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Predatory combat and tail wrestling in hierarchical contests of the Neotropical rattlesnake *Crotalus durissus terrificus* (Serpentes: Viperidae)

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Although the combat ritual among snakes has been described as social aggression (Carpenter et al., 1976), the causes of such interaction remain not entirely well known. The combat ritual has usually been recorded during the reproductive season, and in some species it is an agonistic behaviour which aims at dominance and would result in a mating for the winning male (Klauber, 1972; Gillingham et al., 1983; Andr n, 1986; Schuett and Gillingham, 1989), or obtention of resources, mainly when they are scarce (Carpenter, 1984).

Sutherland (1958) suggested that food competition explained the combat ritual of *Crotalus horridus horridus*. Among captive and free-ranging *Vipera berus*, ritualized combats were reported both during competition for mates at springtime and competition for food (the so-called predatory combat) at different times of the year (Naulleau, 1967; Kelleway, 1982; Andr n, 1986; Luiselli, 1995; Capula and Luiselli, 1997).

In *Pseudechis porphyriacus* (Serpentes: Elapidae), Shine et al. (1981) described the agonistic behaviour of pulling the copulating rival's tail from the female involved in the mating. This "tail wrestling" behaviour was also reported in *Natrix natrix* (Serpentes: Colubridae), as a less dramatic dominance tactic compared to the combat ritual (Madsen and Shine, 1993), but Capula and Luiselli (1997) described the same interaction as an "electric" gregarious courtship.

Territoriality has been pointed out as a release to several types of interaction among snakes (Lowe, 1948; Lowe and Norris, 1950; Perry, 1978). Andr n and Nilson (1981) reported that male *Vipera berus* defended receptive females in small areas during the mating season and the existence of a hierarchy among males during this time. This behaviour was called "copulatory guard" (Andr n, 1986) and later on interpreted as a type of mating system called "female defense polygyny" (Duvall et al., 1992) or "vigilance" behaviour (Luiselli, 1993 a, b).

Ritualized combats in the Neotropical rattlesnake *Crotalus durissus terrificus* from the southeastern region of Brazil have always been recorded during the austral autumn, when they exhibit peaks of activity (Salom o et al., 1995), have the mating season (Langlada, 1975; Santos et al., 1990; Almeida-Santos et al., 1997), followed by the formation of a copulatory plug and long-term sperm storage (Almeida-Santos and Salom o, 1997). However, the causes of such behaviour are still unclear.

