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Alternative male mating tactics in garter snakes, *Thamnophis sirtalis parietalis*

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Alternative mating strategies occur in many animal lineages, often because males adopt tactics best suited to their own phenotypes or to spatiotemporal heterogeneity in the distribution of females. Garter snakes near a communal overwintering den in Manitoba show courtship in two contexts: competition from rival males is intense close to the den, but weak or absent when males court solitary dispersing females in the surrounding woodland. Larger size enhances male mating success near the den, but not mate location rates in the woodland. As predicted by the hypothesis that males match their tactics to their competitive abilities, our mark–recapture data show that larger, heavier individuals remained near the den, whereas smaller and more emaciated males moved to the woodland. To locate mates, woodland males relied upon substrate-deposited pheromonal trails and visual cues (rapid movement), whereas males in the crowded den environment ignored such cues and instead tongue-flicked every snake they encountered to check for sex pheromones. In arena trials, den males adjusted their courtship intensity to the presence of rival males, whereas woodland males did not (perhaps reflecting the lower probability of interruption by a rival). Thus, male garter snakes adjust the times, places, form and intensity of their reproductive behaviours (mate-searching tactics, intensity of courtship) relative to both their own competitive abilities and spatial heterogeneity in mating opportunities.

Although the broad outlines of male reproductive behaviours such as mate searching, courtship and copulation are relatively invariant within a species, individual males none the less differ substantially in the form, intensity and effectiveness with which those behaviours are manifested (Gross 1996). Part of that variation may be non-adaptive, perhaps reflecting individual variation in genetics, health or vigour. However, a significant proportion of variation in the reproductive behaviour of males within a population may represent adaptive matching between an individual's mating 'tactics' and two factors: (1) the male's own phenotype (especially his ability to outcompete his rivals) and (2) spatiotemporal heterogeneity in factors such as the availability of females, the ease with which they can be located, and the intensity of competition from rival males. Although links between a male's behavioural tactics and other aspects of his phenotype are genetically determined in some taxa (i.e. the population contains multiple genetically distinct morphs), this situation evolves only under relatively restricted conditions (Lank et al. 1995; Zamudio & Sinervo 2003). More commonly, alternative male tactics reflect flexibility by individual males, often reflecting differences in body size and thus competitive ability (Hazel et al. 1990; Gross 1996; Immler et al. 2004).

Matching phenotype to mating tactics is a simple and intuitive idea. For example, a male that is too small to win physical battles with larger conspecifics may benefit from avoiding such battles, focusing instead on alternative tactics such as 'sneaking' whereby mating success depends upon characteristics other than prowess in battle (Andersson 1994; Moczek & Emlen 2000; Bro-Jorgensen & Durant 2003). Similarly, a male that is unable to attract a female successfully may benefit by intercepting her as she approaches a larger male, or by attempting to inseminate her forcibly. The scientific literature on alternative mating tactics in males includes many examples of such status-dependent shifts, whereby smaller males act as 'satellites' to intercept females approaching larger males (Brockmann 2002; Eggert & Guyetant 2003; Immler et al.

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2004; Sato et al. 2004), or wait until larger rivals leave before courting the female (Cade 1979; Dominey 1984; Howard 1984; Gross 1996).

A second reason for males to be flexible in their mating tactics is in response to heterogeneity (in both time and space) of the mating opportunities available, and the tactics that would maximize such opportunities. Females of different body sizes and reproductive condition will be distributed in a highly nonrandom fashion, such that adjacent habitats or time periods may favour very different male tactics (e.g. remain at one site and defend it versus move about widely to find unaccompanied females: Luiselli 1995). Thus, variation in male mating tactics can arise from spatiotemporal heterogeneity in the availability and location of females, as well as the specific phenotypic traits of the males themselves. Optimality models predict that male reproductive behaviours should be flexible in response to this heterogeneity, with males adopting mating tactics best suited to their own phenotypes (e.g. competitive abilities) as well as to the precise mating opportunities afforded by local conditions (Brown & Weatherhead 1999; Thomas 2002). One of the most critical factors may be the operational sex ratio (the ratio of fertilizable females to reproductive males). For example, large male European bitterling, *Rhodeus sericeus*, defend territories and are aggressive towards conspecifics under equal sex ratios, but shift to participating in multimale spawning aggregations at higher male densities (Mills & Reynolds 2003). Similar flexibility is widespread in other taxa also (e.g. Gross 1996; Immler et al. 2004).

