



Confusion within 'mating balls' of garter snakes: does misdirected courtship impose selection on male tactics?

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Although courting males are under intense selection to recognize the sex of potential partners, mistakes sometimes occur. Using descriptive and experimental data on garter snakes, *Thamnophis sirtalis parietalis*, from courting aggregations around a communal den in Manitoba, we tested two previously proposed hypotheses that suggest evolutionary significance to such mistakes. One idea, that female mimicry enables a 'she-male' to confuse his rivals within a mating ball, predicts that many mating balls will concurrently contain both she-males and females; where both types of sexual targets are present, males will frequently align their bodies with she-males rather than females. The second idea, that small body size confers a selective advantage to males because it facilitates sex recognition and thus reduces misdirected courtship by other males, predicts that larger males will receive more courtship than their smaller rivals within mating balls. Our results falsify these predictions. Natural courting groups rarely contained both females and female-mimicking males. When both potential sexual targets were present, males essentially ignored she-males. Similarly, male snakes rarely attracted courtship even when they were larger than females. The sensitive chemosensory apparatus of male garter snakes enables these animals to focus their courtship on females, ignoring males that resemble females either physically (body size) or chemically (pheromones). The degree to which a male garter snake resembles females thus has little or no significance for his mating success within a communal mating ball; further work is needed to evaluate the generality of this conclusion for other snake species.

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The ability of reproducing organisms to discriminate between potential mates has usually been examined in the light of species-isolating mechanisms (Panhuis et al. 2001) or the fitness benefits accruing to choosing the best mate from those available (Andersson 1994; LeMaster & Mason 2002). However, reproducing organisms are commonly faced with conspecifics of both sexes in areas where courtship occurs, and hence must also be able to discriminate between males and females of their own species. Such an ability has been documented in many taxa, based on a range of attributes (e.g. scent, colour, size, behaviour: Andersson 1994). This discriminatory ability is not surprising: Darwinian theory predicts that males should be under strong selection for the ability to determine the sex of other individuals, so as to avoid courting other males.

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The situation is complicated by potential advantages to reducing the efficiency of this communication. First, if courtship imposes costs on females, in terms of energy or risk, this sex may evolve to mimic males (Burley 1982; Robertson 1985; Panhuis et al. 2001). Second, a subset of males may benefit from confusing other males as to their sex (Trivers 1976; Rohwer et al. 1980; Kodric-Brown 1986; Laufer et al. 1994; Laufer & Ahl 1995; Gonçalves et al. 1996; Saetre & Slagsvold 1996). Males that resemble females thus might incur a cost, because their activities are impeded by courtship directed to them by other males, or a benefit, because they can thereby manipulate the behaviour of other males to their own advantage. How important are such selective forces? Males of many species do indeed devote substantial courtship to other males (Bagemihl 1999). The more interesting question, however, is whether these 'errors' represent simple mistakes, or reflect evolutionary pressures (i.e. selection on mating tactics). Have such mistakes been sufficiently frequent to impose selection on reproductive traits (Barlow & Siri 1997; Sherratt & Forbes 2001)?

Alternatively, sexually dimorphic traits that function in sex recognition might have been secondarily coopted for this function (West-Eberhard 1979; West-Eberhard et al. 1987; Sherratt & Forbes 2001).

Selection on sex discrimination may be trivial in some kinds of mating systems but important in others. Notably, 'scramble' competition for mates will require many mate recognition 'decisions' by courting males, and hence increase the costs or benefits of male inability to discriminate between males and females (Sherratt & Forbes 2001). Many snake species show such scramble polygyny (Duvall et al. 1992, 1993), with males identifying the sex of other individuals primarily by chemosensory cues (Mason et al. 1989; Mason 1992; Weldon et al. 1992). The ophidian vomeronasal system is extremely sensitive, allowing males to follow substrate-deposited pheromone trails of reproductive females over long distances (Ford & Low 1984; Slip & Shine 1988; LeMaster et al. 2001). None the less, male-male courtship has been reported in several snake taxa from disparate lineages, including colubrids (*Thamnophis* spp.: Noble 1937), elapids (*Notechis* spp.: J. Weigel, personal communication), viperids (*Bitis* spp.: Akester 1983), and boids (*Eunectes* spp.: Rivas & Burghardt 2001).

