Snakes in search of sex: the relation between mate-locating ability and mating success in male garter snakes

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Is a male's ability to find fertilizable females an important determinant of his mating success? We exploited unique logistical advantages offered by courting aggregations of garter snakes, *Thamnophis sirtalis parietalis*, in Manitoba, Canada, to ask: (1) does the order at which a male arrives at a solitary female affect either his courtship tactics or his chances of inseminating her; and (2) does a male's body size affect his probability of arriving before his rivals? Experimental trials in the field and in outdoor arenas (to control group size and arrival intervals) suggested that, in the area near the main den, being the first to find a solitary female conveys limited or no fitness benefits to a male snake. Other males were likely to arrive before the male could achieve copulation; and early arrival did not guarantee optimal positioning within the mating ball. Thus, late-arriving males were as likely to obtain copulations as were early arrivers. Male body size enhanced mating success more in early arrivers than latecomers, but did not affect arrival times. However, although mate-finding ability was unimportant for male garter snakes competing near the den, it was critical in surrounding woodland where densities of rivals were much lower.

To obtain a mating, a male must perform a series of tasks that include finding a fertilizable female, inducing sexual receptivity and, perhaps, overcoming attempts at displacement by rival males. Individual males presumably differ in their abilities at each of these activities, so that any traits that facilitate success at these endeavours enhance male fitness and, hence, are under active sexual selection (Darwin 1871; Andersson 1994). However, the relative importance of these different phases of male–male competition can differ substantially between species and even between populations within a single species, or between years within a single population (Parker 1984). For example, stochastic (prey-induced) variation in the numbers of reproductive females from year to year may substantially modify the probability that a male can find a female in the absence of rival males and, hence, the degree to which success in male–male combat contributes to mating success (Madsen & Shine 1992). Similarly, the dispersion of reproductive females across the landscape,

and the ease with which they can be located by mate-searching males, may vary even between adjacent populations of the same species (Brown & Weatherhead 1999).

An extensive published literature attests to the importance of effective courtship tactics and ability to defeat rival males in fights as determinants of mating success for males (e.g. Arnold 1983; Andersson 1994). However, there is less empirical evidence on the other major task facing a reproductive male: that is, to locate a fertilizable female. The complexity and sensitivity of adaptations for mate location, such as the ability of males of many species to detect extraordinarily low concentrations of female pheromones (Conner et al. 1981; McElfresh & Millar 2001; O'Donnell et al. 2004), provide indirect evidence of strong selection on such traits. None the less, direct empirical measures of male performance in mate location are rare for most kinds of animals. Ideally, we want to know whether the first male to locate a female thereby obtains a reproductive advantage (i.e. is more likely to achieve a mating), and whether a male's ability to locate females differs consistently according to his phenotypic traits (such as body size) or his location. If the first of these statements is true, we predict selection to favour improved mate-finding ability (because it is likely to enhance male fitness). If the second statement is true, we predict that

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patterns of selection on male phenotypes will be driven at least partly by fitness differentials caused by mate location abilities and (or instead of) abilities to induce female receptivity or to defeat rival males. Even if body size per se does not influence mate-locating ability, a correlation between size and rate of mate location might arise as a by-product of selection for alternative male tactics. For example, smaller males (which are less able to win fights) may be favoured if they devote their effort to searching for solitary females rather than attempting to court already accompanied females (Gross 1996). If so, we might predict a correlation between male body size and order of arrival at unaccompanied females.

To evaluate the role of mate-locating ability in the mating system, we conducted simple experimental trials on a snake species that is ideally suited to studies of this kind: a garter snake that courts and mates in large aggregations around communal dens on the Canadian prairies.

METHODS

Study Species and Area

Red-sided garter snakes, *Thamnophis sirtalis parietalis*, are small (males average 45 cm snout–vent length [SVL], females 55 cm), nonvenomous colubrid snakes. South-central Manitoba, in the Canadian prairies, is close to the northern limit of the geographical range of this species (Rossman et al. 1996). The snakes in this area gather in large aggregations at suitable den sites each autumn, and spend 8 months inactive underground (Gregory 1974; Gregory & Stewart 1975). The animals mate soon after spring emergence, before they leave the vicinity of the den. Among a sample of 317 courting groups near one den, the mean group size was four males plus a single female (Shine et al. 2001a). The present study was based on research in May 2001, 2002 and 2003 at a large den 1.5 km north of the town of Inwood (50°31.58′N, 97°29.71′W).

