Courtship tactics in garter snakes: how do a male's morphology and behaviour influence his mating success?

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The behavioural determinants of male mating success play a pivotal role in sexual selection, but remain poorly known for most kinds of organisms, including most reptiles. In Manitoba, Canada, large numbers of red-sided garter snakes, *Thamnophis sirtalis parietalis*, court and mate in early spring near communal overwintering dens. To understand how a male's morphology and behaviour might influence his mating success, we videotaped 21 groups of snakes each comprising four males of varying body sizes plus a female. All males engaged in courtship, and mating occurred in all groups. Males with better body condition courted more vigorously and successfully than their smaller rivals did. The males that obtained matings were those that maintained their own cloaca closest to that of the female, aligned most of their body with the female, showed high rates of caudocephalic waving, chin pressing and tail searching, and did not allow other males to insert their body beside the female's. These behavioural differences between 'winners' and 'losers' were apparent from the beginning of each trial. Thus, male mating success in this 'scramble' system is determined not by chaotic, stochastic struggle (as has often been inferred) but instead is strongly linked to male courtship tactics. Energy stores (as evidenced by good body condition) may be critical determinants of mating success in these vigorous courtship episodes.

There are immense logistical obstacles to understanding the way in which individual phenotypic variations, in behaviour as well as morphology and physiology, translate into differential fitness (Endler 1986). Simply quantifying variation in mating success in natural populations is difficult in most kinds of organisms, and the causal link between phenotypic variation and fitness is even more elusive. This is especially true when dealing with traits with no direct relation to survival or reproductive success. Because of its strong impact on fitness, male mating success has been studied extensively. It is clear that the pathways are complex: for example, male phenotypic traits can enhance mating success via several routes ranging from female choice to forcible insemination and male–male combat and a single phenotypic trait (such as body size) can simultaneously influence the male's performance in all these activities (Clutton-Brock 1988; Andersson 1994). Variation in the effectiveness of courtship has been studied in many organisms, mostly focusing

on the role of female choice. For example, female flies may consent to mate only with males that can perform a complex series of species-specific athletic manoeuvres (Markow et al. 1978), and female birds may require complex visual or sound stimuli from the male before mating (Gibson et al. 1991).

Simply demonstrating high variation in reproductive success among individuals within a cohort does not constitute convincing evidence of sexual selection in progress, because much of this variation may have arisen through chance rather than through deterministic processes (Sutherland 1985, 1987). The overall variance in mating success within males of a given cohort will consist of two components: deterministically generated and random. Quantifying the relative magnitude of these two components poses a daunting task (Clutton-Brock 1988). Detailed studies sometimes reveal no phenotypic correlates of male mating success, even in cases where other information (such as consistent individual differences in success) clearly indicate an underlying deterministic process (McVey 1988). Thus, to understand the ways by which sexual selection operates on males within a population, we need to identify the relation between a male's morphology, his behaviour and his mating success.

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Such data are available for relatively few kinds of organisms (see Table 6.A in Andersson 1994 for a summary of examples of sexual selection operating on morphological and behavioural traits). Much of the reason for this scarcity of information is logistical: for most kinds of animals, it is difficult or impossible to quantify such variables. We have taken advantage of a model system that provides a unique opportunity (at least among reptiles) for identifying the proximate causes of variation in male mating success. Red-sided garter snakes, *Thamnophis sirtalis parietalis*, court and mate in large numbers near overwintering dens, and virtually ignore human observers (Gregory 1974). Thus, we can set up replicated experimental groups with consistent numbers and body sizes of courting males, in identical surroundings, to investigate the relation between male morphology, courtship behaviour and mating success. We focused on a series of related questions.

(1) Is male mating success essentially a random 'scramble', whereby male tactics are irrelevant to mating success (as implied by many authors, e.g. Blanchard & Blanchard 1941; Crews & Gartska 1982; Joy & Crews 1988) or is the process deterministic with specific predictors of success (as suggested by Mason & Crews 1985; Shine et al. 2000a, e)?

(2) If male mating success is determined by male behaviour, over what timescale do these effects occur (i.e. is there relatively long-term consistency in the behaviour of individual males, enabling us to predict success some time before copulation occurs)?