Among reptiles, alternative male mating tactics have primarily been studied in lizards (Sinervo & Lively 1996; Whiting 1999; Sinervo et al. 2000; Sinervo 2001; Calsbeek et al. 2002). Most of these cases have focused on territorial mating systems in which physical battles provide a strong advantage to larger body size in males (Zamudio & Sinervo 2003). In such a system, smaller males allocate their reproductive effort in times and places where competition from their larger rivals is minimized (Zamudio & Sinervo 2003). Alternative male mating tactics in lizards often involve visual (coloured) 'badges' that indicate male tactics and status (Hews & Quinn 2003; Whiting et al. 2003). In contrast, defence of territories is virtually unknown among snakes (Greene 1997), and snake sociality is oriented around chemoreception rather than vision (Cooper & Greenberg 1992). Perhaps in consequence, alternative male mating tactics have been described only rarely in snakes. The most 'lizard-like' example of alternative mating tactics in snakes comes from ontogenetic (size-related) shifts in male tactics in the European adder, *Vipera berus* (Madsen et al. 1993). Males fight with each other for dominance, larger males win fights, and smaller males adopt cryptic tactics whereby they wait near a female until the larger males have departed (Madsen et al. 1993). Plausibly, however, alternative male mating tactics might evolve even in systems that lack direct male–male combat; for example, subsets of males might differ in the times and places where they court, or in the kinds (sizes?) of females that they court. Indeed, an example of the latter phenomenon has been reported from spring aggregations of garter snakes on the Canadian prairies; although males do not engage in any overt battles, alternative male mating tactics co-occur within the den population based on body size. Courtship (and thus mating) is size assortative, with a male's body size determining his response to pheromonal cues from small versus large females (LeMaster & Mason 2002; Shine et al. 2003). Thus, small males court and mate small as well as large females within this system, whereas large males focus their efforts on large females (Shine et al. 2001b, 2003).

We exploited the unique logistical advantages of the garter snake dens to explore male mating tactics in more detail, and to see whether there is diversity in male tactics on a spatial as well as ontogenetic scale. In particular, we focused upon a surprising result from an earlier radiotelemetry study (Shine et al. 2001a). Although many courting snakes can be seen near the den, much of the courtship and mating actually occur after the snakes have dispersed into the surrounding woodland (Shine et al. 2001a). Because snake densities are dramatically lower outside the den, these woodland groups are much smaller and male–male competition is less intense (Shine et al. 2001a). Does this different context for courtship favour divergence in male tactics? Both descriptive and manipulative studies have shown that a male garter snake's ability to obtain a mating within a courting 'ball' depends upon his body size, his body condition (mass relative to length) and his agility (Shine et al. 2000f, 2004a). In contrast, mate-locating ability is unrelated to male body size (Shine et al. 2005a). Thus, we might expect that larger, heavier, more agile males would stay near the den and compete in large courting groups, whereas smaller, thinner, slower males would move to the surrounding woodland and search for unaccompanied females. The much lower densities of unmated females in the woodland than the den might also favour divergence in male mate location modalities and mating tactics. We set out to test these predictions.

METHODS

Study Species and Area

South-central Manitoba, in the Canadian prairies, is close to the northern limit of the geographical range of red-sided garter snakes (Rossman et al. 1996). These small (males average 45 cm snout–vent length [SVL], females 55 cm), nonvenomous colubrid snakes gather in large aggregations at suitable den sites each autumn, and spend 8 months inactive underground (Gregory 1974; Gregory & Stewart 1975). The snakes court and mate in early spring, immediately after emerging from the den, before dispersing up to 18 km to their summer ranges (Gregory 1974; Gregory & Stewart 1975). Extensive studies in the Chatfield area north of Winnipeg have documented many aspects of the physiology, communication systems and behavioural ecology of these snakes (e.g. Mason 1993; Shine et al. 2000b; LeMaster et al. 2001; LeMaster & Mason 2002, 2003). This work has revealed intense sexual conflict: for example, males obtain matings by inducing female cloacal gaping via a hypoxic stress response rather than (as previously assumed) by stimulating female sexual receptivity, and females actively avoid male scent (Shine et al. 2004b). Thus, male 'courtship' in this system might less euphemistically be termed 'attempts at forcible insemination'.

The present study was based at a large den 1.5 km north of the town of Inwood (50°31.58′N, 97°29.71′W). The main den lies in an open rocky area beside a limestone quarry; the snakes emerge from between the rocks. The surrounding area is dominated by aspen woodland, extending to within 5 m of the den. During the spring emergence period, courting groups of snakes can be found both within the den itself, and up to 200 m away through the woodland (Shine et al. 2001a). We worked at the Inwood den from 5 to 22 May 2003 and 9 to 21 May 2004, encompassing most of the snake's emergence period in each of those years.

Substrate and Body Temperatures

Because locomotor performance in snakes is highly sensitive to body temperature (e.g. Greene 1997), any difference in behaviours between males in two sites might be secondary consequences of location-specific differences in body temperature rather than a genuine divergence in male 'tactics'. To address this issue, we collected 25 males and 25 females in the open, rocky den itself and another 25 males and 25 females in the surrounding aspen woodland. We immediately took their cloacal temperatures with an electronic thermometer, as well as the surface temperatures of the sites at which they had first been seen.

Sampling and Mark–Recapture Studies

In May 2003 we patrolled the den each day to collect newly emerged snakes (i.e. those on their first day out after their 8-month winter inactivity). Females disperse soon after emergence, and attract intense courtship (Whittier et al. 1985); thus, newly emerged females were easy to locate. Newly emerged males also attract courtship by other males for the first day postemergence (Shine et al. 2000c) and thus surveys for courted snakes were effective in locating recent emergers of both sexes. We measured (SVL) and weighed all of these snakes, gave each an individual painted number on the dorsal surface, then released them in the den the same day (or rarely, the following day). The nontoxic paint marks were generally readable for about 2 weeks, so that recaptures of these animals provided data on correlates of emergence, movements and philopatry (see below).

