Mechanisms and consequences of sexual conflict in garter snakes (*Thamnophis sirtalis*, Colubridae)

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Red-sided garter snakes (*Thamnophis sirtalis parietalis*) court and mate in early spring around large communal overwintering dens in central Manitoba. Emerging females are immediately covered by dozens or hundreds of vigorously-courting males, potentially imposing significant costs to the female. By manipulating numbers of courting males (both directly and by applying anticourtship pheromones), we quantified the degree to which female dispersal from the den is hindered by courtship. Courted females dispersed only about half as fast as did solitary females. Blood lactate levels were higher in mating than in courting or noncourting snakes of both sexes; the high levels of lactate in mating females support the idea that courtship is physiologically stressful to these animals, perhaps via constraints to female respiration. In arena trials, females that were exercised to exhaustion before courtship mated with smaller males than did control females. The spatial distribution of snakes around the den exhibits substantial heterogeneity, with densities often varying markedly between adjacent areas. Arena trials mimicking this heterogeneity showed that unmated females avoided parts of the enclosure containing scent cues from males. Our data support the hypothesis that courtship in *T. s. parietalis* confers significant costs to females, and that female behaviors have evolved to reduce those costs. *Key words:* courtship, dispersal, harassment, mating, reptile, stress. *[Behav Ecol 15:654–660 (2004)]*

Males and females maximize their reproductive success in different ways, so that conflict between the sexes is almost inevitable (Chapman et al. 2003; Rowe and Arnqvist 2002). That is, the behavior of one sex will generally impose some "cost" to members of the other sex, in currencies such as increased energy expenditure or an enhanced risk of injury or death. For example, females of many species require vigorous and persistent courtship before accepting a copulation. This behavior (sales resistance by the female; Arnqvist and Rowe 2002; Williams, 1966, 1975) may enhance her fitness by ensuring that she mates only with vigorous (genetically suitable, nondiseased) partners but also imposes a substantial energy cost on the male. Similarly, a female that accepts a mating but then does not use that male's sperm for fertilizing her eggs also imposes a cost (in nutrient allocation, energetics and risk associated with courtship, etc.; Watson et al. 1998) for no fitness benefit to the male (Brooks and Jennions, 1999; Gavrilets et al. 2001; Olsson and Madsen, 1998; Olsson et al., 1996).

In the same way, males may impose costs on females. This is most obvious in species in which reproductive males kill the offspring of other males or inflict significant injury to females in the course of forcible insemination attempts (Berry and Shine, 1980; Clutton-Brock and Parker, 1995; LeBouef and Mesnick, 1990; McKinney et al., 1983; Smuts and Smuts, 1993; West-Eberhard et al., 1987). There may be more subtle negative consequences for courted females even in taxa without such overt aggression by males, in which scientists have traditionally interpreted male-female courtship interactions in terms of ritualized persuasion. For example, a male's courtship behavior may attract the attention of predators to the female (Andersson, 1994; Gregory, 1977; Slip and Shine,

1988) or reduce her opportunity to feed (McLain and Pratt, 1999; Rowe et al., 1996; Stone, 1995; Watson et al., 1998).

Snakes offer a good example of a major lineage in which male-female interactions traditionally have been viewed as cooperative rather than in conflict. An influential review by Devine (1984) argued that forcible insemination was impossible in snakes because their elongate body form prevents males from restraining females for forced intromission. Devine speculated that this lack of forcible insemination (e.g., unlike in lizards) was an underlying cause for many of the patterns observed in snake reproduction. Subsequent investigators have generally followed Devine's suggestions, and the possibility of forcible insemination and sexual conflict has attracted little attention in discussions of mating systems in snakes (Duvall et al., 1992, 1993; but see Schuett, 1992). The putative impossibility of forced insemination has direct implications for interpretations of other aspects of reproductive biology. For example, a recent major analysis of mating seasonality in viperid snakes was based on the premise that the seasonal timing of female receptivity ultimately determines the seasonal timing of mating (Aldridge and Duvall, 2002). Similarly, multiple mating by females is often attributed to cryptic female choice among sperm from rival males (Birkhead and Moller, 1998). If forcible insemination is possible, such interpretations may be in error.

