

Do Female Garter Snakes Evade Males to Avoid Harassment or to Enhance Mate Quality?

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ABSTRACT: Females of many species behave in ways that make it difficult for males to locate, court, and inseminate them. Two hypotheses have been advanced to explain such behavior: either a female thereby minimizes costs of harassment (sexual conflict model) or by playing “hard to get” she discourages inferior suitors (indirect mate choice model). Our studies of garter snakes (*Thamnophis sirtalis parietalis*) at a communal den in Manitoba support an interpretation of sexual conflict rather than indirect mate choice. Female snakes dispersed rapidly from the den through areas with relatively few males rather than waiting for additional courtship. Many females dispersed without mating. Experimental (pheromonal) manipulation of the intensity of courtship accelerated rates of female dispersal rather than delaying dispersal, as would be predicted if females wait to obtain matings. The behaviors of females escaping from courting groups were maximally effective in losing their suitors regardless of the number of courting males or whether or not the female was capable of mating (recently mated females cannot mate again because of a mating plug). In total, our data are most consistent with the hypothesis that female garter snakes at communal dens evade males to escape harassment rather than to enhance mate quality.

Keywords: dispersal, mate choice, mating system, sexual conflict, sexual selection.

In many animal species, females display distinctive behaviors that impair the ability of males to find, court, and inseminate them. Such behaviors include direct rebuffs to

male attempts at courtship and mating, fleeing from the approach of a male, and selecting habitats where the female will be more difficult to find or court (e.g., Booth and Peters 1972; Partridge and Hurst 1998; Pilastro et al. 2003). Although such behaviors are widespread, their adaptive significance remains controversial, with two main opposing interpretations: sexual conflict and indirect mate choice.

The simplest interpretation of female evasion behavior is that it functions to reduce costs due to sexual harassment; for example, courtship may inflict physical injury or incur energy costs, and matings may introduce risks of disease and vulnerability to predation (Partridge and Hurst 1998; East et al. 2003). In this “sexual conflict” view, females behave to minimize such costs (Arnqvist and Rowe 1995, 2002; Arnqvist et al. 2000; Cooper and Telford 2000; Moore et al. 2003). However, an alternative and more complex interpretation also is consistent with such behaviors. If potential mates vary in quality (in terms of the genes they will provide to progeny and/or the resources they can provide during the reproductive bout), a female may benefit from mating only with the “best” male, discouraging all others (Eberhard 2002; Eberhard and Cordero 2003). Thus, female behaviors that impaired male attempts at courtship might function as a mechanism of indirect mate choice whereby only the fittest males would be able to surmount these obstacles and obtain matings. In anthropomorphic terms, a female benefits from playing “hard to get” because she thereby discourages inferior-quality males.

Despite the profoundly divergent nature of these two interpretations, in practice they generate almost identical predictions, and indeed, they are not mutually exclusive: a single behavior might influence fitness by both pathways (e.g., Cordero and Eberhard 2003). We cannot hope to objectively assess the female’s “motivation” for such behaviors and thus can test between these alternative interpretations only by gathering detailed information on the form and consequences of female behavior. A vigorous debate about how we could proceed to resolve this ambiguity has generated calls for additional studies, especially

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under field conditions and on a more diverse array of organisms; for detailed mechanistic data on the nature and consequences of interactions between males and females; and for novel methodologies (e.g., Chapman et al. 2003a, 2003b; Córdoba-Aguilar and Contreras-Garduño 2003; Eberhard and Cordero 2003). Especially if experimental manipulations of traits such as female behavior or the intensity of courtship are feasible, we may be able to quantify functional associations between female behaviors and male responses and thus identify situations where the hypotheses of “sexual conflict” and “indirect mate choice” generate divergent predictions.

Garter Snakes as a Model System

Although they have rarely been utilized in this context, snakes provide excellent model organisms for studies on sexual conflict and indirect mate choice. In particular, recent research at large communal dens of red-sided garter snakes (*Thamnophis sirtalis parietalis*) has revealed intense sexual conflict. Near the northern limit of their geographic range in the Interlake region north of Winnipeg, Manitoba, in central Canada (Rossman et al. 1996), these small (<1 m total length) nonvenomous snakes spend about 8 months/year inactive in communal winter dens, emerging in early May to court and mate before dispersing to feed and give birth in the surrounding swamps and grasslands (Gregory 1974, 1977; Gregory and Stewart 1975). Because dens may contain >50,000 snakes, densities of snakes close to the den may exceed 100/m² (Shine et al. 2001b).

