



FORUM

Body size enhances mating success in male garter snakes

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In many kinds of animals, larger males tend to defeat smaller rivals in bouts of physical combat and may thereby enhance their mating opportunities. Does larger body size also enhance male mating success in species that do not display overt male–male combat? The only detailed evidence on this topic for snakes comes from a study on red-sided garter snakes, *Thamnophis sirtalis parietalis*, by Joy & Crews (1988), who concluded that body size did not influence male mating success. We repeated their study and came to a different conclusion.

Snakes vary in their degree of sexual size dimorphism: females grow much larger than males in many species, whereas the reverse is true in others (e.g. Shine 1978, 1994; Fitch 1981). Evolutionary theory suggests that the sexes diverge in body size mostly because of different advantages and disadvantages associated with larger size in males versus females (e.g. Trivers 1972; Andersson 1994). In particular, we expect to see an association between mating systems and sexual size dimorphism because mating systems that involve direct physical rivalry among males might provide a substantial mating advantage to large body size in this sex (e.g. Bartholomew 1970; Gibbons 1972). Comparative analyses have supported this prediction for many taxa, including snakes (e.g. Shine 1978, 1994), but it is logistically difficult to test the functional basis for this linkage (i.e. quantify the relationship between male body size and mating success) for many kinds of organisms.

Thus, although the determinants of male mating success have been studied intensively in a subset of taxa (such as birds, mammals, amphibians and insects) with attributes that facilitate this kind of study, we know very little about the processes by which a male's body size influences his mating success in other taxa. This is

especially true for species that are difficult to observe in the course of their mating activities. The majority of snakes fall into this category because they are relatively rare, highly secretive, frequently inactive, and difficult to observe without disturbance (e.g. Seigel 1993). Consequently, quantitative information on the determinants of male mating success are available for only a few snake species. Larger males tend to win combat bouts in at least two viperid species (Schuett & Gillingham 1989; Schuett 1997; Madsen et al. 1993), and this success in combat is known to translate into enhanced mating success in one of them (the European adder, *Vipera berus*: Madsen et al. 1993). However, recent work challenges Shine's (1978) assumption that body size does not influence male mating success in the absence of overt combat between males. Larger males tend to achieve more matings in the European grass snake, *Natrix natrix*, apparently because they can physically displace the tails of rival males in mating balls (Madsen & Shine 1993; Luiselli 1996). Larger body size enhanced male mating success in 1 of 2 years in a study on Canadian watersnakes, *Nerodia sipedon*, another species without overt combat (Weatherhead et al. 1995). However, body size has been reported to have no effect on male mating success in two other snake species that lack male–male combat behaviour (Australian filesnake, *Acrochordus arafurae*: Shine 1986; red-sided garter snake: Joy & Crews 1988).

Interpretation of this diversity is complicated by small sample sizes in some of these studies, and by the possibility of temporal variation in the intensity of sexual selection on male body size. Such variation has been documented in European adders, in response to year-to-year variation in the operational sex ratio (and, hence, the degree to which success in male–male combat determines male mating success: Madsen & Shine 1992; Weatherhead et al. 1995). The only clear evidence (i.e. experimental as well as observational, and with large sample sizes) for a lack of size advantage to mating male snakes is Joy & Crews's (1988) study. They took

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advantage of a system that is well suited to test such ideas; large numbers of red-sided garter snakes gather at communal hibernacula in southern Manitoba, and mate immediately after emergence in spring. The snakes are highly tolerant of disturbance and readily continue courting and mating in outdoor enclosures. Hence, Joy & Crews (1988) were able to obtain many mating pairs in the field, and to run many mating trials with selected groups of snakes in arenas. Their clear result was that larger body size did not enhance male mating success, either by facilitating more matings or by increasing the average body size (and, hence, probable litter sizes) of the females with which they mated. This conclusion stands in strong contrast to other work on natricine snakes, suggesting a mating advantage to larger males (Madsen & Shine 1993; Weatherhead et al. 1995; Luiselli 1996).

