Pheromonal inhibition of male courtship behaviour in the brown tree snake, *Boiga irregularis*: a mechanism for the rejection of potential mates

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Pheromones play a central role in coordinating the events leading up to copulation in snakes. We report here a novel pheromone system in the brown tree snake in which females release a pheromone that inhibits male courtship behaviour. In a previous study, we made observations of female brown tree snakes releasing cloacal secretions (CS) during courtship that appeared to cause courting males to cease courtship. All snakes have glands that release CS through ducts located along the cloacal orifice. Although CS have been studied for many years, their function in the mediation of snake behaviour has not been experimentally well determined. We examined the role of CS in the reproductive behaviour of male and female brown tree snakes. We conducted four experiments to test the effect of both male and female CS on brown tree snake behaviour under two behavioural contexts, courtship and male–male ritualized combat. Within each experiment, we compared the effects of CS to a control. Female CS caused a decrease in the time that males spent courting females and a decrease in the intensity of courtship compared with the control treatment. Male CS did not, however, affect the time that males spent displaying courtship or the intensity of that courtship. Neither male nor female CS had significant effects on male ritualized combat behaviour, including time that males spent in combat or the intensity of combat behaviours displayed. Furthermore, neither female nor male CS had an effect on female courtship versus controls. The inhibition of brown tree snake reproductive behaviours is specific to female CS inhibiting male courtship behaviour. This pheromone acts in concert with the female sex pheromone to regulate the events leading to copulation.

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In snakes, the coordination of the male and female behaviours leading to copulation are mediated, in large part, by pheromones. Snakes use pheromones for sex identification, to attract potential mates, to release courtship or other associated behaviours such as male combat, and to advertise mated status (reviewed in Mason 1992; Mason et al. 1998). By examining the pheromone systems of a single species, we are able to understand how pheromones regulate the events cumulating in copulation, such as female mate choice. In this study, we investigated the pheromonal inhibition of male courtship behaviour by female brown tree snakes, a novel pheromone system in reptiles.

The brown tree snake is an arboreal, rear-fanged colubrid native to the forests of Australia, Papua-New

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Guinea and the Solomon Islands (Cogger 1992; Rodda et al. 1997). This species was accidentally introduced to the island of Guam, where it has caused significant economic and ecological damage, including the extinction or extirpation of nine forest bird species (Rodda et al. 1992, 1997). Individuals maximally attain snout-to-vent lengths of 3 m and masses of 2 kg, with a sexual dimorphism consisting of longer and heavier males (Cogger 1992; Rodda et al. 1997).

Male courtship behaviour in this species is released by a female sex pheromone consisting of a suite of nonpolar, nonvolatile skin lipids (Greene & Mason 1998). Male brown tree snakes also display ritualized combat behaviour, which presumably serves as a contest between males for access to potential mates during the breeding season (Greene & Mason 2000). Males also follow pheromone trails of conspecifics (both sexes) under breeding conditions (Greene et al. 2001).

Female brown tree snakes are unusually active in courtship compared with other snake species, displaying

behaviours that elicit male courtship and possibly allow the female to assess the quality of courting males (Greene & Mason 2000). We have observed females displaying courtship behaviours normally associated with male courtship, including head-jerking, mounting and chin-rubbing, in response to attractive males. We have also observed females eliciting courtship from males using head-lifting displays, in which the individual bobs its head nearly perpendicular to the ground, a behaviour commonly observed in male–male combat. We hypothesized that female brown tree snakes measure the response of males to these displays to assess winners and losers of male–male combat bouts, much like female *Agkistrodon contortrix* (Schuett & Duvall 1996; Greene & Mason 2000).

In contrast, other female courtship behaviours seemingly inhibit male courtship (Greene & Mason 2000). In response to male courtship, females have been observed to lift their tails nearly perpendicular to the ground, gape their cloacae and release a bolus of liquid. Cloacal secretions (CS) originate from both of the paired cloacal glands in the snakes' tails and from the urogenital opening in the cloaca. CS consist of a clear, viscous liquid containing a yellow or white precipitate. The release of CS has profound effects on male courtship; males that were vigorously courting females stopped displaying courtship in all cases where females were observed to release CS (Greene & Mason 2000). In these cases, males typically remained near the female, following her around the enclosure and investigating her with tongue-flicks.