In two of these cases, confusion in sex identification leading to male-male courtship has been interpreted as a significant selective force on male traits. Both systems involve scramble competition and no overt male-male combat, with multiple males simultaneously struggling to copulate with a larger female. In communally denning garter snakes, *Thamnophis sirtalis*, in Canada, Mason & Crews (1985) showed that some males produce female-like pheromones and hence attract courtship by other males. Mason & Crews suggested that these 'she-males' redirect courtship within a mating ball, thus benefiting the female mimic's attempts to mate. Rivas & Burghardt (2001) suggested that in Venezuelan populations of the anaconda, *Eunectes murinus*, small body size in males reflects selection to diverge from females and hence facilitates sex recognition by rival males. The putative advantage in this case is to reduce the amount of courtship directed to a male, thereby enabling him to focus on courtship rather than on repelling other males.

Despite the wide divergence phylogenetically, ecologically and in body size between the species used in these two studies, the mating systems of garter snakes and anacondas are broadly similar. Both hypotheses suggest that, within a mating aggregation, males become confused about the sex of other participants and thus redirect courtship to other males rather than to the female. The hypotheses differ in whether this redirection constitutes a cost (Rivas & Burghardt 2001) or a benefit (Mason & Crews 1985) to the male that is the courtship recipient. Both hypotheses suggest that the misdirection of courtship is sufficiently frequent, with such a high impact on fitness (cost or benefit) that it has imposed significant selection on male attributes (pheromone profile or body size). Thus, both hypotheses rely upon two assumptions: (1) natural courtship groups around females contain males that differ in the degree to which they resemble the female (i.e. she-males plus he-males for the Mason

& Crews hypothesis; large males plus small males for the Rivas & Burghardt hypothesis); and (2) males that resemble females (in terms of pheromones or body size) attract courtship to themselves and away from the female. If either of these assumptions is falsified, then the hypotheses cannot be valid for that study system. We tested these ideas on communally denning garter snakes in Canada.

METHODS

Study Species and Area

Red-sided garter snakes, *T. s. parietalis*, overwinter in huge communal dens in central Manitoba, presumably to avoid lethally low soil temperatures (Gregory 1974, 1977; Gregory & Stewart 1975). These snakes are small (adult males average 45 cm snout-vent length, adult females 60 cm) and nonvenomous. They emerge from their dens in spring (May) and court and mate near the den before dispersing to their summer ranges (Mason 1993; Shine et al. 2001a). Because males remain near the den for about 2 weeks whereas females disperse almost immediately, the operational sex ratio around the den is highly male biased (Shine et al. 2001a). Most newly emerging females are hidden by dozens or hundreds of suitors, all attempting to align their bodies with that of the female (Hawley & Aleksyuk 1975, 1976). Female skin lipids act as sex pheromones, eliciting vigorous courtship from males (Mason 1993). Some males ('she-males') produce female-like lipids and thus attract courtship (Mason & Crews 1985; Shine et al. 2000a, b, c). We worked at a communal den containing approximately 10 000 garter 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).

Diversity of Phenotypes within Mating Balls

We searched the area around the den, looking for courtship in relatively isolated groups of snakes (i.e. where we could clearly distinguish between snakes that were part of a courting group and those that were not). We then collected the focal snake(s) that were the target of courtship and all other snakes in direct physical contact with that animal. For the pheromonal mimicry study, we attempted to find relatively equal numbers of groups with females and she-males. Within 30 s of collection, the entire group was placed into an open-topped nylon arena (1 × 1 × 1 m) erected near the den. Courtship typically recommenced within 60 s. We then observed the group for 10 min. Any animal that was courted was immediately removed and its sex determined. In practice, all courtship had ceased by 4 min (but recommenced if we added a female or she-male, showing that males were still prepared to court but had no suitable 'targets'). Thus, we are confident that our methods revealed all snakes attracting courtship within each group. We used a separate series of groups to examine the distributions of male and female body sizes within mating balls. We collected

all animals within a group, determined their sexes (by eversion of hemipenes) and measured snout–vent length (SVL).

