

Cryptic Forcible Insemination: Male Snakes Exploit Female Physiology, Anatomy, and Behavior to Obtain Coercive Matings

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ABSTRACT: Whether males can inseminate uncooperative females is a central determinant of mating system evolution that profoundly affects the interpretation of phenomena such as multiple mating by females, mate choice, reproductive seasonality, and courtship tactics. Forcible insemination is usually inferred from direct physical battles between the sexes and has been dismissed on intuitive grounds for many kinds of animals. For example, snakes have elongate flexible bodies (making it difficult for a male to restrain a female physically), males are typically smaller than females, and copulation requires female cloacal gaping to enable intromission. Male garter snakes (*Thamnophis sirtalis*) do not display any overt aggression during courtship and simply lie over the female and exhibit rhythmic pulsating caudocephalic waves of muscular contraction; previous studies have interpreted this behavior as a mechanism for eliciting female receptivity. In contrast, we show that male garter snakes forcibly inseminate females. They do so by taking advantage of specific features of snake physiology, respiratory anatomy, and antipredator behavior. The snake lung extends along most of the body, with the large posterior section (the saccular lung) lacking any respiratory exchange surface. Rhythmic caudocephalic waves by courting male garter snakes push anoxic air from the saccular lung forward and across the respiratory surfaces such that females cannot obtain oxygen. Their stress response involves cloacal gaping, which functions in other contexts to repel predators by extruding feces and musk but in this situation permits male intromission. Thus, superficially benign

courtship behaviors may involve cryptic coercion even in species for which intuition dismisses any possibility of forcible insemination.

Keywords: female choice, forcible insemination, pulmonary anatomy, sexual selection.

Sexual conflict is widespread and may be an important influence on mating systems of many kinds of organisms (Trivers 1972; Ghiselin 1974; Olsson 1995; Sakaluk et al. 1995; Bisazza et al. 2000, 2001). Extensive empirical data support the prediction from theoretical models that the sexes will often have different fitness optima for courtship duration, mating frequency, and numbers of mating partners (Andersson 1994). Males of many species may be under significant selection to obtain copulations, and females may be under equally strong selection to avoid such matings (e.g., Williams 1966, 1975). One potential option for males to increase their mating success may thus be forcible copulation (Ghiselin 1974; Berry and Shine 1980; McKinney et al. 1983; Smuts and Smuts 1993; Clutton-Brock and Parker 1995).

Understanding whether forcible copulations occur is one of the most crucial questions that one can ask about any mating system. Most obviously, forcible insemination may impose direct costs on females, including survival and energy balance (LeBoeuf and Mesnick 1990; Stone 1995; Rowe et al. 1996; Watson et al. 1998; McLain and Pratt 1999). On a longer timescale, this behavior will impose selection on traits such as body size, body shape, and behavior that increases a male's ability to overpower females (e.g., Ghiselin 1974; Berry and Shine 1980) and also on corresponding female traits that minimize the incidence of, or disadvantages of, forced copulations. For example, females may modify habitat selection in order to avoid harassment by males (Smuts and Smuts 1993; Brooks and Jennions 1999). Forcible copulations also reduce the opportunity for female mate choice to influence fitness, although cryptic sperm choice remains possible (Olsson et al. 1996; Birkhead and Moller 1998; Olsson and Madsen

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1998). Hence, in order to interpret phenomena such as multiple mating by females, the seasonal timing of mating activity, and the significance of interspecific and intraspecific variation in traits such as courtship behavior and genital morphology, we need to understand whether some or all matings result from males forcing themselves onto uncooperative females rather than male-female cooperation in mating.

Unfortunately, there are substantial logistical impediments to distinguishing forcible insemination from alternative possibilities, such as females enhancing their fitness by mating only with males strong and persistent enough to overcome vigorous rejection (Andersson 1994). Many published interpretations of mating systems have been forced to rely on intuition in this respect to evaluate whether a male would be capable of copulating with an unreceptive female. Snakes offer an excellent example of this situation. In an influential review, Devine (1984) argued that one distinctive feature of snakes (especially in comparison with their sister group, the lizards) was that the elongate and flexible body of the female made it impossible for a male to forcibly inseminate his partner. When we combine the facts that males of most snake species are considerably smaller than conspecific females (Shine 1994) and that females apparently can prevent intromission by refusing to gape their cloacae (Gillingham 1987), the strong inference is that mating in snakes involves cooperation rather than conflict between the partners. This has remained a fundamental assumption of most subsequent studies and has shaped the interpretation of courtship behaviors in terms of male tactics to induce female receptivity (Carpenter and Ferguson 1977; Gillingham 1987) and prevention of interspecific hybridization (Gillingham 1979) as well as more general aspects such as the timing of mating in terms of seasonality (Aldridge and Duvall 2002) and its relationship to female reproduction (Naulleau et al. 1999). Theoretical models of mating system evolution within snakes (Duvall et al. 1992, 1993) also have assumed no significant role for forcible insemination.

Although the putative lack of forced copulations in snakes is thus critical to interpretation of many facets of the mating systems of these animals, the evidence for this claim is weak. No empirical studies have clarified why females mate with particular males at particular times. The functional significance of the considerable interspecific and intraspecific diversity in male courtship behaviors among snakes remains entirely speculative. For example, why do males of many snake species expend much time and energy in rhythmic posterior-to-anterior contractions of their body musculature during courtship, whereas males of other species bite females or prod them with the snout (Carpenter and Ferguson 1977; Gillingham 1987)?

Recent studies have challenged the paradigm of non-

forcible mating in snakes on the basis of indirect evidence. For example, matings with dead females show that active female cooperation is not essential for mating to occur (Hardy 1998; Shine et al. 2000c). Matings with other males and with heterospecific females also imply that cooperation may not be essential for intromission (Hardy 1998; Pfreder et al. 2001). Specific female behaviors and pheromones to discourage male copulatory attempts (Perry-Richardson et al. 1990; Greene and Mason 2000, 2003) suggest sexual conflict over mating. In large courting aggregations of garter snakes (*Thamnophis sirtalis parietalis*), some females are suffocated by courting males (Shine et al. 2001b), and juvenile females copulate although they are too small to produce offspring (Shine et al. 2000c). Mating is size assortative (Shine et al. 2001d), with larger males being generally more successful (Shine et al. 2000a), except with exhausted females (Shine et al. 2003b). Females attempt to avoid courtship (Shine et al. 2000c; LeMaster et al. 2001). Last, blood lactate levels are higher in mating females than in other groups (Shine et al. 2003b). Because courted females show few overt movements, this switch to anaerobic metabolism suggests that courtship somehow impedes female aerobic respiration. These patterns hint at high levels of stress to females during courtship, but any inference of forcible insemination remains unconvincing in the absence of a plausible mechanism.

