Battle of the sexes: forcibly inseminating male garter snakes target courtship to more vulnerable females

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In communal dens of garter snakes, *Thamnophis sirtalis*, in Manitoba, males obtain copulations forcibly, by inducing hypoxic stress in females. Females emerging from their 8-month winter inactivity are weak and slow, but recover strength and speed within a day or two of emergence. Thus, males may benefit by targeting newly emerged females that are too weak to resist, and by courting females under conditions that maximize the male's physical advantage. Fieldwork at a Manitoba den supported these predictions. Both in the field and in outdoor enclosures, males focused courtship on to newly emerged (weak) rather than dispersing (postrecovery) females. Experimental trials showed that males based this choice on female skin lipids (pheromones) that predict time since emergence, rather than correlates of recent emergence that reflect female physiological state per se (low body temperature, low resistance to hypoxia, high breathing rates during courtship). Male superiority in locomotor speed was maximal at high temperatures, and males targeted courtship to hotter females. The postemergence recovery of females in this system substantially shifts the balance of power in physical encounters between males and females, and provides a fitness benefit to male ability to recognize and exploit more vulnerable females. Male ability to discern and exploit differentially vulnerable females is likely to be widespread, but less overt, in many other populations.

Although the transfer of sperm between males and females is critical to reproductive success in both sexes of all sexually reproducing animal species, the sexes often differ in the optimal timing and frequency of such transfers (Trivers 1972; Parker 1979). Thus, although traditional analyses of mating systems have tacitly assumed a largely cooperative interaction between males and females, recent work suggests that the sexes may often be in substantial conflict (Alonzo & Warner 2000; Rowe & Arnqvist 2002; Chapman et al. 2003). In such a situation, either sex may evolve reproductive behaviours that exploit vulnerabilities in the other sex. For example, mate recognition signals of females may evolve to be more cryptic, thus making it difficult for the male to recognize a female as a potential mate (Andres & Arnqvist 2001; Sirot et al. 2003), or males may evolve to select mating territories that control access to resources that females require for reproduction (West-Eberhard et al. 1987; Eggert & Guyetant 2003).

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Forcible insemination provides the most dramatic manifestation of sexual conflict. Males of several animal species have been reported to copulate forcibly, sometimes inflicting severe injuries to females in the process (Shane et al. 1986; LeBoeuf & Mesnick 1990; Smuts & Smuts 1993; Sakaluk et al. 1995). However, recent studies on snakes show that forcible insemination can occur even without overt violence. The superficially benign courtship behaviours of male red-sided garter snakes, *Thamnophis sirtalis parietalis* (lying above or beside the female's body, with rhythmic caudocephalic waves of muscular contraction) impede the female's respiration, induce hypoxic stress, and thus stimulate the cloacal gaping that provides an opportunity for intromission (Shine et al. 2003a). In such a mating system, males may benefit by targeting courtship to the most vulnerable females: that is, those in which hypoxic stress could be induced most easily. Garter snakes at large communal dens in the Canadian prairies provide an ideal system with which to test this prediction, because there is a great range in female vulnerability. Snakes emerging from their 8-month period of winter inactivity are weak and slow, but recover locomotor ability within a day or two of emergence (Shine et al.

2000a, 2001c). Thus, male snakes have a choice between potential courtship targets that are weak and slow (and presumably less able to resist) versus others that are stronger and faster (and thus better able to resist). In such a case, we might expect males to court the more vulnerable (newly emerged) females.

To test this prediction, we gathered data on male mate choice criteria as well as on associated variables relevant to female vulnerability (locomotor performance, body temperatures) of garter snakes near a communal den in Manitoba. These data allowed us to identify the circumstances that would maximize a male's physical superiority over a female (and hence facilitate forcible insemination), and thus to see whether or not males focus courtship based upon cues that predict female vulnerability.

