# DOES LARGE BODY SIZE IN MALES EVOLVE TO FACILITATE FORCIBLE INSEMINATION? A STUDY ON GARTER SNAKES

RICHARD SHINE[1,2] AND ROBERT T. MASON[3,4]

[1]*School of Biological Sciences A08, University of Sydney, Sydney, New South Wales 2006, Australia*
[2]*E-mail: rics@bio.usyd.edu.au*
[3]*Department of Zoology, Oregon State University, Cordley Hall 3029, Corvallis, Oregon 97331-2914*
[4]*E-mail: masonr@science.oregonstate.edu*

*Abstract.*—A trend for larger males to obtain a disproportionately high number of matings, as occurs in many animal populations, typically is attributed either to female choice or success in male-male rivalry; an alternative mechanism, that larger males are better able to coercively inseminate females, has received much less attention. For example, previous studies on garter snakes (*Thamnophis sirtalis parietalis*) at communal dens in Manitoba have shown that the mating benefit to larger body size in males is due to size-dependent advantages in male-male rivalry. However, this previous work ignored the possibility that larger males may obtain more matings because of male-female interactions. In staged trials within outdoor arenas, larger body size enhanced male mating success regardless of whether a rival male was present. The mechanism involved was coercion rather than female choice, because mating occurred most often (and soonest) in females that were least able to resist courtship-induced hypoxic stress. Males do physically displace rivals from optimal positions in the mating ball, and larger males are better able to resist such displacement. Nonetheless, larger body size enhances male mating success even in the absence of such male-male interactions. Thus, even in mating systems where males compete physically and where larger body size confers a significant advantage in male-male competition, the actual selective force for larger body size in males may relate to forcible insemination of unreceptive females. Experimental studies are needed to determine whether the same situation occurs in other organisms in which body-size advantages have been attributed to male-male rather than male-female interactions.

*Key words.*—Coercive mating, reptile, sexual conflict, sexual size dimorphism.

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Evolutionary biologists seek to understand how variation in phenotypic traits translates into variation in organismal fitness. The task is a formidable one, requiring two kinds of information: the empirical association between phenotype and fitness, and the mechanism responsible for such a link (Arnold 1983, 2003; Lande and Arnold 1985). The first of these challenges is straightforward conceptually but difficult logistically, especially for traits (such as locomotor speed and foraging behavior) that affect fitness only indirectly. Unfortunately, this link with fitness is very indirect for most aspects of an organism's phenotype. The second challenge—to identify the mechanisms by which fitness variation is induced by phenotypic variation—holds even greater obstacles. Even if a strong quantitative link between fitness and phenotype can be shown, any such link might result from a wide range of processes (Arnold 2003). Distinguishing between these alternatives often will require experimental as well as descriptive approaches, preferably on free-ranging animals in the field.

The role of body size in enhancing male mating success provides an ideal system with which to investigate the nature of adaptation. Both body size and mating success are amenable to quantification in the field, and the latter variable is so intimately tied to fitness (i.e., individual reproductive success) that there is no need to assume fitness relevance, as is the case for most other traits. Empirical work has revealed that larger males experience higher mating success in a wide variety of organisms, but interpretations of the functional basis for such an association generally are inferential only. For example, imagine a mating system in which rival males struggle with each other while simultaneously attempting to inseminate a female. Higher mating success of larger males

in such a system would generally be attributed to the advantages of larger body size in vanquishing rivals. However, other possibilities also exist: for example, the greater success of larger males might be due to their interactions with females, not with rival males. Females might accept copulations more readily from larger males, or larger males might be better able to overcome female resistance and, hence, obtain coercive matings (Thornhill 1987; Smuts and Smuts 1993; Olsson 1995; Eberhard 2002; Eberhard and Cordero 2003).