A New Hypothesis on Mating in Snakes

In our study population, male garter snakes are much smaller than females (means of <40 vs. >80 g) and do not show any overt aggression toward the female during courtship; for example, there is no biting. Thus, if males somehow force females into mating, they must do so by way of other courtship behavior. Males align with the female at the beginning of courtship, and their only overt movements involve regular muscular contractions (caudocephalic waves) plus adjustment of the tail to ensure that the two cloacae are adjacent (Noble 1937; Blanchard and Blanchard 1941; Pisani 1976; Carpenter and Ferguson 1977). How could caudocephalic waving by a small male somehow force a much larger female to submit to copulation?

The answer may lie in specific features of pulmonary anatomy in snakes. These elongate animals have similarly elongate lungs that extend for most of the total body length (Bartlett et al. 1986; Wallach 1998). In the majority of snake lineages (including garter snakes), the left lung is very small, and the main respiratory function is carried out by the right lung. Despite its great length, however, only a relatively small thick-walled anterior segment of the lung is involved in gas transfer. The posterior section of the lung comprises a simple thin-walled sac, with gas

exchange occurring only in a clearly demarcated vascular portion that runs from immediately posterior to the heart back for about 10% of body length. Although the functional significance of the saccular lung remains controversial (Rosenberg 1973; Stinner 1982; Wallach 1998), direct sampling shows that air inside the saccular lung is relatively anoxic compared with air in the vascular component of the lung (Gratz et al. 1981).

Given this respiratory anatomy and physiology, caudocephalic waves by courting males might severely impact a female's ability to breathe. Anteriorly directed pressure waves compressing her dorsal surface (as occurs with caudocephalic waves) will tend to force anoxic air from the saccular lung anteriorly to cover the limited gas-exchange area in the vascular lung. This effect will be exaggerated by the ease with which the thin-walled saccular lung can be deformed by pressure (Stinner 1982). Pressure on her dorsal surface (because of the male) also will reduce her ability to take in fresh air. Thus, male courtship (and, especially, caudocephalic waving) may compromise female respiration much more significantly than would be suggested by intuition. High lactate levels in mating females (Shine et al. 2003b) strongly support this component of the hypothesis. Because anoxia induces quiescence in reptiles (C. Daniels, personal communication), stressed females are unlikely to escape from the courting ball.

The next question is, Why should a female under oxygen stress be more likely to allow a male to copulate by gaping her cloaca and allowing intromission? Again, the answer may lie in aspects of snake physiology and behavior. As in many other snake species, one of the most common responses to stress in garter snakes involves cloacal gaping and accompanying discharge of highly odorous musk and feces (Greene 1988). This behavior has generally been interpreted as an antipredator adaptation (Greene 1988) and presumably evolved within that context. However, it also provides an ideal opportunity for a male to insert his hemipenis into the gaping cloaca because snake anatomy involves a single common outlet to the reproductive and digestive systems. Sexual selection on males may have favored induction of high levels of respiratory distress in females such that they gape the cloaca widely and, hence, provide an opportunity for intromission.

This hypothesis relies on a series of assumptions and makes a series of predictions. All of these assumptions and predictions provide opportunities for empirical testing of the hypothesis. The primary issues are as follows. First, courting male snakes cover enough of the female's body during courtship to interfere with her breathing. If this assumption is falsified, the hypothesis cannot be valid. Second, males can expel a significant amount of air out of the female's lungs during courtship. The hypothesis relies on the males' ability to empty the female's lung, at

least partially. Third, courtship (or simulated courtship) increases the respiration rate of the courted snake. If respiration is disrupted by courtship, females removed from courting groups should breathe rapidly immediately afterward to compensate for their oxygen deprivation. If caudocephalic waves are the mechanism inducing this effect, then simulated courtship (anterior-directed pressure waves along the body) also should induce more rapid breathing. Fourth, anterior-directed pressure waves induce cloacal gaping. The mechanism we have suggested predicts that anterior-directed waves should induce stress (and, thus, cloacal gaping) more effectively than posterior-directed waves (because the latter would not force anoxic air onto the respiratory surface). Fifth, anterior-directed pressure waves facilitate copulation. If males achieve copulation by cloacal gaping of highly stressed females, then simulated caudocephalic waves directed to females in natural courting groups should expedite mating. Sixth, females display behaviors to prevent or terminate copulation. Perry-Richardson et al. (1990) described a distinctive behavior used by female checkered garter snakes (*Thamnophis marcianus*) to terminate copulation; they spun rapidly, and these axial rotations dislodged the hemipenis. If female *Thamnophis sirtalis* are reluctant participants in mating, they may display the same behavior.

Methods

Study Species and Area

The Interlake region of Manitoba, approximately 100 km north of Winnipeg, has a long and severely cold winter and a short, hot summer (Crews and Gartska 1982; Shine et al. 2001d). Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are abundant in this area and overwinter for about 8 mo each year in communal underground dens that may contain >20,000 snakes (Gregory 1974). The snakes court and mate near the dens before they disperse in early spring and migrate up to 20 km to their summer feeding ranges (Gregory and Stewart 1975). Approximately equal numbers of adult male and adult female snakes use each den, but males remain near the den for about 2 wk after emerging whereas females disperse within a few days (Gregory 1974; Shine et al. 2001c). The sex ratio around the den is thus highly male biased (sometimes more than 99% males), and each newly emerging female is immediately courted by dozens or hundreds of males (Whittier et al. 1985; Mason 1993; Shine et al. 2001c). Most unmated females near the den are almost completely covered by a writhing ball of courting males (see fig. 1). The females' ability to disperse from the den entrance is substantially impeded by these males (Shine et al. 2000c).