To sample snakes that concentrated their mate-searching activities away from the den, as well as to capture dispersing animals, in May 2003 we set up a 60-m drift fence of wire mesh ('hardware cloth') 20 cm high, with six evenly spaced funnel traps on either side of the fence. The drift fence was erected in aspen woodland 100 m from the main Inwood den, oriented to catch snakes dispersing away from (or towards) the den. Traps were checked and cleared twice daily (or more often when capture rates were high), yielding data on 6653 animals. All snakes were taken back to the field laboratory where they were measured before release the following morning. For the first 4 days of the study, we paint-marked each trapped snake to record in which trap it had been caught; these animals were then released back at the den to see if they would disperse in the same direction a second time. On subsequent days the trapped snakes were not marked, but simply measured and released on the opposite side of the fence.

Courting in Woodland versus the Den

Radiotelemetry has shown that some courting male snakes remain near the den, some disperse and court in the woodland, and others move back and forth between these two areas (Shine et al. 2001a). If the number of snakes in the two former categories outnumber those in the latter category, then it should be possible to identify individual males as belonging to either a 'den' or 'woodland' assemblage. That is, do individual male garter snakes typically focus their efforts on courting in either the den or the woodland, rather than both? If so, we should be able to detect the existence of a 'woodland' group by examining (1) philopatry: some of the paint-marked snakes (see above) should be consistently recaptured at the drift fence rather than at the den; (2) homing: if we displace snakes, they should return to the drift fence, and perhaps to a site close to where they were originally captured.

Reproductive Activities

To quantify differences in reproductive activities in the den versus the woodland, we surveyed both areas. We recorded the numbers of males in each courting group, and whether or not the females had already mated (as evidenced by a large gelatinous mating plug, which persists for >2 days: Shine et al. 2000e). To quantify the intensity of competition from rival males, we set up standardized trials in both habitat types to characterize the rates at which males were able to locate females, and the cues by which they accomplished that task. To do this we anaesthetized eight unmated females (by intramuscular injection of 5 mg/kg brietal sodium). These animals were quiescent for 25–35 min after injection, and all recovered completely (and were then released) within 60 min; no adverse effects of anaesthesia were apparent. Each anaesthetized female was dragged ventral surface downwards for 5 m to deposit a pheromonal trail, and then laid out at the end of her trail. Adjacent females and their trails were separated by at least 5 m. We scored the time taken for males to arrive and begin courting the female; each male was removed as soon as he commenced courtship. We also scored whether each male found the female by following her substrate-deposited pheromonal trail (evident because of frequent side-to-side head movements and tongue flicking to the substrate: Ford & Schofield 1984) or more simply, by tongue flicking other snakes as they were encountered. Trials were terminated after arrival of the 10th male, or after 15 min (whichever was soonest).

To clarify further the cues used by mate-searching males in the two habitat types, we used a 1.2-m length of nylon rope, attached to a stick so that rapid vibration of the handle caused the rope to whip about at ground level in a sinuous fashion, to mimic the movement patterns characteristic of vigorously courted snakes. The rope was wriggled about for 10 s, 30 cm in front of the head of a solitary (and presumably mate-searching) male either in the den or in a grassy clearing in the surrounding woodland. We scored the focal male's response (approach, retreat or ignore) over the following 30 s.

Focal Sampling of Male Behaviour

An observer (R.S.) walked through both the den and the woodland. He randomly selected a male snake and then recorded its behaviour for the next 60 s. The behaviours recorded were: distance travelled; total straight-line displacement; number of other snakes tongue-flicked; number of rival males within a courting group; and the proportion of the 60-s period spent courting, trail following (tongue flicking the substrate) and 'periscoping' (head and neck raised well above the substrate).

Facultative Responses to Competition Intensity

Any differences between males in the woodland versus the den in the intensity of courtship might be caused by intrinsic differences between the males, or facultative responses to factors that differed between the two areas (e.g. number of rival males in courting groups). To tease apart these possibilities, we erected 24 open-topped nylon arenas (1 × 1 × 0.8 m) in a grassy area near the den, and added either one or 20 male snakes to each arena. In half of the arenas, these males came from the den; in the other half, the males were taken from the drift fence. This design thus generated four treatments: den or woodland males, either by themselves or with 19 other males. In all arenas, a single male was randomly identified as the focal animal, and paint-marked for easy recognition. We then added a single unmated female (recently collected from the den) to each arena, and recorded the intensity of courtship by the focal male at 5-min intervals for the next 30 min. Courtship intensity was scored as the number of observation periods (out of a total of five) during which the focal male was aligned with, and actively courting, the female. We conducted four trials in succession in each arena, for a total of 96 trials.

Statistical Analyses

Assumptions of statistical tests (e.g. normality, homogeneity of variances) were checked before parametric analyses. Yate's correction was applied to all contingency table tests with low sample sizes. The text reports mean ± SEs.