Courtship to Female-like Males

We conducted experimental trials in outdoor arenas to quantify the amount of courtship directed to males that resembled females in either pheromone profiles or body size, and to evaluate whether the presence of such animals within a mating ball diverted courtship away from the female.

Pheromonal mimicry

We set up 10 arenas, as above, each containing either three he-males and an unmated female, or two he-males, one she-male and an unmated female. All snakes were collected at the den immediately before the trials. She-males were identified because they attracted active courtship, whereas he-males did not (Shine et al. 2000a). Two of the he-males in each enclosure were arbitrarily chosen as focal snakes and received distinctive dorsal paint marks to enable individual recognition, as did the she-male (we used nontoxic paint for this purpose, which wore off within 48 h). At 5-min intervals for the next 30 min, we scored whether each of the paint-marked snakes was courting and, if so, who was the target of their attentions. This behaviour is straightforward to score, because courting males show distinctive behaviours (body alignment, chin pressing, caudocephalic waving) seen only in courtship (Whittier et al. 1985). Analysis was based on total numbers of courtship records per male.

Body size divergence between the sexes

To quantify how often courting males align with very large males rather than females within a mating ball, we erected nine arenas. To each of these, we added one very large male and one small unmated female, and five smaller males. The large male, the female and one (arbitrarily chosen) small male were paint marked as above. At 2-min intervals for the next 18 min, we scored courtship activity and targets for these males. We added the total numbers of courtship records across all observation periods, to provide an index of courtship activity by each snake to each potential target animal. If mating occurred we immediately terminated the trial, removed the mating pair and replaced them with an unmated female and another male of the same size as the successful male, and commenced a new trial. We conducted 24 trials, of which six resulted in mating.

Because snakes in mating balls often move quickly, and the body of one snake can be hidden beneath others, details of alignment can be difficult to score, especially in larger groups. Thus, we set up an additional series of trials in smaller outdoor arenas ('Space Pop', Smash Enterprises, Melbourne, Australia; 48 cm diameter × 56 cm deep) where we videorecorded courting groups. We added either four or 24 males and one unmated female (with the female and four males of different size classes painted for individual recognition), and filmed the animals for

10 min or until mating occurred. Subsequent analysis of these films was based on snake positions two to five times during each trial, depending on the duration of the trial before mating. To avoid pseudoreplication, we calculated mean values for each male in each trial, to see whether larger males attracted more courtship.

The research was conducted under the authority of the Oregon State University Institutional Animal Care and Use Committee and in accord with the U.S. Public Health Service 'Policy on Humane Care and Use of Laboratory Animals' and the National Institutes of Health 'Guide to the Care and Use of Laboratory Animals', and with a permit from the Manitoba Department of Natural Resources.

Analysis

Data were analysed on a Macintosh G4 computer using Statview 5 (SAS Institute 1998). Data were checked for conformity to assumptions of statistical tests before analysis; some variables were log transformed to achieve normality of distributions or equivalence of variances between groups. We report mean values ± SE.

RESULTS

Diversity of Phenotypes within Mating Balls

Pheromonal mimicry

We collected 50 courtship groups, one of which contained only a single animal (a she-male courting himself); the others contained 1–29 he-males. The mean number of he-males did not differ between groups containing females and those containing she-males (female-centred groups: 9.92 ± 1.20 males; she-male groups: 8.03 ± 1.14 ; one-factor ANOVA: $F_{1,48} = 1.30$, $P = 0.26$). No group contained both a female and a she-male. Of the 24 female-centred groups, 22 contained a single female and two contained two females. Of the 26 she-male-centred groups, 23 contained one she-male, two contained two she-males, and one contained three she-males.