Both males and females require a day or two to recover

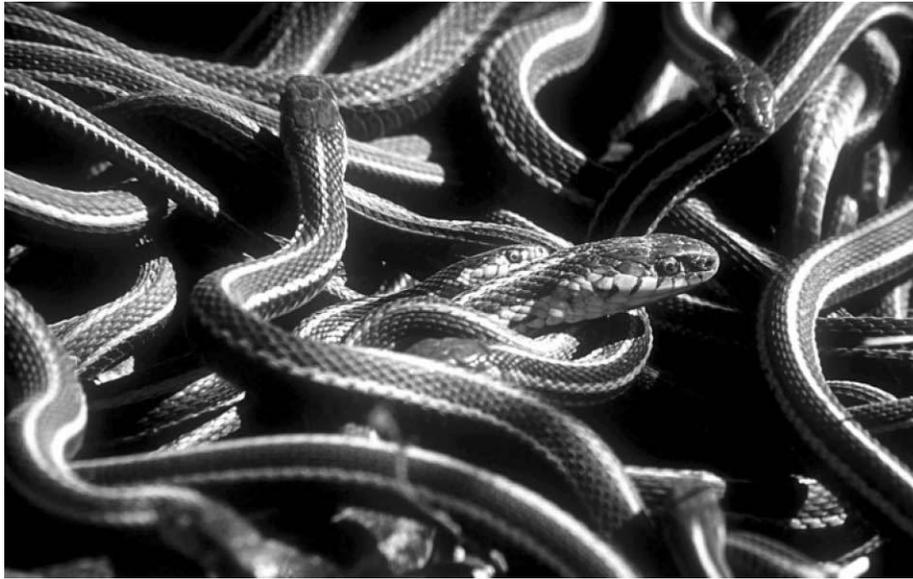


Figure 1: A mating ball of garter snakes (*Thamnophis sirtalis*) at a communal den near Inwood, Manitoba. The single large snake is a female, and the rest are males. See the online edition of the *American Naturalist* for additional color figures and video.

from their long period of winter inactivity and are weak and slow during that time (Shine et al. 2000*d*). In the period between emergence and recovery, most or all males produce female-like skin lipids and thus attract courtship from other males. These “she-males” may benefit because the presence of courting “he-males” provides heat and reduces vulnerability to predatory crows (Shine et al. 2001*a*). Female mimicry is a transient phase, with the animals reverting to he-male status for the duration of their residency at the den.

Courtship in red-sided garter snakes is similar to that seen in many other snake species (Carpenter and Ferguson 1977; Gillingham 1987; see fig. 1). Relying primarily on the vomeronasal system, the male identifies the sex of other snakes by chemoreception of skin lipids (Mason et al. 1987, 1989, 1990). He attempts to align his body with that of the female such that his cloaca is very close to hers and his body is draped along and above hers. Males are smaller than females in this species (in our population, adult males average about 47 cm snout-vent length [SVL], and adult females average 57 cm; Shine et al. 2000*a*), and, thus, the female’s head and forebody may often be unencumbered by courting males. Once he is in position on the female’s body, the male displays rhythmic contractions that pass anteriorly from the region of his cloaca toward his head. Such “caudocephalic waves” are a distinctive feature of courtship by males of many snake species (Noble 1937; Carpenter and Ferguson 1977).

During May 2002, we worked at a communal den con-

taining 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, including analyses of the strong sexual conflict within this mating system (Shine et al. 2000*c*).

Methods

The following methods were used to examine the assumptions and predictions posed in the introduction to this article.

Courting Males Cover Enough of the Female’s Body to Interfere with Her Breathing. To evaluate this assumption, we need data on the position of the vascular lung within the female’s body and the proportion of the female body covered by males in natural courtship balls. Data on lung position were obtained by dissection of snakes (25 females, 20 males) found dead in the field after predator attack. Sexual dimorphism in lung position was relatively minor, so the males provided additional data on lung sizes in small snakes. Each snake was opened with a midventral incision and the anterior-most and posterior-most positions of the vascular segment of the lung were recorded relative to the snake’s SVL. On a total of 68 natural courting groups found near the den, we scored the position of the head of the anterior-most male and the position of the cloaca of the posterior-most male, relative to the fe-

male's own SVL (measured immediately afterward), to quantify the length of the female's body on which courting males were applying pressure.

Males Can Expel a Significant Amount of Air from the Female's Lungs during Courtship. To measure the potential ability of courting males to push air out of the female's lungs by caudocephalic waving, we deeply anesthetized two large (63.0 and 69.5 cm SVL) females by intramuscular injection of brevitall sodium at 0.01 mL/g body mass. We used only two animals for ethical reasons to minimize potential suffering. Each was then intubated with a soft catheter (1.6 mm i.d., 2.4 mm o.d.) directly into the trachea through the glottis. At the beginning of each trial, we fully inflated the snake's lungs by forcing air down the tubing and then allowing air to be expelled until the pressure inside the lungs equilibrated with the outside air. The free end of tubing was then placed into a container of water where it was bent into a U shape, with the open end of the tubing directly below a graduated cylinder (the barrel of a 100-mL syringe). Thus, any air expelled from the snake's lungs was captured (and measured) in the syringe barrel. Calibration trials showed that after the lungs were artificially inflated, they reached a stationary volume soon after the female was laid out on flat ground near the middle of the den. The area had previously been cleared of snakes. Voluntary respiration by the anesthetized females occurred only rarely during the testing period and was easily detected and, thus, eliminated from the analysis.

After waiting 2 min to ensure that lung volumes were stable (no spontaneous exhalation or inhalation), we allowed courting males access to the anesthetized snake. Females were courted by an average of 20–30 males during the trials, and we recorded volumes of air expelled at 30-s intervals. A trial was stopped when no further air was expelled for 2 min. At this time, we pushed down firmly on the female's body and rolled a hand anteriorly to expel (and measure) all remaining air from the lung. Trials were discontinued after the females began to recover from anesthesia and recommence regular breathing.

Courtship (or Simulated Courtship) Increases Respiration Rates of the Courted Snakes. We quantified breathing rates (breaths/min) for 30 he-male, 30 she-male, and 40 female garter snakes under three conditions: in the den, where he-males were mate searching, whereas females and she-males were being courted; after 30 min without disturbance inside a clean cotton bag; and after being removed from a bag after a similar 30-min period and then stroked anteriorly across the dorsal surface to mimic caudocephalic waves during courtship (i.e., to push air inside the lungs anteriorly in the same way that occurs during courtship) for 2 min. For the "stroking" treatment, the snake was

held dorsal side uppermost with its neck lightly restrained between the observer's closed knees and with its tail held back toward the observer in one hand so that the animal was firmly stretched out. We used the fingers of the other hand to exert pressure against the snake's dorsal surface and moved from the cloacal area to the neck (approximately one stroke per second). After this treatment and the other treatments were concluded, respiration rates for the next 60 s were scored by watching overt movements of the snake's anterior lateral surface; thus, very slight shallow breaths may not have been detected. We tested he-males and she-males as well as females to ensure that any responses we detected were not female-specific motor patterns related to sexual receptivity.