All snakes have a pair of cloacal glands (also called scent glands or cloacal sacs) in their tails that open into the cloaca through two small ducts found along the cloacal orifice (Graves & Duvall 1988; Mason 1992). It is common for disturbed snakes to release a bolus of CS, distributing the malodorous and distasteful secretion by lashing their tails. Because snakes have few glandular secretions, the function of CS has been examined for years. It has been hypothesized that CS act as a defensive mechanism, being distasteful to predators (Mason 1992). Furthermore, because CS in snakes are volatile and have a noticeable odour, it has been hypothesized that they serve an alarm signal function to warn conspecifics of danger, as has been shown in the rattlesnake *Crotalis viridis* (Andrén 1986; Graves & Duvall 1988). The secretions of a blind-snake, *Leptotyphlops dulcis*, repel ants during feeding attempts (Gehlbach et al. 1968; Watkins et al. 1969). Chemical analyses of the cloacal gland secretions from garter snakes (genus *Thamnophis*) have shown that the secretions are composed of a variety of nonvolatile lipids and proteins and at least seven volatile components including trimethylamine, acetic acid and propanoic acid (Weldon & Leto 1995; Wood et al. 1995).

Although the function of CS has long been studied, few experimental data clearly explain the function of this secretion in snakes. The experiments conducted as part of this study were designed to test the hypothesis that female CS inhibit male courtship. Furthermore, the experiments were designed to determine whether the pheromone acts under specific behavioural contexts and whether the pheromone is present in the CS of both males and females.

METHODS

Husbandry

Subjects were collected in the field on Guam and housed in our laboratory for 6 years before the study under an established laboratory protocol (Greene et al. 1997). The snakes ($N=7$ females and 10 males) were housed in Plexiglas cages designed specifically for arboreal reptiles (Mason et al. 1991) and were fed a diet consisting of thawed mice or chicks every 3 weeks (Greene et al. 1997). Males in the colony had a mean ± SD snout–vent length of 162.2 ± 22.1 cm and a mean ± SD mass of 647.5 ± 265.7 g. Females had a mean snout–vent length of 137.9 ± 9.9 cm and a mean mass of 385.7 ± 81.5 g. Temperatures cycled from 25 to 30°C and relative humidity in the room ranged between 75 and 80%. Lighting (about 14:10 h light:dark cycle) was provided by overhead fluorescent lights and ambient sunlight entering the room through windows. All snakes were in breeding condition during the study.

General Experimental Conditions

We conducted four experiments to characterize the effects (sex specificity and context specificity) of cloacal secretions on male behaviour, as follows: (1) female CS versus a control on male courtship behaviour ($N=7$; CS from female of pair), (2) male CS versus a control on male courtship behaviour ($N=7$; CS from male of pair), (3) female CS versus a control on male combat behaviour ($N=5$; CS from randomly chosen female) and (4) male CS versus a control on male combat behaviour ($N=5$; CS from both males). Because brown tree snakes are particularly sensitive to handling, we conducted separate experiments to provide approximately 1-week breaks between experiments to reduce stress and fatigue on the animals, and to provide an opportunity to feed and maintain them. The order of the experiments was randomized. The control solution was composed of a 5% aqueous solution of cologne (Aqua Velva, JB Williams Company, White Plains, New York, U.S.A.).

Different male–female or male–male pairs were randomly selected for each experiment. Within an experiment, we tested the pairs using a switchback, or counterbalance, approach, where on the first night of an experiment, we randomly treated the pairs with either CS or a control solution. On the second night of the experiment, we applied the other treatment to the pair.

Experiments were conducted during scotophase, when the snakes were most active, in a clear Plexiglas arena designed specifically for the observation of brown tree snake courtship behaviour (Greene & Mason 2000). The arena was constructed with sides measuring 1.5 m, providing 2.25 m² of floor area. Clear Plexiglas doors on opposite sides of the arena allowed access to the inside of the cage for cleaning and for transfer of snakes. Two red

7-W incandescent lights, mounted above the roof of the arena, provided sufficient light for videotaping the trials through the walls. Data were later collected from video-tape by an observer blind to the treatments. Between trials, the floor and walls of the arena were cleaned using soap and water, dried using paper towels, and allowed to air-dry with the doors open for 30 min before the next trial was conducted. Environmental conditions (ambient temperature and relative humidity) remained constant over the entire study.

CS were collected immediately before a trial by gaping a snake's cloaca and applying light pressure anterior and posterior to the vent. The CS collected in this manner were composed primarily of a clear, viscous liquid with some yellow or white precipitate and appeared and smelled identical to CS voluntarily released by females during courtship. CS were collected into a clean 15-ml screw-top vial and stored at room temperature until used in the experiment. All samples were used in a trial within 15 min following collection.