(3) Does male morphology influence courtship behaviour, generating correlations between mating success and morphology?

METHODS

Study Species and Area

We studied red-sided garter snakes near the northern limit of their geographical range in the Interlake region north of Winnipeg, Manitoba, in central Canada. These small (<1 m total length) nonvenomous snakes spend about 8 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). Because dens may contain more than 10 000 snakes and courtship occurs close to the den, densities of snakes are very high (sometimes >100/m²: Shine et al. 2001a). All newly emerging females are rapidly located and vigorously courted by dozens or hundreds of males. However, radiotelemetric monitoring indicates that many females disperse tens of metres before mating, and most courting groups away from the den centre are relatively small (Shine et al. 2001a). The mean size of 238 courting groups near a den was 4.0 males plus one female (Shine et al. 2001a). Excluding cases where a single male was found with a female (because there is no male–male competition in such cases), four males was also the modal group size. The range from two to six males plus one female encompassed more than 60% of all multimale groups (Shine et al. 2001a, unpublished data). The number of males in a group was not significantly correlated with

the mean body size of those males (Pearson correlation: $r_{236} = 0.06$, $P = 0.35$).

Courtship in *T. s. parietalis* has been described by many authors (Noble 1937; Blanchard & Blanchard 1941; Crews & Gartska 1982; Whittier et al. 1985). Skin lipids on females serve as sex pheromones, enabling males to locate females using the vomeronasal system (Mason 1993). Males align their bodies with that of the female, pressing their chins against her dorsal surface and their cloacae firmly 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. Larger males may push the tails of their smaller rivals out of the way (Luiselli 1996; Shine et al. 2000e). 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). The function of this behaviour has remained obscure. Our recent studies suggest that these waves push anoxic air from the female's nonrespiratory air sac anteriorly to her respiratory lung, thus inducing the stress response of cloacal gaping (Shine et al. 2003b). 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 north of the town of Inwood, 250 m east of Highway 17 in central southern Manitoba (50°31.58′N, 97°29.71′W). This den has been the focus of considerable previous research (e.g. Shine et al. 2000a, b, c, d, 2001b).

Methods

We set up small outdoor arenas ('Space Pop', Smash Enterprises, Melbourne, Australia; circular, 48 cm in diameter, 56 cm deep) in a flat sunny area <10 m from the den, to videorecord courting groups. Unmated females (i.e. lacking a mating plug: Shine et al. 2000d) were collected as they emerged, and one such female plus four males (taken from courting groups immediately before the video trials) were added to each arena. We recorded snout–vent length, tail length (measured by stretching the snake out beside a metre rule) and mass (with an electronic balance) for all animals. In each trial, the four males comprised one from each of the four arbitrarily defined size classes, encompassing the normal size variation for males at the Inwood den. All snakes were painted with a coloured mid-dorsal stripe for individual recognition. Nontoxic paint was used; it had no overt effect on snake behaviour, and wore off within a day or two. We filmed the animals with Sony Handycam CCD-TRV46E digital video cameras set up on tripods above each of the three arenas. The trials were terminated after 15 min unless mating occurred; 29 trials did not result in mating. All snakes were released unharmed at the conclusion of the trials.

We present data only for the 21 trials in which mating occurred. In these cases, we examined the videotapes to score male behaviours and positions at five times: immediately before mating, 30 s earlier, and 1, 2 and 5 min earlier. The variables that we scored

were: (1) distance between male cloaca and female cloaca; (2) proportion of male's body aligned with that of the female; (3) number of caudocephalic waves performed in the previous 30 s; (4) number of other males whose bodies separated the courting male from the female; (5) whether the male attempted a tail-search in the previous 30 s; (6) whether the male chin-pressed the female in the previous 30 s; and (7) whether the male was mistakenly aligned to another male in the previous 30 s.