Exactly this ambiguity occurs in our understanding of the mating system of red-sided garter snakes, the most intensively studied reptile species in this respect. Data from natural matings as well as experimental trials in outdoor arenas (with two, four, or 24 males per female) show that larger males obtain more matings than do smaller males (Shine et al. 2000a), and videotape analysis has shown that larger, heavier males are more vigorous courters and are better able to maintain their own cloaca in an optimal position relative to the female's cloaca within a communal mating ball (Shine et al. 2004a). Courting males appear to push their rivals' tails out of the way with their own tails, and the mating advantage of larger males has been attributed to greater success in this male-male rivalry (Shine et al. 2000a). However, recent work on this species at large communal dens has revealed that most or all matings are coercive, with males inducing cloacal gaping by females as a stress response, by impeding female breathing (Shine et al. 2003a). Accordingly, the mating advantage to larger body size in males might be due to a greater ability to overpower females rather than (or as well as) to displace rival males. In this study, we evaluate this possibility.

### Study Species and Area

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small (average snout-vent lengths [SVLs] = 45 cm for adult males, 60 cm for females), nonvenomous, natricine colubrids that are abundant in the severely cold prairies of south-central Manitoba, in central Canada (Rossman et al. 1996). Snakes in this area congregate in large communal overwintering sites for eight months each year to escape lethally low temperatures (Gregory 1974; Gregory and Stewart 1975). Males emerge earlier in spring than do females and remain longer near the den prior to dispersal; thus, sex ratios near the den are highly male biased (Gregory 1974). As soon as females emerge, each is vigorously courted, immediately becoming the nucleus of a mating ball that may contain anything from a single suitor to dozens of males (Mason 1993). To obtain a copulation, a male must induce the female to gape her cloaca open, and then insert a hemipenis before any of his rivals can do so. At least for matings by newly emerged (and thus, weak and slow) females, cloacal gaping by females results from coercion rather than sexual receptivity. By impeding female breathing, courting males induce a stress response (cloacal gaping to expel odoriferous antipredator secretions from the cloacal glands) that enables copulation to occur (Shine et al. 2003a).

The present study was conducted in May 2004 at a den containing more than 50,000 garter snakes, located 1.5 km north of the town of Inwood in south-central Manitoba (50°31.58′N, 97°29.71′W). The den lies at the edge of a limestone quarry, among aspen woodland, and has been described in detail in previous work (Shine et al. 2003a,b).

### Effect of Male Body Size on Mating Success

If larger size enhances mating success via male-female rather than (or as well as) male-male interactions, larger size should be an advantage even in the absence of rival males. Previous studies have used multiple males per female in such trials (Joy and Crews 1988; Shine et al. 2000a, 2004a). Thus, we placed single unmated females (newly emerged and lacking a mating plug; Mason 1993) with either a single male or two males, one large (>45 cm SVL) and one small ($\leq$ 45 cm SVL), in open-topped nylon outdoor arenas (1 $\times$ 1 m, 0.8 m high) erected beside the den. We allowed trials to proceed for 20 min or until copulation occurred (if <20 min). The time taken and the identity of the copulating male were recorded. Snakes for these trials were collected from the adjacent den immediately prior to use. All snakes were released as soon as they had been weighed and measured after completion of a trial. Each snake was used in only a single trial. We recorded behaviors as well as mating success during these trials, as follows.