METHODS

Study Species and Area

We studied garter snakes near the northern limit of their geographical range in the Interlake region north of Winnipeg, Manitoba, in central Canada (Rossman et al. 1996). These small (<1 m total length) nonvenomous snakes spend about 8 months per year inactive in communal winter dens, emerging in early May to court and mate before dispersing to feed and give birth in the surrounding swamps and grasslands (Gregory 1974, 1977; Gregory & Stewart 1975). Because dens may contain more than 10 000 snakes, densities of snakes close to the den may exceed 100/m² (Shine et al. 2001a). Newly emerging females are rapidly located and vigorously courted by dozens or hundreds of males. However, radiotelemetric monitoring indicates that many females disperse tens of metres before mating, and most courting groups away from the den centre are relatively small (mean about 4 males/female: Shine et al. 2001a).

Courtship in *T. s. parietalis* has been described by many authors (Noble 1937; Blanchard & Blanchard 1941; Crews & Gartska 1982; Whittier et al. 1985). Skin lipids on females serve as sex pheromones, enabling males to locate females using the vomeronasal system (Mason 1993). The male aligns its body with that of the female, pressing its chin against her dorsal surface and its cloaca firmly next to hers. Larger males may push the tails of their smaller rivals out of the way (Luiselli 1996; Shine et al. 2000d). The most distinctive courtship tactic by males involves caudocephalic waving, a series of muscular contractions that travel from the male's cloacal area to his head (Noble 1937; Gillingham 1987). These waves push anoxic air from the female's avascular lung anteriorly to her respiratory surfaces, thus impeding breathing and inducing the stress response of cloacal gaping: this latter behaviour by the female allows intromission of the male's hemipenis (Shine et al. 2003a).

Methods

During May 2003 and May 2004 we worked at a communal den containing more than 50 000 snakes 1.5 km north of the town of Inwood, 250 m east of Highway 17 in central southern Manitoba (50°31.58′N, 97°29.71′W). This den has been the focus of considerable previous research (e.g. Shine et al. 2000a, b, c, 2001b). In both 2003 and 2004, our studies encompassed most of the snake's emergence period that year. At the beginning of our studies each year few snakes had emerged; by the end, most had dispersed. For the experiments described below, we used each individual animal in only a single trial, after which it was measured and released back at the den. Given that the den contained more than 50 000 animals, inadvertent reuse of the same individual in more than one trial would have been very unlikely.

The study was conducted under the authority of the Oregon State University Institutional Animal Care and Use Committee.

Locomotor Speeds

Snakes were collected at the den or from the woodland 100 m away, placed individually in numbered cloth bags, and brought to a range of temperatures from 7 to 35°C by placing the bags either inside a cooled, insulated container or exposing the bags to sunlight. We ran locomotor trials by placing the snake at one end of an open-topped (U-shaped) 1.4-m-long wooden raceway. The rough wooden floor provided traction for the snakes, and walls 12.5 cm high encouraged snakes to travel along the raceway rather than climbing out. We gently tapped snakes on the tail with a leafy twig to keep them moving. We recorded cloacal temperatures before each trial, and the times (by electronic stopwatch) at which the snakes crossed marks made at 0, 40, 80 and 120 cm on the floor of the raceway. We also recorded any stops or reversals. Each snake was run five times in quick succession, then rebagged for later measurement, after which it was released. Because each snake was used for tests at only one temperature, these trials used a total of 169 animals. Our statistical analyses were based on the mean and maximum speeds for each snake for the 40-cm segments (3 segments × 5 runs; thus, $N = 15$) over which its speed was measured.

Is Courtship Targeted to Newly Emerged Females?

Because newly emerged females are relatively weak, cold and slow (Shine et al. 2000a; Shine & Mason 2001; and see below), we predicted that males (1) might find it easier to force copulations with them and hence (2) might focus courtship on newly emerged animals rather than females that were dispersing (i.e. had emerged at least 24 h previously). To test these predictions, we set up open-topped arenas with nylon walls (1 × 1 m and 0.8 m high) in an open grassy area near the Inwood den. We placed 12 males (recently collected at the den) in each arena, then added two unmated adult females. Their unmated status was assessed by the absence of cloacal (mating) plugs (Crews & Gartska 1982; Shine et al. 2000c). One of these females was taken from the den (a recent emerger) whereas the other was taken from the woodland 100 m away

(a disperser; lack of muddy scales indicates that such a female has been out for at least a day, rather than being an unusually rapidly dispersing animal captured on her first foray out from the den). The females were marked with nontoxic paint that wore off within 24 h. We recorded the numbers of males courting each female at 5-min intervals for the next 30 min (continuous courtship for more than 30 min is very common in natural courting groups: Shine & Mason 2001). These scores were summed for each female and divided by the number of observations to yield a mean courtship score per female. We terminated trials as soon as a mating occurred, and recorded which female had mated.