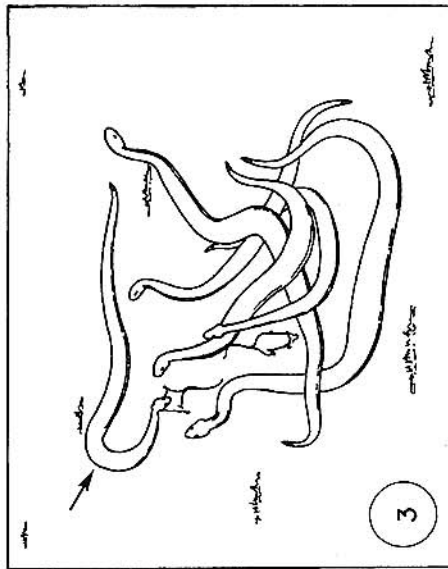
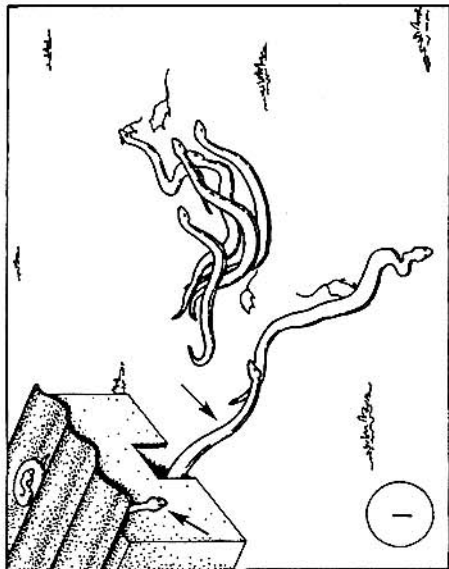
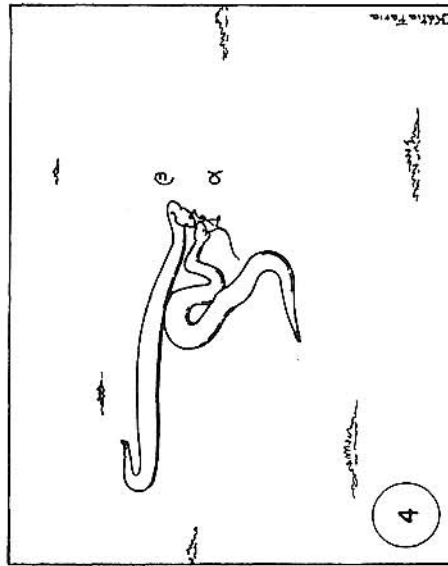
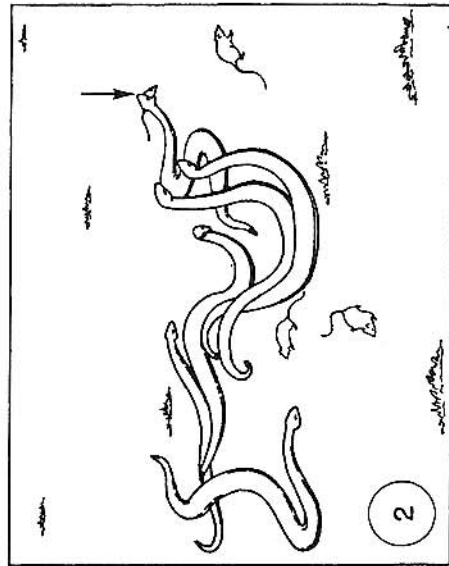
The aim of this paper is to describe a combat ritual stimulated by the presence of food and a dominant-subordinate relationship among male *Crotalus durissus terrificus*, including displacement of a copulating rival. The observations are discussed with reference to mating success, sexual dimorphism and dominance, reproductive success, as well as the phylogenetic implications of such behaviour among snakes.

A captive group of *Crotalus durissus terrificus* ($n = 17$: 9 adult males with SVL > 100 cm; 3 juvenile males with SVL about 65 cm and 5 adult females with SVL about 90 cm) from Vale do Para ba in the east of the State of S o Paulo (23 02'S; 45 33'W; 23 C average annual temperature; altitude about 600 m), was housed in a large circular enclosure (16 m²). This serpentarium was built to resemble the snakes natural habitat,

including some vegetation, basking sites and a pond. The snakes have been maintained there for about 8 years. During 1995, on different days, but always in the afternoon and early evening, different types of interaction among them were recorded ($n = 9$). Snakes ate once every 15 days (20 mice from 60 to 80 g). Competition for food items ($n = 6$) and also competition for females ($n = 3$) were observed, photographed and subjected to analysis. All snakes had previously been given individual marks by painting small coloured dots on their tails. Adult snakes which participated in the combat had approximately 80-110 cm SVL, whereas young snakes were about 60-65 cm in SVL. The male snakes were designated according to their final hierarchical status (α the dominant and β , λ and γ the subordinates). The terminology used for describing and discussing the ritualized combats was based on that proposed by Wilson (1975), Carpenter et al. (1976), Martin (1984) and Gillingham (1987) and will be cited always in quotation marks. In the text, means are followed by the standard deviation.

Competition over food items, the predatory combat, in *Crotalus durissus terrificus* was recorded not only during the mating season (April to June), but also in winter (July to September) and late spring (December). They may last up to 180 minutes (63 ± 54 minutes). Soon after the mice were released, snakes left the basking sites (fig. 1.1.) and started tongue flicking and searching movements. Females exhibited chasing activities followed by a strike, and after envenomation the prey items were ingested. Females did not take part in predatory combats. Males, however, started raising the first third of their body length, initiating combat behaviour (fig. 1.2.). The combatants adopted the "vertical display" (going from horizontal to vertical position), "solicitation display" (vertical posture in male-male contests indicating challenge), "orientation" (side-to-side movements), "overtopping" (action forcing the opponent to the substrate), "corkscrewed" postures (physical contact with spiral movements) and "recovery" (the interaction begins again). No biting or striking was recorded despite the fact that "head butting" was employed. Groups of six to eight males participated in these combats (fig. 1.3.), but always fought in pairs. Combats came to an end when several participants (β , γ and λ) retreated rapidly, followed by some pursuit of the male designated as α . Male α took part in and won all the predatory combats. On one occasion, he disputed a mouse already envenomated and partially ingested by a subordinate male. Male α removed the mouse from the other, and ate it (fig. 1.4). The subordinate remained still. Three juvenile male snakes, SVL about 60 cm, were also observed to combat in the presence of food, first among themselves and then with male α . The postures and the sequence of events were very similar to