A trial began when a male–female or a male–male pair was placed into the arena and allowed to initiate court-ship or combat behaviour. After 90 s of courtship or combat behaviour commenced at the level of chin-rubbing (see Greene & Mason 2000), we added approxi-mately 1 ml of CS or control to the arena using a Pasteur pipette. Treatments were added to the arena through a hole in one of the cage walls, which was covered with paper to prevent the snakes from observing the investigator adding the treatment. The treatment landed in the centre of the arena, well away from the snakes, which typically interacted near one of the arena walls or in a corner.

A 10-min observation period followed the introduction of the treatment. During the observation period, we recorded the time that males spent courting or combating and the time that members of the pair spent in direct contact to quantify the inhibitory effects of CS on male behaviour.

To quantify the intensity of courtship or combat, we used the following formula (modified from Lahav et al. 1999):

$$\frac{\sum_{i-1}^{n} S_i \times t_i}{T}$$

where S_i is the courtship or combat score, t_i is the duration of time spent courting or combating at each score and T is the total time that the snakes of the pair spent in direct contact with each other. We assigned courtship and combat scores using hierarchical scales of courtship and combat behaviour that summarize a pre-vious analysis of courtship and combat in this species (Greene & Mason 2000). Higher scores indicate a behav-iour closer to copulation or winning a combat bout. We used a 0–5 scale to determine courtship scores: (0) no courtship, (1) head-jerking, (2) chin-rubbing, (3) body-alignment, (4) tail-search copulatory attempts and (5) copulation. We used a 0–6 scale to determine combat score: (0) no combat, (1) head-jerking, (2) mounting and
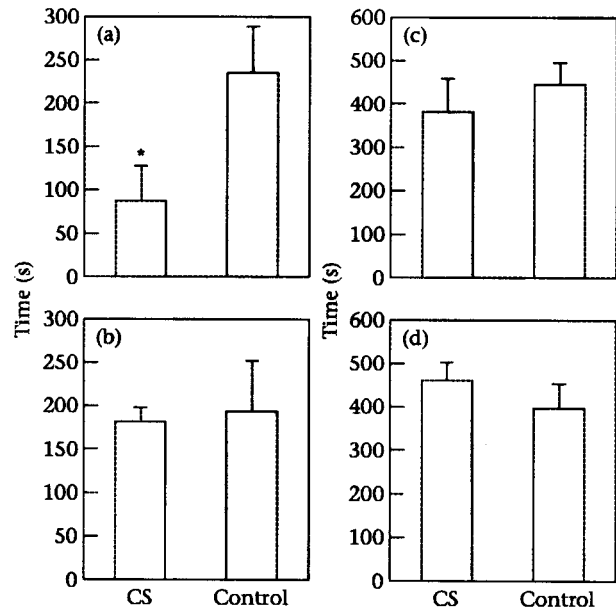

Figure 1. Mean±SE time that male brown tree snakes spent either courting or combating in each experiment when treated with cloacal secretions (CS) or a control. Time that males spent courting females when treated with (a) female CS or control and (b) male CS or control. Time males spent combating when treated with (c) female CS or control and (d) male CS or control. *P<0.05 (Wilcoxon matched-pairs signed-ranks test).

chin-rubbing, (3) body-alignment, (4) head-pinning, (5) body-entwinement and (6) fleeing by loser. For example, an observation of a male chin-rubbing a female during courtship would be assigned an S_i value of 2.

Finally, to determine whether CS have an effect on female courtship, we measured the mean amount of time females spent actively courting males during experiments 1 and 2 when treated with CS or the control.

All statistical comparisons were made by comparing paired data from within each experiment. We used the Wilcoxon matched-pairs signed-ranks test to compare both time and courtship/combat intensity data (Sokal & Rohlf 1995).

