Battles for mates and food: Intraspecific combat in island tigersnakes (*Notechis ater*) from southern Australia

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Abstract. Male-male combat occurs in mainland populations of tigersnakes (*Notechis scutatus*), but authorities have disagreed as to whether or not this behaviour also occurs in island tigersnakes (*Notechis ater*). In this paper, we confirm that intraspecific combat frequently occurs between island tigersnakes maintained in captivity. Two different kinds of combat bouts were observed. We interpret the first type (ritualised "wrestling" matches between large adult males) as a reflection of sexual competition. This behaviour was seen in snakes from each of the island populations investigated, including Tasmania. Agonistic behaviour was exhibited by females and juveniles as well as by adult males: however, this second type of combat was always initiated by the introduction of food items to the enclosure, and incorporated vigorous biting as well as (or instead of) wrestling. Further observations, in the field as well as in captivity, are needed before we can interpret the functional significance of this behaviour. The food-induced combat may be an artifact of high densities of captive snakes, or alternatively may be exhibited in the wild also. We speculate that the high abundance of tigersnakes on some islands, and the highly clumped nature of prey resources (e.g. muttonbird chicks) in both space and time, may have favoured direct interference competition for prey items between island tigersnakes. If so, some elements of the social system of island tigersnakes may resemble the condition seen in many lizard species, rather than in other snakes.

Introduction

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Although snakes are generally thought to be relatively asocial animals, combat behaviour occurs in many species and takes several forms (Shaw, 1951; Shine, 1978, 1994; Akester, 1979; Carpenter, 1986). For example, combat generally is highly ritualised ("wrestling matches") in venomous species, whereas biting is a common component of male-male combat in nonvenomous snakes (Shine, 1994). Unfortunately, because most reports of combat bouts in snakes are based on opportunistic observations, it is difficult to interpret the *absence* of records of combat in a particular species. Perhaps combat occurs in many more species than is currently realised, and simply has yet to be reported. Extensive observations may be necessary before combat is recorded. For example, Fleay (1951b, p. 86) remarked that the presence of male-male combat in Australian blacksnakes (*Pseudechis*) and brownsnakes (*Pseudonaja*) offered a strong contrast to the absence

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of such behaviour in tigersnakes (*Notechis*) and copperheads (*Austrelaps*): "Though I have grown up and 'lived' with copperheads and tigersnakes, no evidence has ever accumulated to show that combat occurs between the males in either of these well known Australian species". In fact, we now know that combat between rival males occurs in both of these taxa (Shine, 1977; Shine and Allen, 1981; R. Jenkins, pers. comm.; Lintermans, 1992), but is reported much less often than the spectacular "combat dances" observed in blacksnakes and brownsnakes (Shine et al., 1981).

Tigersnakes (Notechis ater = N. scutatus of some authorities: Schwaner, 1985) from the Bass Strait islands and Tasmania, off the southeastern Australian mainland, are of particular interest in this regard. Through the elegant ecological studies of T. D. Schwaner and his colleagues (Schwaner, 1985; Schwaner and Sarre, 1988, 1990), these snakes rank among the most intensively-studied elapid snakes in the world. Despite many hours of fieldwork, and detailed observations of reproductive activities (including courtship and mating) in free-ranging snakes on Mount Chappell Island, Schwaner and Sarre (1988) reported that they had never observed combat behaviour in these snakes. However, observations on snakes from another Bass Strait island (New Year Island), maintained in a large outdoor enclosure in Melbourne, revealed frequent combat among adult males during the breeding season (C. Tanner, in litt. to R. Shine; cited by Shine, 1977). There are also anecdotal reports of combat in Notechis ater from Tasmania (Anthony, 1981) and more recently, from Mount Chappell Island itself (I. Norton, cited in Fearn, 1993). The question of whether or not the Bass Strait tigersnakes engage in combat, apart from its intrinsic interest, is also directly relevant to interpretations of the adaptive significance of sexual dimorphism in this species. Males attain larger body sizes than do females in most populations of tigersnakes, and the degree of size difference between the sexes may vary among island populations (Schwaner and Sarre, 1988; Shine, 1987, 1993). Shine (1978, 1994) interpreted this male size superiority to result from selection for greater success in male-male combat, whereas Schwaner and Sarre (1988) advocated a hypothesis concerning seasonal fluctuations in thermal conditions and prey availability. Clearly, the existence of male-male combat is a necessary assumption of Shine's sexual selection hypothesis. Selection on combative abilities might also explain the greater strength of male than of female tigersnakes (Schwaner and Sarre, 1988, 1990). Hence, information on the presence or absence of combat behaviour in island tigersnakes is of significant value.