Ethical Note

Research was conducted under the authority of Oregon State University Institutional Animal Care and Use Committee. All research was conducted in accord with the U.S. Public Health Service 'Policy on Humane Care and Use of Laboratory Animals' and the National Institutes of Health 'Guide to the Care and Use of Laboratory Animals'.

RESULTS

Substrate and Body Temperatures

Substrate temperatures at places where snakes were found were similar in the den and the surrounding woodland (two-factor ANOVA; main effect of location: $F_{1,96} = 1.26$, $P = 0.26$), but males were generally on cooler substrates than were females ($F_{1,96} = 18.83$, $P < 0.0001$), with no significant interaction between these factors ($F_{1,96} = 0.02$, $P = 0.88$; Fig. 1a).

Patterns were different for cloacal temperatures, however; males and females had similar mean body

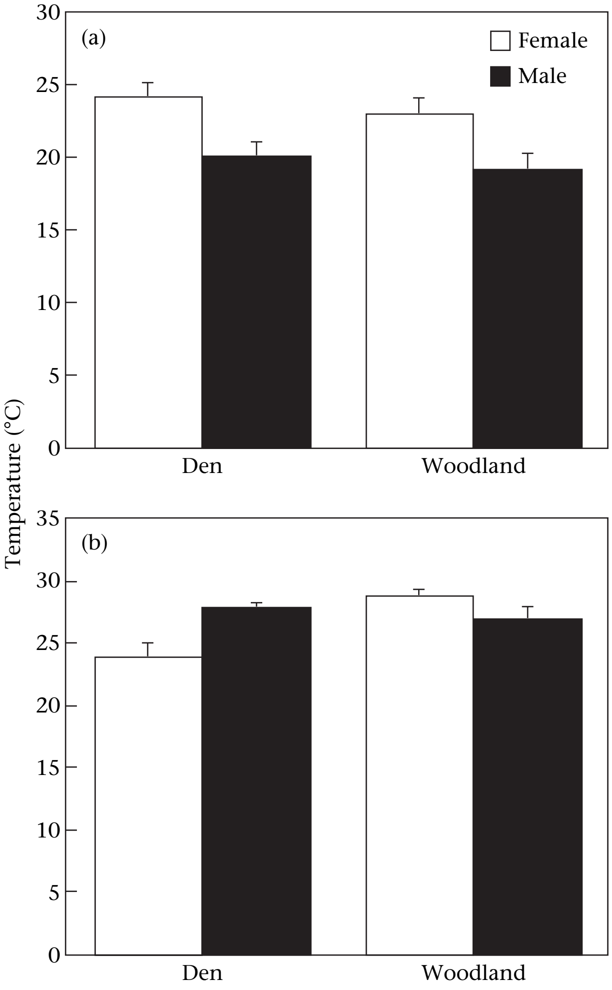

Figure 1. Temperatures of (a) substrates in a communal den and in the surrounding aspen woodland and (b) garter snakes in these sites. Means are shown + SEs; $N = 25$ for each sex/location group.

temperatures ($F_{1,96} = 1.76$, $P = 0.19$), but woodland snakes were hotter than den snakes ($F_{1,96} = 6.86$, $P = 0.01$). Snakes were always considerably hotter than the substrate (Fig. 1). The interaction between sex and location was significant ($F_{1,96} = 14.70$, $P = 0.0002$) because females were colder than males at the den, but hotter than males in the woodland (Fig. 1b).

Morphology and Mark–Recapture Studies

We captured and paint-marked 1895 newly emerged snakes in May 2003, with approximately equal numbers of males ($N = 939$) and females ($N = 956$). The numbers of emerging snakes per day peaked early in May, with the sex ratio shifting rapidly through time: early emergers were primarily males, whereas females emerged later (Pearson correlation between days since 5 May versus %male: $r_{14} = -0.86$, $P < 0.0001$). Mean body sizes also shifted over the course of the emergence period, with a trend for smaller males to emerge later than larger conspecifics (based on one mean data point per day: $r_{14} = -0.57$, $P < 0.025$; based on all male snakes as data points: $r_{937} = -0.11$, $P < 0.002$).

Comparing our samples of snakes captured at the den ($N = 1529$ males, 959 females) versus the drift fence ($N = 5143$ males, 1510 females), both sexes averaged larger body sizes (SVLs) at the den than at the fence, but with a significant interaction between sex and location (interaction: $F_{1,9137} = 116.68$, $P < 0.0001$) because, although den snakes were larger in both sexes (main effect of location: $F_{1,9137} = 320.45$, $P < 0.0001$), the size disparity was greater for females than for males (Fig. 2a). Body condition (mass relative to length) was also better at the den than at the drift fence, especially in males (ANCOVA with ln SVL as the covariate, ln mass as the dependent variable yields a significant interaction term between sex and location: $F_{1,3450} = 5.09$, $P < 0.025$; Fig. 2b).