RESULTS

Effect of CS on Time Males Spent Courting or Combating

In experiment 1, female CS reduced the amount of time males spent courting females when compared to the control treatment (Wilcoxon matched-pairs signed-ranks test: $T=27$, $N=7$, $P<0.030$; Fig. 1a). When treated with CS, males spent a mean ± SE of 87.1 ± 43.0 s courting versus 234.7 ± 52.8 s when treated with the control. In contrast, there were no significant differences in time spent court-ing by males when exposed to male CS versus the control ($T=9$, $N=7$, $P<0.844$; Fig. 1b). Neither female CS ($T=6$, $N=4$, $P<0.250$; experiment 3) nor male CS ($T=2$, $N=5$, $P<0.188$; experiment 4) significantly reduced the mean
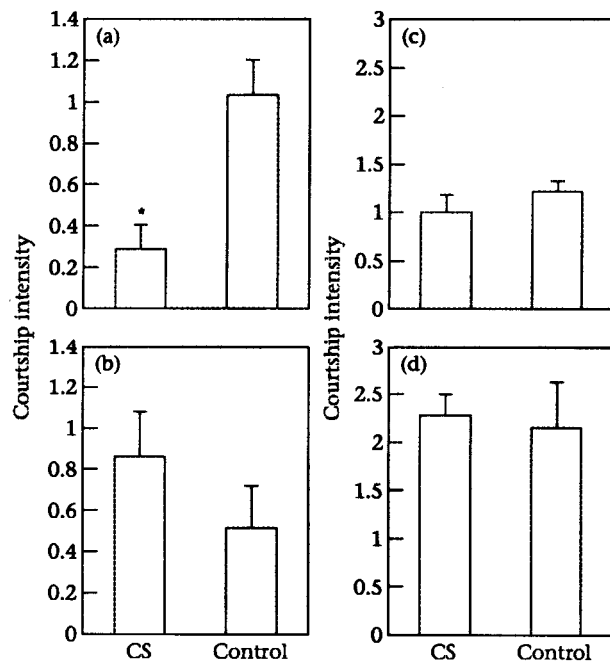
Figure 2. Mean±SE courtship or combat intensities displayed by male brown tree snakes when treated with cloacal secretions (CS) or control. Courtship intensity when treated with (a) female CS or control and (b) male CS or control. Combat intensity when treated with (c) female CS or control and (d) male CS or control. *P<0.05 (Wilcoxon matched-pairs signed-ranks test).

times males spent in combat compared with the control treatment (Fig. 1c, d).

Effect of CS on the Intensity of Male Courtship and Combat

In experiment 1, female CS also reduced the intensity of male courtship when compared to control-treated males (T=28, N=7, P<0.018: Fig. 2a). CS-treated males had a mean ± SE courtship intensity of 0.28 ± 0.12 versus 1.02 ± 0.17 for control-treated males. Male CS did not significantly reduce the intensity of male courtship (T=6, N=7, P<0.345; Fig. 2b). Neither female nor male CS reduced combat intensity compared with the control (T=9, N=4, P<0.144 and T=7, N=5, P<0.892, respectively; Fig. 2c, d).

Effect of CS on Time Pairs Spent in Direct Contact

CS did not significantly reduce the time that members of the pair spent in contact with each other versus the control solution in any of the four experiments (experiment 1: T=14, N=7, P<1.000; experiment 2: T=6, N=6, P<0.875; experiment 3: T=2, N=4, P<1.000; experiment 4: T=1, N=5, P<0.125)

Effect of CS on Time Females Spent Courting Males

There were no significant reductions in the mean time that females spent actively courting males after females

were treated with their own CS versus the control solution (T=16, N=7, P<0.813) or after male CS and the control were added to the arena (T=37, N=6, P<0.818).

DISCUSSION

The results of this study confirm previous observations of male courtship inhibition by females in the brown tree snake (Greene & Mason 2000). Furthermore, we were able to determine the context under which the pheromone operates. This pheromonal signal was present only in female CS and was effective in the context of courtship. Pheromonal effects were observed only on males and not on females. These results represent a novel mechanism of courtship inhibition in a reptile and strong experimental evidence to implicate cloacal secretions in the mediation of snake behaviour (Watkins et al. 1969; Graves & Duvall 1988).

Observations made during the experiments provide insights into the chemical nature of this courtship inhibition pheromone. Brown tree snakes, like other snake species, are highly thigmotactic in nature, preferring to stay near edges, such as the arena wall, even during courtship or combat. In our experiments, CS were added so that they landed in the centre of the arena floor, and away from the snakes, which were typically along the arena walls. It was rare for a male to directly tongue-flick the CS added to the arena (one observation during 24 total trials). In snakes, tongue-flicking serves to deliver primarily nonvolatile chemicals to the vomeronasal organs where they are detected (Halpern & Kubie 1980; Halpern 1987). The behavioural effects of female CS on male courtship thus appear to be mediated via a volatile pheromone, although this hypothesis remains to be tested experimentally.

Most pheromones studied in snakes are nonvolatile integumental compounds (Noble 1937; Gillingham & Dickinson 1980; Halpern & Kubie 1980; Andrén 1982; Mason et al. 1989, 1990; Mason 1992), and little experimental attention has been paid to volatile snake pheromones (Watkins et al. 1969; Graves & Duvall 1988). Because snakes have few glands that release volatile signals, particular attention has been paid to the paired cloacal glands in the tail of all species of snakes. Studies have most often studied cloacal secretions in the context of alarm signals, although little experimental data support this idea (Graves & Duvall 1988). In this study, female CS did not seem to inhibit male courtship behaviour through a generalized alarm response. If this were the case, sex- and context-specific responses like the ones that we observed would not have occurred. Female CS affected males only during courtship and not during combat behaviour, and male CS had no effects on females or other males during combat. This result does not, however, preclude the use of CS as an alarm pheromone or predator deterrent in another context outside of reproduction, because brown tree snakes release CS when disturbed.