Early Arrival and Mating Probability

Mating success

We set up small open-topped nylon arenas ('Space Pop', Smash Enterprises, Melbourne, Australia; circular, 48 cm in diameter, 56 cm deep), in a flat sunny area within 10 m of the den. One unmated female plus four males (taken from courting groups immediately before the video trials) were added to each arena. These densities are similar to those frequently observed in the field at this and nearby dens (Shine et al. 2001a, 2004b). We recorded SVL, tail length and mass for all animals. In each trial, the four males comprised one from each of four arbitrarily defined size classes (35–40, 41–45, 46–50, 51–55 cm SVL), encompassing the normal size variation for males at the Inwood den. The snakes were all placed into the arena at the same time, and we recorded the sequence in which they began courtship, and which male obtained the mating. All snakes were released unharmed at the conclusion of trials.

The research was conducted under the authority of the Oregon State University Institutional Animal Care and Use Committee and with permission of the Manitoba Department of Natural Resources.

Indirect predictors of male mating success, and intensity of courtship

The above trials used a wide size range of males, and allowed males to determine the time they commenced courting. Potentially, variation in those traits, and a stochastic element to which male succeeded in copulating, may have swamped any underlying relation between male order of arrival and advantage in attributes that are likely to enhance mating success. Our previous work has identified several such consistent correlates (Shine et al. 2004a). Thus, we also conducted trials in which we restricted the size range of males, and standardized the rates of arrival of additional males. We collected 140 average-sized males (i.e. excluding atypically small or large individuals, and animals with incomplete tails) and 30 females from the den on 15 May 2003. To quantify the position of snakes in courting groups, we paint-marked each male dorsally (a stripe of red, green, black, or blue) with a Sanford Magnum 44 marker. A silver line was also drawn around the circumference of each male at his cloaca. Similarly, females were paint-marked with a ring around the cloacal area as well as at 10-cm intervals along the body. This nontoxic paint had no overt effect on snake behaviour, and wore off within a day or two. Given that the den contained about 50 000 male snakes (based on unpublished mark–recapture data), the probability that any single male was used more than once during the week we conducted these trials is vanishingly small.

After collection and marking, males were placed in an open-topped nylon arena (1 × 1 × 0.8 m) set up near the den, and allowed to court 'extra' females (i.e. not those used in the courtship trials). For each trial, a female was placed into a smaller nylon enclosure (Space Pop, as above) with a 10-cm grid marked on the bottom. Trials were videotaped from directly over the centre of the arena for later analysis using a Sony Handycam CCD-TRV46E digital video camera set up on a tripod. The first male was selected at random and introduced to the arena with his head directed at the female's back, so that order of introduction corresponded with the order in which males found the female. A second male was added in the same manner 60 s later. The second male was selected at random from among the remaining colours. This process was repeated with a third and fourth male, such that each trial included four differently coloured males. The trial ended 5 min after the introduction of the first male, and 2 min after the introduction of the last male. Trials were videotaped as above. After the trials, all snakes were measured (SVL, mass, tail length) then released near the point of capture.

All males courted the female in all trials, beginning as soon as they were introduced; indeed, some males commenced chin rubbing the female's dorsal surface even before we had released them. In one of the 28 trials, mating occurred before all of the males were introduced.

Data for this trial were deleted from the analysis. We used videorecordings of the remaining trials to score the following variables at 60-s intervals, beginning 30 s after each male was added to the arena:

(1) the distance between each male's cloaca and that of the female;

(2) the number of rival males whose bodies lay between each male and the female;

(3) the proportion of each male's body that was aligned with that of the female;

(4) the total number of caudocephalic waves (rhythmic muscular contractions: see Whittier et al. 1985; Shine et al. 2004a) by each male in a 30-s period, beginning 30 s after the most recent introduction;

(5) whether or not each male tail-searched (i.e. moved his tailbase about in an apparent attempt to remain close to the female's cloaca: see Shine et al. 2004a for a description of this behaviour) within that 30-s period; and

(6) whether or not each male chin-pressed the female (see Whittier et al. 1985 for a description of this behaviour) within that 30-s period.