Anterior-Directed Pressure Waves Induce Cloacal Gaping. If males obtain copulations because their caudocephalic waves induce cloacal gaping in females, mimicking these posterior-to-anterior waves might stimulate gaping also. The hypothesis that caudocephalic waves push anoxic air anteriorly suggests that equally vigorous stroking in the opposite direction would not be as effective in generating gaping by females. Thus, we used the same methods as above (i.e., after 30 min rest in a bag, the snakes were held stretched out) and stroked the animals in either an anterior or posterior direction. We recorded the number of strokes until the snake fully gaped the cloaca for at least one full second (i.e., such that a male would have had a clear opportunity to insert a hemipene). In practice, most snakes that gaped the cloaca kept it fully open for at least 10 s and often much longer. If a snake did not open its cloaca widely after 40 strokes, the trial was discontinued, and a score of 40 was used in the subsequent analysis.

Plausibly, the amount of stimulation (stress) required to elicit cloacal gaping might be affected by several aspects of a snake's phenotype (e.g., sex, body size, body temperature) as well as the nature of the stimulus (e.g., whether the pressure waves are applied in an anterior or posterior direction). Thus, we recorded all of these attributes and tested he-males and she-males as well as females. If the same behaviors are seen in all of these groups, the cloacal-gape response cannot be interpreted as a specific behavior related to female receptivity.

Anterior Pressure Waves Facilitate Copulation via Induction of Gaping. The remarkable tolerance of garter snakes of disturbance allows a more direct test of the hypothesis that caudocephalic waves enhance male mating success by stimulating cloacal gaping by females (and, thus, an opportunity for male intromission). When we located courting groups at the den, the observer sat down beside the group and gently pressed the female's forebody down against the ground so that she was unable to move away.

Courtship continued unabated in all cases. In half of the groups that were tested, the observer also stroked his fingers anteriorly along the female's dorsal surface to mimic strong caudocephalic waves. We then recorded whether the female gaped her cloaca and whether a copulation occurred within the following 3 min. After the trial, we measured the female's SVL and body temperature.

Females Display Behaviors to Prevent or Terminate Copulation. We videotaped courting groups in small outdoor arenas (Space Pop, Smash Enterprises, Melbourne; circular with 48-cm diameter, 56 cm deep). We added either four or 24 males plus one unmated female (with the female painted for individual recognition), filmed the animals for 10 min or until mating occurred, and examined the films to count the number of times that females rotated axially and whether these rotations coincided with intromission.

Throughout this study, we avoided pseudoreplication by using each snake in only a single trial. Data were analyzed using the software package Statview 5 (SAS Institute 1998) on an Apple Macintosh G4 computer. The text reports mean values ± 1 SE.

Results

Courting Males Cover Enough of the Female's Body to Interfere with Her Breathing

The anterior-most part of the vascular segment of the lung was located slightly closer to the snout in female than in male garter snakes ($16.3\% \pm 0.20\%$ vs. $17.8\% \pm 0.20\%$ of SVL, respectively; $F = 30.42$, $df = 1, 43$, $P < .0001$). The same pattern was evident but not statistically significant for the posterior-most point of the vascular segment ($27.6\% \pm 0.40\%$ vs. $28.5\% \pm 0.40\%$ of SVL, respectively; $F = 2.84$, $df = 1, 43$, $P = .10$; see fig. 2a).

Courting males covered most of the females' bodies in the majority of natural courting groups (fig. 2b). Males almost always had their cloacae immediately beside the female's so that the only significant variation in coverage involved the distance between the anterior-most male's head and that of the female. This distance (as a proportion of female SVL) was lower in larger females than in smaller animals (female SVL effect, standardized coefficient from multiple regression = 0.31 , $P < .008$) and was lower if fewer males were present in the courting group (coefficient = -0.38 , $P < .002$). In consequence, very large females sometimes had no males over the anterior part of the vascular segment of their lung, but for most females, males completely covered this part of the body (i.e., the head of the anterior-most male extended past the anterior limit of the vascular lung; fig. 2b).

Males Can Expel a Significant Amount of Air from the Female's Lungs during Courtship

Both anesthetized females recovered consciousness soon after the trials were terminated. Lung volumes at full inflation were higher in one snake than the other, but residual volumes after courtship were similar (around 15 mL; fig. 3). Measurements of the volumes of air at 30-s intervals revealed rapid expulsion by the activities of court-

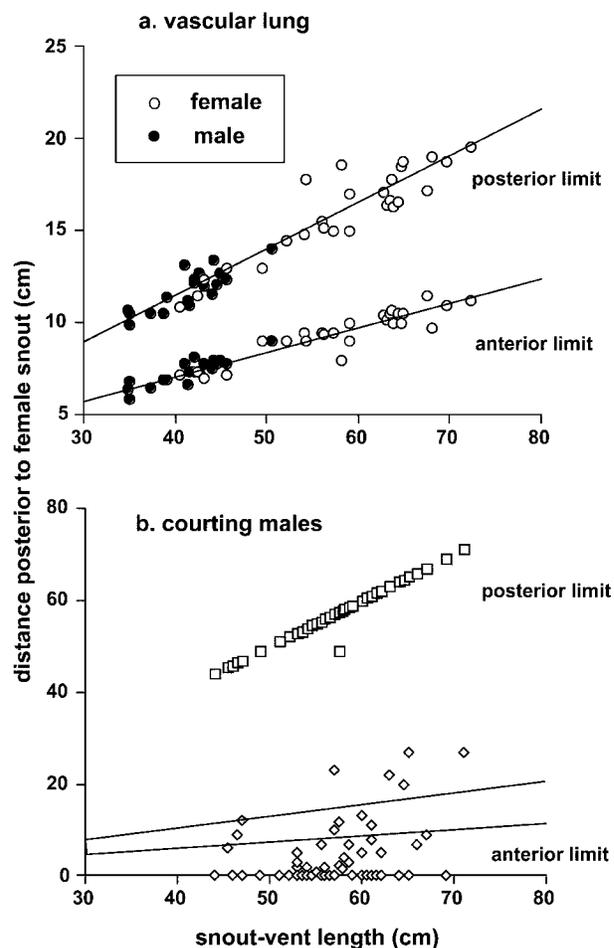


Figure 2: Position of the vascular segment of the lung within garter snakes (*Thamnophis sirtalis parietalis*) and the proportion of the female's body covered by males during natural courtship. *a*, Based on dissection of 25 females and 20 males and shows the distance anterior to the snake's snout at which the vascular lung begins and terminates. *b*, Positions on the bodies of 68 courting females corresponding to the head of the anterior-most courting male and the cloaca of the posterior-most courting male. The two lines show the anterior and posterior limits of the female's vascular lung (i.e., the regression lines fitted to the data in *a*). In most courting groups (especially for small females), males lie above most of the female's vascular lung (i.e., the anterior-most male's head was closer to the female's snout than was the anterior limit of her vascular lung).

ing males (fig. 3). Control trials without males revealed no depletion in lung volumes over equivalent periods.