### Effect of Male Body Size and Presence of a Competitor on Courtship Intensity and Body Position during Courtship

Rings were painted around the body of females using non-toxic paint that wore off in less than 24 h. A white ring was centered on the cloaca, with colored rings at 2-cm intervals from 20 cm anterior to the cloaca back to 10 cm down the tail. Males were marked with a single ring centered on the cloaca. We began recording snake behaviors 5 min after the animals had been introduced to their arenas; courtship had commenced in all cases and in a few trials already had proceeded to copulation (in which case we recorded the identity of the successful male, but did not obtain behavioral data on courtship intensity or position). In the other trials, we recorded either one or two variables for each male at 10-sec intervals for 200 sec, beginning at a random time within the next 10 min: courtship intensity, on a 4-point scale (0 = no courtship, 1 = alignment, 2 = chin-rubbing, 3 = caudocephalic waving; for more details see Whittier et al. 1985); position of the male's cloaca relative to the female's cloaca (i.e., the location of the male's cloaca in terms of the number of rings anterior or posterior to the female's cloaca). Because of frequent changes in position, the second variable was more difficult to score (requiring two observers and one data-recorder), so our sample sizes were smaller for this trait than for courtship intensity (which required only one observer and one data-recorder). Our previous studies have shown that courtship intensity and cloacal positioning are robust predictors of mating success in this system (Shine et al. 2004a).

### Female Ability to Resist Hypoxia as a Determinant of Mating

If male body size affects mating success via male-female rather than male-male interactions, the mechanism might involve either female choice (active preference for larger males) or forcible insemination (inability of females to resist hypoxic stress induced by courtship; Shine et al. 2003a). To discriminate between these possibilities, we measured female ability to withstand hypoxic stress immediately prior to each trial. We did this by holding the female stretched out and stroking her dorsal surface with a finger in a posterior-to-anterior direction to impede breathing, as occurs with the caudocephalic waves of courting males (Shine et al. 2003a). We recorded the number of strokes (up to a maximum of 20) required to elicit cloacal gaping.

### Effect of Male Body Size on Ability to Resist Displacement by Rival Males

To quantify the effect of body size on the amount of force that a rival would need to apply to displace a courting male's tail from the vicinity of the female's cloaca, we conducted experiments on natural courting groups at the den. A live female was held by the tail to keep her immobile; she was soon covered in courting males that aligned their bodies with hers and began active tail-searching with their cloacas near hers. Courting males loop the tailbase around the female's body near the cloaca, providing a conveniently placed loop wherein we could insert a small metal hook with which we could pull the male's tail posteriorly, away from the cloaca, in the same way as other males push their rivals away. A Pesola spring balance attached to the wire hook allowed us to measure the amount of force required to move the male's tail. We then collected the male and measured his body length (SVL) and body temperature (the latter with a quick-registering cloacal thermometer).

## Statistical Analyses

Data were checked for the assumptions of parametric testing; no transformations were necessary except that body mass and SVL were ln-transformed to generate residual scores (from ln mass vs. ln SVL) as indices of body condition. We used one-tailed $P$-values for cases in which there was a clear unidirectional prediction, and two-tailed tests elsewhere. All nonsignificant ($P > 0.05$) values were $P > 0.20$, rendering power analyses unnecessary (Day and Quinn 1989; Peterman 1990).

## RESULTS

### Effect of Male Body Size on Mating Success

Small males averaged 39.51 cm SVL (SD = 3.39) and 21.41 g mass (4.66), large males averaged 49.36 cm SVL (3.60) and 43.31 g mass (9.23), and females averaged 55.23 cm SVL (6.07) and 68.05 g mass (26.35). Logistic regression with male body size (SVL or mass) and number of males per trial as independent variables and mating success as the dependent variable showed that larger males obtained more matings overall (for SVL as the measure of male body size: log-likelihood effect of male size $\chi^2 = 7.88$, df = 1, $P < 0.005$; for body mass, $\chi^2 = 9.83$, df = 1, $P < 0.002$). The probability of obtaining a mating was not reduced by the presence of a competing male (using SVL, $\chi^2 = 1.45$, df = 1, $P = 0.22$; using mass, $\chi^2 = 1.57$, df = 1, $P = 0.21$), nor was mating success affected by any significant interaction between male body size and number of competing males (using SVL as the measure of male body size, $\chi^2 = 0.76$, df = 1, $P = 0.38$; using mass, $\chi^2 = 0.90$, df = 1, $P = 0.34$). That is, male body size enhanced mating success in one-male as well as two-male trials, with the importance of body size in this respect slightly but not significantly greater in the two-male trials (Fig. 1). Mating success was not affected by the presence of a competing male because two-male trials were almost twice as likely to result in the female mating as were one-male trials (16 vs. 26%, $\chi^2 = 1.17$, df = 1, $P = 0.28$). In trials where mating did occur, it happened sooner in two-male trials than one-male trials (means 27.4 vs. 40.3 min; $F_{1,58} = 5.34$, $P < 0.025$).

