THE OPPORTUNISTIC SERPENT: MALE GARTER SNAKES ADJUST COURTSHIP TACTICS TO MATING OPPORTUNITIES

by

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Summary
Reproductive males encounter potential mates under a range of circumstances that influence the costs, benefits or feasibility of alternative courtship tactics. Thus, males may be under strong selection to flexibly modify their behaviour. Red-sided garter snakes (Thamnophis sirtalis parietalis) in Manitoba overwinter in communal dens, and court and mate in large aggregations in early spring. The number of males within a courting group varies considerably, as do the body sizes of both males and females. We manipulated these factors to set up replicated courtship groups in outdoor arenas, and analysed videotapes of 82 courtship trials to quantify courting behaviours of male snakes. Larger and more heavy-bodied males courted more vigorously than did their smaller, thinner-bodied rivals, and large females attracted more intense courtship. The major effect, however, involved the number of rival males competing for copulation. Males in large groups not only reduced their overall vigour of courtship, but also modified their tactics in such a way as to benefit from the courtship activities of rival males. That is, they devoted less energy to inducing female receptivity (which requires energy-expensive caudocephalic waving) and more effort to behaviour (tail-searching) that enhanced their own
probability of mating if the female gaped her cloaca. This social parasitism reveals an unsuspected plasticity and complexity in the behavioural tactics of reproducing male snakes.

**Keywords**: operational sex ratio, plasticity, reproductive success, reptile, sexual selection.

**Introduction**

A high proportion of all behaviours in most kinds of organisms display some degree of plasticity: aspects of the organism’s physiological state or environmental cues modify the expression of the behaviour. Plasticity of this kind is likely to enhance fitness when (as is often the case) the animal unpredictably encounters situations that modify the relative fitness consequences of alternative behaviours (*e.g.* Jackson & Pollard, 1996; Eltz, 1997; Schatz *et al.*, 1997; Henen *et al.*, 1998). Even very ‘simple’ organisms display flexible behaviours, indicating that behavioural plasticity does not require complex information-processing capabilities (*e.g.* Demott & Moxter, 1991; Jurgens & DeMott, 1995; Bushmann, 1999; Corbara & Dejean, 2000). In many cases, organismal responses are modified by local circumstances in ways that plausibly enhance fitness (*e.g.* Maynard Smith, 1976; Sinervo & Lively, 1996; Alonzo & Sinervo, 2001; Candolin & Reynolds, 2002).

Some of the best examples of adaptive behavioural plasticity involve mating tactics. For example, the optimal tactics for mate location often depend upon local conditions (resources, topography, *etc.*) that determine the spatial distribution and ease of location of receptive females (Emlen & Oring, 1977; Duvall & Schuett, 1997; Brown & Weatherhead, 1999). In the same way, a male’s optimal tactics after finding a female will depend on factors (such as the numbers and sizes of rival males) that may vary unpredictably over relatively short timespans and spatial scales (Travis & Woodward, 1989; Dodson & Schwaab, 2001; Candolin & Reynolds, 2002). Hence, the tactics of reproductive males offer a useful system with which to examine plasticity in behavioural traits, and the ways in which such plasticity might enhance mating success.

Reptiles have attracted relatively little attention in this respect, perhaps reflecting an assumption that they display limited behavioural plasticity. However, recent studies have revealed remarkable complexity in reptilian social systems, including polymorphic male strategies. For example, side-blotched
lizards (*Uta stansburiana*) occur in multiple male morphotypes with distinctive mating tactics (Sinervo & Lively, 1996; Sinervo *et al*., 2000a, b, 2001; Sinervo, 2001). Does significant diversity also arise via behavioural plasticity within single individuals? Studies on snakes have lagged well behind those on lizards in this respect, but recent research on one species (the garter snake *Thamnophis sirtalis*) has revealed flexible reproductive tactics. For example, males shift between alternative tactics based on their body size (size-assortative courtship: Shine *et al*., 2001b), their ability to compete with other males (female mimicry: Shine *et al*., 2000a, 2001c), and the numbers and body sizes of rival males (participation in courtship: Shine *et al*., 2000b). Male mate choice is influenced also by attributes of the female, with large and heavy-bodied females attracting more courtship than small, thin conspecifics (Aleksiuk & Gregory, 1974; Hawley & Aleksiuk, 1976; Gartska *et al*., 1982; Shine *et al*., 2001b). Operational sex ratios within courting groups also may modify the intensity of courtship by each male (Joy & Crews, 1985).