Material and methods

Snakes were captured as part of a commercial snake-farming enterprise, and maintained in captivity at the Koorang Snake Farm near the town of Cressy (41°42'S 147°05'E) in central Tasmania. Observations were made by one of us (MF) from January 1991 to October 1992, on groups of snakes maintained in outdoor pits. Shelter in the pits consisted of large sheets of tin resting on wood or roofing tiles and underlain with

straw. Water was provided in plastic-covered holes dug into the ground. Because of the considerable variation in body sizes and morphology of tigersnakes among different islands (Schwaner, 1985; Schwaner and Sarre, 1988, 1990), we present information separately for the following groups:

- (i) Group 1: Snakes from Babel Island (148°19′E 39°58′S) and Cat and Storehouse Islands (both 148°21′E 39°58′S) were captured in January 1991 and housed in a square outdoor enclosure 9 × 9 m in size. All of the 35 snakes in this group were relatively small (maximum snout-vent length (SVL) 1.18 m).
- (ii) Group 2: Ten snakes collected from Forsyth Island (148°18′E 40°31′S) and Preservation Island (148°05′E 40°28′S) in January-February 1991 were housed in an outdoor enclosure measuring 8 × 4 m. Most of these snakes were very large (maximum SVL 1.55 m).
- (iii) Group 3: Snakes were removed from Christmas and New Year Islands (both $143^{\circ}50'E \ 39^{\circ}41'S$) in western Bass Strait in January to March 1991. More than 100 adults (> 0.9 m SVL) were kept in a square outdoor pit 9×9 m. During November 1991 all of the females (approximately 50) from this group, together with ten males, were moved to a circular outdoor pit of diameter 9 m.
- (iv) Group 4: Eight snakes from various parts of Tasmania were caught during January-February 1991 and kept in an outdoor enclosure of diameter 3 m.

As well as these adult snakes in the outdoor pits, we also observed juveniles born in captivity from each of the above groups (and also from Mount Chappell Island: $147^{\circ}55'E$ $40^{\circ}17'S$). The young snakes (and occasionally, adults) were kept in cages measuring $80 \text{ cm} \times 40 \text{ cm} \times 30 \text{ cm}$ inside a constant-temperature room (at $28^{\circ}C$). Depending on the sizes of the snakes, between one and six animals were kept per cage.

Results

Combat was observed frequently among captive tigersnakes, and could be divided into two types. The first kind involved only adult males, and consisted of ritualised "wrestling" matches rather than biting. The second type of combat bout involved juveniles as well as adults, was initiated by the introduction of a prey item into the snake's cage, and often incorporated vigorous biting rather than (or as well as) intertwining. We infer that the function of the two types of bouts may be quite different (note that Shaw (1951) made the same distinction with data on American colubrid snakes), and hence, we describe these two types of combat behaviour separately below.

"Sexual" combat bouts

Combat bouts initiated independent of feeding were observed in snakes from all areas. Most bouts involved only two snakes within each enclosure, whereas food-related combat sometimes involved simultaneous "wrestling" by several intertwined snakes (fig. 1).

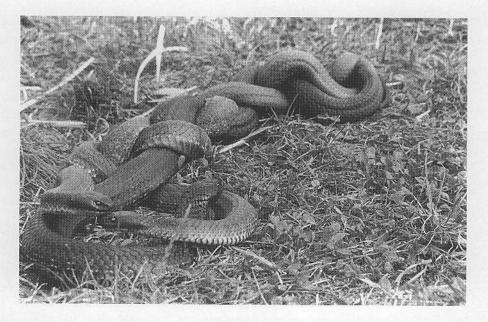


Figure 1. Unlike "sexual" combat bouts, food-related bouts sometimes involved more than two snakes. This photograph shows three male snakes from Christmas-New Year Islands (Group 3) in the course of a battle over prey. Note the horizontal loops of the forebody, a common feature of combat bouts in snakes from these islands.