### Effect of Male Body Size and Presence of a Competitor on Courtship Intensity

Two-factor ANOVA with male body size and number of males per trial as factors and maximum courtship intensity per male as the dependent variable revealed a significant interaction term ($F_{1,195} = 5.92$, $P < 0.016$; Fig. 2A). That is the degree to which a male's courtship intensity was affected by the presence of a rival differed between large and small males. We then conducted separate one-factor ANOVAs for trials involving one versus two males. A male's body size did not affect his courtship intensity if he was alone with a female ($F_{1,53} = 1.11$, $P = 0.30$), but larger males were more vigorous than their smaller rivals if both size classes were present in the trial ($F_{1,142} = 27.51$, $P < 0.0001$). That is, the presence of another male reduced courtship intensity more for small males than for large males.

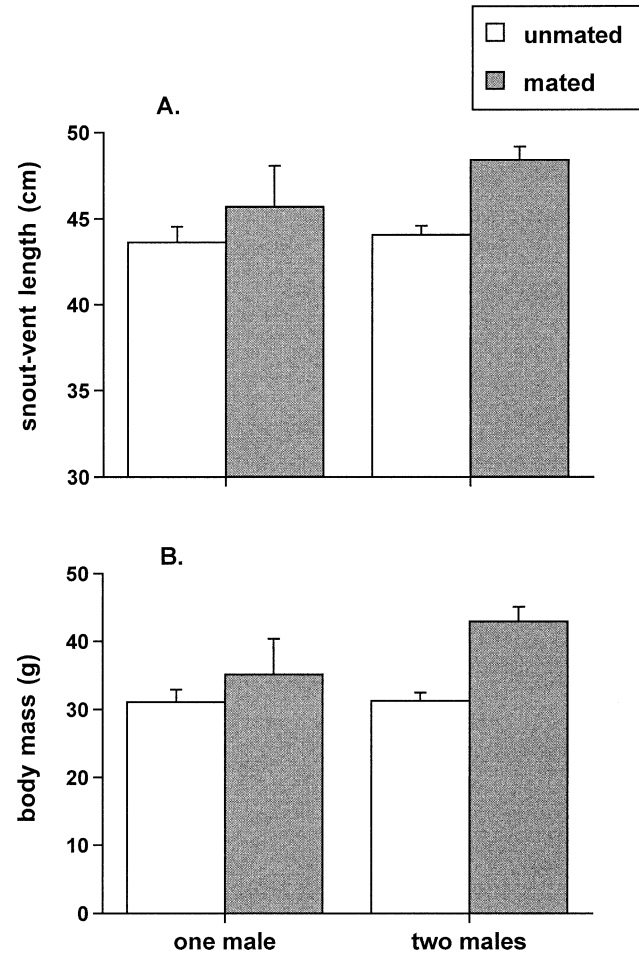Within two-male trials that proceeded to copulation, the



FIG. 1. Body sizes of male garter snakes that obtained matings in trials in outdoor arenas, compared to males that did not obtain matings: (A) snout-vent lengths; (B) body masses. In each case, means are shown plus associated standard errors. Sample sizes (bars left to right): $n = 42, 8, 130, 7$.

more vigorously courting male obtained the mating in 14 cases; the winner and loser exhibited equal maximum courtship intensity in another five trials. Thus, courtship vigor was highly associated with mating success (14 vs. 0, $\chi^2 = 49.0$, df = 1, $P < 0.001$). Adding courtship vigor into the multiple logistic regression for mating success (above) did not change the result: a male's probability of mating was enhanced by larger body size ($\chi^2 = 5.08$, df = 1, $P < 0.03$) and by more intense courtship ($\chi^2 = 10.27$, df = 1, $P < 0.002$) but was not affected by the presence of a rival male ($\chi^2 = 0.37$, df = 1, $P = 0.54$; all interactions were nonsignificant).