Effect of Location and Male Body Size

We set up standardized trials to quantify the rates at which males were able to locate solitary females. To do this we anaesthetized unmated females (by intramuscular injection of 5 mg/kg brietal sodium), dragged them ventral-surface-downwards for 5 m to deposit a pheromonal trail, and then laid each female out at the end of her trail. Females recovered from anaesthesia in 20–30 min with no ill effects. Adjacent females and their trails were separated by at least 5 m. We sat quietly beside the female; mate searching and courting males ignore human observers under such conditions (Shine et al. 2000b). We scored the time taken for males to arrive and begin courting the female; each male was removed and measured (SVL only) as soon as he commenced courtship. Trials were terminated after arrival of the 10th male, or after 15 min (whichever was soonest). Trials were conducted both in the main den area (rocky and open) and in a grassy glade among the aspen woodland 100 m away from the den. Snake densities, and thus sizes of courting groups, decrease dramatically further from the den (Shine et al. 2001a).

Statistical Methods

Data were analysed using Statview 5 and JMP 5.01 (SAS Institute 1998, 2002). Assumptions of parametric tests (normality, variance heterogeneity, etc.) were tested before analysis; no transformations were necessary for any variables except those linked to time since arrival (see below). Comparisons of body sizes and behavioural traits between males that differed in order of arrival were based on single-factor ANOVA, with MANOVA to check for overall significance levels. Arrival rates were compared between den and woodland sites using ANOVA also. To examine possible influences of male body size and arrival time (as well as the interaction between these variables) on mating success, we used multiple logistic regression.

Log-likelihood ratio tests from such regressions provide chi-square statistics to evaluate the statistical significance of each main effect and interaction term. Nonparametric Wilcoxon signed-ranks tests were used to assess changes through time in courtship intensity. Because many of our analyses failed to reject the relevant null hypotheses, we need to ensure that statistical power was sufficient for an acceptably low probability of type 2 error. Following recommendations of Day & Quinn (1989) and Peterman (1990), we conducted such tests (based on noncentral F distributions) only for cases where the test generated a nonsignificant P value < 0.20. Because all animals were used in only a single trial, there are no issues with pseudoreplication.

RESULTS

Early Arrival and Mating Probability

Mating success

Males averaged $\pm$ SE 45.40 ± 0.50 cm SVL, and 30.7 ± 1.00 g. The order in which males began courting was not significantly related to either their mass or SVL (ANOVA with order of arrival as factor: Fs = 1.13–2.63, Ps = 0.06–0.34). All trials involved vigorous courtship, and 21 resulted in mating after a mean of 11.09 ± 3.14 min (range 2.6–55.8 min). Of these 21 trials, similar numbers of copulations were obtained by the first male that began courting ($N = 6$), the second ($N = 5$), the third ($N = 5$) and the fourth ($N = 5$). Thus, the sequence in which males commenced courting was unrelated to their probability of mating (against a null of equal probabilities: $\chi_3^2 = 0.26$, $P = 0.96$).

If we include male SVL as well as order of arrival as independent variables, multiple logistic regression confirms that a male's mating success was not affected overall by his order of courtship commencement ($\chi_1^2 = 0.37$, $P = 0.54$) but was higher for larger males ($\chi_1^2 = 4.27$, $P < 0.04$) and, more importantly, was affected by an interaction between male SVL and order of courtship commencement ($\chi_1^2 = 4.30$, $P < 0.04$). This significant interaction term reflects a pattern whereby successful males were larger than unsuccessful males for the first, second and third males to begin courting, but not for the fourth. Among males that obtained a mating despite being the last (fourth) to join the courting group, smaller males were more successful than their larger rivals (Fig. 1).