Newly emerging females are rapidly located and vigorously courted by dozens or hundreds of males. The most distinctive courtship tactic by males involves caudocephalic waving, a series of muscular contractions that travel from the male's cloacal area to his head (Noble 1937; Gillingham 1987). These waves push anoxic air from the female's avascular lung anteriorly to her respiratory surfaces, thus impeding breathing and inducing the stress response of cloacal gaping and thereby allowing intromission of the male's hemipenis (Shine et al. 2003a). Thus, males obtain matings by forcible insemination via induction of hypoxic stress in females (Shine et al. 2003a); indeed, some females die from suffocation within large mating balls (Shine et al. 2001a). However, sexual conflict is less intense as soon as the females disperse into the woodland surrounding the den. Radiotelemetric monitoring indicates that many females disperse tens of meters before mating (Shine et al. 2001b). The mean number of males per mating ball decreases rapidly away from the center of the den, so most courting groups in the surrounding woodland are relatively small (mean 4.0 males plus one female: Shine et al. 2001b). Radiotelemetric monitoring reveals that females are solitary as they disperse (Shine et

al. 2001b); thus, a female that leaves the den without mating is unlikely to mate thereafter, at least during dispersal to the summer range (which may be up to 18 km away from the den; Gregory and Stewart 1975). Females can use stored sperm from autumn mating to produce offspring; however, this is rare because spring mating plays an important role in inducing vitellogenesis, and stored sperm are evacuated as soon as a female remates in spring (Halpert et al. 1982). We do not know if mating also occurs immediately prior to ovulation, at the summer range.

Previous research has suggested that courtship impedes female attempts to disperse from the den (based on displacement rates of courted and noncourted females over short distances) and that females actively avoid the scent of males in arena trials (Shine et al. 2004) as well as when following substrate-deposited pheromonal trails (LeMaster et al. 2001). Although attributed to sexual conflict, such avoidance behavior might equally be viewed as a form of indirect mate choice whereby females impose selection for traits such as courtship persistence or superior mate-finding ability in their male partners (Eberhard 2002). We quantified the behavior of female garter snakes at a large den to explore the degree to which female movement patterns are consistent with either sexual conflict or indirect mate choice.

Potential Forms of Mate Choice by Female Garter Snakes

The “cooperative view” of snake mating systems would suggest that females benefit from mating prior to dispersal from the den; the availability of such mating opportunities (for both sexes) has been suggested as a possible benefit of communal overwintering in this species (Gregory 1982). Nonetheless, it is difficult to envisage how a female garter snake could exert mate choice, especially in large mating balls near the center of the den. Although male mating success is highly nonrandom (large, heavy-bodied, vigorous males obtain most matings), these biases are generated by direct coercion and male-male rivalry rather than active selection of a particular male by a female (Shine et al. 2000a; R. Shine, unpublished data). Indeed, it is difficult to imagine how a female garter snake could select a specific mating partner from within a jumbled mass of rivals, all of them actively and simultaneously attempting to insert their hemipenes into her cloaca (Shine et al. 2000a, 2003b).

Although the nature of courtship in this population thus reduces opportunities for mate choice by females, proponents of a mate-choice model might nonetheless argue that by remaining in the woodland near the den, a female could benefit by one of two pathways. First, a female that evaded courting males might thus delay mating until she is courted by only a small number of suitors; under such

circumstances, she might be able to discriminate between them and perhaps influence which male obtained the mating. Second, a female that remained close to the den would have the opportunity to mate with more than one male. Multiple paternity of litters is common in garter snakes (Garner et al. 2002), so a multiply mating female potentially could enhance the quality of her offspring by increasing opportunities for sperm competition within her reproductive tract (e.g., Olsson et al. 1996). However, because the gelatinous mating plug occludes the female cloaca for about three days postmating (Shine et al. 2000*d*), such a female would need to remain near the den for at least this period.