Previous studies on reproductive behaviour in garter snakes have been based on visual observation, precluding detailed quantification of the activities of individual snakes within ‘mating balls’ (which often contain several animals in simultaneous vigorous activity). Based on previous research (above), we predicted that male snakes might modify either the intensity or form of their courtship behaviours in response to three factors: (1) aspects of their own phenotype (body size and condition) that could influence their ability to compete with other males; (2) the potential fitness benefits from a mating (body size, and thus probable fecundity, of the female being courted); and (3) the intensity of male-male competition (numbers of rival males). Thus, we videotaped courting snakes in experimental arenas (allowing us to manipulate all three of the above variables) to test these predictions.

**Methods**

*Study species and area*

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small (<1 m total length) non-venomous snakes with a broad geographic distribution in North America. We studied these snakes in the Interlake region north of Winnipeg, Manitoba, in central Canada. Snakes in this severely cold region spend about eight months per 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 & Stewart, 1975). Dens may
contain >10,000 snakes and courtship occurs close to the den; thus, densities of snakes are very high at this time (sometimes, >100/m²: Shine et al., 2001a). Newly-emerging females are rapidly located and vigorously courted by dozens or hundreds of males, but the mean size of courting groups (numbers of males) decreases rapidly as one moves away from the den (Shine et al., 2001a). In the grasslands surrounding the den, some females are courted by single males (Shine et al., 2001a).

Male garter snakes locate females using the vomeronasal system, with skin lipids on females serving as sex pheromones (Mason, 1993). Males align their bodies with that of the female, pressing their chins against her dorsal and lateral surfaces and positioning their cloacae next to hers. Males maintain this position with frequent attempts to intertwine their tailbase beneath that of the female; any movement by the female provokes an immediate flurry of activity by male tails (‘tail-searching’: Noble, 1937; Blanchard & Blanchard, 1941; Crews & Gartiska, 1982; Whittier et al., 1985). Large males may push the tails of their small rivals out of the way at such times (Luiselli, 1996; Shine et al., 2000f). 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). Recent studies suggest that these pressure waves push anoxic air from the female’s non-respiratory posterior air sac anteriorly to her respiratory lung, thus inducing the stress response of cloacal gaping (Shine et al., 2003a). This gaping facilitates intromission of the male’s hemipenis.

During May 2002 we worked at a communal den containing approximately 10,000 snakes 1.5 km N of the town of Inwood, 250 m E 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., 2000b, c, d, e, 2001b, 2003a, b).

**Procedures**

We set up four small outdoor arenas (‘Space Pop’, Smash Enterprises, Melbourne; circular with 48 cm diameter, 56 cm deep) in a flat sunny area <10 m from the den, to video-record courting groups. Unmated females (i.e. lacking a mating plug: Devine, 1977; Shine et al., 2000e) were collected as they emerged, and one such female was placed in each arena. For later analysis we grouped these animals into four size categories such that each category contained approximately equal numbers of snakes (23.7-53.6, 53.7-57.2, 57.3-60.0, 60.1-70.0 cm SVL). We then added either one, four or 24 males (collected from courting groups immediately prior to the video trials) to each arena. We conducted 24 trials involving one male plus a female, 25 trials with 24 males plus a female, and 33 trials with four males plus a female. In the one-male and four-male trials, all snakes were painted with coloured mid-dorsal stripes for individual recognition. In the 24-male trials, we painted four ‘focal’ males (and the female) in the same way, but the other males were unpainted. The four painted males in each four-male and 24-male trial comprised one from each of four arbitrarily-defined size classes, encompassing the normal size variation for males at the Inwood den (as above, divided such that equal numbers of snakes fell into each of the four size classes). We filmed the animals with Sony Handycam CCD-TRV46E digital videocameras on tripods. From the resulting videotapes, we randomly selected two 30-sec samples three minutes apart, and at least two minutes prior to actual mating. At each of these two time periods we scored four nominal variables for each focal male: whether or not (a) his body was aligned with that of the female; (b) he attempted a tail-search; (c) he performed one or more caudocephalic waves; and/or (d) he chin-pressed the female, within the 30 sec period. We also scored three
continuous variables: (a) the distance between his cloaca and the female’s cloaca; (b) the proportion of his body aligned with that of the female; and (c) the number of caudocephalic waves that he performed during 30 sec.