To see whether the same effect occurred in free-ranging snakes, we collected newly emerged females and held them at our field laboratory for 3 days under one of two treatments (randomly allocated) as follows. Some of the females were kept in cloth bags in a cool (8 °C) dark basement, similar to conditions underground in the den. The others were kept in the basement at night, but taken outside every morning and placed in open-topped nylon arenas where they could sun-bask, drink and move around. After 3 days we marked these two groups of females as above, released them simultaneously in the den, and 30 min later recorded the numbers of males courting each marked female.

Because these trials showed that males preferentially court newly emerged females, we examined the cues used for this selectivity. Potentially, males might assess female vulnerability to forcible insemination directly, or instead use traits correlated with time since emergence (i.e. features in which newly emerged females differ from postrecovery females). Such traits include lower body temperatures (Shine & Mason 2001), distinctive pheromonal (skin lipid) profiles (M. LeMaster, personal communication), and lower ability to maintain effective respiration if exposed to caudocephalic waves (Shine et al. 2003a). Thus, we examined whether males targeted courtship based on the following factors.

(1) Female body temperature. To test this factor, we offered males in outdoor arenas a choice between a hot and a cold female. These small elongate animals warm up and cool so quickly that we could not simply modify female temperatures before the trial; the thermal disparity was abolished almost as soon as courtship commenced. Thus, we generated 'cool' females (mean body temperature $\pm$ SD = 19.38 $\pm$ 2.74 °C, $N = 8$) by taping the animal's ventral midbody to a refrigerated 'cooler brick' (15 × 8 × 2 mm); the 'warm' female (29.25 $\pm$ 2.22 °C, $N = 8$; $F_{1,14} = 7.85$, $P < 0.015$) was taped to a similar-sized block that had not been cooled. This procedure did not cause any overt distress (struggling, etc.). We then scored the numbers of males courting each female at 5-min intervals over the next 20 min.

(2) Skin lipids. Paper towels soaked in hexane were rubbed twice in an anterior to posterior direction along the bodies of each of six recently emerged and six dispersing (postrecovery) females, less than 10 min after the females were collected. The towels were laid out in random order on the floor of the den, and responses of the first 10 males to encounter each paper towel were recorded (no interest; tongue flicking; or tongue flicking plus adpressing the chin). Analysis was based on the relative numbers of males showing these different responses.

(3) Resistance to caudocephalic waving. Males might be able to assess the physiological state of individual females, especially their ability to resist anterior-directed pressure waves. If so, courtship should be more intense to females that are less able to resist such pressure. To test this idea, we held females (all collected as recent-emergers less than 60 min earlier, and thus presumably similar in pheromone profiles) and stroked their dorsal surfaces in a posterior to anterior direction with a finger. We recorded the number of strokes (up to a maximum of 20) required to elicit cloacal gaping, and then recorded the intensity of courtship that these females attracted when they were added to arenas containing a single male. We also recorded the duration of courtship (up to a maximum of 60 min) prior to copulation, to test the assumption that resistance to our manipulation provides a valid index of a courted female's ability to resist hypoxia. As in all of our other experiments, the animals were released at their point of capture as soon as trials and measurements had been concluded.

(4) Respiratory rates. Because forcible insemination in these snakes impairs female respiration, courted females breathe rapidly (Shine et al. 2003a). Thus, males might concentrate their efforts on females that rapidly increase breathing rates when courted. We tested this idea by tracheally intubating a freshly predator-killed female and using a 50-ml syringe to inflate and deflate her lungs either rapidly (60 cycles/min, simulating respiratory distress) or slowly (6 cycles/min, simulating normal respiration). Because we had noticed that any movements by a courted female tend to increase male courtship intensity, we included two other treatments as controls: vigorously wriggling either the anterior or posterior end of the female's body. In each case we allowed about six males to align with the female's body and then scored whether courtship intensity (rate and amplitude of tail searching and caudocephalic waving: see Shine et al. 2003b) by a focal male increased, decreased or remained constant in a 10-s period immediately after the treatment was applied. In practice, this change in intensity was easier to score unambiguously than were measurements of absolute rates of courtship activities.