Indirect predictors of male mating success

Males averaged 45.80 ± 0.26 cm SVL, and weighed 28.34 ± 0.47 g. There were no significant differences in mass or SVL according to the order in which males were introduced (ANOVA: Fs = 0.15–1.15, Ps = 0.30–0.65). A male's order of arrival had no significant effect on the distance between the focal male's cloaca and that of the female at either 4 or 5 min after the trial started (ANOVA: 4 min: $F_{3,104} = 0.54$, $P = 0.65$; 5 min: $F_{3,104} = 0.31$, $P = 0.82$; Fig. 2a, b), the proportion of his body aligned with that of the female (4 min: $F_{3,104} = 1.16$, $P = 0.33$; 5 min: $F_{3,104} = 0.42$, $P = 0.74$; Fig. 2c, d), or the number
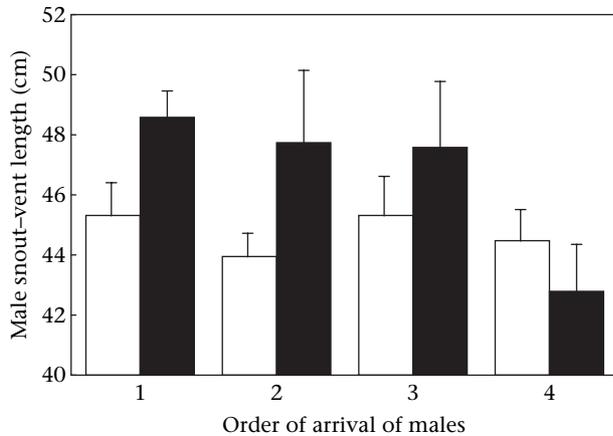
Figure 1. Body sizes (snout–vent lengths) of male garter snakes as a function of the order in which they commenced courting the female in an arena trial, and whether or not they succeeded in obtaining a mating with that female. □: unsuccessful; ■: successful. Mean values $\pm$ SE are shown. N (left to right) = 15, 6, 16, 5, 14, 5, 14, 5. See text for statistical analysis of these data.

of rival males separating his body from that of the female (4 min: $F_{3,104} = 2.76$, $P = 0.05$, power = 0.65; 5 min: $F_{3,104} = 0.74$, $P = 0.53$; Fig. 2e, f). Multivariate ANOVA on these data similarly revealed no significant effect of a male's order of arrival on the variables analysed above (Wilk's lambda: 4 min: $F_{9,248} = 1.21$, $P = 0.29$; 5 min: $F_{9,248} = 0.52$, $P = 0.86$).

Intensity of courtship

We also looked at whether a male's order of arrival at a female modified his overall intensity of courtship. As for the positional variables (above), we detected no consistent influence of arrival order on the number of caudocephalic waves per 30 s (ANOVA: 4 min: $F_{9,248} = 1.15$, $P = 0.33$; 5 min: $F_{9,248} = 0.17$, $P = 0.91$; Fig. 3a, b), nor on the proportion of males tail searching (4 min: $F_{9,248} = 3.11$, $P < 0.03$; 5 min: $F_{9,248} = 0.89$, $P = 0.45$; Fig. 3c, d) or chin pressing (4 min: $F_{9,248} = 0.66$, $P = 0.58$; 5 min: $F_{9,248} = 1.57$, $P = 0.20$, power = 0.39; Fig. 3e, f). The single significant result reflected a trend for earlier-arriving males to continue tail searching very actively 4 min into the trial; however, this pattern had disappeared a minute later (Fig. 3). Multivariate ANOVA on these data revealed no overall effect of a male's order of arrival on his intensity of courtship (Wilk's lambda: 4 min: $F_{9,248} = 1.66$, $P = 0.10$; 5 min: $F_{9,248} = 1.12$, $P = 0.35$).

Last, to see whether courtship intensity (using the same variables as above) changed as group size changed, we followed the first male's behaviour through time. To obtain a single measure per variable per male (and thus avoid pseudoreplication), we used the slope of a regression linking the courtship measure to time for each male. This procedure generated a single measure of change in courtship intensity through time for each male. We used a two-tailed Wilcoxon signed-ranks test on the slopes to see if they differed from zero. We found declines through time in the number of caudocephalic waves ($Z = -1.93$, $N = 27$, $P = 0.054$), the incidence of chin rubbing

($Z = -2.80$, $N = 27$, $P = 0.005$), and the proportion of the male's body aligned with that of the female ($Z = -2.44$, $N = 27$, $P = 0.030$) but not in the incidence of tail-searching attempts ($Z = -0.35$, $N = 27$, $P = 0.72$).