Analysis

Each animal (either male or female) was used in only a single trial, to avoid pseudoreplication. Data were analysed on an Apple Macintosh G4 computer using the statistical software package Statview 5 (SAS Institute, 1998). Relevant assumptions of tests (normality of distributions, equality of variances) were checked prior to analysis. The text presents mean values ± one SE.

We examined male body sizes using two-factor ANOVA with the factors being trial type (number of males per female) and male size class. Body sizes of males were similar among the trial types ($F_{2,244} = 0.41$, $p = 0.67$), with no significant interaction between trial type and male size class ($F_{6,67} = 1.43$, $p = 0.20$). However, the four size classes of males differed consistently ($F_{3,244} = 107.39$, $p < 0.001$). The ‘extra-large’ males averaged $50.08 ± 0.37$ cm snout-vent length (SVL) and $37.76 ± 0.96$ g; ‘large’ males were $46.70 ± 0.30$ cm and $31.21 ± 0.81$ g; ‘medium’ males were $42.98 ± 0.30$ cm and $24.24 ± 0.63$ g; and ‘small’ males were $40.00 ± 0.35$ cm and $19.78 ± 0.67$ g. Analysed in the same way, data on female sizes showed the same pattern: mean body sizes of females did not differ between these three types of trials (two-factor ANOVA: $F_{2,70} = 0.89$, $p = 0.42$), but differed between our four size classes ($F_{3,70} = 64.80$, $p < 0.0001$; mean SVLs = ‘extra-large’, $63.39 ± 0.28$ cm; ‘large’, $58.47 ± 0.12$ cm; ‘medium’, $55.22 ± 0.16$ cm; ‘small’, $49.19 ± 0.54$ cm), with no significant interaction between trial type and female size class ($F_{6,70} = 0.83$, $p = 0.55$).

Previous work has shown that courtship vigour and success in red-sided garter snakes is influenced by female body size (large females attract more courtship: Aleksiuk & Gregory, 1974; Hawley & Aleksiuk, 1976) as well as by male body size (large heavy-bodied males court more vigorously and obtain more matings: Shine et al., 2000f). Thus, we included female size (SVL) as well as male size (SVL) and shape (body condition, calculated as residual scores from the linear regression of ln mass vs ln svl), together with trial type (= number of males per female) as independent variables in multiple logistic regressions. The behaviours we scored as presence/absence for each focal male were used as the dependent variable, with the behaviour scored as present if the male showed it during either of the two observation periods. Because data from the two periods were thus combined into a single response variable for the analysis, each male contributed only a single data point.

Results

Log-likelihood ratio tests from these logistic regressions yielded very similar results for the four behaviours we examined in this way (Table 1). A male’s body size and condition did not influence his courtship except that heavier-bodied males were more likely to perform caudocephalic waves. Figures 1 and 2 show courtship behaviours of males as a function of female body size (divided into four equal-sized groups) and trial type (number of males).
TABLE 1. Results of log-likelihood ratio tests from multiple logistic regressions to evaluate whether phenotypic traits of garter snakes (Thamnophis sirtalis parietalis), and numbers of males per courting group, influenced behaviours exhibited by courting males