Predictions from Conflicting Hypotheses

Because of our inability to determine what kinds of male traits might be selected by females, we have framed our hypotheses in terms of female opportunity to exert mate choice rather than specifying or predicting what kinds of male traits would be the targets of such choice. The hypothesis of indirect mate choice generates specific predictions concerning the behavior of female garter snakes: (1) they will remain near the den longer than is required to recover from their overwinter inactivity (to allow mate choice or remating); (2) they will not leave the vicinity of the den without mating (because once they leave, their opportunity for mate choice is reduced; Shine et al. 2001*b*); (3) if a female postpones dispersal until she has received sufficient courtship to identify a suitable mate, a reduction in courtship intensity (for whatever reason) will delay her departure from the den; (4) as females leave, they will use routes where they will encounter (and thus, be courted by) many males; (5) females will tolerate prolonged courtship rather than attempting to evade their suitors (because prolonged courtship would allow the female to assess male phenotypes and thus select an appropriate mate); (6) females will attempt to escape from large courting groups but not small courting groups (because the latter provide better opportunities for mate choice); and (7) mated females will show different male-evasion behaviors than unmated females (because the former animals cannot remate until they have lost the mating plug and thus derive no benefit from assessing mate quality).

It is important that all of these predictions differ from those expected under the "sexual conflict" hypothesis. If females simply try to avoid males, we predict that (1) they will disperse as soon as possible; (2) many females will leave the den without mating; (3) a reduction in courtship intensity will expedite and not delay female dispersal; (4) females will select dispersal routes that are not used by males; (5) courted females will behave in ways that make it difficult for their suitors to remain with them; (6) fe-

males will attempt to evade all courting males, regardless of group size; and (7) mated and unmated females will behave in similar ways.

Methods

Study Area

During May 2003 and May 2004, we worked at a communal den containing >50,000 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). This den has been the focus of considerable previous research (e.g., Shine et al. 2000*b*, 2000*c*, 2000*e*, 2001*a*). In both 2003 and 2004, our work at the den encompassed most of the snake's emergence period that year.

Procedures

Every morning at the den in May 2003, we collected, measured, and paint marked any newly emerged snakes. These were often found actually emerging from the ground and were distinctive because of their muddy appearance and the frenetic courtship they attracted from males. Because males pass through a transient stage of female mimicry when they first emerge ("she-males": Mason and Crews 1985), the criterion of attracting courtship identifies newly emerged snakes of both sexes. Male snakes are courted only on their first day postemergence (Shine et al. 2000*b*, 2000*e*). We marked 939 newly emerged males and 956 newly emerged females over the 18-day duration of our 2003 study. All of these snakes were measured (snout-vent length [SVL]), weighed, and paint marked with an individual number and/or a daily cohort mark for later recognition. We also recorded whether or not females had recently mated as determined by the presence of gelatinous mating plugs; these persist for about 3 days postcopulation (Shine et al. 2000*a*).

To recapture some of these animals as they dispersed from the den, we set out a 60-m long hardware-cloth drift fence in the woodland 100 m away. Six equally spaced wooden traps with wire funnels, placed beside the fence, allowed ingress but not egress. The traps were cleared at least twice daily yielding data on duration of den residency for 290 marked snakes and directions of dispersal for 6,653 animals.

If females actively solicit copulations, experimental reduction of their attractiveness should delay female dispersal, but if females attempt to disperse without mating, reducing courtship levels should enable them to escape the den area more rapidly. To test this idea, we manipulated female attractiveness by painting the dorsal surfaces of newly emerged females with either peanut oil (control) or

peanut oil containing squalene (a lipid found in the skin lipids of male but not female garter snakes and thus potentially a sex identifier: Mason et al. 1987, 1989, 1990; Mason 1992, 1993). We then released all these females simultaneously in the den and walked around 30–60 min later to score the number of males courting each female and the distance that the female had dispersed from the release point.

If females attempt to avoid courting males, we predict that their patterns of movement when being courted should be those that are maximally effective at escaping from males. To answer this question we need data on what routes and speeds courting females take as they disperse from the den and how these movement patterns make it more difficult for courting males to follow. To answer these questions we quantified the following factors.