Because we placed traps on both sides of the drift fence, we can also compare the phenotypic traits of animals that were caught on the den side (i.e. dispersers as well as animals remaining in the woodland) versus the opposite side (i.e. animals staying in the woodland or returning to the den). These comparisons revealed no significant difference in mean body sizes of females (ANOVA: $F_{1,1508} = 0.49$, $P = 0.49$), but males caught on the side of the fence away from the den were larger than those caught in traps on the den side of the fence ($F_{1,5141} = 21.80$, $P < 0.0001$). This difference suggests that smaller animals kept moving away from the den, whereas larger males either remained in the woodland or returned to the den after dispersing. Our detailed records from recaptures of individually marked snakes reveal both of these behaviours, although returning to the den was less common than remaining near the fence (see below).

Recaptures of individually marked snakes provided more detailed information on dispersal rates and changes through time since emergence. Larger males stayed at the den longer before dispersing than did smaller males (duration from emergence to first recapture at the drift fence versus SVL: Pearson correlation: $r_{255} = 0.16$, $P < 0.015$). Males that emerged earlier in the season (i.e. when mating was at its peak) were heavier at emergence (date versus residual condition score: $r_{235} = -0.20$, $P < 0.003$). In summary, large, heavy males emerged earlier in the season than did their smaller, thinner rivals, and larger animals stayed longer at the den before dispersing.

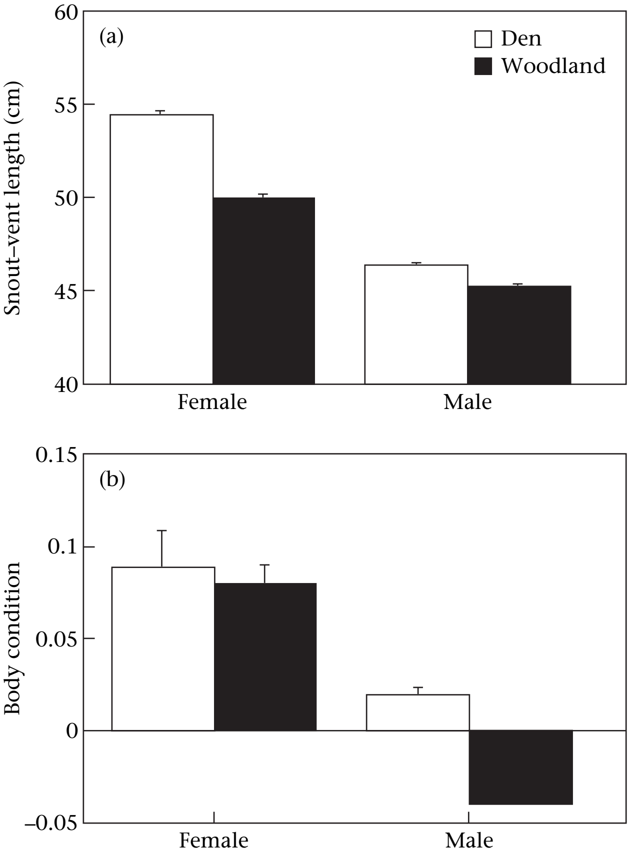

Figure 2. (a) Body sizes (snout–vent lengths) and (b) body condition (residual scores from the general linear regression of ln mass versus ln snout–vent length) for male and female garter snakes captured either in a communal den or 100 m away in the surrounding aspen woodland. Means are shown + SEs; *N* (left to right) = 959, 1510, 1529 and 5143 for each sex/location group.

Courting in Woodland versus the Den

Philopatry

Recaptures from our sample of individually paint-marked snakes comprised only a small proportion of all snakes captured at the drift fence (166 of 5143 males caught at the fence = 3.2%). None the less, these animals provided useful information: most importantly, many of them remained close to the drift fence rather than either returning to the den or dispersing further away. Thus, 27 individually marked snakes caught at the fence were recaptured at the fence 0–13 days later (4.2 ± 0.34 days). This tally includes one male that was captured in traps at the fence four times, and four males that were caught three times each. Contingency table analysis was used to compare the relative numbers of male snakes that were captured at the den or the fence and then later recaptured (excluding newly emerged snakes, since by definition these were always at the den). This analysis revealed a significant assortment of male snakes into 'den' versus 'woodland' groups ($\chi^2_1 = 3.85$, $P < 0.05$): that is, the number of postemergence males moving from the fence to the den or vice versa was significantly lower than the numbers recaptured at their original locations.

Homing

When males captured at the drift fence were taken back to the den and released, many returned to the drift fence and were recaptured a day or two later. These animals consistently returned to the same area of the fenceline at which they had been captured previously, and often ended up in the same trap as before (correlating distance from the north end of the fenceline in successive captures: $r_{59} = 0.31$, $P = 0.016$). In contrast, although females exposed to the same manipulation also dispersed, most of their recaptures on the fenceline were far from their initial point of capture ($r_{39} = -0.46$, $P = 0.11$). Hence, males (but not females) actively homed to specific sites in the woodland. The same pattern was evident in a subset of 96 males, half from the drift fence and half from the den. After these animals were used in the arena trials of courtship intensity (above), they were all released at the den. Only seven of the den males were later recaptured at the fence, whereas 34 of the drift fence males were recaught in the traps ($\chi^2_1 = 28.78$, $P < 0.0001$).