<table>
<thead>
<tr>
<th>Variable</th>
<th>Female SVL</th>
<th>Male SVL</th>
<th>Male condition</th>
<th>Group size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Align to female?</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>14.44***</td>
<td>0.0001</td>
<td>0.47</td>
<td><strong>40.53</strong>*</td>
<td></td>
</tr>
<tr>
<td>Tail-searching?</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.63*</td>
<td>0.32</td>
<td>0.09</td>
<td><strong>24.73</strong>*</td>
<td></td>
</tr>
<tr>
<td>Caudocephalic waving?</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25.74***</td>
<td>0.19</td>
<td>7.07**</td>
<td><strong>36.08</strong>*</td>
<td></td>
</tr>
<tr>
<td>Chin-pressing?</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7.76**</td>
<td>0.08</td>
<td>0.28</td>
<td><strong>40.09</strong>*</td>
<td></td>
</tr>
</tbody>
</table>

SVL = snout-vent length; ‘condition’ = residual score from linear regression of ln mass vs ln SVL; ‘group size’ = number of males courting the female (1, 4 or 24). Text shows χ² values, with significance levels indicated by asterisks (*p < 0.05; **p < 0.01; ***p < 0.001). Values with p < 0.05 shown in boldface.

Large females attracted more intense courtship (alignments, tail-searching, caudocephalic waving, chin-pressing: see Fig. 1). The major effect on all these variables, however, was the number of competing males. Courtship was more vigorous when a male was alone with a female than when he was part of a group with three other males, and courtship intensity decreased still further in a large group (Table 1, Fig. 1).

The higher intensity of courtship to large females was evident for each of the nominal variables that we scored, and this effect was generally stronger in four-male trials than in the other courting groups (Fig. 1). Analysis of the continuous variables (Fig. 2) revealed broadly similar patterns. Males maintained their tailbases closer to the female cloaca in trials with fewer rivals (F₂,228 = 22.75, p < 0.0001; posthoc comparisons all differ at p < 0.05), with no influence of female body size (F₃,228 = 0.72, p = 0.54; interaction: F₆,228 = 1.20, p = 0.31; see Fig. 2). Similarly, the proportion of the male’s body aligned with the female was higher in small courting groups (F₂,228 = 36.24, p < 0.0001; posthoc comparisons all differ at p < 0.05) but was not affected by female body size (F₃,228 = 1.30, p = 0.28; interaction: F₆,228 = 1.35, p = 0.24; see Fig. 2). The frequency of caudocephalic waves was higher in small groups (F₂,228 = 28.16, p < 0.0001; posthoc comparisons all differ at p < 0.05) and was higher for large females (F₃,228 = 4.11, p < 0.008; posthoc tests show that S < L and
Fig. 1. Effects of body size of female and number of courting males per female on courtship behaviours exhibited by garter snakes (*Thamnophis sirtalis parietalis*). Groups contained either 1, 4 or 24 males. We scored whether or not each focal male aligned with the female’s body (a), tail-searched (b), performed caudocephalic waves (c) and/or chin-pressed against the female (d), in two 30-sec observation periods. Size categories of females were extra-large (XL), large (L), medium (M) or small (S). Sample sizes (left to right) = 4, 3, 9, 8, 28, 21, 23, 28, 32, 40, 32 and 28. See text for further explanation and statistical tests.

M), with no significant interaction between these two factors ($F_{6,228} = 0.98$, $p = 0.44$; see Fig. 2).

Figures 3 and 4 show male responses as a function of male rather than female body size. For the continuous variables that we scored for each male, we again calculated a single score for each animal (mean of the two values for successive time periods) and used these as dependent variables in two-factor ANOVAs with trial type (number of competing males) and male size class as the factors. Analyses including female SVL as a covariate (ANCOVA) generated identical conclusions, and so this factor is omitted for simplicity. As for the nominal variables analysed above, male courtship behaviours were affected by the number of rival males. Males were able to maintain their cloacae closer to those of the females if no rivals were present
Fig. 2. Effects of body size of female and number of courting males per female on courtship behaviours exhibited by garter snakes (*Thamnophis sirtalis parietalis*). Groups contained either 1, 4 or 24 males. We scored mean distances between the cloacae of focal males and females (a), the proportion of the males’ bodies aligned with those of the females (b), and the mean number of caudocephalic waves performed by each male within two 30-sec periods (c). Histograms show mean values and one SE. Size categories of females were extra-large (XL), large (L), medium (M) or small (S). Sample sizes as for Fig. 1. See text for further explanation and statistical tests.

