THE PROBLEM WITH COURTING A CYLINDRICAL OBJECT: HOW DOES AN AMOROUS MALE SNAKE DETERMINE WHICH END IS WHICH?

by

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Summary

In order to achieve copulation, a male snake must align his body in the same direction as his mate. This may not be a trivial problem in an elongate limbless animal, especially when the male is much smaller than the female (and hence, his head is far from hers) and when she is simultaneously being courted by many other males (so that much of her body is not visible). This is exactly the situation experienced by red-sided gartersnakes (*Thamnophis sirtalis parietalis*) at communal dens in Manitoba. To clarify this question, we modified cues available to males by manipulating various attributes of females (direction of movement, presence of head and tail, concentration of sex pheromones, *etc.*). Male alignment during courtship does not depend on the visual stimulus provided by the female's head or tail. Instead, male alignment is influenced by the female's direction of movement, and by pheromonal stimuli from her skin. We suggest that courting male snakes obtain directional

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information via their characteristic 'chin-pressing' behaviour. By pressing firmly on each scale with his chin as he passes over it, a male moving anteriorly (but not posteriorly) along the female′s body will open a small gap between that scale and the next most anterior one. This gap enables his tongue-tips to penetrate more easily towards the scale-hinge area (overlain by the more anterior scale) where sex pheromones are concentrated. Thus, the direction of scale overlap provides pheromonal as well as physical cues that permit males to align correctly for copulation.

Introduction

To reproduce successfully, a male must carry out a complex sequence of behaviours, and perform effectively in each of them. Sexual selection for success in these endeavours has provided a strong impetus for the evolution of male abilities to locate prospective mates, determine that they are of the appropriate sex and size, assess their reproductive condition, and court them in such a way as to induce sexual receptivity (*e.g.* Andersson, 1994). Even if we ignore additional behaviours associated with avoiding, evaluating and/or overpowering rival males, the tasks necessary for successful reproduction by males are diverse and often complex. In the process of carrying out these tasks, males utilise a wide variety of cues from their potential mates. Understanding the nature of these cues and the ways in which they are used to overcome particular problems, may clarify the function of specific male behaviours and help to explain the high levels of diversity in male reproductive tactics (Andersson, 1994; Olsson & Madsen, 1998).

In this paper, we focus on a straightforward problem: how does a courting male recognise the orientation of his partner so that he can effectively align his body with hers to achieve copulation? The problem is a trivial one for many kinds of animals, in which anterior-posterior differentiation is so obvious that it provides abundant cues to the male. However, this is less true of elongate limbless species such as snakes. Although snakes show considerable diversity in aspects of the mating system relating to male-male interactions (*e.g.* Duvall *et al.*, 1992, 1993; Schuett, 1997), their courtship and copulatory positions are much less diverse (Carpenter & Ferguson, 1977). The male aligns his body with that of the female, oriented such that both animals are facing in the same direction, and adpresses

his chin firmly against the female while tongue-flicking repeatedly (*e.g.* Carpenter & Ferguson, 1977; Gillingham, 1987). The tongue-flicking clearly relates to acquisition of chemosensory information, especially relating to female pheromones (skin lipids: Kubie *et al.*, 1978; Mason *et al.*, 1987, 1989). However, many questions remain about the other components of reproductive behaviour. In particular:

(i) how does a male snake orient so that he faces in the same direction as his partner during courtship? This is not a trivial problem, given that the head and tail of his partner may look fairly similar to each other, and (in species with strong sexual dimorphism in adult body size) may be a long way from his own head. The female's body is cylindrical, with few overt cues as to orientation. In many taxa, the female's body may also be largely obscured by the bodies of rival males within a 'mating ball' (Whittier *et al.*, 1985; Luiselli, 1996), further reducing the availability of information to the male about the orientation of his potential partner.

(ii) why does a male snake press his chin firmly against the female as he moves his head along her body during courtship? This behaviour might provide information about the female (perhaps including her orientation), either via sensory systems within the chin itself, or by enhancing the effectiveness of tongue-flicking. However, intuition does not immediately suggest that the male would need to press so firmly to achieve either effect.

To clarify these questions, we conducted simple observational and experimental studies on a large aggregation of reproducing snakes.