RESULTS

Locomotor Speeds

Neither of the variables we scored (maximum or mean speed) was significantly correlated with snake body size within any of the groups (for both snout–vent length, SVL, and mass, all $P > 0.14$). Thus, we did not incorporate body size as a covariate in our analyses. However, body temperature significantly affected both speed variables in all groups, and thus was retained as a covariate in ANCOVAs with sex and emergence category as factors, and speed as the dependent variable. These ANCOVAs revealed strong main effects, but also significant interactions. The rate at which both maximum and mean speed increased

with temperature differed between the groups (maximum speed: $F_{4,136} = 3.07$, $P < 0.02$; mean speed: $F_{4,136} = 4.22$, $P < 0.004$), primarily because higher temperatures greatly enhanced performance of snakes that had been out of hibernation for some time (especially den males) but had less effect on the mobility of newly emerged snakes of either sex (Fig. 1). Thus, the locomotor disparity between groups was greatest at higher temperatures. Despite these significant interaction effects, differences in mean values between the groups were so clear-cut that main effects are still interpretable (Fig. 1). Speeds differed between the groups (maximum speed: $F_{4,140} = 12.19$, $P < 0.0001$; mean speed: $F_{4,140} = 21.82$, $P < 0.0001$). Inspection shows that den males were fastest, followed by males in the aspen woodlands and dispersing females (the two latter groups were not significantly different from each other in Fisher's protected least significant difference post hoc tests), followed by newly emerging snakes of both sexes (again, not significantly different from each other). All other post hoc comparisons were significant. In summary, the den contained three types of snakes that differed in locomotor abilities: newly emerged males and newly emerged females that were both slow, plus courting males that were much faster (in post hoc tests, faster than either of the other two groups). The two types of snakes found in the aspen woodlands 100 m away (dispersing females and

males) were relatively fast, and similar in speed (NS in post hoc comparisons).

Is Courtship Targeted to Newly Emerged Females?

Den versus dispersing females

In arena trials with 12 males and two females per outdoor enclosure, den females attracted almost 10 times as much courtship as dispersing females ($F_{1,20} = 36.71$, $P < 0.0001$; Fig. 2a). These differences between treatments were not due to differences in body size between the den and dispersing females (SVL: den: 45.45 ± 0.80 cm; dispersing: 45.30 ± 0.95 cm; mass: den: 29.62 ± 1.54 g; dispersing: 29.77 ± 1.83 g).

Mating frequency by den and dispersing females

In the same arena trials, we recorded matings by six of 25 newly emerged females (collected at the den) but none of 25 dispersing females (collected in the woodland 100 m from the den as they dispersed; $\chi^2_1 = 4.74$, $P < 0.03$). Was this higher rate of mating simply the result of more intense courtship (above), or did den females accept copulations after less courtship than did dispersing females? Multiple logistic regression with female location and
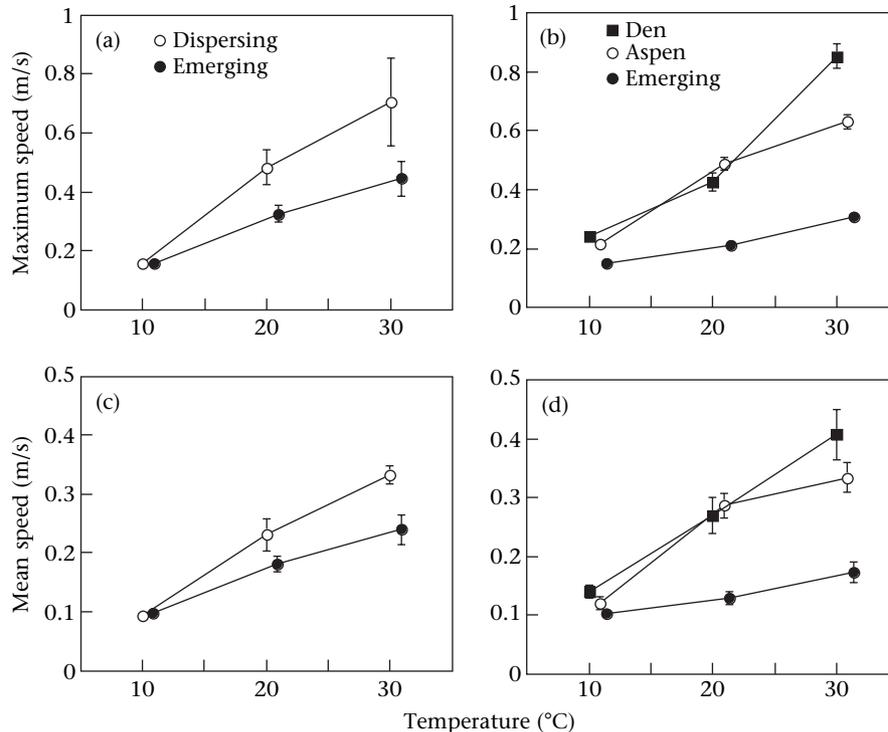