\[ F_{2,228} = 24.83, \ p < 0.001; \text{ see Fig. 4a). There were no significant overall differences among size classes of males in this respect } \left( F_{3,228} = 0.57, \ p = 0.63 \right), \text{ but there was a significant interaction between male size class and number of competing males } \left( F_{6,228} = 2.79, \ p < 0.02 \right). \text{ Larger males maintained their tailbases closer to the female’s cloaca than did small males if the group consisted of only four courting animals, but the pattern was reversed in the 24-male aggregations (Fig. 4a). The proportion of the focal male’s body aligned with that of the female was higher in one-on-one courtship than in large groups (Fig. 4b; } F_{2,228} = 36.98, \ p < 0.0001; \text{ posthoc tests show that all trial types differ at } p < 0.05), \text{ with no influence of male body size } \left( F_{3,228} = 0.38, \ p = 0.77; \text{ interaction: } F_{6,228} = 0.92, \ p = 0.48 \right). \]
Fig. 3. Effects of body size of male and number of courting males per female on courtship behaviours exhibited by garter snakes (Thamnophis sirtalis parietalis). Groups contained either 1, 4 or 24 males. We scored whether or not each focal male aligned with the female's body (a), tail-searched (b), performed caudocephalic waves (c) and/or chin-pressed against the female (d), in two 30-sec observation periods. Size categories of males were extra-large (XL), large (L), medium (M) or small (S). Sample sizes (left to right) = 6, 6, 6, 6, 33, 33, 33, 33, 25, 25, 25 and 25. See text for further explanation and statistical tests.

The same pattern is evident in Fig. 3a, which shows that the proportion of males aligning with the female was lower in groups with more intense male-male rivalry. Caudocephalic waving was displayed by males regardless of group size (Fig. 3c) but the rate of waving was higher in small groups (Fig. 4c; $F_{2,244} = 27.78, p < 0.001$; posthoc comparisons all differ at $p < 0.05$) and more frequent by larger than by smaller males ($F_{3,244} = 4.55, p < 0.005$; posthocs show S differ from XL, L and M at $p < 0.05$). The interaction between male size and number of rivals was close to statistical significance ($F_{6,244} = 2.10, p = 0.054$), reflecting a trend for very large males to court more actively in four-male groups than in either of the other trial types (Fig. 4c).

These analyses show that male courtship behaviours shifted in complex ways as a function of the numbers of competing males, as well as male and
Fig. 4. Effects of body size of male and number of courting males per female on courtship behaviours exhibited by garter snakes (*Thamnophis sirtalis parietalis*). Groups contained either 1, 4 or 24 males. We scored mean distances between the cloacae of focal males and females (a), the proportion of the males’ bodies aligned with those of the females (b), and the mean number of caudocephalic waves performed by each male within two 30-sec periods (c). Histograms show mean values and one SE. Size categories of males were extra-large (XL), large (L), medium (M) or small (S). Sample sizes as for Fig. 3. See text for further explanation and statistical tests.

Female body sizes. Do these shifts reflect simple changes in intensity, or in tactics as well? For example, if males are ‘social parasites’, we might expect that a male in a large group would continue to tail-search (to maximise his chances of intromission if the female gapes her cloaca) but reduce his rate of energy-expensive behaviours such as caudocephalic waving. Figure 5 shows exactly this situation. A two-factor ANOVA with presence or absence of tail-searching as one factor and trial type as the other, with rate of caudocephalic waving as the dependent variable, shows a significant interaction term ($F_{2,250} = 5.63, p < 0.005$; see Fig. 5). That is, males in large groups
continued to tail-search but substantially reduced their rate of caudocephalic waving.