Given this apparent inconsistency in published reports, and the ease with which the Manitoba system permits quantitative tests of such issues, we set out to repeat and extend Joy & Crews's (1988) study. There are at least three plausible pathways by which larger body size could enhance the reproductive success of a male red-sided garter snake: larger males could (1) obtain more matings; (2) tend to mate with larger (and thus more fecund) females; and/or (3) transfer more sperm during copulation, and thus tend to obtain more fertilizations if sperm competition occurs as a consequence of the female remating (Devine 1984). Our data enable us to evaluate aspects of all three of these hypotheses, although we can critically test only the first two. Importantly, these are the two hypotheses upon which Joy & Crews's (1988) study focused.

Methods

Study species and study area

Red-sided garter snakes are slender, surface-active, non-venomous natricine colubrids. In our population, adult females attain much larger sizes (mean 55–60 cm snout-vent length (SVL); mean body mass 70–85 g) than do adult males (mean 45–50 cm SVL; mean mass 35–40 g). We studied this species in Manitoba, at large communal dens within the Chatfield Community Pasture 100 km north of Winnipeg (50°44'N, 97°34'W). At least 50 000 snakes overwinter in these dens every year (R. T. Mason, unpublished data), dispersing out into the surrounding muskeg swampland during summer (Gregory 1974, 1977; Gregory & Stewart 1975; Hawley & Aleksiuik 1975; Mason & Crews 1985). For several years we have studied the snakes during spring (May), when they emerge from the dens and mate. Thus, we encounter snakes either inside the dens (rock-lined sinkholes ca. 20 m long, 3 m wide and 2 m deep) as they emerge from underground cavities, or in the mosaic grassland–aspen woodland habitat surrounding the den. Courting and mating activity occur both inside and outside the den.

Dissections

At one of the dens on 8 May 1997 more than 100 snakes were killed (presumably suffocated) by the mass of

overlying snakes. This event provided an unusual opportunity to confirm the size at sexual maturation, and to examine correlations between the size of male reproductive structures and body size. The snakes were removed from the den less than 3 h after they died, and stored in a snowdrift overnight. We weighed, measured and dissected 76 of these snakes on the following day. The liver and fat body were dissected out of each snake and weighed. We measured (length, width, thickness) the testes, the kidneys and the hemipenes. Although only the sexual segment of the kidney is involved in male reproduction (presumably in producing secretions that are transferred with the semen: e.g. Saint Girons & Kramer 1963), we could not clearly delineate this component and so weighed the entire kidney. We calculated volumes of the testes and hemipenes from their linear dimensions, using equations for the volume of the appropriate geometric shape (e.g. James & Shine 1985).

Field methods

We collected pairs in copulo, placed each pair in a separate bag, and weighed and measured them within 24 h of collection. To compare the sizes of mating males with those of other males in the population, we collected a large sample of other males from the same mating aggregations. Some of these animals may have mated at other times, but were not mating at the time that they were collected.

Arena trials

To control aspects such as body size distributions and the numbers of males attending a female, we carried out a series of mating trials in outdoor arenas. Each arena measured 100 × 120 cm, with vertical walls 90 cm high, and was constructed of nylon fabric. We set out an array of 24 arenas and carried out groups of trials simultaneously to avoid any confounding by weather conditions. A single unmated female (her status as unmated was based on the lack of a mating plug: Devine 1975) was placed in each arena. One set of trials looked at latency to copulation with a single male (either large (>49 cm SVL) or small (<42 cm SVL)) per female; another set looked at mating success with two males (one large, one small; sizes as above) per female; another with four males (of four SVL categories, as follows: <42, 43–45, 46–48, >49 cm) per female; and one with 24 males (six per each of the above four size categories) per female. The trial commenced when the female was added, and finished with copulation. If a female did not accept a mating within 30 min, she was removed from the arena and replaced with a new female. We scored latency to copulation based on the time the male(s) had been courting the female that finally copulated (on the grounds that the other females might have been totally refractory to courtship). We also recorded the total number of females added per trial; this number did not differ significantly between any of the categories of trials (e.g. courtship by a small versus large male). We monitored the enclosures constantly during each trial, and thus detected copulation within 1 min (and usually less) of its initiation. We are confident that