In each case of "sexual" combat, these were the two largest males in the respective enclosure. For example, two large males in the Group 1 enclosure (SVL 1.18 m and 1.05 m) were observed wrestling every day for five days in succession in mid-January 1992. Bouts continued for 15 to 20 min, after which the snakes would retire and resume their conflict the next day at the same time (about 09:45 h). Large male snakes (SVL 1.10 to 1.30 m) from Group 3 were observed in combat unrelated to the introduction of food on four occasions during March 1991. This was the only group where combat bouts involved snakes other than just the two largest males, probably because of the large numbers in this enclosure. Following removal of the females in November 1991, no combat (except that related to food) was observed the next year in the group consisting entirely of males. However, combat continued in the group that contained females. Two male Tasmanian snakes (Group 4: 1.14 m and 1.08 m SVL) were observed wrestling under a sheet of tin during March 1991. These were the largest snakes in the enclosure at the time. Large snakes from Group 2 were observed in "sexual" combat on two occasions: during the second week of October 1991 (1.42 m vs 1.54 m SVL) and in March 1992 (1.42 m vs 1.36 m SVL). A smaller male (1.29 m SVL) was observed to mate in this enclosure the following week.

Combat behaviour was initiated when one snake attempted to press down the head of the other either from a position alongside or from above by sliding dorsally towards the

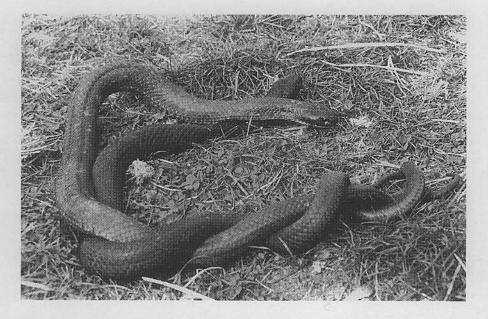


Figure 2. Posture adopted during "sexual" combat between adult male tigersnakes. *Notechis ater*, from Christmas-New Year Islands, Bass Strait (Group 3). Note that the anterior part of the body of each snake remains free, while the posterior part is intertwined.

head. Retaliation of the non-aggressor (by freeing its head, and then attempting to pin the head of the aggressor and vice versa) resulted in a tight corkscrewing effect along the posterior halves of the snakes' bodies (fig. 2). The anterior halves were usually kept free. Whenever the corkscrewing extended to the entire length of the bodies, one snake would attempt either to shake itself free or unwind itself. When the aggressor was notably shorter than its opponent, the larger snake was able to defend itself by forming a vertical loop about 15 cm in height and starting just behind the head, effectively preventing the smaller snake from pinning its head (fig. 3). This loop was ineffective when both snakes were of equal size. The form of the behaviour differed slightly among groups. The most distinctive posture was seen in snakes from Group 3: these animals often formed semicircular, horizontal curves using the anterior 15 to 25 cm of their body. With head pointing inwards, each snake attempted to pin the opponent's head from the side (fig. 1). Combat bouts were observed to last from 2 to 25 min.

Food-related combat bouts

Combat was often associated with the introduction of food in small *Notechis ater* in Groups 1 and 3. No "wrestling" bouts were observed following the introduction of food in either Group 2 (large island snakes) or Group 4 (Tasmanian snakes), but snakes in these latter two groups occasionally bit each other at these times. The lack of wrestling

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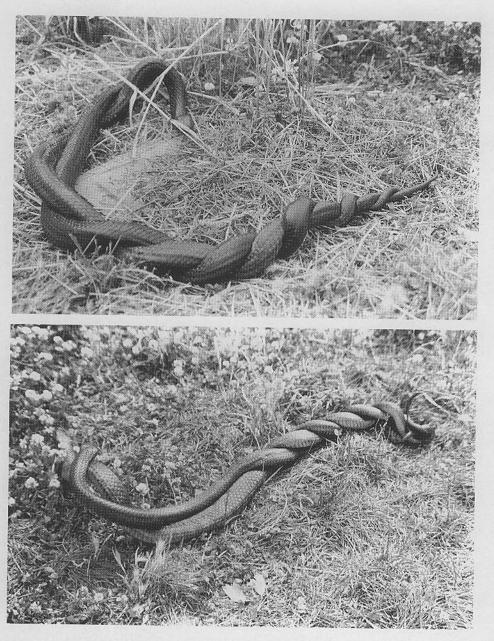


Figure 3. A distinctive posture adopted by during "sexual" combat between adult male tigersnake, *Notechis ater*, from Cat and Storehouse Islands (upper) and Christmas-New Year Islands (lower). The snakes formed vertical loops in their forebodies, thereby making it more difficult for their opponent to exert downwards pressure (with its own head) onto the head of the "looping" snake.