Field studies at large communal dens of garter snakes (*Thamnophis sirtalis*) challenged the view of snake reproduction as an essentially cooperative interaction between the sexes. Instead, males may impose substantial costs on females (Shine et al., 2000b). Many courting males swarm over each newly-emerging female, with the result that some females are crushed to death (Shine et al., 2001b) and survivors are impeded in their attempts to leave the den, thus extending the duration of their exposure to predatory crows (Shine et al., 2000b). Juvenile females accept copulations, either because they are unable to resist them or because the resultant

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copulatory fluids discourage other males from courting and, hence, facilitate the female's unencumbered escape from the den (Shine et al., 2000b).

The present article continues this exploration of sexual conflict in garter snakes. Our main purpose is to build upon the descriptive, inferential data sets of the previous work to conduct experimental studies on aspects of potential male-female conflict and, hence, to obtain more robust tests of relevant hypotheses and assumptions. We focus on the following questions: (1) to what degree does courtship impede a female's ability to disperse from the den, (2) does courtship impair female respiration and cause exhaustion, (3) does exhaustion modify a female's propensity to mate, and (4) do females actively evade courtship, by avoiding areas that contain pheromonal cues from males?

METHODS

Study species and area

In the Interlake region of central Manitoba, winter temperatures fall so low that snakes must use very deep (and thus relatively scarce) underground crevices to avoid freezing. Thus, red-sided garter snakes (*Thamnophis sirtalis parietalis*) return to communal dens in autumn, emerging 8 months later in spring (Gregory, 1974, 1977; Gregory and Stewart, 1975). Juvenile snakes do not use these dens (Gregory, 1974). Adult males typically remain near the den for about 2 weeks, intercepting newly-emerging females, recognizing their sex by vomeronasal detection of pheromonal cues (skin lipids; Mason et al., 1987, 1989), and vigorously courting them in "mating balls" that may contain more than 100 males (Shine et al., 2001a). Adult male *T. s. parietalis* average 45-cm snout-vent length (SVL), smaller than that of females (60 cm). We worked at a communal den containing approximately 10,000 garter snakes 1.5 km north of the town of Inwood, 250 m east of Highway 17 in central southern Manitoba (50°31.58′ N 97°29.71′ W) in May 2001 and 2002, and conducted the following experiments.

Does courtship impede a female's ability to disperse from the den?

Our previous study on the effects of male courtship on female mobility involved very artificial conditions (a dead male taped to a female's back; Shine et al., 2000b). To obtain a more realistic view of the effects of male courtship on female attempts to disperse from the den, we adopted the following procedure. We cut the bases out of plastic garbage cans (diameter, 45 cm; height, 60 cm) and placed them in the center of a flat rocky area, 30 m from the Inwood den. Weather conditions remained fine and clear throughout the trials. We collected 10 adult males from nearby courting groups, placed them in one of the bins, and then added an unmated female collected earlier that day. Unmated females are easily recognized because they lack a mating plug (Devine, 1977; Shine et al., 2000c). The snakes were left for 2 min to allow courtship to commence. We then scored the number of males actively courting the female, before lifting the bin vertically so that the snakes were free to disperse. The female's tail was gently tapped with a meter rule to stimulate her to move, and we continued this practice as she traveled. After she had moved approximately 4 m, we scored her position (distance from the release point), the elapsed time since release, and the number of males still courting her. We measured actual distances traveled rather than straightline displacement. Two other treatments were also used; all had 10 replicate females (one per bin per trial), and the order of treatments was randomized. The control treatment was identical to the procedure above except that no males were added to the bin, and thus, the female was not courted before her release. The second alternative treatment involved addition of 10 males, as above, but before we added the female to the bin we smeared her body with copulatory fluids from mating pairs found nearby. These fluids act as pheromones that discourage courtship (Shine et al., 2000c). Thus, both of the latter treatments serve as controls to evaluate distances traveled by females in the absence of courtship.

Does courtship impair female respiration and cause exhaustion?