Table 1. Morphological traits of male garter snakes in relation to the snake's snout-vent length (cm)

Trait	Intercept	Slope	Regression coefficient (<i>r</i>)	<i>P</i>
Total body mass	-56.59±4.01	1.95±0.09	0.93	<0.0001
Energy stores, in absolute terms				
Mass of the fat bodies (g)	-2.07±0.47	0.07±0.01	0.59	<0.0001
Mass of the liver (g)	-2.55±0.32	0.09±0.01	0.83	<0.0001
Energy stores, relative to lean body mass				
Fat body mass divided by lean body mass	0.02±0.01	0.0002±0.0003	0.07	0.56
Liver mass divided by lean body mass	0.06±0.01	0.0001±0.0002	0.07	0.56
Internal organs				
Combined volume of testes (mm ³)	-145.41±185.89	13.17±4.11	0.35	0.002
Combined volume of kidney (mm ³)	-2593.34±895.61	100.58±19.78	0.51	<0.0001
Hemipenes				
Volume of left hemipenis (mm ³)	-40.81±30.40	2.48±0.67	0.40	0.0004
Volume of right hemipenis (mm ³)	-40.47±26.69	2.37±0.59	0.43	0.0001

Values are given for intercepts and slopes±SE, with associated regression coefficients (*r*) and *P* values, for the least-squares regression between male snout-vent length (the independent variable) and the trait in question. Lean body mass: total body mass minus the mass of the liver and fat bodies. All regressions are based on data from 76 male snakes, dissected the day after they suffocated in the den.

we did not miss any matings that occurred during the trials; copulation continues for ca. 20 min ($\bar{X} \pm \text{SD} = 19.0 \pm 10.0$ min, range 8–50), and females do not mate twice in quick succession unless the mating plug is physically removed by the experimenter (R. Shine, unpublished data). We never found a mating plug in a female that had not been recorded to mate.

To quantify the intensity of male courtship, as well as mating success, we carried out an additional set of trials in which we prevented females from mating by placing adhesive tape across their cloaca. We used 24 males, each paint marked dorsally, so we could recognize him, and then placed with five other unmarked males in an arena. A taped female was added to the arena, and the intensity of courtship by the focal male was scored three times, at 4-min intervals, before the female was removed and another snake added. Every fourth snake added in this way was a female. The others were males and 'she-males' (Mason & Crews 1985), because we also used this experiment to quantify attractiveness of these groups. We used a four-point scale to score intensity of courtship (0: no interest; 1: tongue flicking the female; 2: alignment of the male's body along that of the female; 3: caudocephalic waves and attempts at intromission; modified from Whittier et al. 1985). We used the data on courtship directed towards females only, to see whether a male's body size or condition affected his intensity of courtship. Each snake was used in only a single trial, then released after paint marking (so that we could recognize the animal and avoid using it again). Thus, our data are based on measurements and observations of over 5000 snakes.

Ethical note

We do not believe that our experimental or observational studies induced significant stress or suffering to our study animals. Maintaining snakes in enclosures did not result in any aggression; these are extraordinarily docile animals, and there are no published reports of intraspecific aggression within the entire genus (Rossman et al. 1996). Work on the same population has shown that

handling, and maintenance in bags for some hours, does not result in any detectable rise in the snakes' corticosteroid levels (I. Moore, unpublished data). Overt behaviour is unaffected by handling; for example, male snakes recommence courting immediately even when picked up by the midbody and placed close to a female. All of the snakes were released at the capture site after each experiment. Research was conducted under the authority of Oregon State University Institutional Animal Care and Use Committee. All research was conducted in accord with the U.S. Public Health Service 'Policy on Humane Care and Use of Laboratory Animals' and the National Institutes of Health 'Guide to the Care and Use of Laboratory Animals'.