Figure 1. Locomotor speeds ($\overline{X} \pm$ SE) of garter snakes as a function of their sex, body temperature, time since emergence from overwinter inactivity and habitat. (a) Maximum speed of females, (b) maximum speed of males, (c) mean speed of females and (d) mean speed of males. The two groups of females are newly emerged animals (tested the day they emerged from underground after winter inactivity) and dispersing females (collected 100 m from the den as they dispersed towards their summer ranges). The three groups of males are new-emergers, snakes that stayed at the den to court after emerging ('den' males) and males that were captured 100 m away in the aspen woodland ('aspen'); this latter group may have contained some individuals that were dispersing (like the females captured in the same area) as well as some that remained in the woodland to intercept and court dispersing females. $N = 10$ at each temperature for each group (e.g. emerging females).
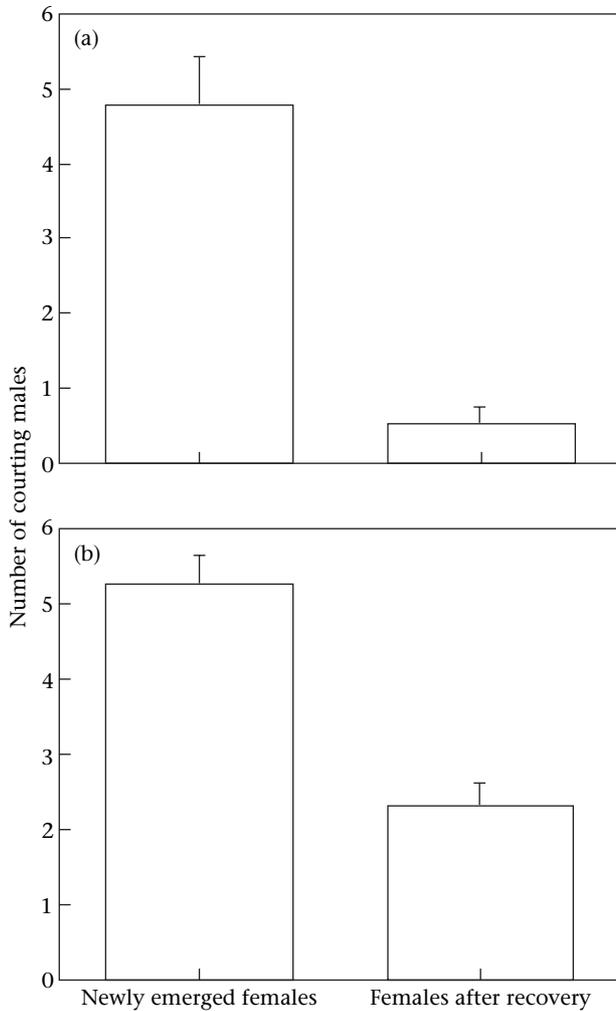
Figure 2. (a) Numbers of males ($\overline{X} \pm$ SE) courting two groups of female garter snakes in outdoor arena trials. Half of the females ($N = 11$) were collected as they emerged at the den; the other half ($N = 11$) were collected as they dispersed through woodland 100 m away. (b) Relative intensity of courtship ($\overline{X} \pm$ SE) directed to female garter snakes as a function of their opportunity to recover from overwinter inactivity in the field, after release at the centre of the den. Some of these females (newly emerged $N = 102$) had been kept indoors under cool dark conditions since emergence, thus delaying their recovery; the others ($N = 75$) were collected at the same time but had been placed outdoors every day for 3 days and allowed to bask, drink and move around, thus allowing recovery. The two groups of snakes were released simultaneously in the den, and we recorded the numbers of males courting them.