*Courtship (or Simulated Courtship) Increases
Respiration Rates of the Courted Snakes*

Figure 4 shows that breathing rates of the snakes were significantly affected by our treatments. He-male snakes displayed relatively slow breathing rates both when collected at the den as they were searching for mates and after being held quiescent for 30 min. However, anterior-directed dorsal stroking substantially increased their rate of breathing (fig. 4; ANOVA, $F = 19.79$, $df = 2, 27$, $P < .0001$; Fisher's PLSD tests show that stroked snakes are higher than both other categories at $P < .05$). Females and she-males also showed slow breathing rates after a period of enforced quiescence, but their respiratory rates were much higher not only after stroking (as occurred for he-males) but also after being courted in the den (fig. 4; females ANOVA, $F = 13.83$, $df = 2, 37$, $P < .0001$; she-males ANOVA, $F = 7.94$, $df = 2, 27$, $P < .002$; in both cases, Fisher's PLSD tests show that stroked snakes were higher than both other categories at $P < .05$). These data are consistent with the hypothesis that courtship (and stroking designed to mimic the caudocephalic waves evident during courtship) induced respiratory distress and, hence, increased rates of breathing.

Anterior-Directed Pressure Waves Induce Cloacal Gaping

We recorded cloacal gaping in 91 of 106 females tested (86%), 69 of 101 he-males (68%), and 29 of 51 she-males (57%; $\chi^2 = 16.83$, $df = 2$, $P < .0002$). Reflecting this pattern, the mean number of strokes before cloacal gaping was highest in she-males, intermediate in he-males, and lowest in females (fig. 5). Analysis of the data in figure 5 with two-factor ANOVA showed that the number of strokes required to elicit gaping varied among the three groups of snakes ($F = 7.91$, $df = 2, 188$, $P < .001$; post hoc tests show that she-males were higher than either of the other groups at $P < .05$) and that anterior-directed strokes stimulated gaping sooner (i.e., with fewer strokes) than did posterior-directed stroking ($F = 8.22$, $df = 1, 188$, $P < .005$). There was no significant interaction between snake sex and stroke direction in this respect ($F = 1.10$, $df = 2, 188$, $P = .33$).

To evaluate the effects of body size and temperature as well as stroke direction, we conducted multiple logistic regression with whether the snake gaped its cloaca during the trial (i.e., after ≤ 40 strokes) as the dependent variable. Log-likelihood ratio tests on data for females indicated that the animal's response was not affected by its body length (SVL $\chi^2 = 0.12$, $df = 1$, $P = .73$) or body tem-

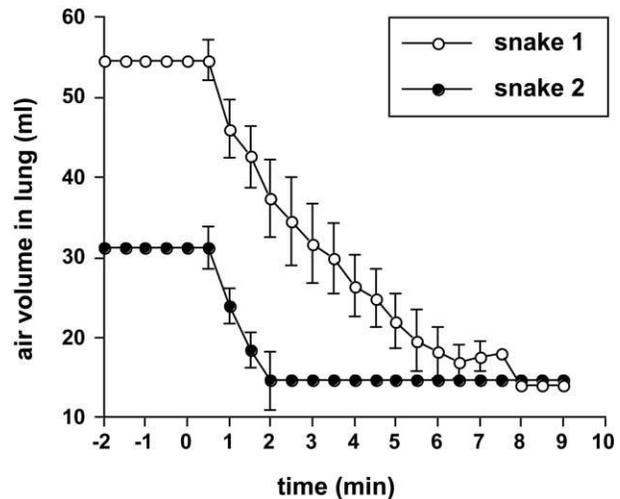


Figure 3: The volume of air remaining within the lungs of two anesthetized female garter snakes (*Thamnophis sirtalis parietalis*) as a function of the duration of time that they were courted by 20–30 male snakes. Data for snake 1 (upper line) are means ± 1 SE on the basis of five trials; data for snake 2 (lower line) are on the basis of four trials.

perature ($\chi^2 = 1.19$, $df = 1$, $P = .28$) but that anterior-directed strokes were more likely to stimulate cloacal gaping than were posterior-directed strokes (89.5% vs. 62.1%, $\chi^2 = 8.58$, $df = 1$, $P < .004$). He-males showed a different response pattern whereby body size was not important ($\chi^2 = 0.001$, $df = 1$, $P = .99$) but gaping was more likely if the snake was colder rather than warmer (mean body temperatures of gapers vs. nongapers = 9.3° vs. 14.6°C , $\chi^2 = 21.81$, $df = 1$, $P < .0001$) and if the stroking was directed anteriorly rather than posteriorly (74.0% vs. 52.5%, $\chi^2 = 12.46$, $df = 1$, $P < .0005$). Last, she-males gaped their cloacae less frequently than did the other groups, with no effect of body size on this response (SVL $\chi^2 = 0.09$, $df = 1$, $P = .77$). Colder she-males were more likely to gape than were warmer snakes (mean body temperatures 14.0° vs. 18.8°C , $\chi^2 = 5.15$, $df = 1$, $P < .03$). Unlike the other two groups, however, she-males were not significantly more likely to gape if stroked anteriorly rather than posteriorly (42.3% vs. 36.4%, $\chi^2 = 1.11$, $df = 1$, $P = .29$).

*Anterior Pressure Waves Facilitate Copulation
via Induction of Gaping*

We conducted trials on 30 courting groups; 15 involved holding the female immobile, and the other 15 also involved stroking the female's dorsal surface in an anterior direction. Cloacal gaping by the female occurred in nine of the 15 trials with stroking and none of the 15 trials

without stroking. Intromission occurred within 3 min in six of the nine trials in which females gaped their cloacae but not in any of the other trials. Log-likelihood ratio tests from a multiple logistic regression showed that whether mating occurred was not affected by the female's body length ($\chi^2 = 1.58$, $df = 1$, $P = .21$) or body temperature ($\chi^2 = 1.20$, $df = 1$, $P = .27$) but was more likely to occur if the female was stroked anteriorly rather than simply held immobile ($\chi^2 = 9.50$, $df = 1$, $P < .003$).

*Females Display Behaviors to Prevent
or Terminate Copulation*

Courted females displayed axial rotation frequently (83 times in 104 courtship trials). Thirty-nine of these cases occurred without effective intromission, although sometimes a male was connected very briefly but dislodged as the female spun her body. Of these 39 cases, the female spun only once in 24 trials, twice in 13 trials, and four and six times in two other trials. Another 44 axial rotations occurred almost simultaneously with effective intromission. Only one copulation was not immediately (<1 s) either preceded or followed by a rapid axial rotation by the female. Some rotations by the female preceded (and indeed may have facilitated) intromission, whereas others appear to have been an immediate response to hemipenis insertion.