Results

Dissections

Unsurprisingly, longer males were heavier than smaller animals, and had larger fat bodies, livers, kidneys, testes and hemipenes (Table 1). However, the relative size of the main energy stores (i.e. fat-body and liver mass relative to lean carcass mass) was unrelated to the snake's SVL (Table 1).

Natural matings

Sizes of successful versus unsuccessful males. We have data on the body sizes (SVL, mass) of mated versus unmated males for 5 years (1995–1999 inclusive). Analysis of these data reveals a small but statistically significant difference in mean body size between males in these two categories (overall means 45.6 cm for mated males, 45.2 cm SVL for unmated males; ANOVA: $F_{1,3315} = 5.30$, $P = 0.02$). However, mean body sizes of adult males also varied significantly between years. Thus, a two-factor ANOVA with year and mated/unmated as factors revealed significant body size differences not only between mated and unmated males ($F_{4,3307} = 10.17$, $P < 0.002$), but also between years ($F_{4,3307} = 7.19$, $P < 0.001$) and in the interaction effect (i.e. relative sizes of mated and unmated males

varied between years: $F_{4,3307}=5.03$, $P<0.001$). Inspection of the data for each year separately showed that mated males were significantly ($P<0.05$) longer than unmated males in 3 of the 5 years, and significantly heavier than unmated males in 4 of the 5 years (including both years when no size advantage was evident in terms of body length). Thus, the general pattern was that larger males obtained more matings.

Data sets on body sizes relative to mating status are strongest for the 2 years (1997 and 1998) when we specifically set out to examine this question (and, hence, attempted to sample mated and unmated males from the same areas at the same times). In these years, mated males were not only heavier (and longer) than unmated males, but also, on average, heavier-bodied (i.e. weighed more relative to SVL; Fig. 1). A one-factor ANCOVA (with mated status as the factors, SVL as the covariate and ln mass as the dependent variable) confirmed that mass increased more rapidly with SVL in mated males than in unmated males (heterogeneity of slopes: $F_{1,584}=9.41$, $P<0.003$).

Size-assortative mating. Measurements of mated pairs found in the field showed that larger males tended to mate with larger females. This correlation was evident for both body length (SVL) and body mass, and was evident in each year of our study (although it was statistically significant in only 2 of those years). Although the body sizes of mated males were correlated with the body sizes of their female partners, the scatter was wide. Least-squares regressions explained less than 1.5% of the overall variation in female body size in each case ($r^2<0.015$), despite the high level of significance ($P<0.006$ for SVL; $P<0.015$ for mass).

These significant results were not an artefact of combining data from the 5 years of our study; indeed, the relationship between male and female body sizes was even stronger after between-year differences in body size were removed from the analysis. One-factor ANCOVA (with year as the factor, male body size as the covariate and female body size as the dependent variable) confirmed the significant link between male and female body sizes within copulating pairs (for the covariate SVL: $F_{1,889}=18.35$, $P<0.0001$; for the covariate mass: $F_{1,863}=16.34$, $P<0.0001$). The relationship between male and female body sizes in copulo varied significantly between years (SVL: slopes homogeneous; intercepts: $F_{4,893}=3.92$, $P<0.004$; mass: slopes: $F_{4,863}=2.94$, $P<0.02$).

Arena trials

Intensity of courtship. We detected no consistent relationship between a male's body size (SVL) and his mean intensity of courtship ($r_{22}=-0.25$, $P=0.26$). However, heavier-bodied males were more vigorous courters (using the residual score from the linear regression between ln mass and SVL as an index of condition, versus mean courtship intensity: $r_{22}=0.45$, $P<0.04$).