courtship intensity as factors, and 'mated or not' as the dependent variable, shows that trials that ended in mating did not involve more vigorous courtship than did other trials ($\chi_1^2 = 0.02$, $P = 0.88$), and that mating occurred more often with den rather than dispersing females even after the analysis was standardized for courtship intensity (log-likelihood ratio test: $\chi_1^2 = 4.77$, $P < 0.03$).

Female recovery and courtship intensity

Females that had been given 3 days to recover after emergence attracted significantly fewer suitors after their release at the den than did females kept in cool dark conditions over the same period ($\overline{X} \pm$ SD $= 5.26 \pm 0.38$ versus 2.31 ± 0.30 males/female; $F_{1,175} = 32.22$, $P < 0.0001$; Fig. 2b).

How Do Males Recognize Newly Emerged Females?

Hot versus cold females

In arena trials with 20 males plus two females in each arena, where males could court either hot or cold females, more males courted the hot than the cold animals (hot: $\overline{X} \pm$ SE $= 4.36 \pm 0.58$ males; cold: 3.00 ± 0.24 males; $N = 16$ females in each group; paired $t_{15} = 2.23$, $P < 0.05$).

Skin lipids

Paper towels impregnated with lipids from newly emerged females attracted more intense male responses than did towels with the scent of postrecovery females. Of 60 males, 48 tongue-flicked in response to the lipids from den females (80%), compared to only 31 of 60 males encountering lipids from the dispersing females (52%: contingency table $\chi_1^2 = 10.95$, $P < 0.001$). For the data from males that tongue-flicked, the proportion of animals that showed the most intense response (chin rubbing) was higher for lipids from den females (50%) than for lipids from dispersing females (26%; $\chi_1^2 = 4.71$, $P < 0.04$).

Resistance to caudocephalic waving

Females that gaped rapidly in response to dorsal stroking mated sooner in experimental trials than did females that resisted for longer (Pearson correlation: $r_{26} = 0.44$, $P < 0.02$). Thus, a female's ability to resist simulated caudocephalic waves offers a valid index of ability to resist real caudocephalic waves. However, the intensity of courtship to these females was not significantly correlated with resistance to dorsal stroking ($N = 96$ trials, resistance score versus % of observations when courting was recorded: $r_{94} = 0.01$, $P = 0.92$; versus maximum courtship intensity: $r_{94} = 0.05$, $P = 0.61$).

Female respiratory rate

The relative numbers of males that increased, decreased or did not change courtship intensity differed between treatments. Vigorously moving the female's tail region elicited strong increases (27 of 30 males increased), and movements of the female's head and neck stimulated weaker responses (16 of 30 males increased). However, changes in the female's respiratory frequency did not influence courtship vigour (no increases in either treatment); the control treatment (no manipulation) similarly showed no changes in courtship intensity during the observation period. Contingency table analysis confirmed that the response to tail movement was greater than that to head movement ($\chi_1^2 = 10.57$, $P < 0.002$), which in turn was greater than to either of the breathing-rate treatments, or the control (for each of these comparisons: $\chi_1^2 = 28.13$, $P < 0.0001$).