Discussion

Male garter snakes are much smaller than conspecific females and display no overt aggression during courtship. Intuition and previous studies suggest that it would be impossible for these animals to forcibly inseminate females. Nonetheless, they clearly do so. The males elicit a stress response from the female and thereby induce cloacal gaping and gain an opportunity to intromit. Our data support all of the predictions of the "hypoxic stress" hypothesis in terms of the mechanisms (anterior-directed waves induce respiratory distress and cloacal gaping), consequences (gaping leads to copulation), and female responses (frequent axial rotation immediately post-intromission, a behavior previously identified as a female tactic to terminate copulation). Most convincing are the experiments where we induced rapid mating within natural courting groups by manually simulating caudocephalic waves along the female's body.

This conclusion runs directly counter to conventional interpretations of snake courtship. Although a minority of workers have suggested that males may play an active role in opening the female's cloaca (Pisani 1976; Crews and Gartska 1982; Hardy 1998), the firm consensus has been that courtship functions to excite the female and make

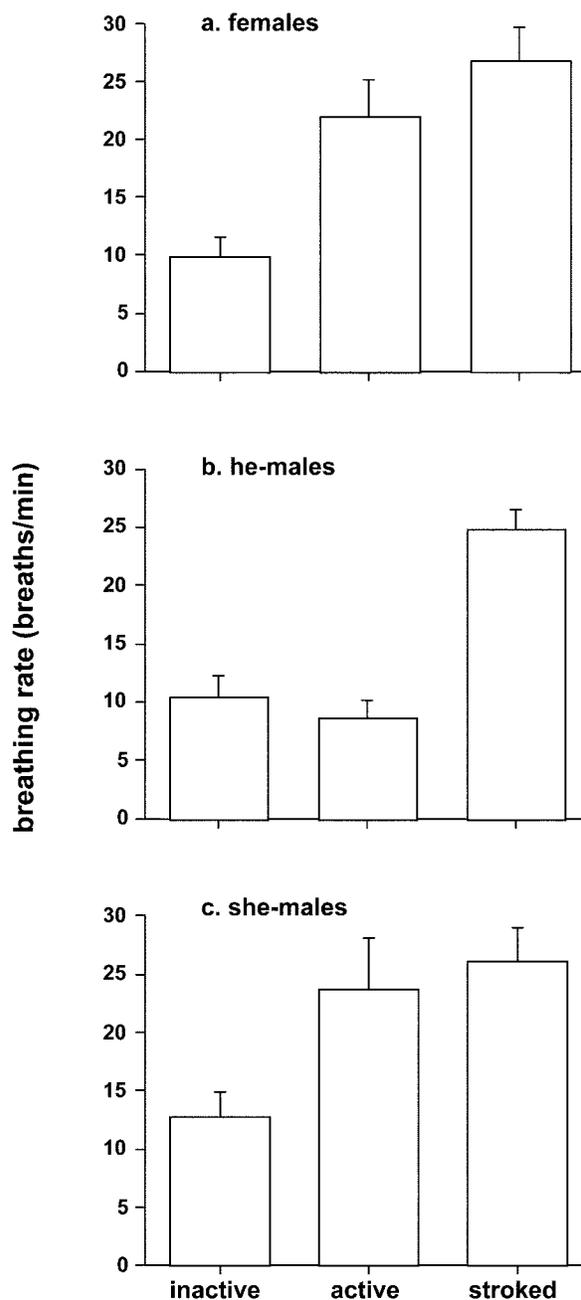


Figure 4: Breathing rates (breaths/min) for garter snakes (*Thamnophis sirtalis parietalis*) as a function of their activity before measurement. Females (a) were inactive (held inside a bag for 30 min) before scoring or collected at the den after being courted ("active") or stroked anteriorly by hand along the dorsal surface to mimic the caudocephalic waves by males that are a distinctive feature of courtship in this species. For he-males (b), the "active" snakes were mate-searching in the den area when collected. For she-males (female mimic; c), the "active" animals were collected while being courted in the den. Histograms show mean \pm 1 SE. See text for statistical analysis of these data.

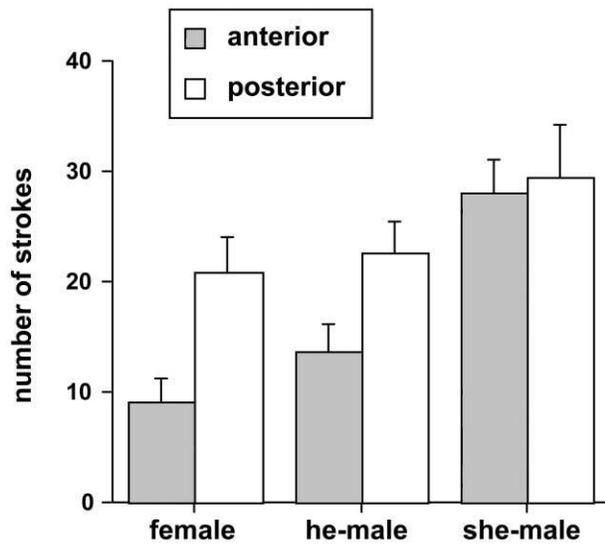


Figure 5: The number of strokes applied to the dorsal surfaces of garter snakes (*Thamnophis sirtalis parietalis*) required to initiate cloacal gaping by the snakes. Trials terminated after 40 strokes, and any snake not gaping by that time was accorded a score of 40. Data are shown separately for female, he-male, and she-male (female mimic) snakes and for trials in which the stroking was applied in an anterior versus posterior direction along the snake's body. Histograms show mean ± 1 SE. See text for statistical analysis of these data.

her more receptive to mating (e.g., Gillingham 1979, 1987; Gillingham et al. 1983; Greene 1997). This latter scenario is not consistent with our data. The fact that respiratory distress and cloacal gaping occur in response to anterior-directed pressure waves in males as well as females, and in snakes collected and manipulated by us as well as those in natural courting groups, means that these behaviors cannot be viewed as a specific component of female sexual receptivity. Indeed, cloacal gaping and defecation in response to predator attack is extremely widespread not only among snakes but also among their sister group, the lizards (Greene 1988). Thus, the co-option of this response by males during courtship reflects exploitation of a preexisting response that has occurred in the evolution of several other sexually selected morphologies and behaviors (Ryan et al. 1990; Andersson 1994).