Figure 1. Predatory combat in *Crotalus durissus terrificus*. Snakes are leaving the basking sites (arrows), whereas others have started the "solicitation display", soon after mice have been introduced in the serpentarium. Two adult males combating in the presence of food showing the posture of "orientation", while a female (arrow) has already caught a mouse without any participation in the interaction. A group of five males exhibiting combat ritual in the presence of mice, while another female is already feeding (arrow). The postures assumed by the males in the predatory combat are visually similar to those recorded in the sexual combat. Subordinate male (β) trying to dispute a mouse with the dominant male (α).



those observed among adults. Once, one of the juvenile snakes (male λ) challenged male α raising the first third of his body to elicit combat, which was won by male α . Once more, a juvenile snake tried to remove a half swallowed mouse from the mouth of male α . The dominant male reacted by pushing the young snake, which left while male α finished eating that mouse. Satiated males (those which fought and ate) did not respond to any "solicitation display" and were not involved any further in predatory combat.

On another occasion, in autumn, a female and a male (β) were trying to copulate, then male α left a basking site on the opposite side of the serpentarium and started tongue flicking. When male α touched the mating couple, he challenged male β , raising the first third of his body. Male β did not show any visible reaction. The male α then inserted his tail in between the tails of the couple, pulling the tail of male β away from the female in a typical tactic of "tail wrestling". Male α succeeded after the third attempt when male β left the female which remained still. Then male α raised the first third of his body length adopting a posture of "agonistic display" towards male β , which did not respond. Male α did not court or mate. Male β approached the same female again, trying to copulate. In response, male α approached the couple and, crawling backwards, separated the female and male β . Immediately after the second separation, male α again assumed a posture of "agonistic display" towards male β , which remained still. Then male α started touching and trying to raise the body of male β . Male β raised the first third of his body length and then male α struck male β twice, biting his head. Male β was leaving when it was bitten again by male α , in the middle of the body. Soon after, male α started chin rubbing the snakes around him in the serpentarium crawling towards that female (the one male β was courting) which remained still. As soon as he reached her, he coiled up on top of her body, but did not attempt courtship or copulation.

The same type of agonistic behaviour was observed on a different day, involving a different female and a different subordinate male (γ), but the same dominant male (α). Again, male α , using "tail wrestling", separated the copulating couple, and after that remained on the female's body. Male γ left, whereas male α stayed on the female, contracting his muscles from the neck towards the tail in a mounting tactic called "cephalocaudal waves".

Concerning the participation of the female during the male interactions, it seemed that in the three occasions she was neutral or inactive towards the fight. However, once the disputed female was seen to raise her tail and exhibit her open cloaca to the subordinate male in a behaviour known as "cloacal gape", indicating that females may interact with the fighting males. Despite her receptivity, no mating occurred after the dominant male had disturbed the subordinate. No aggression toward the females was noticed.

Predatory combat may be distinguished from the sexual combat, only when food works as a release, because in both interactions the different displays assumed by the snakes are similar. As observed in *V. berus* (Kelleway, 1982) and *V. aspis* (Naulleau, 1967), satiated *C. d. terrificus* did not participate further in the combat. Relative food

shortage and dense populations may elicit this competition (Kelleway, 1982) leading to the establishment of a hierarchy (Brattstrom, 1974). In the case of *C. d. terrificus* the density of 1.06 animals per m² in our serpentarium seems to be too high and/or the amount and frequency of food offered was low. In *V. berus* predatory combats occurred in captive populations at a density of 0.5 animals per m² if food supply was maintained at low levels (Kelleway, 1982). In free-ranging populations the competition for food is probably much lower due to the low density of snakes. So, if this interaction occurs in nature, it must be quite rare. However, the multiple function of combats (competition for foraging areas, food and territory including females) should not be forgotten (see Hersek et al., 1992 for details). Female *C. d. terrificus* were not observed to participate in combats, leading us to conclude that they did not participate in the hierarchy different from *V. aspis* (Naulleau, 1967) and *V. berus* (Kelleway, 1982). Juvenile males (sexually mature according to Salomão and Almeida-Santos, in preparation), however, disputed for food with adults, indicating an attempt to establish a new hierarchy in the serpentarium. They did not win any predatory combat probably due to their smaller size, since size seems to be as important for juveniles as it is for adults in establishing dominance (Blem, 1987; Schuett, 1997).