Methods

In the Interlake region of southern Manitoba, adult red-sided gartersnakes (*Thamnophis sirtalis parietalis*) gather in large numbers every autumn at communal hibernacula (*e.g.* Gregory, 1974; Gregory & Stewart, 1975; Gregory, 1977). The snakes court and mate as they emerge the following spring, providing a unique opportunity to study reproductive behaviour. Males recognise the sex of other individuals primarily through skin lipids (sex pheromones: Mason *et al.*, 1989), but also use visual and thermal cues for this purpose (Shine & Mason, unpubl. data). Unmated females attract vigorous courtship from one to many males, with some 'mating balls' containing dozens of snakes (*e.g.* Hawley & Aleksiuk, 1975, 1976). Adult females are much larger than adult males (averages of 65 *vs* 45 cm snout-vent length: Shine *et al.*, 2000 a, b).

We worked primarily at a large den in a gravel quarry 1.5 km N of the town of Inwood, 0.5 km E of Highway 17 (50°31.58′N 97°29.71′W), in southern Manitoba, in May 1998 and 1999. Additional animals (both live and dead) for our trials were collected at dens in the Narcisse Community Pasture, 30 km N of the Inwood den. Recently-dead animals found around the dens (usually due to predator attack) provided enough material for our tests of experimentally manipulated attributes (see below); we did not kill any animals during the study.

We hypothesised that males might orient by means of five types of cues, or a combination of them:

(i)   direction of female movement. Males may distinguish the female's orientation by the direction in which she travels.

(ii) anterior-posterior asymmetry in morphology. Males may recognise the difference between the female's head and her tail visually, and use this information to align themselves in the same orientation.

(iii) physical attributes of the female's skin, such as scale microstructure or the direction of scale overlap, could provide reliable cues to orientation.

(iv) chemical (pheromonal) gradients along the female's body might provide directional information.

(v)   tactile sensation. Can a male use tactile receptors in his hindbody (*e.g.* male-specific enlarged scales beside the cloaca: Blanchard, 1931) to distinguish the female's body from those of rival males?

We carried out a series of simple experiments to clarify whether or not males took advantage of these potential cues. For most of these trials, our dependent variable was the direction in which the male was aligned with the female's body at the time that he initiated intense courtship. In practice, orientation can be scored simply and unambiguously at this time. A male sometimes moves backwards and forwards along the female's body in the early stages of courtship, but he then adopts a position in which the entire length of his body is fully aligned with hers, prior to commencing spasmodic contractions (caudocephalic waves: see Whittier *et al.*, 1985). We scored the male's orientation at the time of the first caudocephalic wave. In practice, we never saw a male reverse his orientation after this point.

Direction of movement

We tied string to the head and tail of a recently-dead female snake, and dragged the carcass either forwards or backwards (in random order) close to a group of mate-searching male snakes. We attempted to attract only one male per trial, and usually succeeded. When more than one male began courting the female, we scored the first male only. As noted above, we recorded the courting male's direction of alignment (*i.e.* with his head either towards the female's head or towards her tail) when he first displayed caudocephalic waves. Four different females were used in these trials.

Anterior-posterior asymmetry in morphology

We gathered three data sets to address this question. First, we scored courtship orientation (as above) for males encountering stationary (dead) females that we stretched out on flat open ground such that the female's head and tail were clearly visible. If males use visual cues

(*e.g.* location of the head), we would expect that they would immediately adopt the 'correct' orientation more often than would be predicted by chance. Second, we repeated the same trials with a female after the head had been removed. Third, we repeated the procedure after the tail as well as the head had been removed.

Scale ultrastructure and direction of scale overlap

To see if males can orient based only on cues associated with the female's skin, we removed the entire skin (minus head and tail) from a recently-dead female and draped it on a hollow metal rod (23 mm diameter × 1 m long). We recorded courtship responses (as above) of males encountering this stationary object.

In hot weather, dead females lose their attractiveness to males after a few hours (pers. obs.), presumably due to breakdown of pheromones. Thus, we repeated the above trials with female skins that had lost much of their attractiveness, to see if reduced pheromonal cues modified male ability to align correctly.

To see if males rely on directional cues associated with the ultrastructure of female scales, we sprayed the posterior three-quarters of the bodies of eight unmated female snakes with a 'plastic skin' (Smith and Nephew #66004976, OpSite). This substance, normally used as a surgical dressing, is permeable to moisture-vapour and (based on courtship behaviour of the snakes) apparently does not impede passage of the methyl ketones that red-sided gartersnakes use for sex identification (Mason *et al.*, 1987). The snakes showed no overt signs of discomfort at the procedure. Because we applied the spray very thickly, any fine striations on the female's scales would have been occluded.

