

COURTSHIP, MATING, AND MALE COMBAT OF THE BROWN TREE SNAKE, *BOIGA IRREGULARIS*

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ABSTRACT: The brown tree snake, *Boiga irregularis*, is an introduced pest species on the island of Guam where it has caused significant economic and ecological damage. Despite the need for basic biological information about this species to manage it effectively, little is known about its reproductive behavior. We report here the repertoire of reproductive behaviors displayed by this species. The courtship behavior of the brown tree snake parallels that of other colubrids, adhering to the triphasic schema developed to standardize descriptions of colubrid courtship; nonetheless, there are differences in the specific behaviors displayed. Unlike most other colubrids, female brown tree snakes employ courtship behaviors normally displayed only by males. In addition, females can inhibit male courtship through the use of a pheromone released in a liquid secretion from the cloaca. Male brown tree snakes show ritualized combat behavior similar to that observed in other colubrid species. Longer and heavier males always won combat events in the study.

Key words: Courtship behavior; Male combat behavior; Brown tree snake; *Boiga irregularis*; Pheromones; Reptilia; Colubridae

REPRODUCTIVE and ritualized combat behaviors have been described in detail for many species of snakes (Andr n, 1986; Carpenter and Ferguson, 1977; Davis, 1936; Lowe, 1948; Schuett and Gillingham, 1988, 1989; Secor, 1987, 1990; Shaw, 1951). These behaviors tend to be "ritualistic" in snakes and can be divided into clearly identifiable motor patterns comparable among species when standardized terminology is used (Carpenter 1980; Carpenter and Ferguson, 1977; Gillingham, 1979; Secor, 1987). However, the vast majority of these reports have been conducted on northern temperate species while few descriptions of tropical snake behaviors have been published (Barker et al., 1979; Gillingham and Chambers, 1982).

The purpose of our paper is to describe the repertoire of courtship, mating, and ritualized combat behaviors displayed by the brown tree snake (*Boiga irregularis*), a rear-fanged colubrid native to the forests of Australia, Papua New Guinea and the Solomon Islands (Cogger, 1992). This species is nocturnal and forages on a generalized diet of mammals, reptiles, amphibians, and birds which are killed by a combination of constriction and envenomation (Greene, 1989; Savidge, 1988; Shine,

1991; Vest et al., 1991). The brown tree snake is arboreal and has a relatively slender body that is characteristic of arboreal snakes (Lillywhite and Henderson, 1993). Brown tree snakes can attain snout-vent lengths (SVL) of 3 m, masses of 2 kg, and are sexually dimorphic with males being both longer and heavier than females (Fritts, 1988).

The brown tree snake was accidentally introduced onto the island of Guam sometime during or after World War II where it proliferated, reaching densities of up to 100 snakes per hectare (Rodda et al., 1992). The snakes have caused the extinction or extirpation of nine native forest birds and have affected nearly all vertebrate populations on the island through predation (Rodda and Fritts, 1992; Savidge, 1987; Wiles, 1987). They have also become economic pests, causing power outages while searching for prey on power lines and preying upon domestic animals and pets (Fritts and McCoid, 1991; Fritts et al., 1987).

Despite organized efforts to manage this economically and ecologically important pest species, little is known about its basic reproductive biology (McCoid, 1994; Whittier and Limpus, 1996). To date, no descriptions of its reproductive behavior have been reported. A comprehensive

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knowledge of a pest species' reproductive biology is crucial to management efforts. The brown tree snake management plan (Brown Tree Snake Control Committee, 1996) calls for research on brown tree snake reproduction to develop strategies to eliminate reproductive adults and their progeny. We report here, for the first time, the sequences of male courtship, female courtship, and ritualized male combat in captive individuals of *B. irregularis*.

MATERIALS AND METHODS

The animals used in this study were collected in the field on Guam and have been housed in our laboratory for the past 6 yr under an established protocol (Greene et al., 1997). The snakes (10 males and seven females) were individually housed in Plexiglas cages designed specifically for arboreal reptiles (Mason et al., 1991). They were fed a diet consisting of thawed frozen mice or chicks every 3 wk. Males ranged in SVL from 132.5–199.5 cm (mean \pm SD: 162.1 ± 22.1 cm) and in mass from 350–1175 g (647.5 ± 265.7 g). Females ranged in SVL from 129–156 cm (137.9 ± 9.9 cm) and in mass from 300–525 g (385.7 ± 81.5 g). Ambient room temperatures ranged from 23–30 C ($\bar{x} = 25$ C) and relative humidity ranged between 75 and 80% in the room. Lighting (14L:10D) was provided by overhead fluorescent lights and ambient sunlight entering the room through windows during the study.