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

Mean body sizes ± 1 SE for the four groups of male snakes were as follows: small: 40.73 ± 0.46 cm snout−vent length (SVL), 21.53 ± 1.00 g; medium: 43.87 ± 0.49 cm, 27.11 ± 1.02 g; large: 46.72 ± 0.53 cm, 33.68 ± 1.71 g; extra large: 50.16 ± 0.67 cm, 39.54 ± 1.52 g. Thus, males from the largest size group weighed approximately twice as much as males from the smallest. ANOVA and Fisher's protected least significant difference (PLSD) post hoc tests on these data confirmed that each of these size classes differed significantly from each of the others (SVL: $F_{3,80} = 54.84$, $P < 0.0001$; mass: $F_{3,80} = 33.73$, $P < 0.0001$). Females were larger than any of these male size groups (56.26 ± 0.33 cm SVL, 68.38 ± 2.62 g; versus combined males: SVL: $F_{1,103} = 90.92$, $P < 0.0001$; mass: $F_{1,103} = 124.91$, $P < 0.0001$).

Male Morphology and Mating Success

To evaluate determinants of mating success, we used paired t tests to compare attributes of winners with mean values for losers in the same arena. Mated males were slightly longer ($\overline{X} \pm$ SE $= 46.76 \pm 0.97$ versus 44.91 ± 0.52 cm SVL; paired t test: $t_{20} = 1.56$, $P = 0.13$) and heavier (34.39 ± 2.10 g versus 29.16 ± 1.09 g; $t_{20} = 2.04$, $P = 0.055$) than unmated males, but these differences fell short of statistical significance. However, winners were significantly heavier bodied than losers (using residual scores from the general linear regression of ln mass to ln SVL; $t_{20} = 2.10$, $P < 0.05$). Males that had lost part of their tails through injury rarely mated (1 of 21 winners versus 8 of 63 losers) but this difference was not statistically significant (contingency table test: $\chi^2_1 = 0.37$, $P = 0.54$). There was no significant correlation between the body sizes of females and of the males that mated with them (Pearson correlation: $r_{19} = 0.06$, $P = 0.81$).

Male Tactics and Morphology

Many measures of male vigour in courtship were intercorrelated. For example, males that chin-pressed the female more often (averaged over the observation periods) also tail-searched more often (Pearson correlation: $r_{81} = 0.83$, $P < 0.0001$), displayed higher rates of caudo-cephalic waving ($r_{48} = 0.54$, $P < 0.0001$), had more of their body aligned with that of the female ($r_{46} = 0.91$, $P < 0.0001$), and kept their own tailbase generally closer to the female's cloaca ($r_{49} = -0.83$, $P < 0.0001$) than males that chin-pressed less frequently (note that sample sizes vary in these analyses because some males were not aligned with females and thus not scorable). Thus, males generally used relatively similar tactics (rather than one animal mostly chin pressing whereas another mostly tail searching, etc.), but differed in the intensity with which they performed these activities.

Links between male morphology and tactics were evident but weak. Males that were more heavy bodied relative to SVL (based on residual scores from the linear regression of ln mass versus ln SVL) performed more chin-presses (Pearson correlation: $r_{79} = 0.23$, $P < 0.04$) and had higher proportions of their bodies aligned with that of the female ($r_{45} = 0.29$, $P < 0.05$). Heavier-bodied males also tended to show higher rates of tail searching ($r_{79} = 0.20$, $P < 0.07$) and to maintain their cloacae closer to that of the female ($r_{45} = -0.25$, $P < 0.08$). Thus, heavier-bodied males tended to be more active and effective courters. No other morphological variables were significantly correlated with male courtship behaviours.