If courting males make it difficult for females to breathe normally (as suggested by the observation of females being suffocated, in extreme cases, by the mass of courting males), then females may switch to anaerobic metabolism because of their inability to maintain aerobic function. This scenario predicts that levels of blood lactate (indicating anaerobic metabolism) of females should increase during prolonged courtship (Moore and Mason, 2001; Moore et al., 2001; Ruben, 1976; Schuett and Grober, 2000). If such an increase is part of male tactics to induce cloacal gaping (as suggested by Shine et al., 2003), then we expect females found mating at the den to exhibit higher lactate levels than other females (i.e., that are not being courted, or are being courted but have not yet mated). All females at the den are courted and virtually all males spend most of their time courting, so in order to include noncourted controls, we placed females and males separately for 60 min in outdoor arenas (open-topped nylon boxes, $1 \times 1 \times 1$ m) near the den. Pilot studies showed that lactate levels of snakes in arenas were indistinguishable from those of free-ranging snakes of the same sex and behavior category sampled from the den (data not shown). We obtained data on blood lactate for both sexes of snakes, and on three behavior categories: no courtship (in single-sex arenas), courtship (in the den), and mating (in the den). We took blood samples from the caudal vein by using heparinized 1-cm^3 syringes and 25-gauge needles. Blood samples were stored on ice until centrifuged and the plasma separated. Plasma samples were then stored in liquid nitrogen until return to Oregon State University, where they were stored at −70°C until assayed.

We measured plasma lactate concentrations spectrophotometrically with a Beckman model DU-530 spectrophotometer and a lactate oxidase colorimetric test kit (Sigma Diagnostics; procedure no. 735). Plasma was thawed at room temperature (21°C) and vortexed before assay; all samples were analyzed in duplicate. Briefly, plasma lactic acid is converted to pyruvate and hydrogen peroxide by lactate oxidase. Peroxidase catalyzes the oxidative condensation of Chromagen precursors to produce a colorimetric change in the solution that is read spectrophotometrically at 540 nm. A series of lactate standards (Sigma Chemical Company) were included with each assay to control for interassay variation and to generate a standard curve. Lactate concentrations (milligram per deciliter) of plasma samples were calculated by using the appropriate standard curve. If sample lactate concentrations were higher than 120 mg/dl (the highest lactate concentration provided in the Lactate Standards Kit; Sigma), then those samples were diluted with distilled water appropriately. Final lactate concentrations of diluted samples were adjusted accordingly to account for the dilution.

Does exhaustion modify a female's propensity to mate?

If females accept copulations only when they reach some level of physiological stress, we might expect females that were exhausted before courtship (by experimental manipulation)

to mate sooner than females that were not exhausted. Also, we might expect smaller males to be more successful at obtaining matings with exhausted rather than "fresher" females, because of lowered female resistance under these conditions. In unmanipulated systems, larger males obtain more matings both in the field and in outdoor arenas (Shine et al., 2000d, contra Joy and Crews, 1988). To test these predictions, we set up six open-topped nylon arenas near the den. Ten unmated females were added randomly to each arena. When first added to an arena, females move to the sides and attempt to escape. In three of the arenas, all females were picked up and repeatedly placed back in the center of the arena as soon as they crawled to the sides, for an hour. By the end of this time, females were noticeably slower, and many remained sedentary after displacement. Females in the other three arenas were left alone and soon settled down. We introduced 20 males to each arena at 1125 h and recorded the time at which copulations occurred. We removed all copulating pairs for later measurement, removing an additional unmated male at the same time to maintain constant sex ratios in all of the "courtship" arenas.

Do females actively avoid the scent of males?

Courtship activity at the den appears to be highly focused around sites where females emerge from the ground, with adjacent areas often containing few or no "mating balls." Thus, females that attempted to avoid courtship (as predicted under the hypothesis of sexual conflict) might be able to do so by selecting sites with fewer pheromonal cues from males. Such females would still have opportunities to mate as they dispersed from the den toward their summer ranges (Shine et al., 2003). To evaluate this idea, we conducted two studies:

Survey of snake densities
To document the highly nonrandom distribution of snakes, we set out eight equally spaced transects 15 m long and radiating out from a common origin, an emergence hole at the center of the den (i.e., 45 degrees apart). We scored the numbers of snakes in each 1×1-m quadrant centered along those transect lines, and did so six times at different times of day. These data thus provide a picture of the spatial distribution of snakes within the area around the den and, especially, the potential for a female to evade male attention by moving a few meters. If snakes are distributed uniformly through the entire area around the den, there would be little opportunity for females to avoid males.