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bouts in snakes from Groups 2 and 4 may reflect the much lower densities at which these snakes were maintained, suggesting that crowding may have contributed to the initiation of food-related combat bouts. Food-related combat between small "Group 1" snakes was observed during April, October and November 1991 and March and April 1992. "Group 3" snakes were observed wrestling over food during March, October, November and December 1991, and March 1992. Combat of this type was often preceded (initiated?) by one snake biting another's head when both attempted to seize the same prey item. Both male and female snakes in Group 1 often bit their rivals in this situation. Bites in this group were vigorous, usually of short duration and directed at the rival's head. Group 3 snakes also directed bites at the head of their rivals, but these bites were less vigorous, and appeared more like feeding responses than aggression. Indeed, bites in this group often led to attempted cannibalism. Biting was also observed infrequently in Group 2 and Group 4, always around food, but attempts at cannibalism were not observed in these snakes. Although biting was a common component of combat bouts that had been induced by the introduction of food, biting was not observed during "sexual" combat bouts (i.e. those unrelated to food). Biting caused no apparent harm to any snake.

Aggression in juvenile snakes

Juvenile snakes kept in boxes showed a high degree of aggression at feeding time, often ignoring food and attacking each other. Aggression consisted of a vigorous bite, usually directed at the head of the rival. No "wrestling" matches were seen. Snakes from all populations (including the animals from Mount Chappell Island) exhibited this biting behaviour. Attempted cannibalism often followed if the snakes were not separated. Aggression and cannibalism in juveniles away from feeding time occurred in all populations.

Combat in adult female snakes

During the last week of January 1992, two females from Group 1 were placed in one of the cages in the thermostatically controlled room. Snake A measured 915 mm SVL and weighed 493 g, whereas snake B measured 930 mm SVL and weighed 486 g. Fifteen days later, and five minutes after introduction of prey (6 two-week-old mice), the snakes were discovered in typical combat posture with the posterior halves of their bodies tightly entwined. Snake A bit the head of snake B three times, and snake B retaliated with a bite to the head of snake A. More wrestling ensured for three minutes at which point a mouse was offered to each snake. After about two minutes, when snake A had finished its meal and snake B was nearly finished, snake A again bit the head of snake B. More wrestling broke out, and continued for another four minutes at which point snake A was removed from the box.

Both of these snakes were confirmed to females (as judged by tail shape, and by probing for hemipenes). Prior to this event, all combatants in the Group 1 enclosure

were assumed to be males. It is possible that females were engaged in combat in this group and not recognised as such, due to the less obvious sexual size dimorphism in this group. It is not possible that females from any other enclosure could have been involved in combat without being noticed: either females were much smaller than males in these groups, or were individually recognisable.

Discussion

Our results are interesting in a number of respects. Firstly, they confirm Tanner's original report (in Shine, 1977) of male-male combat in reproductive male tigersnakes from New Year Island. Secondly, they suggest that such behaviour is widespread among tigersnakes from Tasmania and islands both in western Bass Strait, and in the Furneaux group. Hence, the absence of field records of combat from behavioural ecology studies on the Chappell Island tigersnakes (Schwaner and Sarre, 1988) may mean that combat is rare, or difficult to observe, rather than being entirely absent. Rarity of combat seems more likely than absence, based upon our observations and a recent brief report of combat in tigersnakes on Mount Chappell Island (I. Norton, in Fearn, 1993). The records of male-male combat in captive tigersnakes seem likely to represent sexual behaviour, as has been reported in many other kinds of snakes (e.g. Shine, 1994). Notechis have been observed mating in autumn in Victoria and Tasmania (Fleay, 1951a, b; Fearn, 1993, pers. obs.), spring in Western Australia (Bush, 1983), and both autumn and spring in New South Wales (Shine, 1977). This seasonality broadly coincides with the times of male combat bouts observed in the present study. The observations that only males engaged in such battles (as far as we could determine), that they occurred close to the time of mating, and that this behaviour ceased in a group of males after females were removed, all seem to be consistent with the interpretation of sexually-motivated combat. The occurrence of this behaviour (and its restriction to unusually large individuals) suggests that sexual selection for ability to win combat bouts (and hence, obtain matings) offers a plausible selective force for the evolution of larger body size in male than in female Notechis ater. The postures adopted by wrestling males are consistent with the hypothesis that the greater muscular strength of male tigersnakes, compared to conspecific females, also results from selection for ability to win combat bouts. However, it is important to recognise that our data do not offer convincing evidence for the sexual selection hypothesis relative to alternative explanations for sexual dimorphism in this species (e.g. Schwaner and Sarre, 1988); we have simply shown that one of the assumptions of the sexual selection hypothesis is likely to be valid.