Movement Patterns of Females. Courted females frequently flee from the groups of males that are courting them, often in response to very vigorous courtship (especially male attempts to lift the female's tail from the ground; R. Shine, personal observation). We approached natural courting groups and lifted the female's tail with a stick, mimicking intense courtship. After one or two touches the female typically moved away rapidly, with some or all males attempting to remain beside her. We mapped the distance and direction she moved before stopping again and recorded the numbers of males courting her before and 10 s after her displacement. Where possible, we then collected the female to check whether she was mated or unmated (based on the mating plug).

Factors Influencing Male Ability to Relocate a Female. Fishing line was tied around the neck of a recently predator-killed female snake (65 cm SVL); this animal's movements were controlled with a 1-m stick tied to the other end of the 1-m length of fishing line. The dead snake was dragged near a mate-searching male or males; after they commenced vigorous courtship the female was moved (at normal crawling speed of 0.4 m/s; R. Shine, unpublished data) in one of four ways: straight-line, continuous movement for 4 m; straight-line movement, but stopping after 2 m; 1 m straight-line movement, then abrupt (110°) change in direction, then continue in that new direction; 1 m straight-line movement, then abrupt (110°) change in direction, then stop after 20 cm. In each case the number of males remaining with the female was scored as above.

Male Responses to Other Males. Our observations both of natural groups and of males following the dead female (above) suggested that the "turn-then-stop" behavior of females was effective in losing males because of the males' shift to visual rather than pheromonal cues for mate re-

location under these conditions. Thus, males that suddenly lost contact with the female (as she fled) generally stopped tongue flicking and instead lifted their heads well above the substrate ("periscope" position) as they moved rapidly in the direction in which the female had gone. Males followed any fast-moving snake in the vicinity, and typically these were either the female herself or another male in her pursuit. This reliance on movement meant that when a female stopped, the pursuing males generally kept going and often passed right over her body; because their heads were raised well off the substrate without tongue flicking, they generally failed to detect her presence.

To test the hypothesis that males use visual cues from other males during mate relocation, we attached a recently predator-killed male (47 cm SVL) to a fishing line as above, and laid him on the ground 20 cm from a natural courting group. We then induced the female to flee (as above) and pulled the male along the ground such that he crossed behind the female's tail at an angle of approximately 45°. We scored the number of males initially in the courting group and the number that approached and tongue flicked the "target" male over the next 10 s. We also scored male approaches to the dead male when he was simply laid out on the ground immobile 20 cm from a courting group and when he was moved along the ground beside the group but without inducing the female to flee beforehand.

Results

Our data reveal several strong patterns that help to distinguish between the "sexual conflict" and "indirect mate choice" hypotheses.

Females Dispersed Rapidly from the Den

The mean interval between a female's emergence at the den and her recapture at the drift fence 50 m away in the woodland was only 2.36 days (SE = 0.23, $n = 33$). Eight females reached the fence the same day they emerged, 21 in 2 days, and the remaining four in 3 days. In contrast, most males remained near the den for several days (mean = 6.16 days, SE = 0.25, $n = 239$; comparing duration of residency between the sexes, $F = 17.16$, $df = 1, 288$, $P < .0001$).

Many Females Dispersed without Mating

Overall, only about one-third (37.1%) of females contained mating plugs when they were captured at the drift fence as they left the vicinity of the den. This proportion varied with female body length, from 0% in females <35 cm SVL to >67% in the largest size groups (>55 cm SVL; fig. 1). Thus, approximately one-third of the largest fe-