Successful Versus Unsuccessful Males

Repeated measures ANOVA with male status (winner or loser) as the factor and time period (from 5 min before mating to immediately before) showed that successful males behaved differently from unsuccessful ones, and did so throughout the courtship period. As mentioned above, these tests are based on mean values for unmated males within each enclosure, compared with values for mated males. Both groups of males managed to manoeuvre their cloacae closer to that of the female as the trial progressed ($F_{4,96} = 4.52$, $P < 0.003$) but successful males were strikingly more adept at this task ($F_{1,24} = 40.46$, $P < 0.0001$; Fig. 1a). The rate at which males decreased the average distance between their cloaca and that of the female did not differ between the successful and unsuccessful suitors (interaction: $F_{4,96} = 2.13$, $P = 0.08$). The proportion of the male's body that was aligned with the female showed a similar pattern, increasing through time ($F_{4,96} = 2.38$, $P = 0.05$) at a similar rate in the winners and losers ($F_{4,96} = 0.80$, $P = 0.53$), but averaging higher throughout in the successful males than in their unsuccessful counterparts ($F_{1,24} = 56.48$, $P < 0.0001$; Fig. 1b). The rate of caudocephalic waving did not change through time ($F_{4,96} = 0.23$, $P = 0.92$; interaction: $F_{4,96} = 0.78$, $P = 0.54$) but was higher for mating males than for nonmating males ($F_{1,24} = 12.63$, $P < 0.002$; Fig. 1c). Winning males also managed to keep their body closer to that of the female (i.e. with fewer intervening rivals) than losing males did ($F_{1,16} = 27.90$, $P < 0.0001$; time effect: $F_{4,64} = 1.94$, $P = 0.11$; interaction: $F_{4,64} = 0.71$, $P = 0.59$; Fig. 1d).

The nominal variables that we scored (whether a male chin-pressed or tail-searched during 30-s periods) also revealed differences associated with whether a male
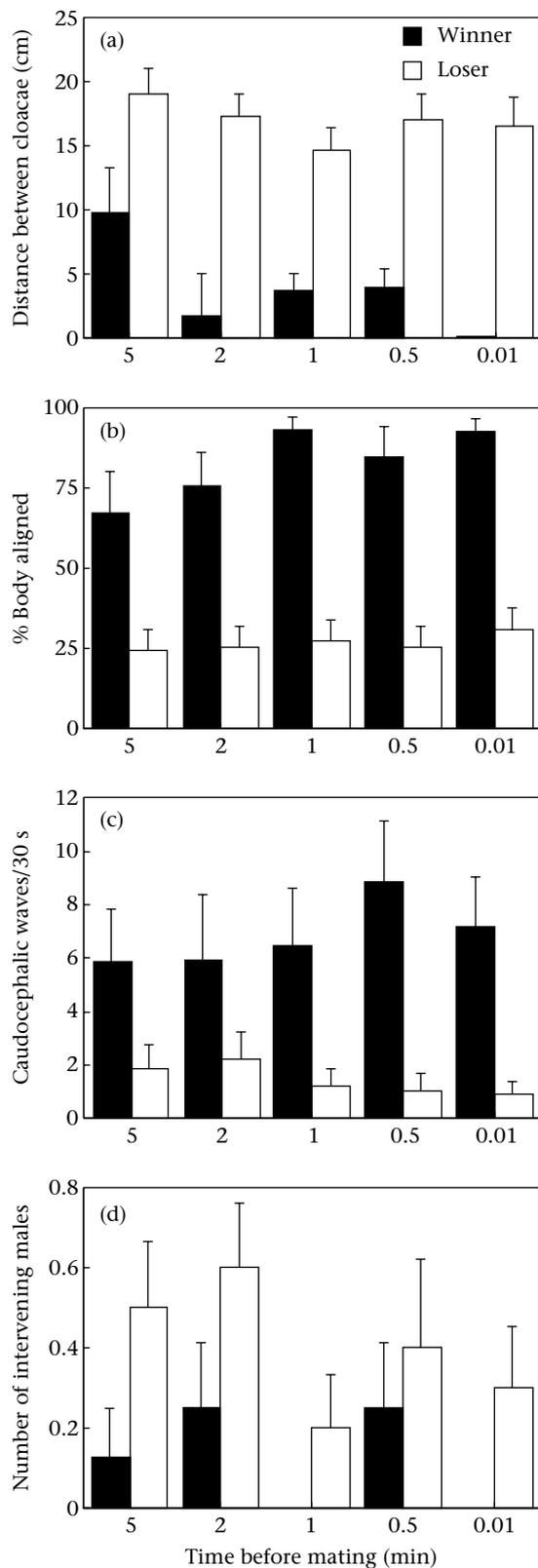
Figure 1. Behavioural attributes of male garter snakes, *Thamnophis sirtalis parietalis*, at successive periods before mating in trials filmed by videocamera at a communal den near Inwood, Manitoba. Data are shown separately ($\overline{X} \pm 1$SE) for the males that eventually mated (winners) and those that did not (losers). In each of the 21 trials, we quantified the following behaviours for four males (one of which