Effectiveness of courtship. If a male's body size influences his ability to elicit matings, the courtship time prior

to mating should be consistently lower for a large male than for a small male, when both are alone with a receptive female within an arena with no interference from other males. In fact, our data do not reveal any such bias. The most direct test comes from the trials in which we simultaneously added females to arenas with either very large (>49 cm SVL) or very small (<42 cm SVL) males; there was no difference between the two size classes in their mean duration of courtship prior to copulation (large males: $\bar{X} \pm SD=11.2 \pm 9.7$ min, $N=21$ matings; small males: 13.9 ± 12.0 min, $N=19$; ANOVA: $F_{1,38}=0.62$, $P=0.44$). Thus, it appears that large and small males are equally adept at inducing females to lift their tails and thus allow intromission. Overall, we did not detect any significant correlations between male size (SVL, mass and condition) and the time taken to induce female receptivity (all $P>0.5$).

Male-male competition. If males compete physically for matings, then larger body size may enhance a male's ability to displace his rivals. As predicted from this hypothesis, the mean body length of successful males in the arena trials was substantially higher than the mean size of unsuccessful males (Fig. 2). This size superiority was evident in all three sets of trials that we conducted, using two, four or 24 males per female. A two-factor ANOVA with group size and mated/unmated as the factors, and male SVL as the dependent variable, showed that we were successful in maintaining similar mean body sizes of males in all three group sizes ($F_{2,538}=0.04$, $P=0.96$). Mated males were larger than unmated males ($F_{1,538}=16.83$, $P<0.0001$), with no significant interaction term between group size and mated status ($F_{2,538}=1.83$, $P=0.16$). Although this analysis suggests that larger body size enhanced male mating success under all three of our experimental treatments, independent analysis of data from each set of trials reveals substantial differences in the magnitude of the effect (see Fig. 2). The size advantage was stronger in trials involving two males (one-factor ANOVA with mated or not as factor: $P<0.005$) than for the four-male groups ($P=0.12$) or 24-male groups ($P=0.059$; see Fig. 2).

Analyses based on body mass rather than SVL provided a very similar result. Heavier males obtained more matings (ANOVA: $F_{1,530}=9.59$, $P<0.003$), with no significant effects of group size or any interaction ($P>0.20$ in both cases). To examine effects of body condition (since heavier-than-average males obtained more matings in the field), we used two-factor ANCOVA (with number of males per group and mated/unmated as the factors, male SVL as the covariate and ln mass as the dependent variable). Males obtaining matings did not differ consistently in body condition from their unsuccessful competitors (slopes: $F_{1,524}=1.46$, $P=0.23$; intercepts: $F_{1,531}=3.10$, $P=0.08$).

Discussion

Our main conclusion is clear: larger body size enhanced mating success of male garter snakes, and this was true for