Effect of Location and Male Body Size

In 15 trials at the den, at least 10 males arrived at each female within 8 min of the trial's commencement (mean arrival rate $\pm$ SE = 3.04 $\pm$ 0.25 males/min). However, females laid out in seven trials in the aspen woodland attracted only one or two males within the 15-min time limit (mean arrival rate $\pm$ SE = 0.13 $\pm$ 0.02 males/min; comparing the two areas: ANOVA: $F_{1,20} = 61.99$, $P < 0.0001$). We thus analysed the body size data from these two sets of trials separately. A male's body size did not affect the order of his arrival at a female in either location (Pearson correlation: den males: $r_{148} = 0.13$, $P = 0.12$, power = 0.63; woodland males: $r_8 = 0.24$, $P = 0.52$; Fig. 4).

DISCUSSION

Our study suggests there is little or no fitness benefit to enhanced mate-finding ability for male garter snakes that court in large aggregations around the Manitoba dens. This result stands in strong contrast to many published speculations; for example, Schwagmeyer (1988) concluded that both theoretical and empirical studies support the idea of a mating advantage for highly mobile males when precopulatory competition consists largely of nonaggressive searching. Why, then, did earlier arrival at a female not enhance mating success in our male garter snakes, at least near the communal den? Potentially, such a benefit could arise in two ways: either the first male to find a female is able to court her uninterrupted (without any rivals) for a long-enough period that he can induce her to accept a copulation; or alternatively, other males arrive before that time but, none the less, the first male to arrive is more likely to achieve a mating. In turn, such an advantage might arise if early arrival enables the male to take an optimal courtship position relative to the female. Our data argue against both propositions, at least for snakes in the main mating aggregation. First, the rates of arrival of rival males at the main den were high ($>$3/min) relative to the usual time of courtship required before intromission (mean = 11.1 min in our arena trials with four males courting: see above). Thus, copulation before the arrival of another male is very unlikely. Second, as soon as other males arrived, the first male's advantage was lost; he was no more likely to mate, or to be able to maintain a position that would facilitate mating, than were his more tardy rivals.