Reproductive behavior was induced in our captive colony of brown tree snakes by reducing the ambient temperature in the snake colony room, a common technique used by snake breeders and researchers (Crews and Garrick, 1980). A 7-wk cooling period of 5 C below normal room temperature (25 C) was sufficient to bring all members of the snake colony into breeding condition. During the cooling period, humidity remained unchanged and the amount of light entering the snake room changed slightly, decreasing until winter solstice and slowly increasing thereafter. Courtship and combat behavior was observed from all snakes in the colony for the next 11 mo, waning until the next cooling period was initiated.

We conducted experiments during scotophase, between 1900 and 0200 h, when the snakes were normally active. Observations of reproductive behavior were made by introducing a male-female or a male-male pair into an arena constructed of clear Plexiglas. The arena had walls measuring 1.25 m on each side, providing 1.6 m² of floor area. The snake pairs were left together in the arena for 1 h, and their behaviors were recorded by an observer hidden behind a blind or by a video camera. Combat trials were continued to completion if both males of the pair were actively engaged in combat at the end of the 1 h observation period. The arena was cleaned using soap and water, rinsed, and dried between trials. Lighting was provided by a red 7-W incandescent light mounted above the arena. We recorded 20 courtship trials and 20 male-male combat trials (individuals were used more than once). The snakes had no courtship, mating, or combat experience during the previous 6 yr in captivity. No females were present during the combat trials.

Behaviors were described using standardized terminology (Gillingham, 1979, 1980; Gillingham et al., 1977). To allow comparison to other studies of colubrid male courtship behavior, the triphasic system developed by Gillingham (1979) that partitions male courtship into three phases (Phase I: tactile-chase, Phase II: tactile-alignment, and Phase III: intromission) was used to describe male courtship behavior in the brown tree snake. The following descriptions catalog all behaviors observed during courtship and combat trials in the temporal order in which they were observed.

RESULTS

Male Courtship Behavior

Phase I.—Courtship begins when a male tongue-flicks the dorsal integument of the female. In snakes, sex pheromones are detected by the vomeronasal organ via tongue-flicking (Halpern, 1992). After tongue-flicking the female's dorsum, the male displays head-jerking behavior in which the male rapidly tongue-flicks the

female while rhythmically jerking his head in a lateral direction. The male will mount the female soon after displaying head-jerking by placing his chin on the female's dorsum while subsequently chin-rubbing the female, a behavior in which the male advances along the female's body while pressing his chin to the female's dorsum. Chin-rubbing is accompanied by forward-body jerking, rhythmic forward surging movements of the male's head and body, and periodic snout-probing, in which the male presses his snout to the lateral side of the female's body while displaying short tongue-flicks only with the tips of his tongue. After several minutes of chin-rubbing, the male will periodically display head-lifting by coiling his head and neck region into an S formation and bobbing it up and down at a 45–90° angle to the ground for several seconds. At this point in the courtship sequence, males will display chase behavior by following a retreating female or chase-mount behavior by pursuing a female while remaining mounted on the female's body and chin-rubbing her. A period of chase-mount behavior eventually leads to body-alignment where the bodies of the courting pair are aligned side by side or the male's body is mounted on the female's body.

Phase II.—Tail-search copulatory attempts follow, in which the male repeatedly attempts to align his cloaca with the female's cloaca by wrapping his tail under the female's tail. Mating was observed only twice during this study, as most mating pairs were separated before reaching this phase to avoid confounding other studies being conducted simultaneously with the same snakes (Greene and Mason, 1998). In the two complete mating trials, the males displayed one and six tail-search copulatory attempts, respectively. Cloacal gaping by the female prior to copulation was not observed. No caudocephalic waves or body writhing were displayed by the males.

Phase III.—If the female is receptive to the male's courtship, the male will intromit one of his hemipenes into the female's gaped cloaca. During copulation, the male remains motionless except for periodic

tongue-flicking. No copulatory plugs were deposited into the female's cloaca at the termination of copulation.