Female responses to male scent
We set up four outdoor arenas (as above) near the den. Newspapers moistened with water covered the floors of all arenas, taped to the nylon sides to avoid snakes crawling beneath them. Half of the floor area of each arena was covered by newspapers that had been scented by exposure to 50 male garter snakes for 30 min; the other half of each arena was covered in newspapers that had been treated similarly but without exposure to males. Thus, half of each arena comprised a "stimulus" floor, and the other half consisted of "control" (unscented) newspaper. We added 12 unmated adult female snakes to each arena and let them settle down for 10 min. At 5-min intervals after that time, we scored the numbers of females on either side of the arena, then disturbed the snakes so that they moved around (to ensure that a snake's initial "decision" as to where to stay would not influence the entire data set). The newspaper covering the entire floor of the arena was sprayed with water at these times also. The location scores (position of each female's head in control vs. stimulus side) were taken 10 times for each arena, and the resulting data were
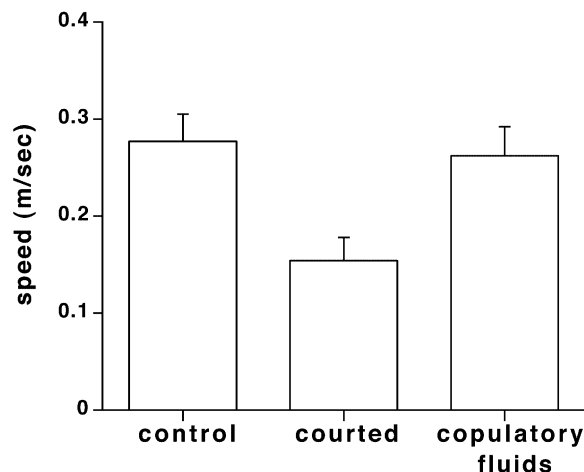

Figure 1
Locomotor speeds of female garter snakes (*Thamnophis sirtalis parietalis*) when tested over a distance of approximately 4 m under three conditions: alone (control), courted by an average of about seven males (courted), and smeared with copulatory fluid to discourage courtship. Sample size = 10 females per treatment. Graph shows mean values and one standard error. See text for statistical analysis.

analyzed with repeated-measures one-way ANOVA. The dependent variable for this ANOVA was the number of females with their heads above each half of the arena.

RESULTS

Does courtship impede a female's ability to disperse from the den?

Analysis revealed no significant differences among treatments in the mean body sizes of females (mean = 54.4–57.7 cm SVL, $F_{2,26} = 0.45$, $p = .64$) or in the distances over which they traveled during the trial (mean = 3.6–4.3 m, $F_{2,26} = 2.09$, $p = .14$). The number of males actively courting the female at the commencement of the trial obviously differed among treatments (zero for controls, 0.22 for copulatory-fluid trials, and 6.90 for courtship trials; $F_{2,26} = 57.49$, $p < .0001$). Females in the courtship treatment were accompanied by an average of 2.4 males at the end of the trial (versus zero for the other treatments, $F_{2,26} = 8.99$, $p < .0015$). Crawling speeds were much lower for females being courted by males than for females that were not courted ($F_{2,26} = 6.18$, $p < .007$) (Figure 1). Posthoc (Fishers PLSD) tests showed that courted females were significantly ($p < .05$) slower than were females in either of the other groups, with a decrement in speed of almost 50%.

Does courtship impair female respiration and cause exhaustion?

Do females mate only after they are under respiratory stress, such that they have to shift from aerobic to anaerobic metabolism? Two-factor ANOVA with sex and behavior as factors showed that the sexes exhibited similar mean levels of blood lactate (female, 76.16; male, 88.20 mg/dl; $F_{1,53} = 1.43$, $p = .24$) but that behavior affected lactate levels ($F_{2,53} = 18.79$, $p < .0001$; posthoc tests show mating higher than the other categories at $p < .05$). The effect of behavior on lactate levels was similar in the two sexes (interaction $F_{2,53} = 2.27$, $p = .11$) (Figure 2).
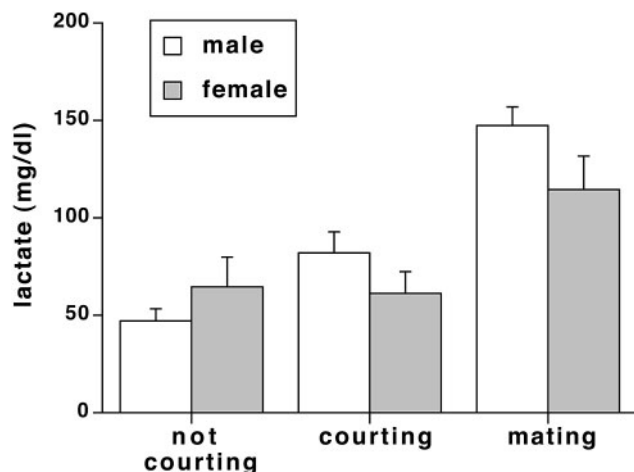
Figure 2
Blood lactate levels of male and female garter snakes
(*Thamnophis sirtalis parietalis*) engaged in three activities: not
courting (in single-sex outdoor arenas), courting (in the field), or
mating (in the field). Sample sizes (left to right) = 10, 11, 10, 12,
8, and 8. Graph shows mean values and one standard error. See
text for statistical analysis.