Intuition suggests that arriving first might enable a male to obtain the best position for subsequent courtship, even if other males eventually arrive. However, our data clearly falsify this prediction. The likely reason is that females frequently move about during courtship, so that males are in constant motion in an attempt to maintain their cloacae close to hers. Hence, any advantage is lost as soon
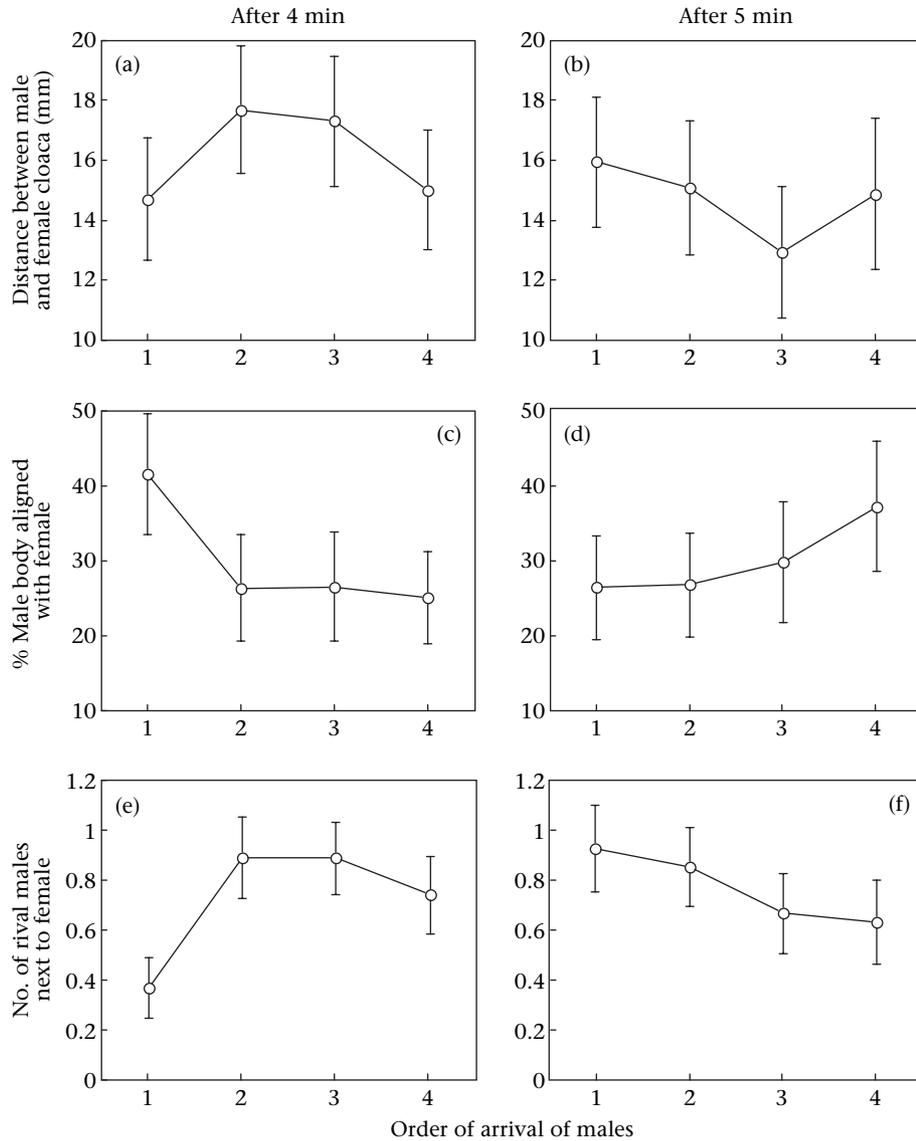
Figure 2. Effects of the order in which a male garter snake arrived at a female (with 1 min between successive arrivals) on the position of that snake within the resulting mating ball after (a, c, e) 4 min and (b, d, f) 5 min. Mean values $\pm$ SE are shown, each based on data for 27 snakes. (a, b) Distance between male and female cloaca, (c, d) percentage of male's body aligned with female and (e, f) number of rival males that had their bodies interposed between the focal male and the female. See text for statistical analysis of these data.

as positions change, which they do almost continuously (Shine et al. 2004b). The only obvious effect of the arrival of additional males was a decrease in the frequency of courtship activities by the males already in place (and, thus, an overall decline in courtship intensity per male in larger groups). We noted the same pattern in a previous study, and interpreted it in terms of social parasitism; that is, males benefit from reducing energy-expensive courtship and allowing other males to stimulate the females while they wait for an opportunity to intromit (Shine et al. 2003).

Although the fitness benefits to efficient mate searching were minimal in large mating aggregations in the den, the same was not true in the nearby aspen woodlands where snake densities were much lower. A male that finds a solitary female in the woodland is likely to be able to court

uninterrupted for an average of about 7.7 min (based on mean arrival rates in our study); in arena trials with courtship by a single male, 29% of copulations (8/28) occurred within that time period (unpublished data). Thus, the ability to locate females may be under strong directional selection in this system, and presumably also in many other snake populations (which typically occur at densities even lower than those in the aspen woodlands surrounding the large dens: personal observation). Mate-locating ability may be a major target of selection even in mating systems that involve male–male combat, because a high proportion of all male–female encounters (and, thus, mating opportunities) may occur in the absence of other males (Madsen & Shine 1992; Duvall & Schuett 1997).