Times spent in the three phases of courtship were recorded for the two complete mating sequences observed. The first mating pair spent 7.3 min in Phase I, 0.1 min in Phase II, and 12.3 min in Phase III of courtship, for a total time of 19.7 min. The second mating pair spent 16.0 min in Phase I, 0.7 min in Phase II, and 15.8 min in Phase III, a total time of 32.5 min. Combining the times for the two pairs, a mean time of 11.7 min was spent in Phase I of courtship, a mean time of 0.4 min was spent in Phase II, and the pairs spent a mean time of 14.1 min in Phase III. The two mating pairs spent a mean time of 26.1 min in the entire courtship sequence.

Female Courtship Behavior

A short (< 20 s) display of head-jerking behavior from females generally resulted from a female tongue-flicking a male. Typically a female that displays head-jerking will mount the male by moving her head along the male's dorsum or she will move along side the male's body towards the male's head. Upon reaching the male's head, the female maneuvers her body under or directly in front of the male's snout in an apparent attempt to elicit tongue-flicks from the male. This typically elicits courtship behavior from the male. The female then retreats from the male while displaying head-lifting behavior identical to that displayed by courting males. Males responded by following the female (chase and chase-mount behavior) and eventually attained body-alignment.

Male snakes cannot force copulation; therefore, mating occurs only if a female is receptive to male courtship and gapes her cloaca to allow the male to insert one of his hemipenes. Like the male, the female remains nearly motionless during copulation. Female brown tree snakes do not display any noticeable tail movements immediately preceding cloacal gaping as has been reported in other species (Holman, 1960; Murphy et al., 1978; Shaw, 1951).

Male courtship may elicit female behav-

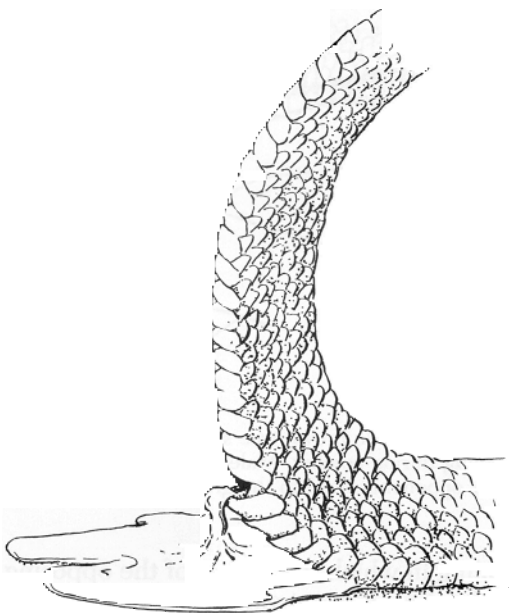


FIG. 1.—A female brown tree snake displaying tail-raising behavior and releasing a bolus of cloacal secretions in response to male courtship.

iors that apparently serve to discourage male courtship. Often, females will hold their heads in a defensive display, as if about to strike (although strikes at males during courtship were never observed) while slowly moving away from the male snake and displaying tail-lashing behavior. Females also responded to male chin-rubbing with body-bridging and body-bumping at the point where the male's head makes contact with the female's body.

In six of 20 courtship trials, male courtship attempts resulted in the female lifting her tail perpendicularly to the ground and releasing a bolus of liquid from her cloaca (Fig. 1). The liquid was clear with a yellow or white precipitate that was observed to originate from the urogenital opening and the paired cloacal glands located in the tail. This liquid appeared and smelled identical to what is released when brown tree snakes of both sexes are disturbed. When disturbed, a fine spray of cloacal gland secretions is released and the snake opens its urogenital opening and releases a bolus of this liquid. Tail-lifting behavior, however, is only displayed by females dur-

ing courtship and never when snakes are disturbed. In all courtship trials in which this liquid was released, the females did not previously exhibit any defensive displays.

A total of four different females were responsible for the six trials where cloacal secretions were released in response to male courtship (two females released cloacal secretion twice). There were no significant differences in SVL ($P < 0.446$; t -test) or mass ($P < 0.235$) between males that were rejected by females with cloacal secretions (SVL: $161.3 \text{ cm} \pm 7.4$ (SE); mass: $583.3 \text{ g} \pm 91.2$) and males that were not rejected by the same females in other trials (SVL: $153.9 \text{ cm} \pm 5.9$; mass: $457.1 \text{ g} \pm 50.8$).