Does exhaustion modify a female's propensity to mate?

We recorded eight matings from the females that had been
exhausted before introduction of males, and 10 matings from
the control group. Larger males mated sooner (regression of
male SVL versus time to mate, $n = 18$, $r^2 = .28$, $p < .03$; the
same pattern was evident but not statistically significant within
both treatment groups). Including male body size as a co-
variate, times to mating were similar in the two groups (mean =
47.4 versus 33.0 min, $F_{1,15} = 0.005$, $p = .95$). However, the
mean body size of males that obtained matings in the
"exhausted female" treatment was lower than that in the con-
trols (mean = 41.08 ± 1.38 versus 46.42 ± 1.35 cm SVL, $F_{1,16} =$
7.52, $p < .02$).

Do females actively avoid the scent of males?

Surveys of snake densities showed that the numbers of animals
decreased dramatically with distance away from the center of
the den (Figure 3a). More than 5 m from the center, densities
averaged less than 20 snakes/m^2, less than a fourth of the
numbers at the center. More than 95% of these snakes were
males, so a female snake would often have the option of
moving to a nearby area where densities of males were much
lower than her current location. The distance she would have
to move would depend on her exact position, but 385 of 720
segments checked (53%) contained no snakes when scored.
Of the remaining 335 segments, 137 (41%) were adjacent to
a 1-m^2 area that did not contain any snakes at the time of
checking. This spatial heterogeneity in densities is apparent
from a plot of densities in adjacent areas (Figure 3b).
Although the two numbers are correlated ($n = 719$ quadrant
samples, $r^2 = .18$, $p < .0001$), there are many instances where
a 1×1-m area containing more than 200 snakes is immediately
adjacent to one with no snakes.

In the arenas divided into halves with either male or no
(control) scent, the relative numbers of females (out of 12 per
arena) in the scented versus control halves of their respective
arenas did not change across 10 observation periods (re-
peated-measures ANOVA, $F_{9,54} = 0.003$, $p = 1.0$). More females
selected the "unscented" than the "male-scented" side of the
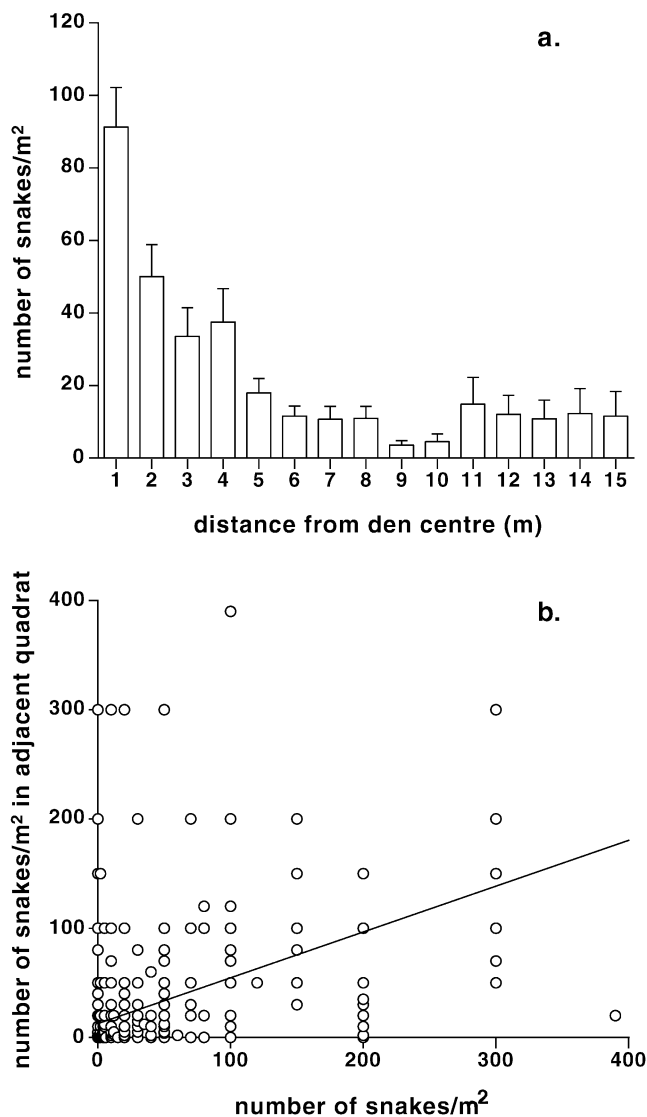arena (means of 4.0 vs. 8.2 females, $F_{1,54} = 60.32$, $p < .0002$).