obtained a mating. Males that eventually copulated had chin-pressed and tail-searched more often than their rivals did (total number of periods during which each behaviour occurred; chin pressing: $F_{1,82} = 15.16$, $P < 0.0002$; tail searching: $F_{1,82} = 10.55$, $P < 0.002$; Fig. 2). Mistaken courtship to other males (whereby the male aligns to another male and not the female) was seen only rarely (mean < 0.2 total records per male across five time periods) and was no more common in losers than in winners ($F_{1,82} = 0.12$, $P = 0.73$).

How do Male Tactics Influence Mating Success?

Our data show that behaviours differed substantially between males that obtained matings and those that did not. A male was more likely to mate if he: (1) kept his tailbase close to the female's cloaca; (2) aligned most of his body with the female; (3) performed frequent caudocephalic waves; (4) did not permit other males to come between him and the female; (5) frequently chin-pressed the female; and (6) actively tail-searched. Misdirected courtship to other males was rare and apparently not an important determinant of male mating success. One consistent pattern was the lack of any significant interaction between a male's status (winner versus loser) and the rate of change in his behaviour over successive time periods. That is, not only did the eventual winners court more vigorously, but they did so from the beginning of our observation periods.

Because many of the behaviours associated with male mating success were themselves intercorrelated, it is difficult to tease apart the causal pathways that link male behaviour to mating success. To clarify this issue, we used principal components analysis (PCA) to extract a smaller number of variables that summarize major (uncorrelated) axes of behavioural variation among courting male snakes. The analysis generated three axes from the original seven variables (Table 1). Factor 1 (explaining 49% of the overall variance in the data set) was highly correlated with scores for body alignment, chin pressing, proximity to the female's cloaca and the rate of caudocephalic waving, and thus provides an index of overall vigour in courtship (Table 1). Factor 2 (16% of the total variance) was related to the rate of tail searching attempts but not to other variables (all $r < 0.30$; Table 1). Factor 3 (14% of the total variance) represented the incidence of alignments to males rather than females but no other variables. We included these three axes plus male body condition in a multiple logistic regression, with male mating success as the dependent variable. To avoid pseudoreplication, we averaged the mean values for all losers within each enclosure, and the scores for each snake (or group of snakes)

eventually mated): (a) the distance from the male's cloaca to that of the female; (b) the percentage of the male's body that was aligned with that of the female; (c) the number of caudocephalic waves performed by the male in the previous 30 s; (d) the number of males with their bodies lying between the focal male and the female. These data were recorded at 5, 2, 1 and 0.5 min before mating, as well as immediately before intromission ($= 0.01$ min). See text for statistical analyses of these data.
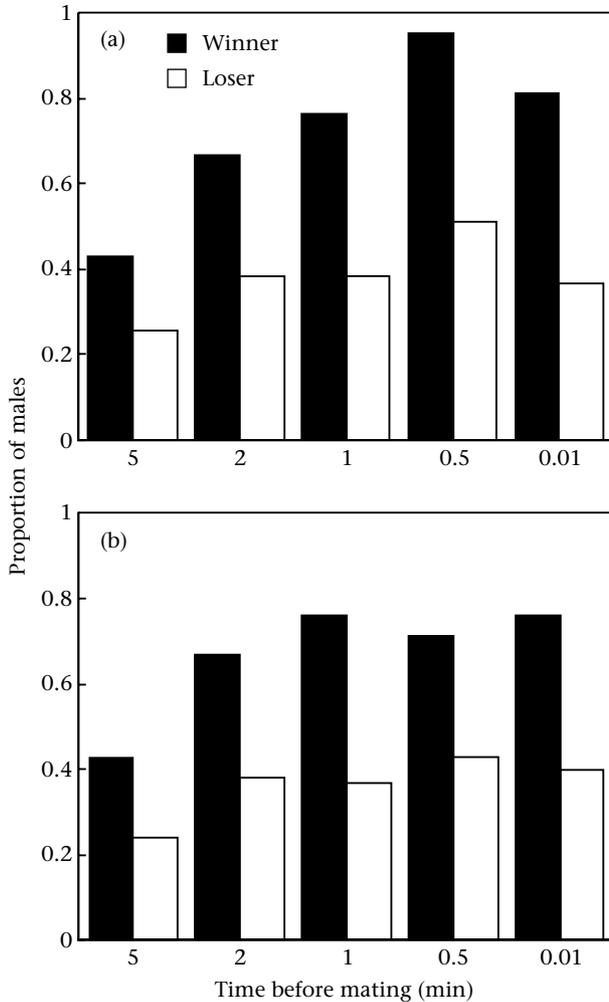
Figure 2. Proportions of male garter snakes, *Thamnophis sirtalis parietalis*, displaying specific behaviours at successive periods before mating in trials filmed by video camera at a communal den near Inwood, Manitoba. Data are shown separately for the males that eventually mated (winners) and those that did not (losers). In each of the 21 trials, we quantified whether the males had (a) chin-pressed against the female or were (b) actively searching with their tail during the previous 30 s. These data were recorded at 5, 2, 1 and 0.5 min before mating, as well as immediately before intromission (= 0.01 min). See text for statistical analyses of these data.