Two of the females that rejected males with cloacal secretions also mated with other males. The first female rejected two males of 169.5 cm and 187 cm SVL and masses of 525 g and 975 g, respectively and mated with a male of 166.5 cm SVL and mass of 700 g. The second female rejected a male of 132.5 cm SVL and mass of 350 g and mated with a male of 156.5 cm SVL and a mass 500 g. Combined, there were no significant differences in SVL of rejected and mated males ($P < 0.948$; t -test) or mass of rejected and mated males ($P < 0.951$) for these two females.

Male Responses to Female Courtship Behavior

After head-lifting displays by females, males would often respond with head-lifting behavior. In addition, males would orient toward females or would approach and tongue-flick females. Upon approaching the female, the male would often move directly to the female's head and would posture his head above the female's head as in hovering behavior displayed during combat. Males were also observed pinning the female's head which usually resulted in the female quickly pulling her head free. In other cases, males approached and mounted a female displaying head-lifting and resumed courtship.

Male behavior changed noticeably after females lifted their tails and released clo-

acal secretions. Prior to this event, males displayed vigorous courtship behavior. After female cloacal secretions were released, however, males stopped courtship, except for periodic, weak head-nodding, and generally stayed near the female, following her around the arena. Identical behaviors were observed in all six cases, although in only one of these cases did a male tongue-flick the female cloacal secretions directly.

Male Combat Behavior

In every case, ritualized combat behavior began only after males tongue-flicked their opponent's integument. In response to tongue-flicking each other, opposing males display head-jerking behavior. Simultaneously, the males mount their opponent's body and display chin-rubbing accompanied by forward-body jerking behavior. Typically, the chin-rubbing initially occurs in the direction of the opposing male's tail and then towards the opposing male's head. During this phase of combat, males will often display body-bridging, where they bridge the section of their bodies upon which their opponent is chin-rubbing, or body-bumping behavior, repeated body-bridges at the point of chin-rubbing. Males will also periodically display snout-probing to each other and will display vigorous bouts of head-lifting for several seconds when chin-rubbing temporarily ceases. Head-lifting by one male was generally followed by a head-lifting display by its opponent or, if separated, the opponent would approach the head-lifting male and continue combat. Eventually, body-alignment is displayed when the bodies of both males are aligned side by side or one male is mounted on the other male's body.

Upon reaching body-alignment, the males begin to display head-pinning behavior where males attempt to pin their opponent's head to the ground using their chin (Fig. 2). This is often accompanied by hovering in which a male will hold its head and body above its opponent's head instead of using a physical pinning action. During head-pinning, males remain in a position parallel to the ground. An extended bout of head-pinning results in body-

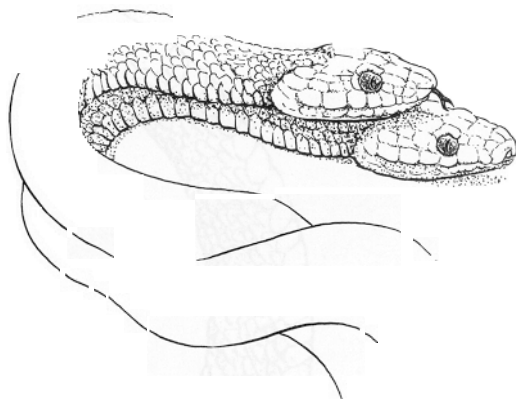


FIG. 2.—Male brown tree snakes displaying head-pinning during combat. Males use their head to pin their opponent's head to the ground.

coiling in which the bodies of the opposing males become entwined from just posterior to the neck region to the cloaca and the males constrict their opponent's body. Ultimately, a winner and loser are decided when the loser flees from its opponent. Fleeing by the loser is accompanied by body and tail lashing. The lashing is not directed at either of the males.

A winner and loser were decided in four of the 20 combat trials. In the remaining trials, males mutually separated without determining a winner, most likely because a female was not present during the trial. In all four cases where a winner was decided, the longer and heavier male won the combat event ($P = 0.014$; Fisher exact test). Winners had a mean SVL of 170.9 ± 9.4 (SE) cm and a mean mass of 687.5 ± 115.7 g while losers had a mean SVL of 148.3 ± 6.9 cm and a mean mass of 537.5 ± 71.7 g. Complete combat trials lasted a mean of 60.5 min with a range from 27–122 min. The difference of winner SVL and loser SVL and the difference of winner mass and loser mass did not correlate to the amount of time it took for combat pairs to determine a winner (linear regression; $r^2 = 0.061$, $P < 0.753$ and $r^2 = 0.136$, $P < 0.631$ respectively).