Body size divergence between the sexes

We collected 26 mating balls, each containing 2–28 males and a single female. Some mating balls contained males over a wide range of body sizes. Females averaged 35.5% longer (15.82 ± 0.70 cm) than the males found courting them. Thus, most males were clearly distinguishable from most females by body size. However, even very small females were sometimes courted, so that the disparity between the body size of a male and the size of the female he courted varied widely (Fig. 1). Mean male size was greater than female size in five of the 26 balls we measured; all of these were small balls (two or three males per female) around small females. Although these were the exception, the overall result supported this assumption of Rivas & Burghardt's model; a minority of males was similar in body size to the females they were courting (Fig. 1).

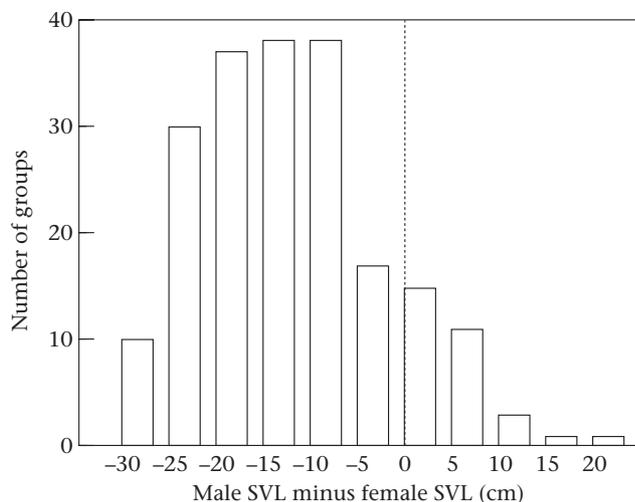


Figure 1. Disparity in snout-vent length (SVL) between male garter snakes and the females they were found courting. Data combined from measurements of snakes in 26 mating balls at the Inwood den in Manitoba. Negative scores show cases where females were larger than courting males and positive scores show cases where males were larger.

Courtship to Female-like Males

Pheromonal mimicry

Body sizes of she-males were similar to those of he-males in the same trials (SVL: she-males: 46.84 ± 1.79 cm; he-males: 45.40 ± 0.90 cm) and both were smaller than females (57.08 ± 1.97 cm; one-factor ANOVA: $F_{3,27}=20.47$, $P<0.0001$); post hoc Fisher's protected least significant difference tests showed that females were larger than either of the two male categories ($P<0.05$). The major result from these trials was that courtship to she-males was rare when a female was present: we recorded only three alignments with she-males (versus 25 with females in the same trials). None of these alignments occurred while the she-male was courting the female; instead, the female and she-male were the foci of separate courtship groups within the arena. Courting was recorded in three of 25 possible trials for she-males versus means of 12.5 by he-males in the same trials and 13.0 for he-males in trials without she-males run concurrently, but this difference was not significant ($F_{1,28}=3.21$, $P=0.084$). Thus, the presence of a she-male in the arena did not reduce the amount of courtship directed to the female (comparing arenas with and without she-males: $F_{1,28}=0.47$, $P=0.50$). Despite vigorous courtship in these trials, we never saw a she-male being courted while he was courting a female.

Body size divergence between the sexes

In trials using large arenas, large males were slightly longer (52.30 ± 0.93 cm) than females (50.36 ± 1.12), and much longer than either the small focal males (40.89 ± 0.81) or the unmarked males (40.40 ± 0.34 ; $F_{3,121}=82.47$, $P<0.0001$); post hoc Fisher's PLSD tests showed that large males were not significantly larger than females and that the 'small' males did not differ from

randomly chosen males; all other comparisons were significant ($P<0.05$). Analyses on body mass produced identical conclusions (large males: 45.66 ± 1.87 g; females: 45.48 ± 2.90 g; small males: 20.57 ± 1.12 g; unpaired males: 19.87 ± 0.44 g; $F_{3,121}=115.68$, $P<0.0001$); post hoc Fisher's PLSD tests showed that large males were not significantly different from females and that the 'small' males did not differ from randomly chosen males; all other comparisons were significant ($P<0.05$).