In most respects, the "sexual" combat behaviour of male tigersnakes is similar to that previously described for other elapid species. For example, the postures adopted during combat in *Notechis ater* are similar to those reported for combat bouts in other Australian elapids. That is, the bout is essentially a horizontal battle, with opponents attempting to pin each other's head to the ground from above (Fleay, 1937, 1951a, b). The durations of

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the bouts we observed were similar to those recorded for other elapids (see Shine et al., 1981). The tight entwining of the posterior body, with the anterior body remaining free and mobile, has been recorded in two other large Australian elapids, *Pseudonaja textilis* (Fleay, 1951a, b) and *Austrelaps superbus* (Shine and Allen, 1981). The significance of this posture, compared to the whole-body entwining of snakes of other species, remains unclear (Fleay, 1951b; Murphy et al., 1978; Carpenter et al., 1978).

The other interesting result to emerge from our study is the readiness with which captive tigersnakes, from some but perhaps not all populations, engage in vigorous combat (including biting) in battles over prey items. There are at least two possible explanations for this food-related combat behaviour:

- (i) The behaviour is an artifact of captivity, as a result of artificial crowding and stress. Tigersnakes are renowned as gluttonous feeders in captivity, and they may simply become over-excited at the presence of food. In keeping with this interpretation, food-related combat was not seen in the two groups of snakes kept at lower densities, and has not been reported by other herpetologists who have maintained tigersnakes in captivity (e.g. Fleay, 1951b; Bush, 1983; Fearn, 1993; but see Worrell, 1958 regarding the high frequency of cannibalism in island tigersnakes during feeding). Previous studies on captive snakes of several species have reported that the introduction of food items can stimulate combat bouts, and that such behaviour can be shown by juveniles of both sexes and by adult females, as well as by males. Juvenile aggression in the cobra Naja n. kaouthia involved hood-spreading and biting, and occurred both with and without food present (Thomas, 1970). Juvenile combat over food, involving ritualised "wrestling" matches, is also known in two species of Vipera (Thomas, 1969; Kelleway and Brain, 1982). Thus, combat-in the form of either "wrestling" or biting, or both—may be initiated by the introduction of food in captive snakes of a wide variety of species (Shaw, 1951; Kelleway, 1982).
- (ii) The behaviour is also exhibited in the wild, and enhances an individual's ability to obtain a food item in competition with other snakes. This scenario would be very unlikely for most snakes in the wild, since it is difficult to imagine many circumstances in which two snakes would simultaneously encounter a potential prey item over which they could compete. For most snake populations, population densities and encounter rates with prey would both be so low that such opportunities for piracy would be vanishingly rare. However, island tigersnakes may be one of the few snakes for which the opportunity may actually arise. Especially on islands where muttonbird chicks are the most important prey items for adult tigersnakes, the prey resource may be highly concentrated both in space (i.e. a rookery) and time (i.e. a few weeks each year after the chicks hatch, and before they grow too large for the snakes to ingest: Worrell, 1958; Schwaner, 1985). Also, population densities of island tigersnakes may be extremely high (Schwaner and Sarre, 1988, 1990). Hence, it would be instructive to look within

natural populations at the appropriate times and places (where snakes and prey resources are both concentrated) to see whether interference competition occurs between snakes at these times.

More generally, these speculations emphasise how little is known of the social systems of snakes in the wild. There are abundant data on social systems of lizards, and these often involve vigorous combat bouts over prey items or territories (e.g. Carpenter and Ferguson, 1977). The general consensus among scientists is that snakes are relatively asocial animals (Carpenter and Ferguson, 1977), but observations of agonistic behaviour in captivity suggest that social hierarchies may be important in lineages as divergent as pythons (Barker et al., 1979) and pit-vipers (Schuett and Gillingham, 1989). Even if social systems involving territorial defence or direct interference competition for prey were widespread in snakes, it is very likely that we would have no direct evidence that this is the case. All we would have would be anecdotal accounts, such as the ones that already exist for territorial defence in large African elapids such as mambas and cobras (e.g. Broadley, 1982). The ease with which food-related combat can be elicited in captive snakes suggests that such behaviour may be exhibited in the wild also, under circumstances that closely mimic those prevailing in captivity. Detailed behavioural studies of free-ranging snakes offer the only way to resolve questions such as these.

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