Reproductive Activities

Of 32 unmated females that we located in the woodland, 17 were alone and the other 15 were being courted by one to three males when we found them (overall mean number of males/female = 0.69 ± 0.15). In 36 groups at the den, none were alone. The mean number of males per female in the den was 14.69 ± 2.57 (range 1–82; versus woodland groups: $F_{1,66} = 26.21$, $P < 0.0001$). In addition to these unmated females, we located many females that had recently mated (as evidenced by mating plugs). The percentage of mated adult-size (>50 cm SVL) females averaged 12.5% (85 of 679 animals) at the den versus 65.2% (481 of 738 animals) at the drift fence 100 m away ($\chi^2_1 = 406.58$, $P < 0.0001$).

In trials where anaesthetized females were laid out at the end of pheromonal trails, the mean time for the first male to arrive and begin courting the female was about 40 times longer in the woodland than the den (means 16.27 ± 4.0 s in the den versus 608.57 ± 84.27 s in the woodland; $F_{1,20} = 111.20$, $P < 0.0001$). The mean rate of arrival of males, averaged across all males within each trial, was about 25 times higher in the den (0.051 ± 0.004 versus 0.002 ± 0.0004 males/s; $F_{1,20} = 61.99$, $P < 0.0001$). None of 150 den males that found the female did so by trail following (tongue flicking pheromonal trails on the substrate); instead, they kept their heads well off the ground and simply tongue-flicked the dorsal surfaces of every snake they encountered. In contrast, eight of the 10 woodland males found the female by tongue flicking along her substrate-deposited pheromonal trail ($\chi^2_1 = 110.03$, $P < 0.0001$).

The rapidly twitching nylon rope elicited a higher response level from males in the woodland (14 approached, three retreated, three ignored) than in the den (five approached, one retreated, 14 ignored; comparing the two data sets: $\chi^2_2 = 13.21$, $P < 0.002$).

Focal Sampling of Male Behaviour

We obtained 60-s focal samples for 16 males in the aspen woodland and 20 males at the den. Figure 3 reveals many differences between behaviours of these two groups of males. Animals in the woodland moved further than did den males ($F_{1,34} = 24.03$, $P < 0.0001$), over greater straight-line displacements ($F_{1,34} = 30.17$, $P < 0.0001$). The woodland males spent a lower proportion of their time courting females ($F_{1,34} = 22.08$, $P < 0.0001$), and instead spent more time tongue flicking the substrate (trail following: $F_{1,34} = 34.43$, $P < 0.0001$). When they found a female, the woodland males competed with fewer rivals ($F_{1,34} = 33.04$, $P < 0.0001$) and, perhaps for this reason, tongue-flicked fewer other snakes ($F_{1,34} = 22.77$, $P < 0.0001$). Lastly, the proportion of time spent in the head-up ('periscope') posture was higher for woodland snakes than for den snakes, suggesting use of visual cues by the woodland snakes ($F_{1,34} = 11.20$, $P < 0.001$).

Facultative Male Response to Competition Intensity

In an outdoor arena with either 0 or 20 other males, den males were more vigorous courters than were woodland males overall ($F_{1,92} = 10.76$, $P < 0.002$) and courtship was more intense if there were fewer competing males ($F_{1,92} = 3.97$, $P < 0.05$; Fig. 4). However, the most important result from these trials was the significant interaction term between male location and number of competitors ($F_{1,92} = 3.97$, $P < 0.05$). Woodland males did not modify their intensity of courtship depending on how many other males were present, but den males courted more fervently if they encountered a solitary female (Fig. 4).

DISCUSSION

Male garter snakes locate and court females in two very different contexts: either in large aggregations in the communal den, or solitarily or in small groups in the surrounding woodland. Although these two areas are separated by only a few metres, the demarcation is clear and the determinants of male mating success are likely to differ. Biotic factors are likely to be more important than abiotic in this respect. Although the woodland is more shaded, mean temperatures at ground level during the day were similar in the two habitats (at least in places where snakes were found: Fig. 1a). Body temperatures of male and female snakes diverged in these two areas, but to a minor degree only (Fig. 1b). In addition, these snakes are