Thus, if males use body size as a criterion for sex recognition, we would expect these large males (larger than the females, on average) to attract significant courtship. Large males did attract some courtship, but much less than females did (28% as much, on average). The total amount of courtship (total of alignment plus chin pressing, summed over the eight observation periods) directed to large males was slightly but not significantly more than to small males (means of 1.21 versus 0.67 courting records per snake; $F_{1,46}=1.88$, $P=0.18$). However, larger males were also more active in courtship (3.13 versus 1.80; $F_{1,46}=4.51$, $P<0.04$). Because a male that is actively courting is by definition close to the female, we might expect males that are active courters to attract more courtship. That is, the most likely 'error' for a courting male will be to align his body with a male that is itself closely aligned to the female. Analysis of covariance confirmed this prediction. With male body size as the factor and intensity of courtship by a male as the covariate, males that courted more often were themselves courted more often (covariate: $F_{1,45}=13.17$, $P<0.001$). The amount of courtship directed to a male was not affected by his body size ($F_{1,45}=0.15$, $P=0.70$), and the relation between courtship to and by a male was similar between large and small males (interaction: $F_{1,44}=0.38$, $P=0.54$). Thus, snakes that were more active courters themselves attracted more 'mistaken' alignments, but male body size did not affect the frequency of this behaviour.

The video trials provided similar conclusions. We ran 33 trials with four males per group and 25 with 24 males per group. Each arena contained four focal snakes of different size categories. The four size classes of males averaged 40.75 ± 0.47 , 43.43 ± 0.49 , 46.50 ± 0.32 and 49.90 ± 0.36 cm SVL ($F_{3,228}=90.50$, $P<0.0001$; all post hocs differed at $P<0.05$) and 21.44 ± 1.18 , 26.08 ± 1.33 , 31.02 ± 0.86 and 37.85 ± 0.88 g in mass ($F_{3,228}=42.11$, $P<0.0001$; all post hocs differed at $P<0.05$). Males aligned with other males only rarely in the video trials, as in the larger arenas (15.9% of records of courtship were directed to males and the other 84.1% to females, despite much larger numbers of males than females in the courting groups). As for the trials in the larger arenas, male snakes that courted females more often were themselves the object of courtship more often, especially in larger groups (Pearson correlation between courtship to and by a male: $r_{98}=0.49$, $P<0.0001$). To examine effects of body size and group size, we conducted analysis of covariance with male body size (sorted into four categories) and number of males per group as the factors, number of male alignments with a female as the covariate, and courtship to those males as the dependent variable. Interaction terms were not significant ($P>0.05$) and were thus deleted so

that we could compare intercepts. A male's own level of sexual activity was a good predictor of the number of times that he was courted by other males (covariate: $F_{1,226}=8.00$, $P<0.006$) but his body size and the number of other males in the group did not affect the number of times that he was courted (body size: $F_{3,226}=0.11$, $P=0.95$; group size: $F_{1,226}=0.96$, $P=0.33$).

DISCUSSION

Our results falsify both of the hypotheses that we tested. In both cases, critical assumptions of the hypotheses were not satisfied within the study system that we used. This finding does not mean that the hypotheses may not apply to other systems, but there are no data to support this possibility. Interpretation of our results for garter snakes is greatly facilitated by extensive background information on mating systems and sexual communication in these animals, much of it based on the same den population that was the focus of the present study.