It is easy to imagine scenarios whereby male body size might correlate with the order in which males arrive at
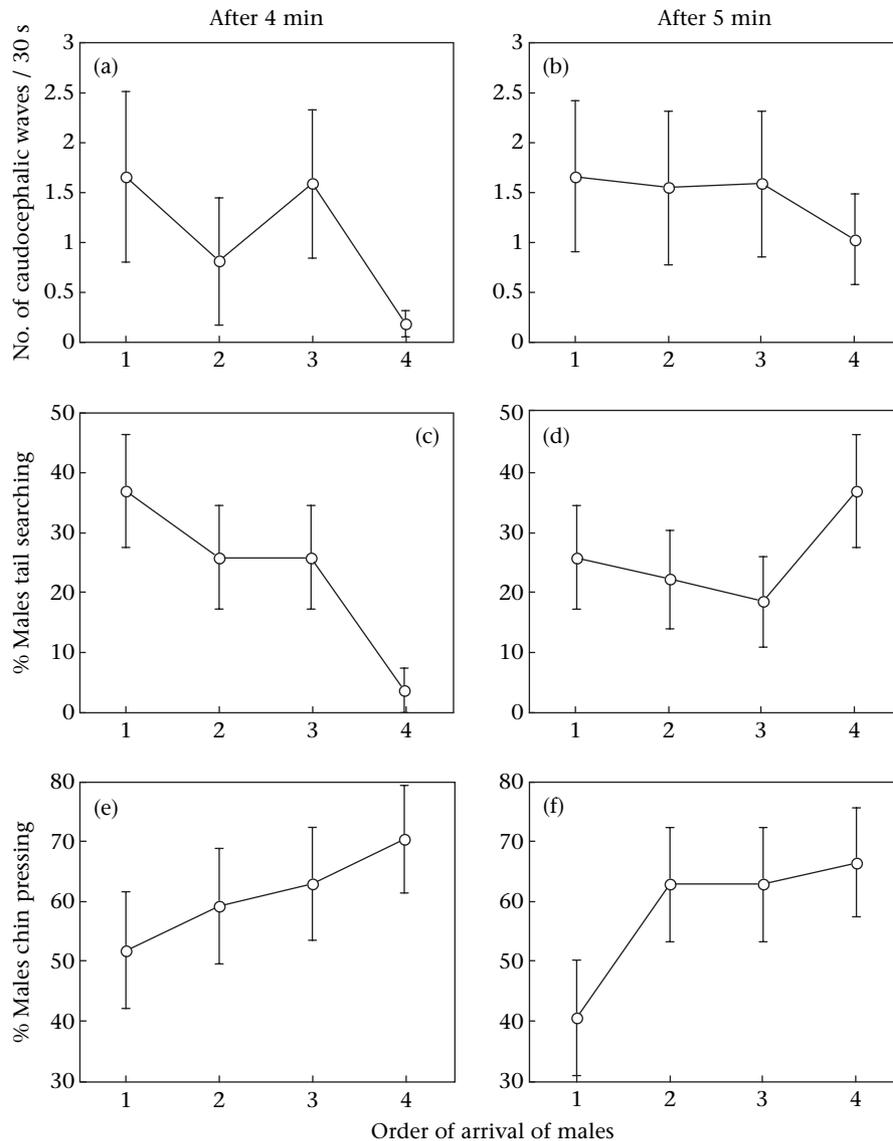
Figure 3. Effects of the order in which a male garter snake arrived at a female (with 1 min between successive arrivals) on the intensity of courtship of that snake within the resulting mating ball. (a, b) Number of caudocephalic waves/30 s, (c, d) percentage of males tail searching and (e, f) percentage of males chin pressing. Mean values ± SE are shown, each based on data for 27 snakes. See text for statistical analysis of these data.

a female: for example, small males might move around more either because of energetic benefits or because they are unable to compete successfully with their larger rivals in mating balls (Gadgil 1972; Emlen & Oring 1977; Olsson & Madsen 1998). However, our study provided no support for this idea. Instead, a male's body size did not affect the order in which he arrived at a female (Fig. 4). Larger male body size enhanced the probability of mating for the first three males to begin courting, but had no such effect on the fourth (latest) male to commence courtship (Fig. 1). The pattern for the first three males accords well with previous studies on the same population, whereby larger body size enhanced a male's probability of mating (Shine et al. 2000b). Why, then, did this trend reverse with the fourth-arriving male (Fig. 1)? Because copulation often occurred soon after the fourth male commenced

courtship, smaller males might have been able to exploit the courtship endeavours of their earlier-arriving, larger rivals; smaller body size may thus have been less of a disadvantage, or may even have facilitated optimal positioning within the courting group.