### Effect of Male Body Size and Presence of a Competitor on Body Position during Courtship

Larger males maintained their tailbases closer to the female's cloaca than did their smaller rivals (Fig. 2B; $F_{1,40} = 8.12$, $P < 0.007$). This was true in both one-male and two-male trials, but the presence of a rival male impeded male positioning ($F_{1,40} = 4.90$, $P < 0.035$) to a similar degree in males of both size classes (interaction $F_{1,40} = 0.001$, $P = 0.98$).
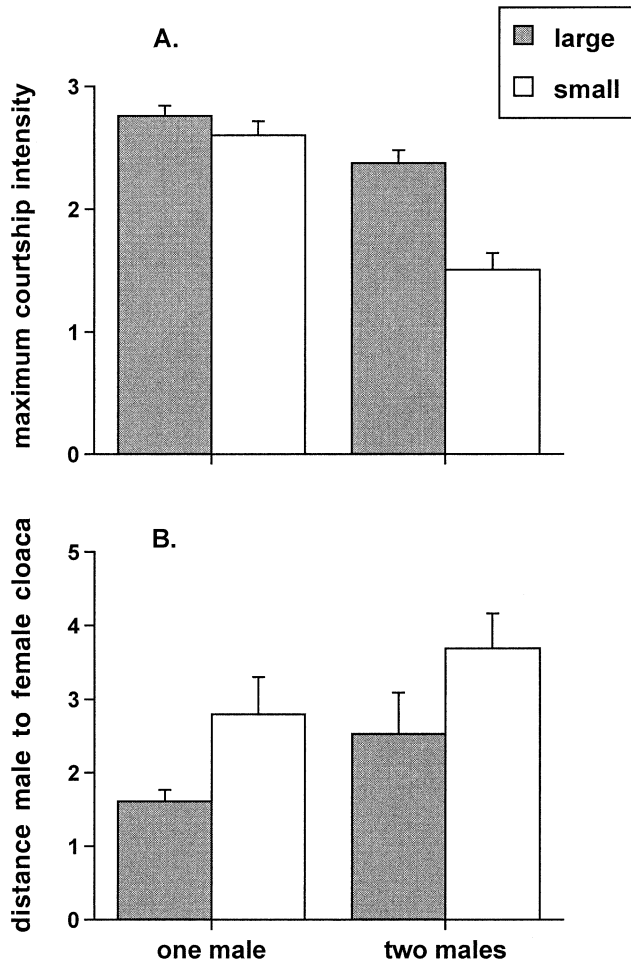
FIG. 2. Effect of the presence of a rival male on (A) maximum intensity of courtship by male garter snakes; and (B) the mean distance between the male's cloaca and that of the female he is courting. Data are shown separately for large (>45 cm snout-vent length) and small (≤45 cm) males and for trials when the male was alone with the female versus when another male was also present. The two-male trials always consisted of one small plus one large male. Means are shown plus associated standard errors. Sample sizes (bars left to right): (A) $n$ = 29, 25, 72, 73; (B) $n$ = 15, 9, 10, 10.
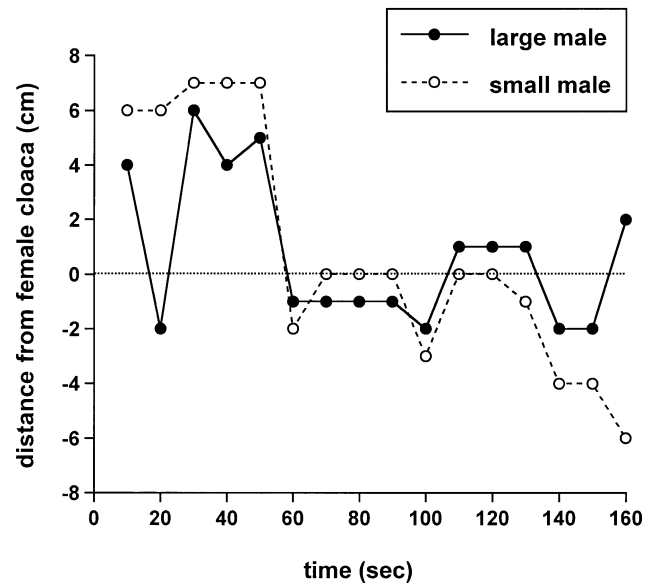