DISCUSSION

Until recently, the role of conflict between the sexes as a driving force in the evolution of mating systems and reproductive behaviour has attracted little scientific attention (Alonzo & Warner 2000; Chapman et al. 2003). However, it is becoming clear that evolutionary arms races between the sexes can play major roles in the evolution of sexually dimorphic morphological and behavioural traits (Andres & Arnqvist 2001; Arnqvist & Rowe 2002) and that conflict can have substantial fitness costs for females (Maklakov & Lubin 2004). In snakes as in most kinds of animals, interpretations of mating systems have traditionally ignored the possibility of sexual conflict; indeed, Devine (1984) suggested that the elongate flexible bodies of these animals precluded forcible insemination. Recent studies at garter snake dens have strongly challenged this view (Shine et al. 2000b, 2003a, 2004), and the current work provides additional evidence for an intense battle between the sexes at the dens. Our data support the hypothesis of sexual conflict, notably the prediction that males will recognize, and court, a subset of females that are less able to resist attempts at forcible insemination.

Both in the field and in arena trials, male garter snakes selectively courted females that were weaker (i.e. newly emerged rather than postrecovery), and at body temperatures that maximize the locomotor advantage of the males (i.e. hotter rather than colder; Fig. 1). This exploitation by males of the transitory weakness of snakes that have just emerged from an 8-month period of winter inactivity may sometimes result in copulations that confer no fitness benefit to either participant, as in the case of males mating with other males, or with juvenile females (Pfrender et al. 2001; Shine et al. 2000b).

Is the tendency of males to court newly emerged rather than postrecovery females (Fig. 2) strong evidence for male tactics in sexual conflict, or is there a simpler explanation? Alternatively, this behaviour could be caused by differences in the female's ability to evade courtship, rather than active male focus upon one versus the other type of female. That is, newly emerged females are cold, weak and slow, and hence less able to escape the male's attentions. All else being equal, we would expect to find more males courting such females than stronger, more agile (and thus more elusive) postrecovery females. Our arena trials resolve this ambiguity, because they prevented females from escaping. These trials showed that low female body temperatures per se were not the reason for more intense male courtship; the same preference was evident when thermal differentials were abolished and indeed, other trials showed that hotter not colder females were preferred. Newly emerged females elicited about 10 times as much courtship as postrecovery females even under conditions when neither female could escape the males (Fig. 2). Thus, although low body temperatures and poor locomotor ability reduce a newly emerged female's ability to evade male courtship, the concentration of male attention on this subset of females is a reflection of active mate selection by males rather than (or, more likely, as well as) differential evasion ability by females.

Are there reasons other than sexual conflict why males might selectively court newly emerged females? One possibility is that, in this multiply mating species (Garner et al. 2002), being the first male to mate a newly emerged female might confer an advantage in sperm competition within the female oviduct. Experimental studies suggest that a first-male advantage occurs in some, but not all, species of squamate reptiles (Olsson et al. 1994; Höggren & Tegelström 2002). Nevertheless, multiple mating by female garter snakes before they disperse from the den is vanishingly rare, because the first male to mate with a female deposits a gelatinous mating plug that precludes her from subsequent copulations until after she has dispersed from the mating aggregation (Shine et al. 2000c). Males do not court already mated females, based on pheromonal cues resulting from copulation (Shine et al. 2000c). Because almost all females mate only once before they leave the den, selectively courting newly emerged rather than dispersing females would not affect mating order or sperm precedence: all of the females that are courted in these circumstances (and that were used in our trials) were animals that had not mated since emerging.

Newly emerged animals (of both sexes) differ in several respects from postrecovery snakes. Thus, newly emerged females were, on average, not only cooler (lower mean body temperatures) and slower (in sprint speeds) than postrecovery females collected in the woodland, but also weaker (less muscular strength: Shine et al. 2000a) and showed cloacal gaping after fewer dorsal strokes (simulating caudocephalic waves; R. Shine, unpublished data). Hence, males can induce hypoxic stress more easily in newly emerged females, before they recover from hibernation. Males might identify vulnerable females by any such correlate of emergence, and mate choice is often based upon multiple cues (Candolin 2003). Although some of these traits are functionally associated with female vulnerability, our experimental trials suggest that males do not use these cues. Instead, males rely primarily upon an indirect indicator of female vulnerability, skin lipids, to discriminate newly emerged from postrecovery females. This sensory modality is also the primary means by which male garter snakes assess another snake's species, sex, body size and condition, and mated status (Shine et al. 2003c), so its use in this additional context is not surprising. Under the hypothesis of an arms race between male and female snakes at the dens (Shine et al. 2000b, 2004), we might expect selection on females to mask these pheromonal changes that indicate vulnerability postemergence. However, skin lipids are important for water proofing (Mason 1993) and, thus, their composition needs to change rapidly when a snake moves from the cold wet den to the hot dry surface; these biophysical challenges may constrain any ability to mask pheromonal (skin lipid) changes coincident with emergence from the den.