DISCUSSION

The repertoire of courtship behavior displayed by the brown tree snake closely

parallels that of northern temperate colubrid species (Secor, 1987). As such, male courtship behavior follows the triphasic schema developed to describe male courtship behavior in colubrid snakes (Gillingham, 1979; Gillingham et al., 1977). In this species, Phase I is characterized by head-jerking, mounting behavior, chin-rubbing, snout-probing, head-lifting, chase-mount behavior, and body-alignment. Phase II is initiated with a tail-search copulatory attempt and terminates with intromission and Phase III consists of intromission, and coitus (Gillingham, 1980).

The duration of time that males spent in Phases I and III of courtship was comparable to what has been observed in other colubrids, although the amount of time spent in Phase II of courtship was shorter than has been reported for most colubrids (Secor, 1987). Only the gray-banded kingsnake, *Lampropeltis mexicana alterna*, has a comparably short Phase II (Murphy et al., 1978).

Although brown tree snakes follow the same general pattern of courtship as other colubrids, they differ in the types of behaviors prominently displayed by males during courtship. Secor (1987) identified body-jerking, writhe/writhe-bump behavior, the presence of caudocephalic waves, and coital biting as major motor patterns in the repertoire of colubrid courtship behavior. Male brown tree snakes only display head-jerking behavior, none of the latter behaviors.

Brown tree snakes display snout-probing which has rarely been reported as a courtship behavior in other snakes (Gillingham, 1974). This behavior, which involves close range, rapid tongue flicking to the integument of the female, seems to be a mechanism to aid in the detection of the female sex pheromone. Behaviors similar to snout-probing are displayed by brown tree snakes in other situations in which detection of a chemical signal elicits some behavior such as feeding on dead prey items and following pheromone trails (Greene and Mason, unpublished data). This may be a mechanism for the snakes to detect semi-volatile components of the sex pheromone using olfaction while si-

multaneously sampling nonvolatile pheromone components via their vomeronasal organ.

Female brown tree snakes take an active role in courtship, displaying courtship behaviors to elicit male courtship and possibly to evaluate the quality of the courting male. These behaviors are displayed only after a female tongue-flicks the integument of a male, suggesting that a male sex pheromone that releases female courtship behavior is present in this species. Several other studies have observed female head-jerking or body-jerking behavior in colubrid females (Gillingham, 1974, 1979; Murphy et al., 1978; Secor, 1987). However, this is the first report in which displays of mounting, chin-rubbing, and head-lifting behaviors were observed in colubrid females.

Female head-lifting behavior has been described in the viperid *Agkistrodon contortrix*, where it serves as a mechanism for female mate choice by allowing females to assess male combat experience (Schuett and Duvall, 1996). Females of *A. contortrix* display head-lifting behavior during the initial stages of courtship in order to evaluate the success of courting males in combat bouts prior to courtship (Schuett and Gillingham, 1988). Males that had recently won combat bouts responded to female head-lifting with a "challenge display", a vertical posture displayed during the initial stages of combat. In contrast, losers of combat bouts were repelled by female head-lifting. Male copperheads without prior combat experience responded to female head-lifting with challenge displays (Schuett and Duvall, 1996).

Male and female brown tree snakes seem to interact during courtship in a similar manner as *A. contortrix*. Male brown tree snakes responded to female head-lifting with head-lifting bouts of their own, by approaching and tongue-flicking the female, mounting the female, hovering over the female's head, or pinning the female's head, each prominent combat behaviors. Although we never observed males being repelled by female head-lifting, the males used in our study had no combat experience during the previous 6 yr of captivity

at the time of the courtship trials. Future studies will be necessary to determine the role of head-lifting in female mate choice in the brown tree snake.

Female brown tree snakes also actively discourage male courtship by the release of cloacal secretions along with the visual signal of the raised tail. This appears to be a mechanism for female brown tree snakes to reject males deemed unacceptable or to signal to males that they are not sexually receptive. Male brown tree snakes in this study ceased courting females that released cloacal gland secretions even though they had been vigorously courting the females previously. After exposure to female cloacal gland secretions, these males still showed interest in the female by following the female around the cage, tongue-flicking her body, but not by displaying courtship behaviors except for periodic, weak head-jerking. In contrast, in other trials, males that voluntarily stopped courting females showed little interest in the female, being occupied with tongue-flicking the floor and walls of the cage instead of the female. These changes in male behavior are suggestive, at least, for the presence of a volatile male courtship inhibitory pheromone in female cloacal secretions.