**Discussion**

Reflecting their remarkable tolerance of disturbance (Moore & Mason, 2001), the garter snakes in our outdoor arenas courted vigorously, and with the same behaviours as seen in natural courting groups in the den a few metres away. The arenas allowed us to control group sizes (operational sex ratios) and body sizes of both males and females, and hence to explore the ways that male tactics are influenced by these factors. Videotaping permitted unambiguous scoring of behaviours for each focal male. The clear result from the study is that male garter snakes exhibit significant plasticity in courtship tactics in response to each of the variables that we manipulated. This plasticity involved not only the intensity of effort that a male devoted to courtship, but also his allocation of effort among different components of courtship behaviour. In each case, the direction of the shift was consistent with the adaptationist hypothesis that male courtship plasticity enhances mating success. Below, we consider each of the factors (and interactions between them) that modified the tactics of male snakes in our trials.
Female body size

Large females attracted more intense courtship than did small conspecifics (Figs. 1 and 2). Similar results have been reported in most previous studies of the same species, with large females attracting more suitors than small females (Aleksiuk & Gregory, 1974; Hawley & Aleksiuk, 1976; Gartska et al., 1982; Shine et al., 2001b). Only one previous study of red-sided garter snakes has reported that female body size did not influence courtship intensity (Joy & Crews, 1985). Large females stimulate higher tongue-flick rates from mate-searching male snakes (Shine et al., 2003c). Large females are courted or mated by more males in at least two other snake taxa (Laticauda colubrina — Shetty & Shine, 2002; Nerodia sipedon — Prosser et al., in press), suggesting that this may be a widespread phenomenon. In red-sided garter snakes, the preference for large females may be driven by pheromonal cues rather than (or as well as) visual cues (LeMaster & Mason, 2002; Shine et al., 2003c). The strength of this preference for large females increases with male body size (Shine et al., 2001b).

Previous work on this topic has interpreted the greater attractiveness of large females in terms of potential fitness benefits to the male because female fecundity increases with maternal body size in this as in most other snake species (Fitch, 1970; Gregory, 1977). Hence, a male that mates with a large female may thereby fertilise more ova. The recent discovery that male red-sided garter snakes force matings by inducing hypoxic stress to females (Shine et al., 2003a) suggests another reason why large females are subject to more vigorous courtship. In natural courting groups, the proportion of a female’s body that is covered by courting males depends upon her body size; large females are less encumbered in this respect, especially in the anterior part of the body containing the vascular lung (Shine et al., 2003a). Thus, males may court (and especially, caudocephalic-wave) more vigorously to large females in order to induce sufficient stress to initiate cloacal gaping.

Male body size and body condition

Large males were more vigorous in many aspects of courtship (e.g. Fig. 4c) and heavier-bodied males performed more frequent caudocephalic waves (Table 1). An earlier study of the same population reported a similar result, with more active courtship by large males (Joy & Crews, 1985). Extensive data from field and arena matings have shown that larger, heavier-bodied
males experience higher mating success than do their small, thinner rivals (Shine et al., 2000f). Videotape analyses of courting trials (4 males, 1 female) that resulted in matings showed that the successful males were those that courted most vigorously (Shine et al., 2003b). Thus, the size advantage for mating in this system may partly be due to a size-associated shift in courtship vigour rather than a simple ability of large males to displace small males. The trend for more vigorous courtship from heavier-bodied males may reflect the fact that these animals have greater energy reserves: males lose mass (and thus, body condition) rapidly during their period of residency at the den during the mating season (Shine et al., 2001a), and leave the den when their reserves fall below some threshold level (Shine et al., 2003d). Our data reinforce the complexity of the relationship between body size and male mating success within red-sided garter snakes. For example, small males not only court less vigorously (perhaps expending less energy per courtship?) and obtain fewer matings, but also tend to mate with small females (Shine et al., 2001b), at least some of which are too small to produce offspring (Shine et al., 2000d).