The use of contest tactics in snakes has normally been related to male reproductive success (Luiselli, 1996). Male size and tail length dimorphism seem to be directly related to the male's greater physical strength (Darwin, 1871; Shine, 1978; Gillingham, 1987; King, 1989; Luiselli, 1996) and ability to displace rivals through tail wrestling (Madsen and Shine, 1993). In *Crotalus durissus terrificus*, males are larger and have larger tails than females (S.M. Almeida-Santos, in preparation), allowing the use of the tail wrestling tactic when struggling for first achieving intromission, as described in the colubrid, *Natrix natrix* (Madsen and Shine, 1993; Luiselli, 1996). Male α *C. d. terrificus* was the largest and oldest snake in the serpentarium suggesting a relationship of dominance, and therefore hierarchy, among them, since hierarchy is dependent on size (Brattstrom, 1974; Luiselli, 1995, 1996; Schuett, 1997) and age (Barker et al., 1979), as described by Andr n (1986), Schuett and Gillingham (1989), Madsen et al. (1993) and Schuett (1997).

Male α was not observed to copulate after displacing rivals, even when the female was receptive, suggesting that mating could have occurred before and the dominant male was simply trying to prevent another male from copulating, preventing sperm competition and multiple paternity (Stille et al., 1986; Andr n and Nilson, 1987; Stille and Niklasson, 1987; Andr n et al., 1997). This behaviour known as post copulatory guarding (Andr n and Nilson, 1981) is part of a mating system of pit vipers called "female defense polygyny" (Duvall et al., 1992). In this system, females that would try to copulate with as many males as possible in order to guarantee fertilization or to improve the quality of the litters via intrauterine sperm competition (Madsen et al. 1992), are prevented from doing so by a successfully fighting male (dominant male). This behaviour would last until a copulatory plug (contraction of the posterior part of the uterus) was formed (24 to 48 hours after mating according to Nilson and Andr n, 1982). After that, even if the female

mated another male, little sperm would reach the uterus (Andrén, 1986), assuring the success of the first male (Andrén and Nilson, 1987). Observations recorded here show that “female defense polygyny” is part of the reproductive strategy in *C. d. terrificus*, including male-male dispute for females, autumnal mating, copulatory guard, the formation of a copulatory plug and obligatory long-term sperm storage (Almeida-Santos and Salomão, 1997). As a consequence of that within-season multiple matings, sperm competition and multiple paternity are plausible events in neotropical rattlesnakes, but further detailed field investigation is needed.

Dominance is a consequence of different interactions among snakes (Carpenter, 1984), occurring mainly in confined spaces (Gillingham, 1987). Assuming that its function in male snakes is the obtainment of food, mate or space (Carpenter, 1984; Hersek et al., 1992), we may say that in *C. d. terrificus*, food worked as a reward for such dominance, explaining why satiated males did not combat any further. Although dominance established by male α was not altered during 1995, it is not possible to define if this is a continual or transient phenomenon or whether it is restricted to captive individuals.

Combat ritual behaviour serves several purposes in a variety of viperid genera (*Agkistrodon*, *Crotalus*, *Vipera*) and it is widely documented among newborn snakes (Fitch, 1960; Thomas, 1969; Blem, 1987) indicating that these behavioural strategies are genetically determined. Tail wrestling is well distributed among snake families including Colubridae (Madsen and Shine, 1993), Viperidae (this work), and Elapidae (Shine et al., 1981). The presence of the same type of behaviour in these three families suggests that these characters could be plesiomorphies present in a common ancestor of the Colubroidea. Investigations of the existence of such behaviour in other members of the Colubroidea would be necessary to test whether this behaviour is due to symplesiomorphy or convergence.

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