cloaca gapes open (personal observatoin). Males may exploit a characteristic anti-predator behavior to induce females to lift their tails. When a human approaches a red-sided garter snake and pins its body to the ground, the immediate response (elicited in <5 s in 25 of 25 trials) by both male and female snakes involves raising the tail-tip and waving it in the air (R. Shine, unpublished data). This response may normally function to attract the predator's attention to the (disposable) tail-tip (Willis et al. 1982), but may also enhance a male's opportunity to intromit.

Nonetheless, a male cannot copulate with a healthy female unless he obtains some limited co-operation from her (i.e., she must relax the musculature around her cloacal opening). If she is too small to produce offspring, why co-operate? Copulatory behavior unrelated to reproductive output has been recorded in females of a wide variety of species (e.g., Hrdy 1986; De Ruiter et al. 1994; Poldmaa et al. 1995). These non-reproductive matings have been interpreted as non-adaptive consequences of high sex steroid levels (e.g., Symons 1979) or because the costs of resisting male courtship may eventually outweigh the costs of accepting an "unnecessary" copulation (e.g., McLain and Pratt 1999). Alternatively, a female may enhance her reproductive success by mating, even if she does not use the sperm obtained in that copulation to sire her offspring. For example, females that mate more often than is necessary for reproduction may enhance their nutritional status through nuptial gifts or sperm acquisition (Ward and Landolt 1995), or may be able to manipulate the subsequent behavior of their male partners (Hrdy 1986; De Ruiter et al. 1994). In garter snakes, females that mate may thus manipulate not only the behavior of their mate, but also of all other males in the vicinity. After copulation, females rapidly lose their attractiveness to males, because the scent of copulatory fluids discourages male courtship (Devine 1977; Ross and Crews 1977, 1978; Whittier et al. 1985; Shine et al., 2000d). Thus, a female that copulates can thereby disperse from the den with less harassment by courting males.

Because studies on reptiles have generally interpreted copulations strictly in terms of sperm transfer, most herpetologists have tacitly assumed that mating only occurs in circumstances where the sperm that are transferred are likely to contribute to paternity of a female's offspring. The inference is logical and plausible, but definitive evidence is weak. In two viperid snake species, field studies indicate that females copulate only in years when they are likely to produce offspring (Isogawa and Kato 1995; Naulleau et al. 1999). However, earlier studies on one of these species reported mating even by non-reproductive females (Saint Girons 1952). The contradictory results may reflect female opportunities to escape; non-reproductive female vipers mate in captivity, but not in the wild (X. Bonnet, personal communication).

What determines the minimum body size at mating for females?

The conventional answer to this question would be that females do not copulate until they are large enough to produce offspring. Instead, our data on garter snakes suggest that females begin copulating at the minimum body size at which they are physically capable of doing so. The most likely physical constraint involves the size of the female's cloacal chamber compared to the size of the hemipenis that it must accommodate during copulation (Fig. 4). Although we interpret the correlation between cloacal size and mating as evidence for a body size constraint on mating, the argument could be reversed. That is, the same pattern would result if relative cloacal size evolved to fit some optimal "body size at first mating."

Consequences of harassment

Mating by non-reproductive females has several implications. The first of these is a methodological one. Studies that use molecular techniques to assign paternity have shown that simply measuring the number of copulations that a male achieves (as is often done in behavioral ecology studies) may provide a misleading measure of his reproductive success (e.g., Poldmaa et al. 1995). In such cases, the error is attributed to unseen copulations, or to post-mating effects (e.g., sperm competition). Our study reveals another source of error: some of the females that copulate may be too small to produce offspring, and hence these matings have no effect on male reproductive success in genetical terms. In turn, this bias could modify conclusions concerning the determinants of male fitness. For example, size-assortative mating within this population means that numbers of copulations substantially underestimate reproductive success of large males relative to smaller conspecifics, not only because larger females tend to have more offspring (e.g., Gregory 1977), but also because many of the smaller females may not actually use that sperm to produce offspring.

Various aspects of garter snake biology may reflect the "costs" of sexual coercion.