**Number of rival males**

Our most striking results involve the effect of operational sex ratio (i.e. number of competing males in a courting group) on the courtship tactics of males. For almost every variable that we analysed, the focal males were most active in courtship when they were alone with a female, less active when they were competing with three other males, and less active again when competing with 23 rivals. To our knowledge, no previous study has reported this kind of decrease in courtship intensity in large groups. Indeed, previous research suggested either an increased courtship intensity in large groups (Joy & Crews, 1985), or (anecdotally) that a male’s zeal for courtship was unaffected by group size (Blanchard & Blanchard, 1941). Nonetheless, the pattern in our data is extremely strong and consistent, with some courtship behaviours an order of magnitude less frequent in large groups than small ones (e.g. Fig. 2c). Because our data are based on values per male, the total number of caudocephalic waves, chin-presses, body alignments and tail-searches to a female would nonetheless increase with group size (i.e. the differences between courtship intensities per male to females in 1-male vs 24-male groups is <24-fold; see Figs.).
Why was courtship vigour of males highest in small groups, and especially if the male was alone with the female? On a proximate level, a male alone with a female may have maximal access to pheromonal cues from her; in large groups the female is obscured by the bodies of rival males. In terms of fitness benefits, two aspects could be important. First, a solitary male would have to court very vigorously in order to induce sufficient hypoxic stress in the female and hence, facilitate mating. Second, opportunities for one-on-one courtship are rare and likely to be short-lived in the crowded den environment (Shine et al., 2001a) and hence, a male in this situation may benefit from inducing female receptivity very rapidly, before any rivals arrive to potentially ‘steal’ a mating that would otherwise be his.

The decreased intensity of courtship in large groups was manifested in a shift in tactics as well as an overall decline in effort. Thus, not only did the proportion of actively tail-searching males decline in large groups (from around 70% in 1-male courtship to 30% in 24-male courtship: Fig. 3b), but even the males that continued to tail-search showed a precipitous decline (about 7-fold: Fig. 5) in their frequency of caudocephalic waving. This latter behaviour is the most vigorous (and presumably, energy-expensive) component of male courtship, and plays a critical role in inducing the female cloacal gaping that is required for successful intromission (Shine et al., 2003a). The continued tail-searching by these males shows that they were aware of the female and were attempting to obtain a copulation, but nonetheless substantially reduced their energy expenditure by reducing their waving rate. Because females in large groups are subject to high rates of caudocephalic waving simply because of the large numbers of (infrequently-waving) males, a male in such a group can ‘afford’ to reduce caudocephalic waving (and thus, save energy) and instead, focus on ensuring that his cloaca is immediately adjacent to the female’s. This positioning is a major predictor of male mating success (Shine et al., 2003b).

Thus, male garter snakes modify both their overall effort and their specific tactics as a function of the operational sex ratio within courting groups. The net effect is to save energy, and perhaps facilitate accurate cloacal positioning because of the reduced need for simultaneous performance of conflicting tasks. In essence, the response constitutes ‘social parasitism’, whereby a male can enhance his own mating opportunities by exploiting the activities of his rivals. Female mimicry in the same population provides another example of this phenomenon: a male that elicits courtship from other males thereby
obtains benefits (protection from predators, warming) at some cost in risk and energy to his rivals (Shine et al., 2001c). Manipulation of the behaviour of other males (and females, through induction of hypoxic stress: Shine et al., 2003a) thus plays a significant role in male mating tactics within this population.

*Interactions between body size and number of rivals*

For two of the variables we measured, a male’s body size influenced his behaviour differently in different-sized groups. In relatively small (4-male) groups, large male snakes performed more frequent caudocephalic waves, and maintained their tailbases closer to that of the female; these patterns were reversed in the large (24-male) aggregations (Fig. 4a, c). If mating success is more deterministic (and thus, more consistently related to male body size) in small groups than in large groups (Crews, 2000), large males may be favoured to specialise on small groups and to devote high levels of effort in such circumstances. In contrast, small males may be at less of a disadvantage in the more stochastic situation of large groups; indeed, their small size may facilitate cloacal apposition with the female amidst the tangle of competing tails (Fig. 4a). Hence, males may adjust their courtship tactics depending on the degree to which greater strength and vigour is likely to enhance their probability of mating.

The end result of these patterns is that male garter snakes flexibly modify the intensity and nature of their courtship depending upon their own body size, their body condition (energy reserves), the size of the female, and the numbers of rival males. These factors also interact with each other in complex ways. In each case, the patterns of response support predictions from the adaptationist hypothesis that males should behave in ways likely to maximise their mating success while minimising their energy costs. Such plasticity is likely to be widespread in snakes as well as in other kinds of organisms.

*References*


