

# Benefits of female mimicry in snakes

She-male garter snakes exploit the amorous attentions of other males to warm up.

Males of several animal species mimic females either in appearance or in the chemical cues they release<sup>1,2</sup>, and this mimicry has generally been interpreted in terms of alternative mating strategies — for example, a male that mimics a female may obtain stolen inseminations or avoid aggression from larger rivals<sup>3</sup>. Our studies of snakes suggest a different explanation, which relies on natural selection rather than sexual selection. Male garter snakes that produce female-like pheromones (she-males) may benefit simply because large ‘mating balls’ of amorous males form around them, transferring heat to the she-male after it emerges from hibernation and reducing its exposure to predators.

Garter snakes (*Thamnophis sirtalis parietalis*) in Manitoba, Canada, court and mate in large aggregations centred around overwintering dens. It has been suggested that the advantage of mimicry lies in a she-male’s ability to confuse other males within the mating balls (which sometimes contain more than 100 males) that form around genuine females<sup>2</sup>, but she-maleness has since been shown to be a transitory phase that is restricted to the first day or two after a male first emerges from his eight-month hibernation<sup>4,5</sup>. The snakes are weak and slow at this time and are therefore highly vulnerable to attack by crows<sup>6</sup>. We have identified no mating advantage to she-males<sup>4</sup>, and propose an alternative explanation for female mimicry in this species.

The primary purpose of males producing female pheromones is to attract courtship from other males; indeed, most she-males are virtually obscured by the bodies of their suitors (Fig. 1). At a den near Inwood, Manitoba<sup>5</sup>, 49 of 53 newly emerged she-males were partly covered by other males when sighted; overall, an average of 58% of the body of each she-male was covered by other males (s.e., 4.0), whereas only 32 of 55 he-males (at more than 2 days after emergence; none of these was courted) were partly obscured, with an average of 25% cover (s.e., 4.3; one-factor ANOVA,  $F_{1,106} = 31.0$ ,  $P < 0.0001$ ).

She-maleness may benefit newly emerged animals (which are cold, weak and slow<sup>4</sup>) for two reasons. First, a snake hidden beneath other individuals may be less vulnerable to attack by crows<sup>6–8</sup>. Second, courting males press vigorously against the object of their affections<sup>9</sup> and may thus transfer heat — newly emerged snakes are cool (ground temperature is below 10 °C), but reproductive males are on average

warmer than 25 °C (ref. 10). Courtship could thus increase a she-male’s body temperature and therefore his locomotor capacity<sup>11</sup>, as well as accelerating his recovery from hibernation. Many dens are deeply shaded and smooth-sided, making it difficult for a newly emerged snake to bask in sunlight. Because reproductive males travel constantly back and forth between the den and surrounding clearings, however, a snake that attracts courtship will be covered in hot males as soon as it emerges.

Does a cold snake warm up faster if it is courted by hot males? To test this idea, we glued miniature thermal data-loggers (Thermochron 1-buttons, Dallas Semiconductor) to the mid-dorsal surfaces of 24 females, which we placed in open-topped outdoor arenas measuring 1 × 1 × 1 m (ref. 4). Six arenas contained only four females each, whereas the others contained four females plus twenty males. The average temperature of females was 4 °C and that of males was 25 °C when we commenced the trials at 11:00 h to mimic newly emerging snakes. The females were heated to 20 °C within 30 min, with courted snakes heating faster than uncourted animals (repeated-measures ANOVA on data from each minute over this period, interaction  $F_{29,638} = 3.87$ ,  $P < 0.0001$ ).

To verify that this effect was due to heat transfer rather than to courtship-induced changes in the behaviour of courted animals, we repeated the study using dead snakes as the courtship ‘targets’, with thermistor leads implanted to measure deep-body temperature. Again, snakes exposed to courtship were heated faster than those that were not (repeated-measures ANOVA,  $F_{29,203} = 1.82$ ,  $P < 0.01$ ). The thermal benefit from courtship often exceeded 3 °C.

Do higher temperatures accelerate recovery from hibernation? We investigated this possibility by capturing she-males soon after they emerged, and then keeping them either warm (28 °C) or cool (10 °C). At 90-min intervals, we brought five she-males from each group to 25 °C and then held them by their tails in the den to quantify their sexual attractiveness. We scored the responses by five mate-searching males to each she-male, using a four-point scale<sup>4</sup>. ‘Warm’ she-males regained their he-male status within 3 hours, whereas ‘cool’ snakes remained as she-males for over 5 hours. The intensity of courtship that she-males attracted from other males therefore decreased more rapidly in snakes that were kept warmer (interaction between thermal



**Figure 1** A newly emerged female-mimicking (she-male) garter snake (*Thamnophis sirtalis parietalis*), still covered in white limestone dust from its underground hibernation den, is enthusiastically courted by five other adult male snakes. The she-male may benefit through heat transfer from its suitors, as well as from reduced vulnerability to predatory crows (photo, D. O’Connor).

treatment and time,  $F_{3,32} = 3.96$ ,  $P < 0.02$ ).

We conclude that alternative male mating strategies such as female mimicry might have evolved through natural selection (for thermoregulation and predator defence), rather than through sexual selection, as has generally been surmised<sup>1–3</sup>. She-male garter snakes may therefore manipulate their rivals’ behaviour not to ‘steal’ matings, but to warm up and to reduce their own vulnerability to predation. Although intuition would favour an interpretation that female mimicry has evolved within the context of alternative mating tactics, simpler explanations should also be investigated.

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- Andersson, M. *Sexual Selection* (Princeton Univ. Press, Princeton, New Jersey, 1994).
- Mason, R. T. & Crews, D. *Nature* **316**, 59–60 (1985).
- Trivers, R. L. *Evolution* **30**, 253–269 (1976).
- Shine, R., Harlow, P. S., LeMaster, M. P., Moore, I. & Mason, R. T. *Anim. Behav.* **59**, 349–359 (2000).
- Shine, R., O’Connor, D. & Mason, R. T. *Can. J. Zool.* **78**, 1391–1396 (2000).
- Shine, R., LeMaster, M. P., Moore, I. T., Olsson, M. M. & Mason, R. T. *Evolution* **55**, 598–604 (2001).
- Olson, D. H. *Copeia* **1989**, 391–397 (1989).
- Hamilton, W. D. *J. Theor. Biol.* **31**, 295–311 (1971).
- Whittier, J. M., Mason, R. T. & Crews, D. *Behav. Ecol. Sociobiol.* **16**, 257–261 (1985).
- Shine, R., Harlow, P. S., Elphick, M. J., Olsson, M. M. & Mason, R. T. *Physiol. Biochem. Zool.* **73**, 508–516 (2000).
- Heckrotte, C. *Copeia* **1967**, 759–763 (1967).

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