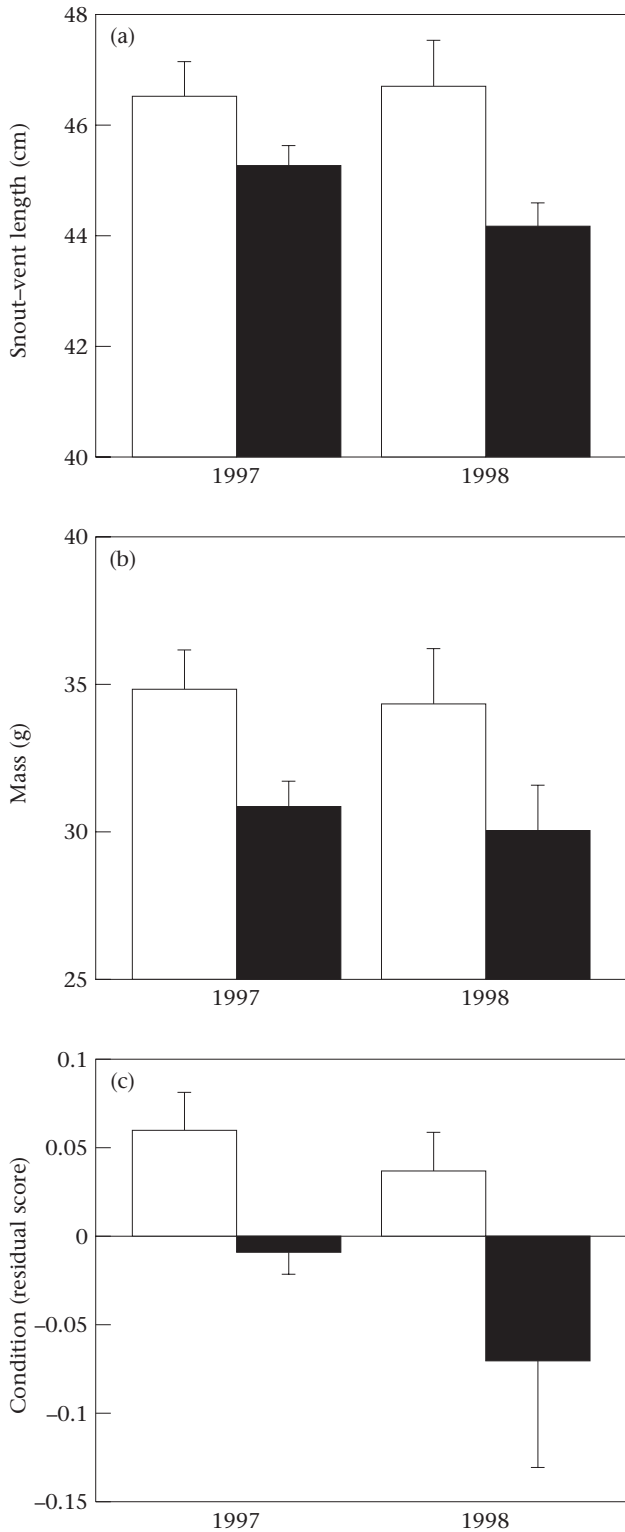


Figure 1. Body size and body condition of male garter snakes collected at communal dens in May 1997 and 1998. (a) Body length (snout-vent length (SVL), cm), (b) mass (g) and (c) condition (mass relative to SVL, calculated as the residual scores from the least-squares linear regression of \ln mass to SVL). The attributes of males found mating in the field (□) are compared with those of unmated males found in the same courting aggregations (■). Data are shown separately for each year of the study. Means are given +SE. See text for statistical treatment of these data.