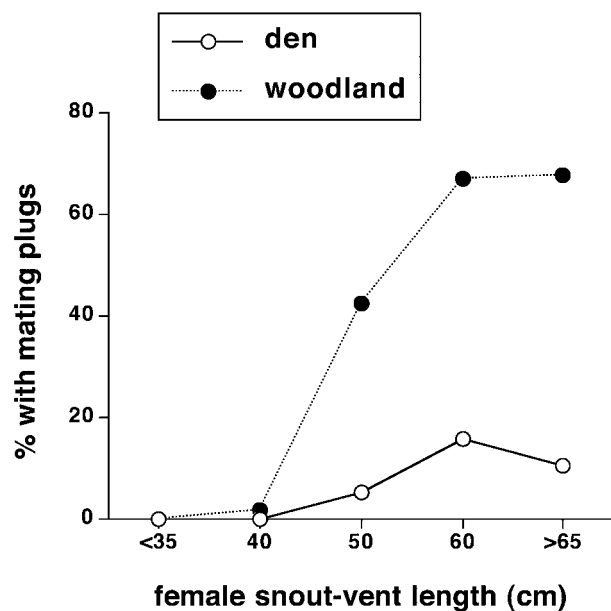


Figure 1: Effect of female body size (snout-vent length) on the proportion of female garter snakes that had mated prior to collection either at the den (shortly after emergence) or when they dispersed to the drift fence 50 m away from the main den. See text for statistical analyses of these data.

males left the den area without mating. Mating plugs provide reliable evidence in this respect, because the plugs persist for longer than the average duration of time taken to disperse (see above), and matings without plugs are very rare (Shine et al. 2000a).

Was the probability of mating during dispersal linked to a female's body size? If so, the relative numbers of mated versus unmated females in different size classes should differ between the den sample and the drift fence sample, as indicated by the interaction term in a multiple logistic regression with plug presence as the dependent variable and location (den/woodland) and female SVL as independent variables. Analysis on the entire data set indeed reveals such an interaction (Wald $\chi^2 = 34.72$, $df = 1$, $P < .0001$), but this test is influenced by the fact that very small females never mated (and thus, the proportion with mating plugs did not change as they dispersed), whereas larger females were mated as they dispersed (fig. 1). Among females >50 cm SVL, no significant interaction between location and female SVL was apparent ($\chi^2 = 0.53$, $df = 1$, $P = .47$), but main effects remained highly significant (location, $\chi^2 = 346.34$, $df = 1$, $P < .0001$; SVL, $\chi^2 = 17.30$, $df = 1$, $P < .0001$). Thus, the increased incidence of mating for females at the drift fence versus the den applied evenly across the size range of adult females.

Females Dispersed in Different Directions than Males

Contingency-table analysis revealed that the relative numbers of male and female snakes in each of 10 traps (total 26 females, 238 male snakes) deviated significantly from the null hypothesis of similar sex ratios in each trap ($\chi^2 = 38.83$, $df = 9$, $P < .0001$). Indeed, sex ratios per trap ranged from 100% female to 100% male.

Decreased Female Attractiveness Accelerated Rates of Dispersal

Experimental reduction of a female's attractiveness to males reduced the duration of her stay near the den. Comparison of free-ranging females to which we applied the "male-identifier" lipid (squalene) and control (peanut oil only) females confirms that squalene reduced the intensity of courtship to which a female was subjected (fig. 2a; number of males courting, $F = 11.60$, $df = 1, 97$, $P = .001$). Females that experienced less courtship dispersed more rapidly than did the control females (distance from release point, $F = 6.96$, $df = 1, 97$, $P < .01$; fig. 2b).

Courted Females Showed Distinctive "Escape" Maneuvers

When induced to flee, females moved rapidly in a straight line and always away from the den center in the direction they had been facing prior to disturbance. Of the 70 females observed during such displacements, about half (33) maintained this straight-line trajectory. Of these animals, 11 kept moving for an average of 3.3 m before stopping, whereas the other 26 stopped abruptly after an average of 1.0 m. In the remaining sample of 33 females, all turned abruptly (at 80° – 140° to the original trajectory) after moving 1–2 m. Of these animals, 12 then kept moving in the new direction, whereas the other 21 stopped 10–50 cm after their turn. In summary, females typically moved only 1–2 m before stopping, often soon after making an abrupt turn.

