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Female mimicry in garter snakes

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In many diverse taxa, males of the same species often exhibit multiple mating strategies[1]. One well-documented alternative male reproductive pattern is 'female mimicry', whereby males assume a female-like morphology[2–8] or mimic female behaviour patterns[9,10]. In some species males mimic both female morphology and behaviour[2,7,11,12]. We report here female mimicry in a reptile, the red-sided garter snake (*Thamnophis sirtalis parietalis*). This form of mimicry is unique in that it is expressed as a physiological feminization. Courting male red-sided garter snakes detect a female-specific pheromone and normally avoid courting other males. However, a small proportion of males release a pheromone that attracts other males, as though they were females. In the field, mating aggregations of 5–17 males were observed formed around these individual attractive males, which we have termed 'she-males'. In competitive mating trails, she-males mated with females significantly more often than did normal males, demonstrating not only reproductive competence but also a possible selective advantage to males with this female-like pheromone.

On emergence from the winter den, female red-sided garter snakes are usually courted by 10–20, but sometimes as many as 100 males simultaneously, although only one male mates with the female[13]. Males begin to court females when rapid tongue-flicks by the male deliver pheromone cues from the female's dorsal surface to the male's vomeronasal organ[14,15]. During the spring of 1983, a census was taken of presumed 'mating balls' at a study site in central Manitoba, Canada. In 33 of the observed 200 (14%) mating balls studied, no female was found; instead a single male was being courted by the other males. These courted males (she-males) possessed normal hemipenes, testes and accessory sex structures and their mean snout–vent length and body weight did not differ significantly from those of other males taken at random from the population.

The attractivity of she-males is not caused by prior physical contact with recently emerged females. Males rubbed against a recently emerged, attractive female were not courted by other

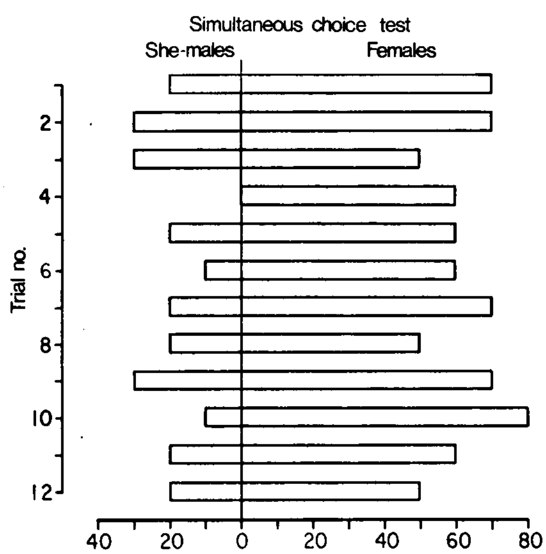


Table 1 Circulating levels of sex steroid hormone in the two male morphs and the female red-sided garter snake

	(n)	Hormone (ng ml^{-1}) Testosterone	Oestradiol	Dihydro-testosterone
Male	9	5.720 ± 1.655	0.061 ± 0.012	0.231 ± 0.066
Female	9	0.233 ± 0.082	7.703 ± 3.440	0.093 ± 0.017
She-male	9	19.785 ± 5.703	0.075 ± 0.013	0.142 ± 0.025
F ratio (d.f. 2, 24)		7.68	3.69	2.45
$F \geq 3.40$, $P > 0.05$				

Plasma levels of dihydrotestosterone, oestradiol and testosterone were determined by steroid radioimmunoassay. Values are the mean ± s.e.m.

males, agreeing with field and laboratory observations in which recently mated males that have been in contact with females for up to 1 h have never been observed to be courted. The attractivity of the she-males appears to be as permanent as that of sexually mature females[16]. All of the she-males tested ($n = 33$) elicted courtship from sexually active males when tested at 3, 18 and 40 weeks after capture.

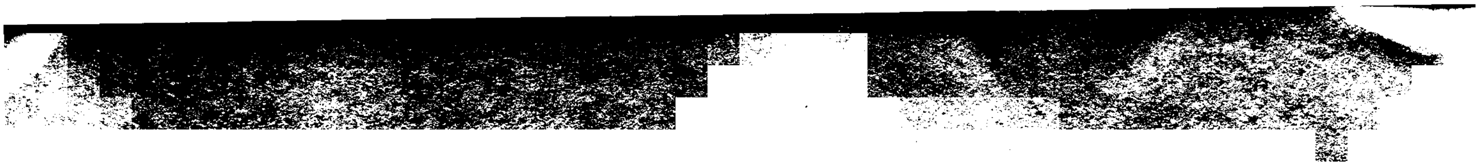
Steroid hormone levels were assayed on blood samples taken in the field from males, females and she-males[17]. Analysis of variance revealed that females had significantly higher circulating levels of oestradiol than either males or she-males ($P < 0.05$, Student–Newman Keuls) (Table 1). Although testosterone levels in males and females were not significantly different, she-males had significantly higher levels of testosterone than either females or males ($P < 0.05$, Student–Newman Keuls). There were no significant differences in circulating levels of dihydrotestosterone. Presumably, the high levels of testosterone in the she-males was a result of either higher secretion or reduced clearance from the circulation.

The pheromone produced by the she-males is apparently indistinguishable from that produced by females. Samples obtained from the skin surface using the non-polar solvent toluene revealed that the skin of females and she-males, but not of males, elicited courtship behaviour from conspecific males at the den site (Table 2). However, in simultaneous choice tests ($n = 12$) in which 10 courting males were able to choose between a female and a she-male, the majority of males preferred the female in every case, although in each trial some males also courted the she-male (Fig. 1). Thus, females may produce more of the pheromone or they may produce a qualitatively different pheromone from that of she-males.

Competitive mating trials were conducted in the field in which groups of five males and five she-males were selected at random and released into an arena (1 m × 1 m) with an unmated, attractive female. In a total of 42 mating trials, 29 resulted in a she-male mating with the female and 13 with a male mating; thus, she-males mated significantly more often than did normal males ($\chi^2 = 11.85$, $P < 0.001$). In field observations, she-males joining an established mating ball caused courting males to ignore the female and begin to court the she-male. A possible advantage to the she-male's attractiveness thus lies in an ability to gain a

Table 2 Transfer of the attractiveness pheromone

Trial no.	Female	Male	She-male
1	+	−	+
2	+	−	+
3	+	−	+
4	+	−	
5	+	−	



better position in the mating ball by confusing other males.

Currently, breeding experiments and future field work are being designed to resolve an enigma: why are all males not she-males if she-males do indeed have a reproductive advantage over normal males?

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