FIG. 3. Changes through time in the positions of the cloacae of two courting male garter snakes relative to the cloaca of the female that they are courting. Courting males attempt to keep their cloaca close to the female's to facilitate intromission if she gapes the cloaca open; rival males push each other's tails out of the way. The large male was 50.7 cm snout-vent length and 46.2 g; the small male was 41.8 cm snout-vent length and 23.3 g.

Detailed inspection of sequential changes in tail position confirmed that males do indeed push the tails of their rivals away from the female's cloaca (Fig. 3). To evaluate this point statistically, we calculated the change through time (between successive 10-sec samples) in the distance between each male's cloaca and the female's cloaca; the positions of the two males changed synchronously in this respect, as would be predicted if they push each other (for data in Fig. 3, $n$ = 15 time samples, $r$ = 0.53, $P$ < 0.05). The female was stationary throughout this trial, so that the synchronized displacements of males indicate direct interaction between them.

### Female Ability to Resist Hypoxia as a Determinant of Mating

Caudocephalic stroking prior to trials elicited cloacal gaping after 0–20 strokes (mean = 5.49, SD = 6.99). Females in poor body condition (low mass relative to SVL, as mea-

sured by residual scores from a general linear regression of ln-transformed mass vs. SVL) gaped after fewer strokes ($n$ = 240, $r$ = −0.12, one-tailed prediction, $P$ = 0.03). Females that gaped readily were more likely to mate (comparing females that mated to those that did not, for time to gape, $F_{1,244}$ = 3.65, one-tailed prediction, $P$ < 0.026). Within the subset of trials in which mating occurred, more rapid pretrial elicitation of cloacal gaping was associated with more rapid mating ($n$ = 56 trials, $r$ = 0.44, $P$ < 0.001). Thus, females in poor condition, who were less able to resist handling stress, were the most likely to mate in our trials.

### Effect of Male Body Size on Ability to Resist Displacement by Rival Males

The force required to displace 20 males (range 37–54 cm SVL) ranged from 10–55 g on the Pesola scale. Male body temperatures were all within a narrow range (28.0–31.4°C) and were not correlated with the force required to displace the male from the female's body; thus, temperature was not included as a covariate in our analyses. Not surprisingly, larger males required more force to displace (force required vs. male SVL, $n$ = 20, $r$ = 0.89, $P$ < 0.0001).

### DISCUSSION

Our data challenge previous interpretations of selective forces operating on male body size in this system. Intense male-male rivalry, including vigorous physical battles for optimal positioning on the female, is a central feature of courtship and mating of garter snakes at the large Manitoba dens. Our data confirm that males do indeed physically displace their rivals, and that larger males are likely to have an

advantage in this endeavor. Courtship vigor is closely associated with mating success (as in our previous studies; Shine et al. 2004a), and males adjust their vigor both to their own body size and to the presence of rival males (Fig. 2). Thus, intuition suggests that the higher mating success of larger males in this population reflects the advantages of larger body size in male-male competition. However, our arena trials showed the same mating advantage to larger body size even when no competitors were present, indicating that male-female rather than male-male interactions are most important in this respect.