During courtship, observations of females releasing CS were always accompanied by tail-raising behaviour. This response suggests that both a chemical and a visual signal

are involved in inhibiting male courtship behaviour, although the results of this study indicate that the release of CS alone is sufficient to inhibit male courtship behaviour. Although visual signals are important in snake courtship and combat (Carpenter 1977; Gillingham 1979, 1980; Secor 1990), pheromones are necessary to release these behaviours (Noble 1937; Kubie et al. 1978; Mason et al. 1989, 1990). It is possible that a more pronounced response would have occurred if the females in this study had displayed tail-raising behaviour or other behaviours associated with a lack of receptivity, such as body-bumping and tail-lashing (Greene & Mason 2000). The effect of the pheromone overrode the effects of courtship displays expressed by females during the courtship trials, demonstrating the stereotypic response of the brown tree snake to the pheromone.

The inhibition of male courtship behaviour by the release of female CS may represent a mechanism for females to reject unsuitable mates or to signal that they are not sexually active at the time of courtship (Greene & Mason 2000). Male snakes cannot force copulation, so females ultimately determine whether copulation will be the outcome of a courtship event. Therefore, there would be clear motivation for a male snake to cease courtship once a female has signalled that she is not receptive, because further displays of courtship with the same female would be costly. Such displays could result in the male missing other mating opportunities or attract predators. Termination of unwanted courtship could also be advantageous to females by reducing their exposure to predators, and protecting them from physical harm from the longer and heavier males of this species. For example, in the garter snake Thamnophis sirtalis parietalis, courting aggregations, called mating balls, comprise up to 100 males and a single female, and females within these mating balls risk being suffocated (Shine et al. 2001).

In other snake species, male length and mass are indicators of male mating success (Madsen & Shine 1993; Weatherhead et al. 1995; Brown & Weatherhead 1999; Shine et al. 2000). Observations in the brown tree snake (Greene & Mason 2000), however, indicate that females do not reject males with CS based upon male mass or snout–vent length. These observations were made in captivity using a reasonably small sample of males, so further experiments will be necessary to understand what male qualities female brown tree snakes assess during mate choice. Winning or losing male combat behaviour in the brown tree snake (Greene & Mason 2000) may be particularly important in determining whether a female rejects a male with CS during courtship; we found that winners of combat bouts were significantly heavier and longer than losers (Greene & Mason 2000). Furthermore, females in the laboratory mate multiply (we have observed multiple mating with different males, but have not tested for multiple mating with the same male). Thus, it is plausible that females may reject males based on mating history; a female may reject males she has mated with but accept those she has not in order to increase sperm competition. However, we have limited data on such phenomena and need further experiments to test such hypotheses.

In concert with the female sex pheromone, which acts to attract potential mates and release male courtship behaviour, the courtship inhibition pheromone can act as a regulatory mechanism to mediate male courtship. The female sex pheromone of the brown tree snake cannot be turned on and off rapidly; it is a skin lipid component present on a female's surface throughout the breeding season. A skin-shedding event would be necessary to change the skin lipid layer and remove the pheromone. As such, female snakes remain attractive to males throughout the breeding season. In contrast, the volatile courtship inhibition pheromone is a temporary and probably energetically cheap mechanism to thwart unwanted courtship. Thus, the female sex pheromone is constituently 'on', but the courtship inhibition is voluntarily released to negatively feed back on male courtship.

Our future work will examine more specifically how female mate choice operates in this mating system, particularly in regard to females' responses to males that win or lose combat events, and will chemically characterize and identify the biologically relevant chemical compounds present in female CS that comprise the pheromone. Field experiments are needed to complement this work and to rule out alternative hypotheses, such as that the observed behaviours were an artefact of laboratory conditions, and to determine under what situations females reject male courtship. It is possible, for example, that this behaviour is more rare in the wild, where individuals interact less often than under captive conditions, where they are also contained in cages during experiments. We will also test whether the pheromone present in female CS acts only during courtship (i.e. in conjunction with the female sex pheromone) or whether exposure to the pheromone before courtship (i.e. independent of the female sex pheromone) can also inhibit male behaviour.

Acknowledgments

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