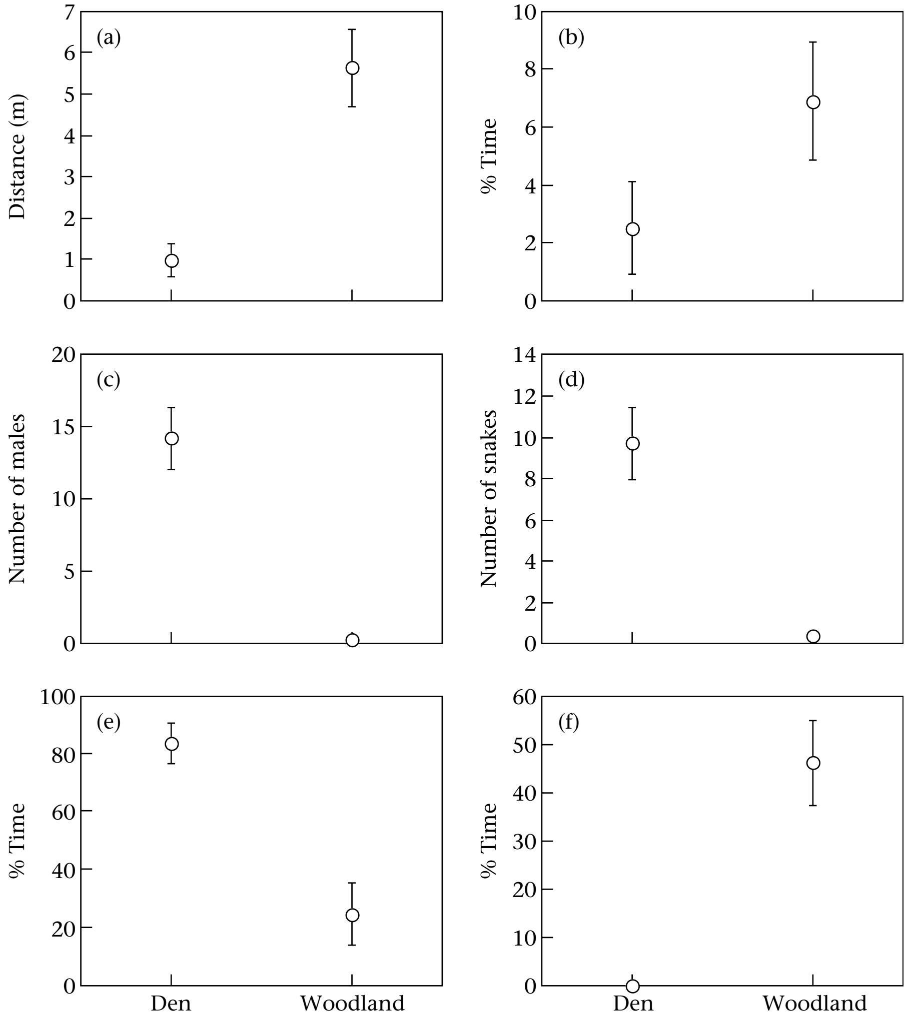

Figure 3. Differences in behaviour of free-ranging male garter snakes in two areas (den and woodland) during 60-s focal observation periods. (a) Distance moved; (b) % time with head raised ('periscoping') (c) number of rival males; (d) number of other snakes tongue-flicked; (e) % time courting; (f) % time trail following. Means are shown ± SEs. See text for statistical tests of these data. *N* = 20 den males and 16 woodland males.

capable of effective locomotion and courtship over a wide range of temperatures, and courting males accord a low priority to behavioural thermoregulation (Shine et al. 2000a). Thus, the most important differences between the den and the woodland for an amorous male garter snake involve the numbers of potential courtship targets (unmated females), the ease with which they can be located, and the numbers of rival males.

Snake densities are much lower in the woodland than the den, and many of the woodland females have already mated (and thus cannot mate again for a few days: Crews & Gartska 1982; Shine et al. 2000e). Thus, locating the (few) potentially receptive females poses a stronger challenge in the woodland than at the den. However, the intensity of male–male rivalry around woodland females is greatly reduced (mean number of males per female 0.69 versus 14.69). Thus, male mating success in the woodland is likely to be determined by mate location ability rather than by the ability to outmanoeuvre rivals within a mating ball. As predicted from the hypothesis that males will flexibly adjust their reproductive behaviour to fit their own abilities and the tactics likely to succeed in specific conditions, our study revealed significant flexibility in both of these respects.

(1) A male garter snake's morphology (size, strength, agility, mass relative to length) affects his probability of obtaining a mating within a courting group (Shine et al. 2000f, 2004a), but his size does not affect his mate-searching ability (Shine et al. 2005a). Thus, if males modify their mating tactics relative to their own competitive ability, large, fast, heavy males should emerge early in the season and stay at the den thereafter. This prediction is supported by overall comparisons between males in the den and the woodland, as well as the more detailed information from marked males. Our measurements of locomotor speeds showed the same shift between den males and woodland males (Shine et al. 2005b), consistent with the idea that male garter snakes select times and places to court based upon their ability to compete with rivals. Our data on homing and philopatry show

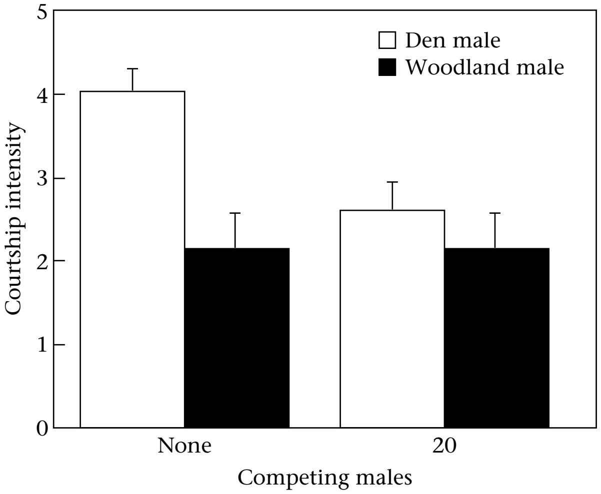

Figure 4. Intensity of courtship by male garter snakes in outdoor arenas as a function of the male's collection location (den versus woodland) and the number of competing males within the arena. Courtship intensity was scored as the number of observation periods (out of a maximum of five, at intervals of 5 min) during which the focal animal was courting the female. Means are shown + SEs. See text for statistical tests of these data. $N = 24$ replicates (courting groups) within each treatment.

that this matching involves relatively discrete subsets of males, such that some animals mostly court at the den and others in the woodland.