Our study also clarifies the nature of those male-female interactions. Although many cases of female choice for larger males have been reported (Andersson 1994; Breuker and Brakefield 2002; Candolin 2003; Eberhard and Cordero 2003), female garter snakes rarely have the opportunity to exercise such a choice. Courtship typically involves attention from multiple males, several of which simultaneously vie to insert a hemipenis as soon as the female's cloaca gapes open. There is no way for the female to choose a particular male under these conditions. Also, cloacal gaping is induced by hypoxic stress rather than sexual receptivity; the response is elicited as easily from males as from females, in response to caudocephalic stroking similar to that performed by courting males (Shine et al. 2003a). Such courtship can rapidly empty the air from the lungs of even a large female (Shine et al. 2003a). The present study found that females were more likely to accept a mating if they were unable to resist hypoxia due to caudocephalic stroking and that females in poor body condition were particularly susceptible in this respect. These data strongly support the hypothesis that larger body size enhances male mating success because it facilitates coercive mating, rather than because of advantages associated with male-male rivalry or a female preference for larger males.

This conclusion stands in strong contrast to those of previous studies. Published discussions on sexual size dimorphism in snakes consistently have focused on male-male rivalry as the primary selective force for larger body size in males (Gibbons 1972; Shine 1978, 1994). Indeed, field studies have confirmed a strong size advantage in male-male combat bouts and hence, mating opportunities, for males of one viper species (*Vipera berus*, Madsen et al. 1993) and one python (*Morelia kinghorni*, Fearn et al. 2005). Data from captive snakes suggest that larger size often may be an advantage in physical combat between males (*Agkistrodon contortrix*, Schuett and Gillingham 1989; Schuett 1997). Despite early reports that such advantages may be minimal in species that lack ritualized male-male combat (Shine 1986; Joy and Crews 1988), detailed studies have revealed significant (albeit more modest) increases in mating success with male body size in such taxa (Madsen and Shine 1993; Weatherhead et al. 1995; Luiselli 1996). This pattern has been attributed to the ability of larger males to physically outmaneuver their smaller rivals during courtship; the most extensive data in this respect come from the subject of the current study, *T. sirtalis parietalis*, in which larger males attained more matings both in the field and in (multiple-male) arena trials (Shine et al. 2000a, 2004a). However, the possibility that male size influences mating success via an ability to force copulations, rather than (or as well as) via male-male rivalry,

has remained virtually untested in reptiles as in other types of organisms.

In combination with previous studies, our data show that body size may enhance mating success in male garter snakes via a surprisingly complex set of pathways: larger males are more vigorous courters (Fig. 2A), are better able to keep their tailbase close to the female's cloaca during courtship (Fig. 2B), are better able to resist being displaced by other males, target their courtship toward larger females (Shine et al. 2001a), and are better able to force female cooperation (Fig. 1). These variables doubtless interact in complex ways; for example, the ability to maintain an optimal position may be related to courtship vigor and resistance to displacement. However, our logistic regression showed that larger males obtained more matings even after courtship vigor was factored out of the analysis, so the body-size advantage to mating is not driven only by vigor of courtship. Similarly, the relationship between male body size, courtship vigor, and extent of male-male rivalry is complex. Males reduce courtship vigor if another male is present, parasitizing the other male's activities so that a mating can be obtained with lower energy expenditure (Shine et al. 2003b). The decrease in courtship vigor is greater in smaller males than in larger conspecifics (Fig. 2). Because the probability that a female will mate is higher if more than one male is present, a male may actually benefit from the presence of a rival. In summary, larger body size enhances a male garter snake's mating success via complex pathways; the only fitness-relevant task in which performance is known to be unaffected by body size is the rate of mate location (male size does not affect rate of arrival at a newly emerged female; and earlier arrival does not increase the probability of mating; Shine et al. 2005).