1. Size-assortative mating. Size-assortative mating in this system can occur even in the absence of male-male interaction (Shine et al. 2000b and unpublished data). Thus, size-matching may be related to physical struggles between the male and female.
2. The tendency of small females to emerge in cold weather. Predation by crows is intense around the dens, with small female snakes disproportionately at risk (Shine et al., unpublished data). The bias in predation toward these animals may reflect both their size and the fact that they are frequently active during unusually cool weather (see above). Plausibly, activity by small females at such times is favored because of lowered levels of coercion. An alternative hypothesis would be that smaller body size enables the young females to heat faster than larger conspecifics, and thus emerge under cooler conditions. This interpretation is not consistent with the similarity in body sizes between adult males and juvenile females, nor

with studies showing that a garter snake's body size exerts only a trivial effect on its rate of heating (Shine et al., in press a).

(3) Avoidance of dens by juvenile snakes. Many studies on garter snakes have shown that young-of-the-year snakes do not return to their parents' den for their first winter. This phenomenon has generally been attributed to the availability of alternative overwintering sites: small snakes can physically penetrate deep underground in the myriad small crevices available, and thus do not need to seek out the few large dens (Gregory 1974, 1982). However, this hypothesis cannot explain the total absence of young-of-the-year animals at the communal dens. We have never seen a single first-year snake at the dens, among tens of thousands of older snakes. Given the suitability of surrounding swamps as summer habitat for garter snakes, chance would dictate that a few hundred yearlings, at least, would overwinter at the dens each year. Their absence suggests that they actively avoid the large dens. The "costs" of harassment offer a plausible reason for such avoidance, especially given the small body size of the yearling animals. This explanation would apply to males as well as females, because newly emerged males are actively courted by other males (Shine et al. 2000a).

Two puzzles remain, however. First, why do yearling females use the communal dens (and thus accept harrassment by males) if other overwintering sites are available? Second, young-of-the year tend to avoid communal dens in other snake taxa, including species that do not mate immediately after spring emergence (Gregory 1982). These observations suggest that ontogenetic shifts in overwintering sites may be affected by several factors, with sexual conflict being only one component.

(4) Copulation by juvenile females. Females copulate at body sizes well below those at which they give birth (Fig. 2). As noted above, the simplest explanation for this phenomenon is that juvenile females benefit from copulation because it means they are ignored by males during the subsequent period of dispersal. Alternatively, juvenile females might store sperm within their oviducts and ultimately use this sperm to fertilize ova the following year. Given the apparent advantages of multiple mating to females in some snake species (Madsen et al. 1992), and the high frequency of multiple mating in female garter snakes in some populations (Schwarz et al. 1989), juvenile females might actually enhance their reproductive fitness by accepting sperm in this way.

(5) Female mimicry. Male red-sided garter snakes at the Manitoba dens exhibit female-like skin lipids in the period immediately after they emerge from hibernation, and thus attract considerable courtship from other males at this time (Mason and Crews 1985, 1986; Shine et al. 2000a). After regaining their strength, locomotor speed, and courtship ability, the males produce a male-identifying lipid (squalene: Mason et al. 1987) and cease to be attractive to other males (Shine et al. 2000a). Although this phenomenon has always been interpreted as males mimicking females, the argument can be turned on its head. Females may have evolved to mimic males, because of the consequent reduction in sexual harassment (as in some butterfly species: Cook et al. 1994). In turn, males would evolve a substance (such as squalene) that unambiguously marks their sex (and hence, makes them unattractive to other males). In the consequent "arms race" between the sexes (e.g., Clutton-Brock and Parker 1995), she-males might reflect the ancestral character state of males, before they have had enough time to produce the male identifier.

Conclusions

How general are our results? In particular, do mating systems in other snakes (or even other populations of garter snakes) also involve sexual conflict, harassment, and forcible copulation? At present, the data are too meager to evaluate this possibility. The high operational sex ratios at the huge Manitoba dens may exacerbate the degree of harassment far beyond that seen in other systems. Nonetheless, courtship behavior among snakes shows considerable diversity, and some of the behaviors of courting males may function to force female receptivity. For example, some male colubrids bite the neck of the female during coitus (e.g., *Elaphe*, *Lampropeltis*, *Pituophis*: Gillingham 1987), some pythons (*Liasis*) grip the female with body coils (T. Madsen, personal communication), and some elapids (*Ophiophagus*) and sea-snakes (*Emydocephalus*) prod the female very firmly with their snout (Guinea 1996; R. Whitaker, personal communication). Unfortunately, the possibility of male-female conflict during courtship has attracted very little attention. We will need detailed behavioral studies on other snakes before we can evaluate whether or not sexual conflict is an important general feature of snake biology.

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