Female Escape Maneuvers Functioned to Evade Courting Males

The observations of females attempting to flee from natural courting groups (above) provide data on the effectiveness of alternative female movement patterns in "losing" suitors. Females that turned then stopped ($N = 21$) lost an average of 79% of the males initially courting them, because in most cases the males kept moving rapidly in the initial direction and thus went past (sometimes, over) the sedentary females. A lower proportion of courting males were evaded by females that turned but did not stop (18%, $N = 12$ groups), that kept moving in a straight line

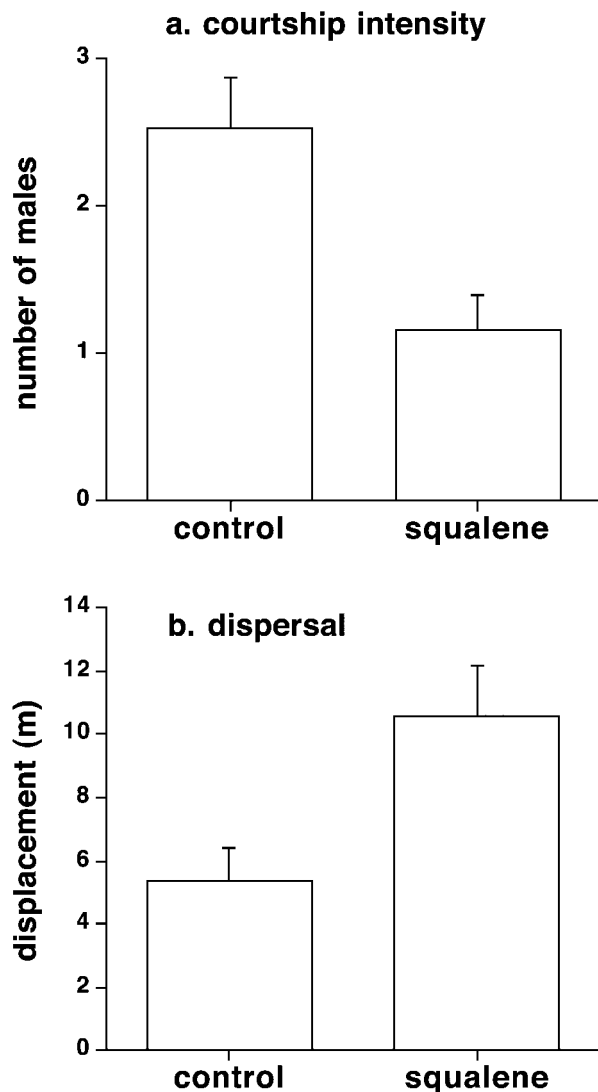


Figure 2: Effects of external application of a male-identifying lipid pheromone (squalene) onto female garter snakes. The graphs show (a) the numbers of males courting manipulated versus control (peanut oil) female garter snakes after their release at the den and (b) the distances that females had moved from their release point when the animals were resighted 30–60 min later (see text for statistical tests). Graphs show mean values and associated standard errors; sample sizes were 48 control females and 51 squalene-painted females.

(13%, $N = 11$ groups), or that moved in a straight line and then stopped (20%, $N = 26$ groups). The trials using a recently killed female snake on a fishing line provided very similar results. As for natural groups, trials in which the female turned and then stopped resulted in a high proportion of males losing contact with the stimulus (fig. 3). We analyzed these data with a three-factor ANOVA; the factors were trial type (natural group vs. dead female),

whether or not the female stopped after 1–2 m, and whether she moved in a straight line or made an abrupt turn. This analysis revealed no overall difference in the proportion of males lost between trials with natural groups and those with the dead female ($F = 0.07$, $df = 1, 142$, $P = .80$) or any significant interaction term involving this factor (all $P > .22$). However, the proportion of males lost during a trial depended on female movement patterns and was highest if the female made an abrupt turn and then stopped (fig. 3; interaction-turn*stop, $F = 32.69$, $df = 1, 142$, $P < .0001$).

Trials using the dead male on fishing line supported our interpretation of the functional basis for the effectiveness of female evasion maneuvers. When the dead male snake was simply laid on the ground, he rarely attracted approaches from other males (mean % of courting males that approached the stimulus = 1.6%, in 15 trials). The dead male attracted more interest when he was moved about rapidly (mean = 19% of males approached the stimulus in 15 trials). However, when he was moved across and behind the fleeing female, a high proportion of males approached and tongue flicked the target snake (mean = 53% in 15 trials). The consequent difference in the proportions of courting males that were distracted by the dead male ($F = 25.69$, $df = 2, 42$, $P < .0001$, all post hoc comparisons $P < .05$) supports the hypothesis that male garter snakes use cues from other males when attempting to relocate females.