Table 1. Pearson correlations between behavioural traits of courting male garter snakes, and three major factors identified by principal components analysis

Behaviour	Factor 1	Factor 2	Factor 3
% Body align with female	**0.94**	−0.15	−0.04
Rate of chin pressing	**0.86**	0.20	0.04
Distance to female cloaca	**−0.85**	0.22	0.09
Rate of caudocephalic waving	**0.72**	−0.28	0.05
Rate of tail searching	0.27	**0.92**	0.16
Alignments of other males	−0.15	−0.20	**0.96**
Number of intervening males	−0.65	−0.12	−0.20

Correlations greater than 0.70 are shown in boldface font.

were averaged across the five time periods over which they were quantified. Analysis suggested that all four of the independent variables contributed significantly to a male's mating success: matings were more likely if a male was in good body condition (likelihood ratio test: $\chi^2_1 = 7.30$, $P < 0.007$), was vigorous in courtship (axis 1: $\chi^2_1 = 48.71$, $P < 0.0001$) rather than tail searching (successful males showed less and not more tail searching: $\chi^2_1 = 12.18$, $P < 0.0006$) and avoided aligning with males rather than females ($\chi^2_1 = 6.06$, $P < 0.02$). Thus, all of these traits had direct links to mating success, even in an analysis that factored out effects of the other traits.

DISCUSSION

Our data reveal that mating success within courting 'balls' of garter snakes is highly nonrandom. The males that succeeded in copulating were those that kept closer to the female and courted her more actively than their unsuccessful rivals. For all the behavioural variables that we recorded, these differences were apparent even 5 min before mating (Figs 1 and 2). This result fits well with our conclusions from other work on snakes at these dens (e.g. Shine et al. 2000e, 2001b), and challenges earlier work that viewed this mating system as a 'scramble' in which male reproductive success was largely stochastic (Blanchard & Blanchard 1941; Crews & Gartska 1982; Joy & Crews 1988). The traits that we measured bear clear and intuitive relations to copulatory success: a male was most likely to win a mating if his cloaca was close to the female's and if his caudocephalic waves were frequent, strong and accurately aligned with the female's body.

Why do caudocephalic waves promote male mating opportunities? Conventional explanations have interpreted mating in snakes in terms of males stimulating females to receptivity, and emphasized the need for a female to gape her cloaca for intromission to occur (e.g. Noble 1937; Blanchard & Blanchard 1941; Carpenter & Ferguson 1977; Gillingham 1987). More recent work suggests a different scenario, whereby the caudocephalic waves of courting garter snakes impede breathing by the female and stimulate stress-induced cloacal gaping that, in turn, allows copulation (Shine et al. 2003b). Although sexual selection via female choice has received intense scientific scrutiny, less attention has been focused on mating systems in which males obtain matings by means of forcible insemination. None the less, increasing evidence suggests that coercive mating may be widespread (West-Eberhard et al. 1987; LeBouef & Mesnick 1990; Clutton-Brock & Parker 1995) and, hence, male traits that facilitate success in obtaining such matings may be under strong selection (Ghiselin 1974). Importantly, forcible matings do not necessarily imply a lack of 'courtship', because males may obtain matings not simply by direct physical battles with females, but also by inducing high levels of stress through prolonged aggravation (e.g. Smuts & Smuts 1993). In such a mating system, females may eventually copulate because they are physiologically unable to resist such prolonged attention or because the stress response elicited by male attention facilitates intromission by males (as in garter snakes).