In one sense, there is a trivial answer to the question 'does misdirected courtship to other males impose significant selection on male tactics?' This mating system favours males that can accurately and rapidly distinguish males from females and thereby allocate courtship appropriately. Thus, costs of misdirected courtship to other males impose selection on the chemosensory abilities of male snakes (Mason et al. 1987, 1989, 1990). However, misdirected courtship within communal mating balls is unlikely to have influenced the evolution of other traits, such as female mimicry and sexual size dimorphism. The major conclusion from our studies is that courting male garter snakes in this situation can distinguish the sex of other participants in the mating ball, and are not confused by similarities between males and females in terms of either pheromones or body size.

The social context within which this discrimination occurs is critical. Female mimics (she-males) do attract vigorous courtship, but only when females are not present. Experimental trials showed that she-males ceased courting females and retreated from their presence if males (especially large males) commenced vigorous courtship (Shine et al. 2000b). This is exactly what happened in our arena trials, and also explains the lack of 'combined' courting groups (containing both a female and a she-male) in the field sample. The behaviour of he-males also shifts with context; solitary mate-searching he-males are more attracted to she-males than are males already in a courting group around a female (Shine et al. 2000a). That is, males seem to search for the most female-like pheromonal stimulus. She-males provide sufficient attraction when no females are nearby, but are abandoned immediately in favour of a real female if one is present. The combination of these two behavioural shifts (she-males avoid females once other males are present, and males ignore she-males if females are present) indicates that the adaptive significance of female mimicry, if any, must lie in advantages to males of being courted in the absence of females. This restriction falsifies the original Mason–Crews (1985) hypothesis that she-males obtain a mating advantage through interactions within

mating balls around females, but is consistent with the suggestion that courtship provides warmth and protection to otherwise solitary she-males (Shine et al. 2001c).

Unlike the Mason–Crews hypothesis, the basic conditions envisaged by the Rivas–Burghardt (2001) model are realistic in this population, as they are in the system for which the hypothesis was originally devised (anacondas in Venezuela). That is, mating balls around female garter snakes contain males of a wide range of body sizes, some even longer than the females (Fig. 1). The size range of males within such balls is less than would be expected under random membership of mating groups with respect to body size, because of size-assortative courtship within this population (Shine et al. 2001b), but is still large enough that one could imagine males mistaking their larger rivals for females. In keeping with this possibility, studies have shown that mate-searching males cannot distinguish between the tails of males and females, and thus align their tail with whichever tail is closest (Shine et al. 2000c). Female body size and shape also act as stimuli for courtship, with larger females attracting more attention than smaller conspecifics (Aleksiuk & Gregory 1974; Hawley & Aleksiuk 1976; Gartska et al. 1982; Shine et al. 2001b). At first sight this preference for larger females implies a strong role for visual cues to body size and hence a substantial possibility that courting males would be distracted by a very large (female-sized) male. In practice, this happened only rarely in our study. Even when males were larger than females, they attracted much less courtship. The most likely explanation for this apparent paradox is that males assess the body sizes of females not simply through visual cues, but also through subtle pheromonal shifts that occur with female body size (LeMaster & Mason 2002; Shine et al. 2002).

In summary, both the Mason–Crews and Rivas–Burghardt models fail primarily because of the effectiveness of the vomeronasal system in courting male snakes. Confusion occurs only rarely within the mating ball, because a male can generally distinguish the sex (and body size) of another animal rapidly and accurately, often with only a single tongue-flick (personal observation). The mating system of the red-sided garter snake may place an unusually high premium on such discriminatory ability; males in most snake species (and indeed, southern populations of *T. s. parietalis*) may encounter conspecifics at much lower rates and hence have more time to assess the other animal's sex and size. At the same time, however, the potential for confusion between alternative potential mates is probably higher in the Manitoba garter snakes than in most other systems. We conclude that selection on male discriminatory ability has been so strong that misdirected courtship within communal mating balls is rare and hence has not acted as a significant selective force for traits to reduce or enhance the similarity between males and females.

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