One important complication with coercive mating, however, is that the females least able to resist forcible insemination may be smaller, weaker, or in lower body condition than most other females within the population and, hence, be less likely to reproduce in the following summer (and/or more likely to produce a smaller litter of less viable neonates if they do so). Thus, the ability to forcibly inseminate females may not increase the number of offspring that a male sires as much as it enhances the number of copulations that he obtains. This situation occurs in Manitoban garter snakes: females that are in relatively poor condition not only are easier to inseminate forcibly (current study) but also are less likely to produce offspring (Whittier and Crews 1990). Also, some of the females that are forcibly inseminated are too small to produce offspring (Shine et al. 2000b, 2004b). However, the reverse effect also may occur, because a larger, stronger male may be able to obtain matings with larger females than could his smaller, weaker rivals. Indeed, larger males do court and mate larger females in this system (Shine et al. 2001a). Thus, forcible insemination might favor larger body size in males because of advantages in mate quality as well as number of matings. Additional data are needed to clarify the relative fitness benefits accruing from forcible insemination versus matings driven by female choice.

Given that larger body size strongly enhances male mating success, why do females attain larger mean adult body sizes than do conspecific males in this population, as in most or all other garter snake species (Shine 1994; Rossman et al.

1996)? Presumably, the answer involves even stronger selective advantages to large body size in females. In keeping with this interpretation, larger females produce larger litters of larger neonates than do smaller conspecifics, and larger females are less vulnerable to attack by predatory crows (Rossman et al. 1996; Shine et al. 2001b).

More broadly, our study identifies a potential flaw in the widely accepted conclusion that in mating systems with overt male-male rivalry, the higher mating success of larger males reflects the advantages of larger body size in male-male competition (Andersson 1994). In practice, it is difficult to distinguish between forcible insemination and male-male rivalry as selective forces for large size in males, because these two behaviors often may occur simultaneously (Berry and Shine 1980; Smuts and Smuts 1993; Andersson 1994; Eberhard and Cordero 2003). For example, Andersson's (1994) encyclopedic review of empirical evidence for the operation of sexual selection (table 6.A) identified 57 case studies in which selection was shown to favor larger body size in males. The selective advantage to larger size was attributed to female choice in 19 of these taxa, male-male contests in 29, and both female choice and male contests in another nine cases. None of these cases were attributed to forcible insemination, although the interpretation might be plausible in several of these taxa. This situation may reflect a widespread reluctance of scientists to interpret sex-specific traits as adaptations for coercive mating (Thornhill and Thornhill 1992). Male-male rivalry is much easier to document than is forcible insemination, especially if the courtship behaviors of males superficially involve gentle persuasion rather than overt harassment (Shine et al. 2003a). Even if coercive mating is suspected, it is difficult to demonstrate, for example, it is hard to distinguish from female choice for vigorously courting males (Thornhill 1987; Eberhard 2002; Eberhard and Cordero 2003).

Some of the best opportunities to resolve this ambiguity may come from situations in which a male's ability to obtain forcible matings is enhanced, not by larger body size, but by some other phenotypic trait less relevant to other potential male-male and male-female interactions. In this case, the functional significance of the trait in question may be more clearcut. For example, smaller (not larger) male body size may enhance a male's ability to obtain coercive matings in viviparous fishes, because agility and inconspicuousness are more important than strength in this system (Bisazza et al. 2000, 2001). Even clearer are cases in which males possess specialized structures that facilitate forcible mating, as in some species of turtles (rugose paracloacal scales, Berry and Shine 1980), scorpionflies (the dorsal clamp, Thornhill 1980; Thornhill and Sauer 1991), water striders (abdominal ventral processes, Arnqvist and Rowe 2002) and crickets (the gin trap, Sakaluk et al. 1995). Unfortunately, larger body size may be the phenotypic trait most commonly linked to performance in a wide variety of fitness-relevant tasks, so that we cannot afford to ignore this issue, despite its logistical difficulties. Disentangling the relative importance of the multiple, fundamentally different pathways (female choice, male-male rivalry, forcible copulation) by which larger body size enhances male mating success remains an important challenge for future work.

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