The high energy costs of courtship to male garter snakes (Shine et al. 2001a) may be responsible for the associations that we documented between male morphology and tactics (and thus between male morphology and mating success). Relatively heavy-bodied males (i.e. those with high mass relative to body length) were more vigorous courters, and thus were disproportionately likely to obtain matings. The same bias towards mating success by heavy-bodied males is apparent in other data on these snakes from natural matings in the field as well as from trials in outdoor arenas (Shine et al. 2000e). The mating advantage of higher body condition may be manifested primarily through the increased courtship vigour of these animals, but our multiple logistic regression showed that higher body condition remained a significant predictor of mating success even after behavioural variables (including courtship vigour) were factored out of the analysis. None the less, we simply recorded the rates of each behaviour, and a more vigorous male might perform each of these activities more strongly or rapidly, and thus successfully, than his less vigorous rivals. Mark–recapture studies show that a male's body mass decreases rapidly during his residency at the den in spring, and that males leave the mating area for their summer ranges after they have lost some threshold level of mass (Shine et al. 2001a, 2003a). Males in better body condition may have greater energy reserves and thus be most capable of courting vigorously.

Males clearly differed in the vigour with which they courted, and it was the more vigorous males that obtained matings. Stepwise deletion of the significant effects in the multiple logistic regression suggested (unsurprisingly) that the most direct proximate determinants of a male's mating success involve behaviours (tail searching and cloacal apposition) that function to keep his cloaca close to that of the female at the time that she gapes her cloaca open. Successive deletion of significant effects suggested that body alignment facilitates this kind of male positioning, that chin pressing and caudocephalic waving facilitate accurate alignment, and that direct physical displacement of rival males allows a male to obtain the optimal position for courtship behaviours. Alternative hypotheses on causal pathways (e.g. removing rivals is a major proximate determinant of mating success) are less consistent with our data. Of the variables that we measured, only the rate of misdirected body alignments was unimportant in determining mating success. Again, this result accords well with other studies showing that mistaken alignments are rare because of the males' ability to discriminate the sex of conspecifics from pheromonal cues (Mason 1993). Hence, our data do not support the hypothesis that such 'mistakes' constitute a significant selective force on sexual size dimorphism in snakes (Rivas & Burghardt 2001).

Snake species display considerable diversity in courtship behaviour; for example, the caudocephalic waves that dominate courtship activity for male red-sided garter snakes are absent in several other snake lineages, and even in some other garter snakes (Perry-Richardson et al. 1990). Thus, the determinants of mating success for males may differ considerably between snake species, between populations within single species, and even between 'mating balls' of different sizes within a single population. In larger courting groups of red-sided garter snakes, mating success may be more stochastic than is the case in smaller groups (Crews 2000). None the less, the groups that we used in our experiments were similar in size to most natural mating balls (Shine et al. 2001a) and hence the determinants of mating success in these groups should be similar to those in natural situations. The similarity in morphological correlates of male mating success between natural matings and those in our arena trials supports this inference.

Our study underlines the importance of quantifying courtship behaviour and mating success under controlled conditions, rather than relying upon simple observation. Intuition is misleading in this respect. To a casual observer, the writhing balls of courting snakes seem chaotic in the extreme, and it is difficult to believe that mating success depends upon anything more than chance. In combination with our previous studies, the present results emphasize the presence of strong deterministic components within this superficially chaotic mating system. The same may well be true for many other organisms in which males scramble for mating opportunities. Unfortunately, logistical obstacles in most study systems may prevent researchers from detecting links between a male's morphology, behaviour and mating success even if such links occur. We should thus be wary of embracing the null hypothesis that male phenotypic traits are irrelevant to mating success.

Acknowledgments

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