Trials using Opsite spray were carried out in outdoor open-topped arenas (1.1 × 1.1 m, 0.9 m high) constructed of nylon fabric. Each female was placed in an arena with five males, and another eight control females were similarly set-up with males in other arenas. We scored the numbers of males courting each female at five-minute intervals over a 70-minute period, and whether these males were 'correctly' aligned to the female.

Pheromonal gradients

There may be a gradient of lipid types or concentrations along the female's body, enabling males to distinguish the female's orientation by olfactory means alone. To evaluate this possibility, we washed the posterior three-quarters of nine females in hexane to remove sex-attractant methyl ketones. As was the case in the Opsite trials, we noted no evidence of any avoidance behaviour or discomfort from these animals as a consequence of the procedure. Another nine females were washed with water as controls (the ketones are not water-soluble) and we then placed each female in an arena with five males and scored courting numbers and alignments as above.

Location of receptors in males

Lastly, we used field trials to directly test the ability of courting males to distinguish between the tails of females *vs* other males, using only the posterior parts of their own bodies. Male gartersnakes can distinguish the two sexes using their vomeronasal system, but they might also possess sensory receptors in the posterior part of the body that enable them to distinguish sex. Especially when most of the female's body is hidden beneath rival males, such an ability

could greatly enhance male courtship success. We used the following procedure to test this possibility. After finding a courting group, we gently moved the males' tails away from the female without disturbing them. We then held the rear of the 'target' female's body (including her tail) inside a closed hand so that it was inaccessible to the tails of the males, and stretched the tails of two other snakes (one male, one female; similar to each other in body sizes) so that they crossed (and were held firmly against) the target female's body 5 cm anterior to the cloaca. The two 'test' tails were held 2 cm apart, parallel to each other and to the body of the target female. The courting males immediately searched for the target female's body with their tails, and aligned with one of the substitute tails. We scored which of the substitutes was chosen (based on the first male tail to align with and wrap around a 'test' tail). We then again disengaged the males, and reversed the position of the two 'test' tails (*i.e.* the one that previously contacted the target female's body more anteriorly was moved to the posterior position). After scoring the new alignment, we selected a new courting group, captured two new 'test' snakes, and repeated the procedure.

Results

Most of our trials provided clear results, and help to identify the cues that male gartersnakes use for alignment during courtship.

Direction of movement

Males use information on the direction of a female's movement to determine which way they should align. When dead females were pulled forwards, all males aligned in the correct orientation ($N = 29$ trials; binomial test against a null of 50% correct orientation, $p < 0.001$). In contrast, females dragged backwards were courted the wrong way round (*i.e.* male head towards the female's tail) in 11 of 25 trials (44%; against a null of 50%, binomial test, $p = 0.35$). Contingency-table analysis confirms that these two results differ significantly ($\chi^2 = 13.42$, 1 df, $p < 0.0002$; see Fig. 1a).

Anterior-posterior asymmetry in morphology

Males encountering a stationary (dead) female in an open location were almost equally likely to align themselves in either direction with respect to the female when they first began courting her (in 7 of 20 trials, the male initially moved towards the female's tail rather than her head, $= 35\%$; against a null of 50%, binomial test, $p = 0.13$). However, they adjusted their positions prior to commencing intense courtship (caudocephalic waving); all of the 15 final alignments were the correct way around (binomial $p < 0.001$;
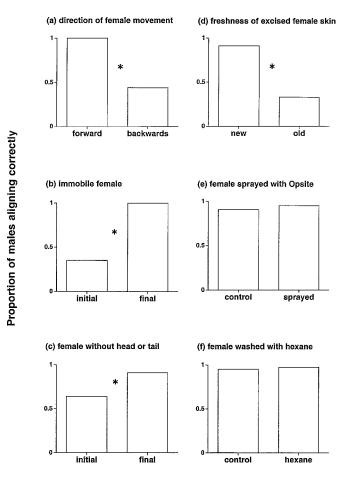
Fig. 1. Effects of experimental treatments on the ability of male gartersnakes to align correctly with the female during courtship. The treatments involved (a) moving a female forwards or backwards; (b) an immobile (dead) female; (c) a dead female with the head and tail removed; (d) an excised skin from a female, tested either immediately after removal or several hours later; (e) a live female sprayed with Opsite ('plastic skin'); and (f) a live female washed with hexane to remove surface lipids. See text for explanation and statistical tests of these results. Asterisks show results that are statistically different ($p < 0.05$) from that expected under the null hypothesis of equal probability of alignment in either direction.