Our current study also clarifies the mechanistic basis for the large-male mating advantage noted above. The higher mating success of larger males (both in the field and in arena trials) has been attributed to male–male rivalry within courting groups. That is, larger males are more able to displace their smaller rivals (Shine et al. 2000b). However, data from the earlier study were also consistent with the hypothesis of a size advantage driven by mate-searching ability; that is, larger males may have obtained more matings because they commenced courting sooner, and thereby obtained more copulations. Our data falsify
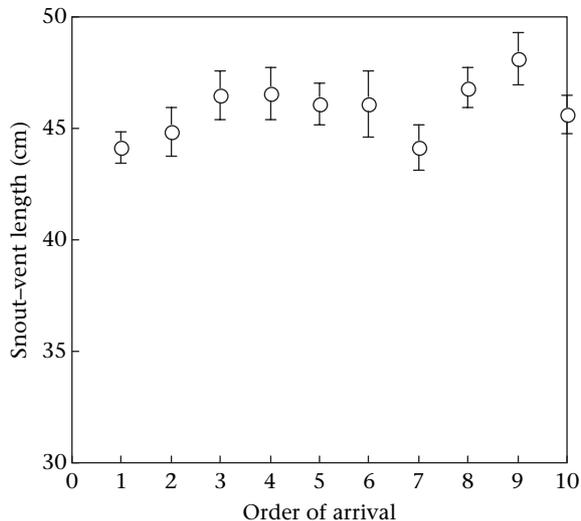
Figure 4. Body sizes (snout–vent lengths) of male garter snakes as a function of the order in which they arrived at anaesthetized female snakes laid out in the communal den. Mean values ± SE are shown. Sample sizes are 15 males for each point. See text for statistical tests of these data.

this latter hypothesis, with large male body size enhancing mating success regardless of order of arrival at the female (Fig. 1). Thus, the mechanistic basis for large-male advantage in this system involves courtship per se, not mate-finding ability.

Our data also add to the growing evidence on the fitness consequences of variation in male body size in this population. At the Manitoba dens, small body size increases a male garter snake's vulnerability to mortality by several sources including predation by crows, suffocation in mating balls (Shine et al. 2001b) and roadkill (Shine & Mason 2004). Small body size also decreases a male's chances of obtaining a mating (Shine et al. 2000b), especially if the female is large (Shine et al. 2001c) or if larger males are present (Shine et al. 2000a). None the less, a snake's vulnerability to other mortality sources (such as winterkill and drowning at the dens: Shine & Mason 2004) is not influenced by his body size; and our study shows that a male garter snake's performance in mate location is similarly unrelated to his size.

Although our methods are simple and our results straightforward and relatively intuitive, empirical data on the fitness consequences and phenotypic correlates of mate-locating ability appear to be scarce for most kinds of animals. The primary exception to this statement involves studies on the effects of sperm precedence: that is, order of mating influences the proportional paternity of the resulting clutch (e.g. Birkhead 2000; Tennessen & Zamudio 2003). If a similar first-male advantage applies to garter snakes, it must do so over a longer timeframe than was relevant to our own study. Female garter snakes stay at the den only briefly before dispersing to their summer ranges, and a large gelatinous mating plug occludes the mated female's cloaca throughout that period (Devine 1977; Rossman et al. 1996). Thus, remating at the den is rare (Shine et al. 2000c). None the less, multiple paternity is common (Garner et al. 2002) even though long-term

(across-season) sperm storage is rare (Blanchard 1943); thus, many females must remate later in the season. First-male priority may well occur under such circumstances, but if so would exert selection not on male mate-finding ability per se, but on a male's focus of courtship activity (i.e. at the den versus in the summer range).

We expect that careful studies on other taxa will reveal many of the same patterns seen in our own data set; for example, priority of access to females may be relatively unimportant in determining male mating success if courtship before copulation is prolonged relative to rates of arrival of rival males. In contrast, the first male to find a female may experience a substantial fitness advantage in systems where courtship is brief or rates of arrival of rivals are low (Parker 1984). Thus, the consequences of variation in mate-locating ability may vary enormously at small spatial and temporal scales, and future work could usefully explore the determinants of such variation.

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