(2) Male snakes in the woodland move about actively, tongue flicking the substrate; when they locate a female's trail they follow it to find her. This behaviour is typical of many snake species (Gillingham 1987). Visual cues to a female's location also play a role, at least at short distances; again, this may be common among snakes (Shine & Mason 2001). Male garter snakes near the den display a less usual form of mate location: reliance upon chemosensory information obtained by tongue flicking the bodies of other snakes rather than by following substrate-deposited pheromonal trails. This divergence in mate location tactics makes intuitive sense. The den is in an open rocky area where the large numbers of moving male snakes reduce the information content of visual cues, and where females are likely to emerge close by so that moving long distances is unnecessary; also, the pheromone-soaked substrate may render it difficult or impossible to follow a single trail. In contrast, lower snake abundance in the woodland means that females are widely dispersed. Any rapidly moving animal is likely to be a courted female (mate-searching males move at a relatively sedate pace: Fig. 3a), and pheromonal trails offer excellent opportunities for long-distance mate location (especially because males can detect a female's mated status from her trail: O'Donnell et al. 2004).

Our arena trials offered an even more striking example of facultative adjustment of courtship intensity to local conditions, in this case the degree of competition. Woodland males did not modify their intensity of courtship in response to the number of competing males; in nature, group sizes are fairly stable in the woodland because of low rates of arrival of new suitors. Thus, there may be some optimal level of courtship intensity regardless of group size. In contrast, the den males showed a spectacular increase in courtship intensity if they were alone with a female, as opposed to being part of a large courting group (Fig. 4). Such small (single-male) groups do occur at the den (we recorded 1–82 males per female at the den) but are very transitory; other males will arrive rapidly. Given that den females typically accept copulations after relatively brief courtship (Shine et al. 2000f), a den male may benefit by expending frenetic effort on courtship if he finds a solitary female; his probability of success will decline rapidly with time as other males arrive, whereas this is not the case for a snake in the woodland. The different response to group size in these two groups of males (Fig. 4) thus fits well with the hypothesis that males adjust courtship intensity not only relative to the degree of rivalry they experience, but also to the degree they are likely to experience in the near future.

We do not know the relative importance of matings at the den versus in the woodland (or even later, when females have dispersed to their summer ranges) as determinants of male reproductive success. However, at least three lines of evidence suggest that matings after a female has left the den are significant influences on male fitness. First, radiotelemetry and visual surveys confirm that many matings occur in the woodland (Shine et al. 2001a). Second, the proportion of females that have mated by the time they leave the woodland is lower than the proportion of female snakes that reproduce each year (Gregory 1977; Shine et al. 2000d), so presumably other matings must occur (sperm storage between years is rare: Blanchard 1943). Third, genetic analyses of garter snake litters have revealed high levels of multiple paternity (Gibson & Falls 1988; Garner et al. 2002), even though mating plugs preclude a female from remating during the short time she spends near the den (Shine et al. 2000e).

This divergence in the context of mating results in a surprisingly wide divergence in many other traits between the two adjacent habitats. The most obvious involve male mating tactics, with den males courting in larger groups, more vigorously, and locating females without reliance on substrate-deposited pheromonal trails. However, other attributes also differed between the two habitats that we studied. For example, mean body sizes were larger at the den for both sexes, presumably because smaller individuals of both sexes attempt to escape the intense and potentially dangerous attentions of courting males. They may achieve this result by dispersing when the weather is too cool for active courtship (Shine et al. 2000d, 2004b). Overall, our present results reinforce a major conclusion from our previous work: that the superficially chaotic 'scramble' competition for matings at a garter snake den in fact is far from chaotic. These small snakes use complex and sophisticated mating tactics, and display a remarkable ability to modify their behaviours in the light of the opportunities available to them.

Although our study is the first to look in detail at alternative mating tactics in snakes, our results broadly resemble those obtained by other authors on other kinds of organisms (e.g. Norman et al. 1999; Moczek & Emlen 2000). For example, a male's body condition (energy reserves) may often influence the timing and duration of his involvement in reproductive activities. In the territorial toad *Pelobates fuscus*, males in poor condition joined breeding aggregations later, and left sooner, than did males in good condition (Eggert & Guyetant 2003): this is exactly the same pattern as we saw in garter snakes. Similarly, male bearded seals, *Erignathus barbatus*, in poor condition may roam widely in search of females, rather than defending territories (Van Parijs et al. 2003). Thus, we predict that detailed studies on other snake species will reveal many of the same phenomena as revealed by our study, notably spatiotemporal heterogeneity in male tactics and a matching of male phenotypes to mate location and courtship behaviours. However, the Manitoba snakes are unusual in the short spatial scale (tens of metres) over which the operational sex ratio and effective mate-finding modalities vary. This situation facilitates our ability to identify links between male phenotype, operational sex ratio and male tactics.

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