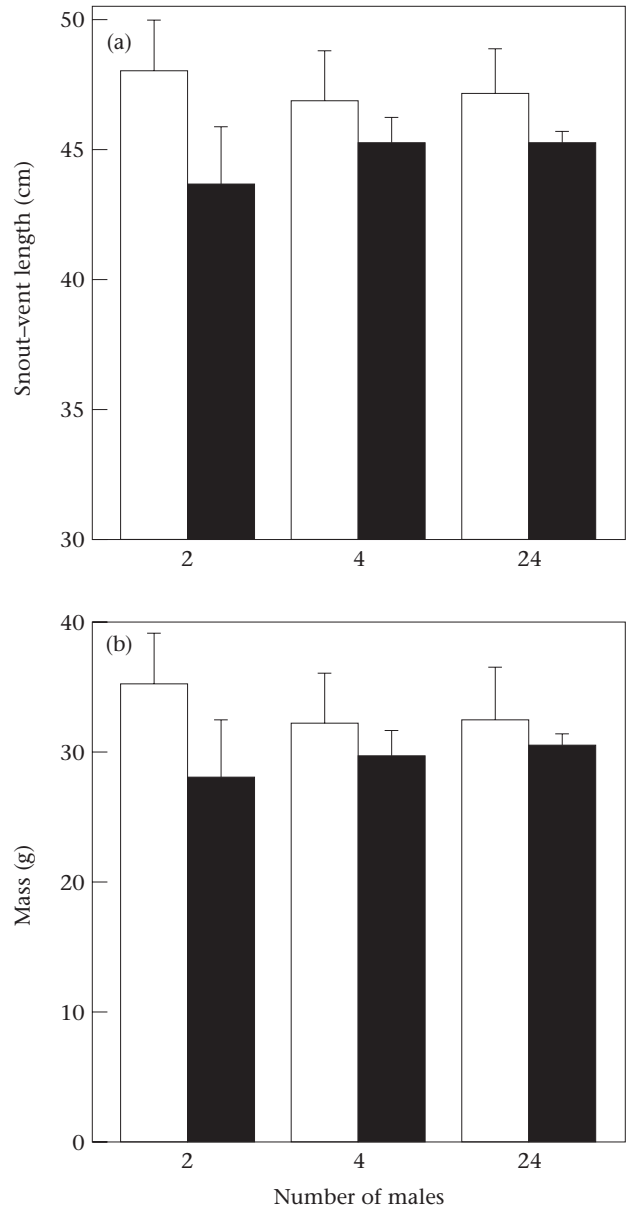


Figure 2. Body size and body condition of male garter snakes used in arena trials to investigate the effect of body size on mating success. (a) Body length (snout-vent length (SVL), cm) and (b) mass (g). The attributes of males that mated in the trials (□) are compared with those of males that failed to obtain matings (■). Data are shown separately for three experimental treatments, in which the female was courted by either two, four or 24 males. Means are given +SE. See text for statistical treatment of these data.

all facets that we investigated. Larger males obtained more matings (both in our arena trials and in the field), mated with larger females, and had larger hemipenes and larger testes (and thus, we infer, produced more sperm). Some of these results are not surprising, and bear in only a limited way on male reproductive success. In particular, the information on relative organ sizes from our dissections simply supports the (fairly obvious) proposition that larger males have larger body parts; we have no data to indicate that larger testes, hemipenes or kidneys

actually enhance male reproductive success. The testes are not actively producing sperm in spring (Krohmer et al. 1987), and so their regressed size may offer a poor indication of their capacity to produce gametes.

Our data on the body sizes of mating snakes are more compelling, and are surprising from two perspectives. First, larger body size in our study conferred a substantial mating advantage for male garter snakes, and yet males of this species are much smaller than females. Second, a previous study on the same system, using techniques very similar to ours (Joy & Crews 1988), came to conclusions that are diametrically opposed to our own. Below, we address the contradiction between the results of these two studies.

Why did mating success increase with larger body size of males in our study (both in the field and arena trials) but not in the analogous data sets of the earlier study? Joy & Crews (1988) offered a possible explanation. They did detect a slight trend in this direction in one of their data sets, but attributed it to the possible inclusion of juvenile animals (defined as males less than 40 cm SVL) among the smallest size classes of snakes. If we had inadvertently included many juvenile animals, we might have spuriously concluded that size enhanced mating success even if no such size effect was present over the size range of adult snakes. We can confidently dismiss this possibility. All of our dissected males were adult (i.e. possessed sperm in the efferent ducts); the smallest of these animals was 37 cm SVL (18.7 g). Also, some of the males that we found mating in the field and in our trial arenas (see below) were among the smallest that we recorded (down to 35.0 cm SVL, 15.1 g). Even if we arbitrarily restricted our analyses to males longer than 45.3 cm SVL (the mean size of males), we still detect a significant difference in body size between the mated versus unmated male snakes ($P < 0.05$ for analyses of mean SVL in mated versus unmated males, in separate tests with data from the field and from the arena trials). Thus, the consistent mating advantage to larger body size in our study is not an artefact of including juvenile males.

Another possible explanation for the disparity in results between the two studies involves the role of the operational sex ratio (OSR). Plausibly, the OSR might affect the degree to which larger body size enhances male mating success. Perhaps success is truly stochastic in very large aggregations (as is typical within the den itself), but deterministic, and hence related to male size, when there are fewer rivals (as is seen in the surrounding pastures)? Our data from arena trials provide limited support for this hypothesis. The body size effect on mating success was strongest in trials involving only two males (Fig. 2), and the group sizes used by Joy & Crews (1988) were larger (16 or 48 males) than in two of our three treatments. If OSR does affect the mating advantages of large male size (despite the lack of a significant interaction term in our analyses), the overall advantage to larger males within the field matings data suggests that many copulations may occur in small rather than large 'mating balls'. In keeping with this inference, our surveys reveal a mean courting group size of four males (R. Shine, unpublished data). The contrast between our conclusions and those of Joy &