Figure 3
Spatial distribution of garter snakes (*Thamnophis sirtalis parietalis*) at
a communal den near Inwood, Manitoba. The upper graph
(a) shows mean values and 1 SE for the number of snakes per
1×1-m quadrat at varying distances from the center of the den.
Data combined for six surveys conducted at different times of day, and
along eight transects radiating out from the den center. The lower
graph (b) plots the number of snakes in a 1-m^2 quadrat against
that in the adjacent quadrat (same transect, but further from the
den center). Data were deleted such that each quadrant appears
only once in this graph. See text for statistical analysis.

DISCUSSION

Our experimental data are consistent with the hypothesis that
courtship imposes a cost on female garter snakes, and that
these animals reduce that cost by avoiding areas with many
male snakes. The only previous analysis of sexual conflict in
snakes was also based on Manitoba *T. s. parietalis* (Shine et al.,
2000b) but provided much less direct evidence than is available
from the present study. The previous work inferred costs to
females based on their responses (e.g., mating by juvenile
females; female dispersal from the den during cold weather
when males were inactive), whereas the present study provides
experimental tests of the "sexual conflict" hypothesis.

Observations at the den show that every newly-emerging female (regardless of her body size, condition, or health) is soon covered by a writhing ball of male snakes, even before she has fully emerged from the ground (Shine R, personal observations). Females almost immediately attempt to begin dispersing from the den, a behavior likely to be under strong selection because of the high abundance of predators in the vicinity of the den (Shine et al., 2001b). Courtship impairs this dispersal; for example, females attempting to climb a steep rocky cliff surrounding the den frequently fall back to the floor of the quarry when they are dislodged by courting males (personal observation). Nonetheless, it is difficult to quantify such effects. The more realistic system adopted in the present study supports the conclusion of our earlier work (Shine et al., 2000b). It also confirms that copulatory fluids serve as sex pheromones in this population, discouraging male courtship to already mated females (Shine et al., 2000c). Finally, these data strongly support critical assumptions of the hypothesis that mating by juvenile females enables these animals to disperse from the den without harassment (Shine et al., 2000b).

Elevated levels of lactate in the blood of mating males (Figure 2) are not surprising; these animals court very vigorously, and virtually nonstop, for very long periods (Joy and Crews, 1985; Shine et al., 2000d). A switch to reliance upon anaerobic metabolism and a consequent lactate accumulation is expected, as it is after any vigorous activity in ectotherms (Ruben, 1976; Schuett and Grober, 2000). Equally high lactate levels in mating females (Figure 2) are more puzzling. Females typically move very little during courtship, so presumably expend relatively little energy at this time. Why shift to anaerobiosis? The most likely answer is difficulty with aerobic supply. The observation that some females are suffocated by courting males (Shine et al., 2001b) suggests that the male's combined mass or courtship behavior somehow obstructs normal respiration by the female. In other studies, we have confirmed that courting males can indeed expel most of the air from a female's lungs (Shine et al., 2003), offering a plausible explanation for the high lactate levels seen in the blood of mating females. The lactate data suggest that merely being courted did not necessarily impair respiration by females; but the only animals that mated were those that had shifted to anaerobic metabolism. Associations between high lactate levels and high cortisone levels after intense social encounters in other snake species suggest involvement of the hypothalamic-pituitary-adrenal axis (Schuett and Grober, 2000); in light of these results, it would be interesting to examine cortisone levels in courted garter snakes also.