Evasion Behaviors of Courted Females Were Unaffected by Group Size or Female Mating Status

A two-factor ANCOVA with number of males initially courting a female (natural groups only) showed no significant relationships between group size and the female's behavior (whether or not she stopped, $F = 0.62$, $df = 1, 66$, $P = .43$; whether or not she turned, $F = 0.97$, $df = 1, 66$, $P = .33$; how far she moved, $F = 0.005$, $df = 1, 66$, $P = .94$). Similarly, mated and unmated females did not differ in the frequency of these behaviors (turn or not, $\chi^2 = 0.82$, $df = 1$, $P = .36$; stop or not, $\chi^2 = 1.57$, $df = 1$, $P = .21$; distance traveled, $F = 1.38$, $df = 1, 61$, $P = .24$).

Discussion

Together with previous work on this system (Shine et al. 2000*d*, 2003*a*, 2004), data from the current study provide strong support for the hypothesis that sexual conflict is a major force driving the behaviors of garter snakes at communal dens in Manitoba. In snakes, as in most kinds of animals, interpretations of mating systems traditionally have ignored or downplayed the possibility of sexual con-

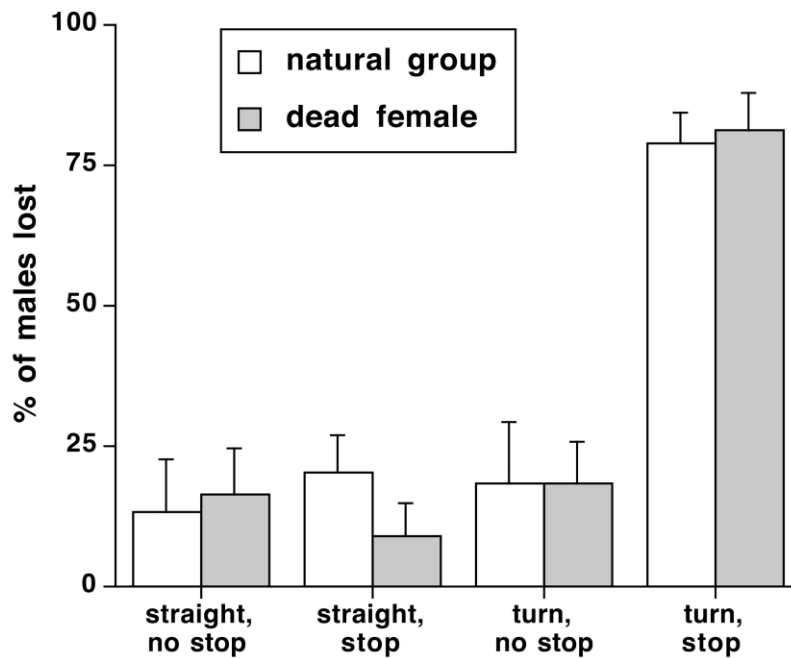


Figure 3: Effects of movement patterns of female garter snakes on the proportion of males that failed to keep up with the female they had been courting after the female moved away. The graphs show data for two sets of trials: (a) natural courting groups, in which the female was induced to flee and we recorded her behavior and the number of males (from those originally present in the courting group) still courting her at the conclusion of her movement, and (b) responses to a dead female snake that we manipulated to move in ways mimicking those seen in natural groups. The graphs show mean values and associated standard errors. Data are shown for four patterns of female movement: the female either continued moving or stopped after 1–2 m and either did or did not make an abrupt turn during that movement. Total sample size was 70 natural groups (see text for details) and 20 of each trial type for the dead female (total = 80 trials).

flict (e.g., Devine 1984; Arnold and Duvall 1994; Chapman et al. 2003b). In the Manitoba garter snakes, however, several lines of evidence point to an intense battle between the sexes. Our data (above) on female behavior support the hypothesis of sexual conflict in that many facets of female movement patterns support the idea that females disperse from the den as rapidly as possible and minimize contact with males as they do so.