Crews (1988) emphasizes the value of replicating important research projects, because otherwise they tend to be accepted without challenge. Because of our work, the emphasis within the field can now shift from 'why does larger size enhance male mating success in some natricines but not others?' (as posed by Madsen & Shine 1993) to 'are there any mating systems and contexts in snakes wherein larger size does not enhance male mating success?'

Why do larger males obtain more matings? The mechanism relates to male–male rivalry, because small and large males were equally effective in courting and inducing copulatory consent from females (above). Our data thus allow us to falsify the hypothesis that body-size-related advantages are due to size-related shifts in courtship intensity or effectiveness (Madsen & Shine 1993; Luiselli 1996). Instead, our observations of courting snakes indicate that the benefit to larger body size comes about via the ability of larger (stronger) males to displace their rivals' tails from the vicinity of the female's cloaca prior to coitus. The males align their bodies with the female, and wrap the anterior part of their tail around the female's tail immediately posterior to the cloaca. When she lifts her tail to gape her cloaca, the males respond rapidly, pushing their own cloaca forward to achieve intromission. Because the males all attempt to maintain the same position, there is continual tail wrestling to maintain that place. Displaced males throw a coil around the female's body and force it posteriorly against the coils of their rivals; the tapering of the female (especially immediately below the cloaca, the prime position for males) means that it is difficult for a male to retain his position against this pressure. Larger, heavier males appear to be more successful at resisting the posterior pressure from their competitors, and thus are more likely to be in the best position when the female is ready to accept a mating.

The same kind of tail wrestling may be widespread in snake species that display 'mating balls'; that is, where more than one male simultaneously attempts copulation. This situation is most likely to occur in species that (1) do not display male–male combat, (2) occur in high population densities, and especially (3) if mating occurs soon after spring emergence, while the snakes are highly aggregated at overwintering dens. These three criteria fit many snake species, especially natricine colubrids (Gregory & Stewart 1975; Slip & Shine 1988; Duvall et al. 1993). Our data, in conjunction with those of other workers (Madsen & Shine 1993; Sexton & Bramble 1994; Weatherhead et al. 1995; Luiselli 1996), suggest that tail wrestling may introduce a significant mating advantage to larger body size in males within such systems.

The second benefit to larger male body size in our garter snakes involves the trend for larger males to mate with larger females. Joy & Crews (1988) detected the same pattern in 1 of their 2 years. Larger females produce more offspring per litter in most snake species, including the Manitoba *Thamnophis* (Gregory 1977; D. Lerner, personal communication), so we infer that mating with a larger female is likely to enhance male reproductive success. If larger females remate more frequently, this inference may

be in error, but our studies do not suggest any such size-related effect (R. Shine, unpublished data). Size-assortative mating has been described in many other mating systems (e.g. Sullivan 1983; Robertson 1990), but the mechanism responsible for this effect remains elusive, at least for the red-sided garter snake.

In summary, then, we conclude that larger body size significantly enhances male mating success in the red-sided garter snake. This result is counterintuitive: a priori, it seems likely that chaos rules within a writhing 'mating ball' of red-sided garter snakes, and that paternity is determined more by random factors than by any deterministic process. None the less, our results fit well with the emerging generalization that larger body size frequently confers a reproductive advantage to male snakes, even in species that do not show the 'classical' form of overt male-male combat (Madsen & Shine 1993; Weatherhead et al. 1995; Luiselli 1996). The magnitude of this advantage is likely to be much smaller than is the case in species that display direct physical combat (Madsen et al. 1993). Importantly, however, the degree to which male size benefits mating success in snakes is likely to be a continuum rather than the dichotomy suggested in earlier work (e.g. Shine 1978).

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