Are our data consistent with the alternative hypothesis that females resist courtship in order to obtain a fitness benefit through mating only with the strongest, most vigorous males? This latter hypothesis assumes that such males are genetically superior and will transfer these traits to their offspring. In passing, we note that there are no data to show such a link; the two phenotypic predictors of male mating success in this system (male body size and body condition; Shine et al. 2000a) change rapidly through

time in individual males (Shine et al. 2001c, 2001d) and, hence, are unlikely to have a strong genetic basis. Although the “forcible insemination” and “resistance as a female ploy” hypotheses make many similar predictions, they differ in important respects, and in each case our data support the former rather than the latter.

Courtship imposes significant stress on a female and substantially increases the risk of her injury or death. A female could test male vigor in many ways that would not threaten her own welfare, whereas the forcible insemination hypothesis relies on significant stress to the female. If male tactics are so stressful that females thereby are killed, the hypothesis that females gain fitness by resisting copulatory attempts is strongly falsified. Not only are female garter snakes under hypoxic stress during courtship (this article), but also many die of suffocation at this time (Shine et al. 2001b). These deaths are inconsistent with the view of female resistance as an adaptation to maximize female fitness.

Males copulate with conspecifics that obtain no fitness benefit from that mating. Reproductive females are the only animals that can gain in fitness from copulating with especially “good” males. If copulation requires female cooperation, we would not expect to see mating by other groups within the population. In fact, male garter snakes copulate with all adult-size females (fig. 2 in Shine et al. 2000c) despite the fact that about half of them will not breed in the current year (Gregory 1974), with juvenile females far too small to produce offspring (Shine et al. 2000c), and even occasionally with weak or sick she-males (Pfreder et al. 2001). These animals do not derive any genetic benefit from mating.

Females do not have the opportunity to select mates on the basis of phenotypic traits. The massive assemblages of garter snakes in Manitoba rarely provide such an opportunity. Many matings occur in the den itself, with the female buried beneath literally hundreds of courting males (see fig. 1); it is inconceivable that a female can control which male inserts his hemipenis from among the dozens of male snakes with their tailbases < 2 cm from her own, all of them racing to intromit as soon as she gapes her cloaca. Female choice among potential partners seems more feasible in smaller groups of courting snakes, but video analysis shows that the successful male often is not in contact with any part of the female other than her tail (Shine et al. 2003a). Female assessment among the phenotypes of competing males is simply not possible within this system.

Stress, per se, without any of the cues usually associated with courtship, stimulates the female to behave in a way that facilitates intromission. We induced cloacal gaping in a highly artificial stressful situation (i.e., manually stroking a captive solitary female) without any of the stimulatory

cues associated with normal courtship. Thus, the female's "receptive" behavior is elicited by stress, with no cues whatsoever about male phenotypes.

The stress response that allows intromission is exhibited by males as well as females. The fact that males showed the same cloacal gaping response to stress further erodes the idea that this behavior is part of some female-specific suite of adaptations that has evolved to optimize mate quality.

Our data also clarify some ambiguities in snake courtship. For example, a review by Gillingham (1987, p. 191) concluded that "Although some authors have speculated that copulatory adjustment is brought about by the male through the use of hemipenial spines to lift the female's cloacal scales, with little or no female participation ... it is now well-established that female cloacal gaping is necessary for intromission." The observation of copulation with dead females shows that this is not strictly true, but available evidence suggests that a live female is capable of preventing copulation by holding her cloaca firmly closed (Hardy 1998; Shine et al. 2000*b*). The issues have usually been framed in terms of whether a male can force a copulation versus whether a female needs to cooperate. Our data show that this is a false dichotomy because a male can obtain a mating not by forcing the cloaca open against a female's muscular resistance (which may well be impossible) but instead by inducing a female to gape her cloaca because of hypoxic stress. Hence, active cloacal gaping does not imply female cooperation in mating.

Although caudocephalic waves are a distinctive and phylogenetically widespread component of courtship in many snake species, the function of this behavior has been obscure. Caudocephalic waves may have multiple functions as suggested by subtle variations among taxa in the exact form and frequency of waving. Indeed, closely related species (and, in at least one case, populations within a single species) may differ in whether courtship includes caudocephalic waving at all (Gillingham 1979; Perry-Richardson et al. 1990; Ford 1996). Caudocephalic waves may have evolved originally for functions such as allowing the male to check that his lower body is aligned with the female rather than with the bodies of other males that are part of the same courting group; the resistance to pressure waves is likely to differ between the (large) female and the (smaller) males. Also, because the waves are applied to the female's lateral surfaces as well as her dorsum, they may tend to push her slightly off balance and facilitate the male's attempts to wedge his hindbody underneath hers to allow close cloacal apposition. Advantages such as these may have favored the initial evolution of caudocephalic waving during courtship, with the incidental consequence that a few females were hypoxically stressed enough to gape their cloacae. Sexual selection could then favor more

vigorous and effective air expulsion through modifications of the form, frequency, and intensity of waving behavior.

Under the "hypoxic stress" scenario, we would expect an arms race between the sexes. First, males would evolve courtship behaviors that more effectively elicit cloacal gaping by the female. Second, assuming that females experience some cost from forced copulations (perhaps relating to the consequent reduction in potential for female choice among alternative mates), females could evolve attributes of morphology, physiology, and behavior that conferred resistance against these male courtship tactics. Several authors have reported female traits that might function in this way, ranging from direct retaliation by biting males and tail wriggling or body spinning to prevent or interrupt intromission (Carpenter and Ferguson 1977; Gillingham et al. 1983; Perry-Richardson et al. 1990) to cloacal pheromones that discourage male courtship (Greene and Mason 2003). Part of the wide diversity in courtship behaviors among snakes (Carpenter and Ferguson 1977) might reflect such arms races between the sexes.

Our own study provides a possible example of this phenomenon that involves the "third sex" present at garter snake dens in Manitoba. She-male (female-mimicking male) garter snakes benefit from attracting courtship from other males (because of thermal and antipredator advantages; Shine et al. 2001*a*) but generally do not allow other males to copulate with them. We have recorded only one such copulation, into a male too weak to resist intromission (Pfrender et al. 2001). The large gelatinous mating plug occluded this male's gastrointestinal tract and distended his hindbody so much that it may have impeded sperm transfer through the efferent ducts running from his testes to the hemipenes (R. Shine, personal observation). Also, copulation might be physically injurious to the cloacal region in males. Thus, we expect that she-males are under strong selection to resist insemination. In keeping with this prediction, she-males were more reluctant to gape their cloacae than were either he-males or females (fig. 5).