Fig. 1b). The males' ability to align correctly remained at 100% after the female's head was removed ($N = 18$ trials; binomial $p < 0.001$) and when the tail as well as the head was removed ($N = 9$ trials; binomial $p < 0.003$). Thus, overt anterior-posterior asymmetry is not essential for

alignment: males are able to align correctly without visual reference to the female's head or tail.

Scale ultrastructu re and direction of scale overlap

Males actively courted the excised snake-skin (headless and tailless) wrapped around a metal pole. As for the intact snakes, initial alignment was apparently random (correct alignment in 14 of 22 trials, = 64%; against a null of 50%, binomial p = 0.14). However, the males adjusted their positions prior to commencing vigorous courtship, so that they were oriented in the correct direction in 10 of the 11 trials that progressed to caudocephalic waves (against a null of 50%, binomial p < 0.007; Fig. 1c).

When these trials were repeated using 'older' skins that had lost much of their attractiveness, males were less efficient at alignment. Of the trials that progressed to intense courtship, males were correctly aligned in only 7 of 21 (33%; against the results from earlier trials with the same skins, χ^2 = 7.43, 1 df, p < 0.007; Fig. 1d).

Spraying live females with 'plastic skin' did not reduce the frequency with which they were courted in our arena trials (average of 14.4 courting records for the sprayed females, *vs* 10.25 for the control females; $F_{1,14}$ = 0.74, p = 0.40). Similarly, the experimental treatment did not reduce the males' ability to align in the correct direction during vigorous courtship (average of 95.4% 'correct' alignments on the sprayed females, *vs* 90.7% on the control females; $F_{1,14}$ = 1.03, p = 0.33; Fig. 1e). For both data sets, binomial tests reject the null hypothesis of random alignment (p = 0.0001).

Pheromonal gradients

Washing females in hexane to remove sex pheromones reduced the frequency with which they were courted. The hexane-washed females attracted an average of 7.1 courtships, compared to 25.9 for the control females ($F_{1,16}$ = 7.10, p < 0.017). Nonetheless, the males' ability to align in the correct direction was unaffected (averages of 97.3 *vs* 95.0% 'correct' alignment to the two groups of females, $F_{1,16}$ = 0.77, p = 0.39; Fig. 1f). For both data sets, binomial tests reject the null hypothesis of random alignment (p = 0.0001).

Location of male receptors

The field trials where we offered 'substitute' tails to courting males revealed no evidence that courting males aligned with the tails of females rather than simultaneously-presented males ($N = 11$ *vs* 9 trials respectively, binomial $p = 0.41$). Instead, males generally aligned with the tail that crossed the 'target' female's body in the most anterior position (and for this reason, might seem most likely to be the female's own tail). This result was observed in 19 of 20 trials, enabling strong rejection of the hypothesis that males will recognise, and consistently align with, the tails of females rather than males.

Discussion

Male gartersnakes were able to align themselves correctly with their female partner in the vast majority of courtship sequences, even when they had access to only a limited set of cues. Our study suggests that the primary features used by males to determine alignment are (1) the direction of the female's movement, and (2) some characteristic of her skin that provides pheromonal information on orientation. Our data also indicate that males do *not* use the female's head and tail as cues for alignment, and that direct pheromonal receptors on the male's body (as opposed to the use of his vomeronasal system) are not likely to play a significant role in alignment. The idea that such receptors may occur was suggested to us by the occurrence of sex-specific enlarged rugose scales near the male's cloaca (Blanchard, 1931; Harrison, 1933; see Shine, 1993 for a review), and by the presence of anterior-posterior duplication of another sensory system (vision) in seasnakes (Zimmerman & Heatwole, 1990). However, our study provided no evidence for any such ability in male gartersnakes.

Our results accord with intuition, in terms of the availability and reliability of alternative cues. First, we consider the cues that were *not* used by male snakes. The location of the female's head and tail seem the most obvious cues to a human observer, but in practice may be difficult for a male gartersnake to assess. Females are courted even when only a small part of their body protrudes from shelter, and (as noted above) when the 'ball' of courting males is so large that the head and tail of the female cannot be seen. Similarly, removing much of the external pheromones (skin lipids) reduced female attractiveness, but not male ability to align. Unfortunately, results

from our the arena trials with hexane-washed and Opsite-sprayed females are ambiguous because we cannot dismiss the possibility that female movement also served as a cue in these cases. Pheromones on the exposed skin surface may not be informative about the female's orientation, especially if a male has access to only a small part of the female's body. The same may be true of ultrastructural characteristics of the scale surface.