Selection might favor males that cease courting females upon detecting female non-receptivity. Male snakes cannot force copulation; therefore, male mating success depends upon the female gaping her cloaca to allow intromission of the male's hemipene (Gillingham, 1979; Secor, 1987). Subsequently, it would prove futile for a male to court a female after the female has signaled that the male is an unacceptable mate or that she is not reproductively competent at that time.

Gillingham (1979) observed identical tail-raising behavior in an analysis of the reproductive behavior of eastern North American rat snakes (*Elaphe*) following coital separation and defecation, although it was observed at a low frequency. Additionally, female "tail-waving" has been reported in *Crotalus atrox* in which females lifted their tails and extruded their cloacae in response to male courtship (Gillingham et

al., 1983). Tail-waving behavior positively correlated to mating success and also resulted in an increased male tongue-flick rate, suggesting that pheromonal communication was involved (Gillingham et al., 1983).

The data collected in this study provided no evidence that females rejected males with the release of cloacal secretions based on the male characteristics of SVL or mass. Additionally, females did not reject males based upon combat experience as the males did not have any combat experience in the 6 yr preceding the courtship trials. This suggests that the females in this study rejected males based on their physiological state or on a male characteristic that was not measured. Females that rejected males with cloacal secretions may have been stressed or were not sexually receptive at the time of the trial despite being sexually attractive.

The ritualized combat display of the brown tree snake is initiated only after males tongue-flick each other. This suggests that a pheromone is present in the male integument that releases combat behavior. Like other colubrids that show ritualized combat, male brown tree snakes are larger than females (Shine, 1978, 1996). The snakes remain in a horizontal posture during combat and display behaviors similar to those displayed by other colubrids including head-jerking, hovering, body-coiling, and head-lifting (Carpenter, 1980). Many colubrids display body-pinning during combat where a loop of a snake's body is used to pin the anterior portion of its opponent's body (Gillingham, 1980). Brown tree snakes, in contrast, use head-pinning where the same motions are utilized but to pin an opponent's head instead of its body.

Large size appears to be an advantage during brown tree snake combat, as the longer and heavier male of the pair won the combat bout in each case during the study. Size advantage in combat has been documented in viperid species (Andr n, 1986; Schuett and Gillingham, 1989), although this relationship has not been reported for other colubrids. Other factors, including variation in aggression between

individual males and prior agonistic experience are also likely determinants of combat success in the brown tree snake, although the latter was controlled for in this study. Differences in SVL and mass between winners and losers did not correlate to the time it took the combat pairs to determine a winner, as might be predicted. This may be explained by variation in individual male behavior as casual observations suggested that some males seemed to be more likely to remain in combat even when seemingly being dominated by a larger male.

Head-lifting during combat in the brown tree snake seems similar, although more vigorous, to what has been reported in other colubrids. In other colubrids where head-lifting has been reported, head-lifting involves an elevation of a snake's head several centimeters above the ground (Brecke et al., 1976; Gillingham, 1980). In contrast, brown tree snakes bob their heads up and down at an angle to the ground. In this species, head-lifting may act as a solicitation display, serving as a visual signal that attracts other males, much like the challenge display seen in viperid combat bouts (Carpenter, 1977, 1984). In response to head-lifting by other males, male brown tree snakes will display head-lifting and approach other males and begin combat.

Although studies have addressed the reproductive physiology of the brown tree snake (McCoid, 1994; Shine, 1991; Whittier and Limpus, 1996), our study is the first description of this species' courtship, mating, and combat behavior as well as one of the few descriptions of these behaviors in any tropical species. The results of our study may also provide a basis for future studies on brown tree snakes, including investigations of the role of pheromones in mediating reproductive behavior.

The courtship and combat behavioral sequences described as part of this study were initiated only after tongue-flicking was observed (never by visual or tactile signals alone), suggesting that these behaviors are released by pheromones. These putative pheromone systems include the

female sex attractant pheromone, a male sex pheromone that releases female courtship behavior, a pheromone that releases male combat behavior, and a potential courtship inhibition pheromone found in cloacal secretions of females. Further experiments are necessary, however, to characterize the role of these pheromones in mediating brown tree snake reproductive behaviors. It is possible that, if identified and synthesized, these pheromones could be used as part of a larger brown tree snake management plan as chemical attractants or reproductive inhibitors (Mason, 1998).

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