Male snakes also directed more courtship to hot rather than cool females, although this bias was much weaker than that based upon pheromonal cues. At first sight, the trend for males to court hot females more intensely runs counter to earlier reports that low female body temperatures stimulate courtship by male garter snakes (Shine & Mason 2001). However, the latter result was based on initial

responses only, and may reflect the fact that most females at the den are newly emerged and thus often colder than males. Hence, low body temperature provides a clue as to the animal's sex (Shine & Mason 2001). In the current study, however, we monitored vigour of male courtship over a much longer (20-min) period, when the sex of the 'target' snake was presumably not in question. Thus, although low body temperature may stimulate a male to check another snake carefully to ascertain its sex, courtship intensity was higher to hot rather than cold female snakes. Another issue involves the fact that locomotor speeds of both sexes increased with body temperature, so that we might expect males to select high body temperatures themselves but to court the coldest (slowest) females. The high rates of heat transfer between courting snakes make this impossible; all snakes within a single courting group rapidly equilibrate to the same body temperature (Shine et al. 2000e, 2001c). Because males are constrained to be at the same body temperature as the females they court, they benefit from courting warmer rather than cooler females.

The sex differentials in both mean body temperature and locomotor performance are transitory, and disappear within a day or two after emergence, by which time the female has dispersed from the main den into the surrounding woodland (Fig. 1). Presumably, this signals a substantial shift in the balance of power between the sexes. Male garter snakes are much smaller than females, so that it may be increasingly difficult for a male to obtain forcible copulations as the female recovers. Not only is she hotter and faster than before, but the densities of males (and hence courting-group sizes) in the woodland are at least 10-fold lower than at the den (Shine et al. 2001a). Thus, a male cannot rely upon his rival's activities to induce hypoxic stress in the female (Shine et al. 2003b). The rapid postemergence recovery of females in this system substantially changes the interaction between males and females. Male snakes at large communal dens respond accordingly to exploit transitory female weakness. However, dispersing females can exert increasing control over their courting and mating partners, and show complex movement patterns that are effective at evading unwelcome suitors (unpublished data). These movements rely upon rapid short-distance displacement and sudden changes of direction, manoeuvres likely to be impossible for a slow recently emerged female. Hence, the mating system may differ substantially between animals at the den versus in the surrounding lands. For logistical reasons, previous research (including our own) has focused heavily upon the den and its near surrounds, so we know almost nothing about male–female interactions within this population after the balance of power has shifted to females. Such studies offer exciting possibilities to explore the role of sexual conflict in the mating system of these remarkable animals.

Our study system is unusual in the abrupt shift in locomotor speeds that follows emergence from the winter den, and thus in the presence of females of very different physiological and locomotor capacities. That diversity has allowed males to exploit female vulnerability by targeting potential mates less capable of resisting forcible copulation. We predict that postemergence changes in the

balance of power between the sexes may be more subtle in warmer-climate reptile populations, because of the lower physiological challenges posed by overwintering in milder climates. None the less, the same general principles should apply even if the mechanisms generating variation in resistance among females are different. For example, it should generally be true that smaller females, or animals in poorer body condition or with injury, parasite or disease problems, may be less capable of resisting forcible insemination. If so, the diversity in mating systems that we have documented as a function of time since emergence will simply map on to variation in body size or health status. In any animal species, most populations will encompass substantial variation in terms of the size and strength of individual males and individual females. Our results suggest that such differentials may provide powerful opportunities for adaptive modification of male (and perhaps female) mating tactics, whereby an individual's behaviour reflects its abilities and vulnerabilities relative to conspecific organisms.

Acknowledgments

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