We turn now to the cues that *were* used by males. First, a female's direction of movement is a simple and well-nigh infallible cue to her orientation. It is not always available, however: many females remain sedentary for long periods, and are often mated before moving far from their initial point of emergence from the den (pers. obs.). Thus, males need additional cues as well. Our experiments show that they must somehow obtain these cues from the female's skin, because males can align successfully when only the excised skin is available. The cues involve pheromones, because males have more difficulty aligning after the pheromones begin to degrade. Paradoxically, however, removing most of the surface pheromones from the exposed portions of the female's skin (with hexane) did not compromise male alignment ability. In combination, these two results suggest that the relevant pheromones must be located in places where they are not removed by brief immersion in hexane. The area beneath overlapping scales is such a location. Histology supports this notion; female sex pheromones in red-sided garter-snakes are concentrated close to the skin surface in an area at the base of each scale, overlain by the anterior scale (Gartska *et al.*, 1982). This 'hinge' area (where the base of the scale inserts into the dermis) is also the place where the underlying epidermis is thinnest, and where the underlying circulation approaches the surface most closely (Gartska *et al.*, 1982). These features should facilitate the male's ability to detect the pheromone.

If pheromones are concentrated in the 'hinge' area deep beneath overlying scales, how can a courting male detect the pheromone? Chin-rubbing may play an important role in this respect. As Gillingham (1987, p. 189) noted, 'dorsal advance and chin rubbing are by far the most ubiquitous courtship acts observed in snakes'. We suggest that firm adpressing of the chin, in combination with frequent tongue-flicking, provides a courting male with information on the female's alignment as well as her reproductive condition. A male that adpresses his chin firmly as he moves along the female's body, will thereby tend to depress each scale that he touches. This effect has two consequences:

(1) physical. A chin moving anteriorly will encounter the leading (free) edge of each scale, whereas a chin moving posteriorly will glide over them. Ophiophagous snakes use the direction of scale overlap as a cue for the direction of prey ingestion (Greene, 1976). Courting males may well use the same cue to ascertain female orientation.

(2) pheromonal. A male's chin moving anteriorly will tend to open a small space between the scale that is being pushed down and the one immediately anterior to it. Thus, his tongue-tips will more easily penetrate the space between adjacent scales, and encounter the higher concentrations of pheromone in the 'hinge' region. In contrast, a male adpressing as he moves posteriorly will push the adjacent scales tightly against each other, thereby reducing access to the 'hinge' region. Thus, anterior movement would expose a male's vomeronasal organ to higher concentrations of pheromones. Such exposure would be enhanced by the tendency of male snakes to move forward along the female's body in an intermittent rather than continuous fashion. These short pauses may provide opportunities for the flickering tongue to penetrate between scales anterior to the male's snout.

Both of these mechanisms offer plausible cues by which males could assess female alignment accurately even when they have only an excised skin to court (above). The two putative functions are not mutually exclusive, because a single behaviour (chin-pressing) provides both types of information (*i.e.* physical as well as pheromonal).

We can envisage only two alternative hypotheses for the functional significance of 'chin-rubbing' in male snakes:

(1) Chin-pressing merely serves to bring the male's tongue close to the female's body. This hypothesis fails to explain why courting males press their chins so firmly against their partners. Sensory input is unlikely to require so much pressure, but it is exactly what we would expect if adpressing functions to physically depress scales to allow access to the otherwise hidden 'hinge' region.

(2) The male's chin contains sensory organs that detect some characteristic of the female. Male snakes of some species do indeed possess enlarged scales in this region, but histological studies reveal no chemosensory apparatus within them (*e.g.* Blanchard, 1931; Jackson & Sharawy, 1980). Covering these scales does not reduce the intensity

of male courtship, whereas blocking the vomeronasal system shuts courtship down completely (Kubie *et al.*, 1978).

In summary, our simple experiments clarify the mechanisms that male gartersnakes use to align themselves correctly during courtship. The snakes rely upon multiple cues, primarily those that provide the most reliable information about the female's orientation. Our results also suggest a novel hypothesis about the functional significance of one of the most distinctive and ubiquitous features of snake courtship: chin-pressing by amorous males.

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