Our data are based on a single population of snakes, and further studies will be needed to establish the generality (or lack thereof) of our hypoxic stress hypothesis. As noted, snakes display considerable interspecific variation in courtship behavior. Part of this variation may relate to alternative mechanisms of obtaining forced copulations and part to ritualized "persuasion" of females. Our hypothesis makes several predictions that are consistent with available data. For example, we would not expect to see vigorous caudocephalic waving during courtship in species that do not gape their cloacae in response to hypoxic stress (prediction supported in *Thamnophis marcianus* [Perry-Richardson et al. 1990] and *Vipera xanthina* [Murphy and Barker 1980]) or in highly aquatic taxa, in which adap-

tations for underwater activity enable females to withstand long periods of apnea without stress. In keeping with this prediction, courtship in laticaudid sea snakes *Laticauda colubrina* involves episodic twitches rather than caudocephalic waves (Shetty and Shine 2002), male queen snakes *Regina septemvittata* bounce their forebodies on the female rather than using caudocephalic waves (Ford 1982), and male turtle-headed sea snakes *Emydocephalus annulatus* have a specialized rostral projection to prod the female during courtship (Guinea 1996). We would also not expect to see caudocephalic waving in legless lizards, which have very different lung anatomy from snakes despite their external morphological resemblance. Caudocephalic waves have not been reported during courtship in such animals (Carpenter and Ferguson 1977). Clearly, enough variation exists in courtship behavior within snakes to provide robust empirical tests of our hypothesis. Species that display caudocephalic waves in some populations but not others (e.g., *Thamnophis radix*; Ford 1996) provide exceptional opportunities in this respect.

More generally, how widely will our hypothesis apply to organisms other than snakes? The hypoxic stress hypothesis relies on specific features of snake anatomy (the nonrespiratory sacculus lung, anoxia-induced quiescence, the common cloacal outlet for excretion and reproduction). Thus, organisms that lack these specific features will not evolve identical mechanisms for inducing female receptivity. Nonetheless, the broader idea that features of anatomy and physiology in specific groups will influence mating tactics by males, including forcible insemination, is likely to be valid. For example, some crustaceans can mate only when the female has recently molted and, thus, has a soft exoskeleton. Males thus focus their courtship activities on newly molted females and in some species may stimulate female molting with pheromonal cues (Cowan and Atema 1990). Prolonged underwater courtship and female sequestration in organisms as diverse as dolphins (Shane et al. 1986; Connor et al. 2001) and ducks (Davis 2002) may function in very similar ways to the garter snake system, with males impeding female attempts to breathe such that the consequent hypoxic stress reduces female resistance to copulation.

Induction of hypoxic stress may explain some puzzling features of male-male as well as male-female interactions. Many snake species display male-male combat that typically involves males intertwining their posterior bodies with those of their rivals (Carpenter 1986; Shine 1994; Schuett et al. 2001). This behavior has generally been interpreted as a highly ritualized test of strength, with success going to the larger male. Instead, it may rely on the stronger snake impairing respiration by his rival because of the compression of the sacculus lung in the same fashion that we have suggested for courtship. Schuett and Grober's

(2000) observation that blood lactate levels were higher in losers of such contests than in winners fits well with this interpretation. Schuett and Grober noted that losers were less active than winners during combat, and, thus, their higher lactate levels could not be attributed to exertion. They invoked a complex stress response to explain their data, but it seems more parsimonious to infer that the shift to anaerobiosis reflected impairment of aerobic respiration of the vanquished animal in the course of the combat bout.

If the physiological mechanisms underlying success in male-male combat are the same as those in courtship, adaptations for one function could enhance a male's ability in the other. If so, we might expect a correlation between the occurrence of combat and the form of courtship. Supporting this prediction, males of many snake species with male-male combat wrap tightly around the posterior part of the female's body during courtship (Tolson and Henderson 1993; Schuett et al. 2001). More generally, adaptations that arise in one social context (either male-male combat or male-female courtship) can influence the feasibility of alternative tactics in the other context. Correlations between male tactics in these two kinds of behavior might thus be usefully examined in snakes as well as other kinds of organisms.

The mating behavior of garter snakes has been described by many authors over a very long period of time, and throughout this period, male tactics universally have been interpreted in terms of stimulating the female to sexual receptivity (e.g., Noble 1937; Blanchard and Blanchard 1941; Pisani 1976; Carpenter and Ferguson 1977). Our study provides a very different interpretation of dynamics and male-female interactions during courtship. Reproductive behaviors and mating systems in other kinds of snakes also warrant reanalysis, in light of the possibility of forcible insemination. For example, the use of hindlimb remnants (spurs) by male pythons may not "excite" the female (Ross and Marzec 1990) so much as torment her and thus elicit cloacal gaping. The same may be true for many other male courtship behaviors. The possibility of coercive matings also might affect both the times and places where mating occurs; for example, laticaudid sea snakes mate mostly on land, where females are relatively helpless and unable to escape from courting males (Shine and Shetty 2001; Shetty and Shine 2002), and in the hydrophiid sea snake *Aipysurus laevis*, courtship often occurs in shallow reef areas on a falling tide, again minimizing female ability to escape (Lynch 1999). Although genetic benefits to multiple mating have been documented in some snake populations (Madsen et al. 1992), multiple matings do not enhance female fitness in other populations of the same species (Luiselli 1993) and might instead reflect coercive insemination. Thus, the functional significance of

multiple matings by females may vary even among con-specific populations. Our study also has obvious implications for attempts to understand the causes of individual variation in male mating success and the phenotypic correlates of such fitness variation.

The most general message from our study is that males may obtain matings from uncooperative females by relatively subtle means without overt displays of aggression or physical manipulation. Thus, intuition provides an unreliable basis for inferring whether courtship involves an element of coercion. We do not doubt that forcible insemination is truly impossible in many kinds of organisms, but we suggest that researchers should consider the possibility carefully before dismissing it. For example, males of many insect species emit pheromones that enhance sexual receptivity (reviewed by Andersson 1994). It is easy to imagine that the mechanism of this effect, especially where pheromones are derived from food plant alkaloids (e.g., Conner et al. 1981) might involve some kind of overall stress to the female rather than a specific modification of female behaviors related to sexual receptivity. Indeed, many behaviors of courting males may be stressful to females, and “sexual competition often involves one or another form of psychological warfare” (Ghiselin 1974, p. 189).

The reality may be that “coercive” and “cooperative” matings represent the ends of a continuum, not a simple dichotomy. In the most extreme cases, males simply seize females and intromit by sheer force. Slightly less extreme are cases where the male somehow stresses the female so she ceases resisting. Even further along this continuum is the situation that we have described in garter snakes, whereby males stress the female such that she responds in a way that facilitates copulation. Still further, male courtship may simply involve so high a cost to females in terms of energy balance (cessation of feeding) or risk (attracting predators) that selection favors female cooperation in response to harassment. Attempts to understand the functional basis of courtship behaviors should consider the possibility that subtle forms of sexual coercion may be much more common than is currently believed to be the case.

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