Stressing a female during courtship might be an integral component of male tactics rather than an incidental consequence of vigorous courtship by males. That is, if stressed females are more likely to accept copulations, male courtship behavior might evolve so as to maximize stress to females (Shine et al., 2000b, 2003). This hypothesis predicts that by exercising females to exhaustion before courtship, we would facilitate male mating attempts. In practice, we saw no such effect; the duration of courtship before mating averaged slightly but not significantly longer in the experimental group (with exhausted females) than in the control group (with rested females). However, larger males obtained matings sooner than did smaller ones, and smaller males successfully obtained matings with exhausted females but not with control females. These patterns are consistent with the notion that prolonged courtship exhausts females, and this exhaustion may play some role in male courtship success.

The high spatial heterogeneity of snakes within the den area means that it is frequently possible to find nearby sites that differ dramatically in the numbers of mate-searching males (Figure 3). In turn, this heterogeneity provides the potential for females to avoid courtship by selecting a resting-site where males are scarce or absent. Realistically, all females close to the main den during warm weather attract courtship virtually all of the time, and males find females by a series of sensory modalities (including vision and temperature as well as chemoreception; Shine and Mason, 2001) that can operate over substantial distances. However, females can indeed find resting sites where they escape harassment during cool weather conditions when relatively few males are active, or in the grassland surrounding the den where snake densities are much lower, or at smaller dens (Shine et al., 2001a; Shine R, personal observations). Our arena studies provide empirical evidence that females avoid male cues. Previous work showed that females were more active when courted, perhaps reflecting attempts to escape (Shine et al., 2000b), and that female garter snakes may avoid pheromonal trails left by males (LeMaster et al., 2001).

In the communal snake-dens of Manitoba, courtship may confer benefits as well as costs. Studies on female-mimicking males (she-males) suggest that courtship to these animals confers benefits in terms of thermoregulation (heat transfer from courting males) and, more importantly, protection against crow predation (because the courted animal is hidden beneath a group of conspecifics; Shine et al., 2001d). Presumably, courted females obtain some of the same benefits. However, females are courted much more intensely than she-males (Shine and Mason, 2001) and therefore the costs are likely to far outweigh any such benefits, resulting in a battle between the sexes that could influence the evolution not only of habitat selection by females (above) but also aspects such as their mating behavior, timing of dispersal, and size-assortative mating (Shine et al., 2000b). Both the pheromonal composition of female lipids and the ability of males to detect such cues may be under intense selection as part of an "arms race" between the sexes, as reflected by geographic differentiation in these traits (LeMaster and Mason, 2003; Panhuis et al., 2001; Shine R and Mason RT, in preparation). Thus, sexual conflict may have played an important role during the evolution of the mating system in this population.

Sexual conflict could influence mating-system evolution via many pathways. For example, the reproductive frequency of females could be depressed by energy expended during courtship, by delays in dispersal from the den leading to reduced feeding opportunities before ovulation or to injuries resulting from predator attack during enforced residency near the den. Avoidance of males may compromise thermoregulation by females, if heavier cover (and thus, lower exposure to solar radiation) offers the only concealment and if females are forced to emerge during cooler periods when males are less active (Shine et al., 2000a). Mortality at the den, either during courtship or through predation, may ultimately affect sex ratios of adult snakes (Shine et al., 2001b). In combination, reduced reproductive frequency and higher mortality of females would exacerbate the male bias in operational sex ratio, further intensifying the magnitude of sexual conflict because males will mainly court the (reduced) number of reproductive females each year (Hawley and Aleksiuk, 1975, 1976; Shine et al., 2001c). Such a positive feedback system might ultimately lead to very substantial conflict between the sexes. Although the massive aggregations of courting animals in this population intensify the extent of sexual conflict, strong phylogenetic conservatism of many features of courtship behavior in snakes (Gillingham, 1987) suggests that conclusions from our study may apply much more widely than to red-sided garter snakes alone.

More generally, sexual conflict may be a significant influence on mating systems in many kinds of organisms for

which interactions between the sexes in courtship have traditionally been interpreted in terms of persuasion rather than costs. Snakes are a good example because their elongate flexible body seems to make it impossible for a male to forcibly restrain (and, hence, copulate with) a female (Devine, 1984). In keeping with this inference, courtship in snakes only rarely includes any elements (such as biting) that are overtly aggressive, and even these have usually been interpreted as mechanisms to facilitate male-female cooperation in mating (Gillingham, 1987). The discovery that courting male garter snakes impair female dispersal and induce physiological stress, and that females attempt to evade males, suggests that sexual conflict may be widespread and important even in superficially nonconflictual mating systems.

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