Rapid dispersal from the den may enhance female fitness via multiple pathways. For example, it reduces the female's vulnerability to crow predation (which is concentrated near the den; Shine et al. 2001a; R. Shine, personal observation) and provides more time for the female to feed on her summer range prior to reproduction. Food is scarce near the dens but abundant in the surrounding woodland: snakes begin to feed almost as soon as they begin dispersing (O'Donnell et al. 2004). Lastly, sexual conflict imposes costs per se: females that remain near the den risk injury or death if they are trapped beneath piles of vigorously courting males (Shine et al. 2001a).

These disadvantages suggest that female garter snakes should disperse from the den as soon as they have recovered from their long period of winter inactivity. The only

potential advantage to delaying dispersal is that it provides an opportunity for mate choice by a female. In such a case, we might predict that a female garter snake would not disperse from the den area immediately but instead would behave in ways that gave her opportunities for mate choice. Although the idea is plausible, our data falsify predictions from this hypothesis and instead accord with the following predictions from the alternative scenario of sexual conflict.

Duration of delay before dispersing. Females dispersed rapidly from the den, generally covering at least 100 m (to the drift fence) within a day or two of emergence.

Incidence of mating prior to dispersal. Many females dispersed from the den without mating (fig. 1), which is inconsistent with the hypothesis that females wait to mate. This result is paradoxical in view of the high frequency of multiple mating in garter snakes as revealed by genetic data (Garner et al. 2002; for the Inwood population, M. Pfrender, personal communication). It seems probable that females remate after they have left the den on their way to (or after arriving at) their summer ranges.

Effect of courtship intensity on duration of delay prior to dispersal. Critically, an experimental reduction in the in-

tensity of courtship to a female resulted in her dispersing faster (as we would expect if courtship impedes dispersal) rather than slower (as we would expect if she waits to mate before dispersing).

Dispersal routes. Dispersing females followed routes that resulted in lower-than-expected rates of encounters with males as evidenced by differing sex ratios of captures in different traps. This pattern must reflect active avoidance of males by females, because focal observations confirm that males in the woodland follow female trails whenever they locate them (LeMaster et al. 2001; R. Shine et al. 2005). Thus, we would expect the numbers of males and females within a trap to be positively rather than negatively correlated unless females actively avoid males. Avoidance of male scent by females has been reported both for substrates in outdoor arenas (Shine et al. 2004) and for trails on the ground (LeMaster et al. 2001).

Evasion behaviors of courted females. The behaviors employed by courted females (especially rapid straight-line movements followed by an abrupt turn and stop) were effective at evading males because of male reliance on visual cues (especially rapidly moving snakes) for mate relocation. A female's evasion tactics were unrelated to the number of males courting her or to whether or not she had already mated (and hence her ability to copulate).

In summary, our data accord better with the "sexual conflict" hypothesis than with the alternative idea of indirect mate choice. In combination with our previous studies at the same den, these results suggest that movement patterns by female garter snakes in this system are driven by attempts to avoid males rather than to enhance mate quality. We note, however, two important caveats. First, we know nothing about sexual interactions of snakes away from the den at their summer ranges. It is plausible that mating might occur there also, and females may be better able to control mate quality under such circumstances than in the frenetic den aggregations. Second, we cannot completely reject the "indirect mate choice" hypothesis even at the den, because a female that evades males may thereby benefit both from reduced costs of harassment and from an enhanced mate quality due to "screening" potential mates (Cordero and Eberhard 2003). One additional criterion to discriminate between these two hypotheses is parsimony: the "sexual conflict" hypothesis invokes a simple reduction in direct costs of harassment, whereas the "mate choice" scenario relies on a more complex and less direct pathway for enhancement of female fitness, that is, via differential mate quality. Although multiple mating enhances offspring fitness in some but not all snake populations (Madsen et al. 1992; Luiselli 1993; Blouin-Demers et al. 2005), there are no data to substantiate the critical assumption of a link between mate choice and offspring viability in garter snakes. Nonetheless, it

remains a challenge for future work to explore the potential fitness benefits of evasion behavior for females. As noted by previous researchers (e.g., Chapman et al. 2003a, 2003b; Córdoba-Aguilar and Contreras-Garduño 2003; Eberhard and Cordero 2003), we need field studies on an ecologically and phylogenetically diverse range of study organisms to obtain a better understanding of the behavioral interactions between males and females in natural populations.

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