

Male-male ritualized combat in the Brazilian rainbow boa, *Epicrates cenchria crassus*

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MALE-male combat is a ritualized behaviour occurring mainly during the mating season (Greene, 1997; Schuett, 1997; Schuett *et al.*, 2001) which is widespread among snake families including Boidae, Elapidae, Viperidae and Colubridae (Shine, 1978, 1994). Male-male combat is an example of intrasexual selection in which males compete for access to females. Typically, the two opponents attempt to physically subdue one another by exerting pressures (e.g., pushing, flipping, entwining) on the anterior part of their body in an attempt to bring their adversary to the ground. (Carpenter, 1977). Among boid snakes male-male combat is recorded in only one erycinae (*Eryx colubrinus* – see Schuett *et al.*, 2001), 21 pythoninae (see Shine, 1994; Schuett *et al.*, 2001) and 14 boinae species – nine of these being Neotropical (see Shine, 1994; Schuett *et al.*, 2001). The genus *Epicrates* includes ten species and combat is recorded for six, including the Brazilian *E. c. cenchria* (Shine, 1994; Schuett & Schuett, 1995; Schuett *et al.*, 2001). Despite the existence of many records in boid snakes, detailed descriptions of combat behaviour are only available for the pythoninae (*Python molurus*; Baker *et al.*, 1979) and the boinae *Sanzinia madagascariensis*.

Here we provide a description of combat in three captive male *Epicrates cenchria crassus*. This mainly terrestrial species feeds on small mammals (Pizzatto L., unpubl. data), and inhabits the Brazilian cerrado, a savanna-like vegetation, where it is probably associated with riparian forests (Peters *et al.*, 1986; Henderson *et al.*, 1995).

The three snakes came from unknown localities in São Paulo State, southeastern Brazil and were maintained in captivity in Bandeirantes city (-50°03'W, -23°02'S), Paraná State, southern Brazil. Male 1 and male 2 were obtained in 1999 and male 3 was obtained in early 2001. These snakes were maintained in individual cages (1.0 m x 0.50 m x 0.40 m) made of wood with screen in the front. Cages were contiguous and disposed side by side in the same room, thereby preventing visual contacts between the experimental subjects. Room temperature was ca. 30–32°C in spring/summer and 22–25°C in autumn/winter. We used heating pads when the temperature fell below 25°C, and sprayed the cages with water when the humidity was low. Water was provided ad libitum, and snakes were fed once a week (one or two young rats). We measured each snake in June 2004: Male 1 was 1130 mm in SVL and weighed 845 g, male 2 was 910 mm in SVL and 800 g, and male 3 was 1060 mm SVL and 910 g. All males were adults (L. Pizzatto, unpubl. data). We used the terminology used by Carpenter *et al.* (1976) for the combat phases.

In April/May in 2001, we observed high snake activity in the cages and decided to introduce males to one another, simultaneously, in the same cage. Then, male 1 and 3 started a combat behaviour. Although male 2 was in the cage with the other 2 snakes it did not engage in combat. The end of the combat was initiated when the loser (male 3) withdrew itself from the fight and became inactive. After trials, all snakes were returned to their individual cages.

In April/May 2002, snakes became very active again. Male 3 was continuously forcing the cage wall towards the cage of male 1 until it broke the cage and entered male's 1 cage, probably attracted by chemical cues. The three snakes were put together again and exhibited combat behaviour. Again, male 2 did not engage in combat. But, in contrast to year 2001, male 3 became dominant over male 1. The same behaviour combat was recorded again in 2003 and 2004 with male 3 being the dominant. During these four years combat occurred from April to June.

The following description is based on two combat events that occurred between 11 and 12-June 2004: in the evening (the main period of activity for this species) we placed the three snakes together in an arena (1.3 m x 1.1 m x 0.7 m) and recorded combat behaviour using a JVC VHS model GR-AX827. As observed in the previous years, only male 1 and 3 engaged in combat. Below, we provide a detailed description of the combat phases:

Recognition-investigation phase – When male 3 and male 1 approached each other they tongue-flicked frontally, male 3 getting the / anterior part of its body in a 15° elevated S-shape, and moved toward the head of males 1. They tongue-flicked and crawled rapidly over each other. This phase lasted 10 sec in each combat event.

Ascent-alignment-orientation – Male 3 moved forward over the dorsum of male 1, and the snakes aligned their bodies and heads. Both males ascended the 1/3 anterior part of their body while keeping the posterior parts in contact. Male 3 had the anterior trunk more elevated and placed anteriorly relative to male 1, and they kept moving.

Topping – Male 3 entwined its 1/3 anterior trunk with the 1/3 anterior trunk of male 1, and forced it to the ground. The remainder of the bodies was loosely entwined. Heads were kept in a vertical position when the trunks were elevated and many times the posterior trunks were firmly entwined (Fig. 1). Sometimes snakes had the whole bodies entwined spinning on the longitudinal axes. Frequently, these males were completely entwined, constricting each other vigorously (Fig.

2) and male 3 pressed the anterior trunk of male 1 against the ground (Fig. 3). In most cases the 1/3 anterior trunks and heads were elevated in a vertical position (Fig. 1).

Submission – Male 1 moved far away from male 3, with head on the ground, showing a submissive position. This behaviour occurred many times, with male 1 chasing male 3.

On the first day, topping was mixed with submissive behaviour but it was more vigorous. After several minutes of submission the ascent-alignment-orientation started again and combat resumed. Combat lasted about 28 min interspersed with 18 mins of intervals.

On the second day, topping was less vigorous, 31 minutes elapsed between the start and the end of the combat. Topping behaviour was interrupted many times because male 1 assumed a submissive position, trying to escape, and male 3 chased it. Total topping time was 12 minutes. Male 2 never engaged in combat. On the first day, male 1 approached male 2 from behind, crawling rapidly forward over the body of its opponent. Male 1 tongue flicked on the dorsum of male 2, moving quickly and anteriorly above the other, apparently trying to align its body with the other snake. Male 2 fled in the other direction. Then, both snakes tongue flicked frontally once again, and male 3 raised its / anterior part of its body in the form of an S-shape at an 15° angle, and moved rapidly over male 2, their bodies facing opposite directions. During the most of this time male 2 continued to move away.

Carpenter *et al.* (1976) suggested that aggressive behaviour in boine and pythonine snakes lacks the vertical components exhibited by viperids. In addition, Greene (1997) pointed out that, in these subfamilies, combat frequently occurs with the bodies on the ground. However, *Sanzinia madagascariensis* use their anterior bodies only to maintain a purchase on limbs and branches (Carpenter *et al.*, 1978). Similar to the Indian python (*Python molurus*) and other Rainbow boas (*E. c. cenchria*, *E. inornatus* and *E. angulifer*), *E. c. crassus* exhibited elevation of the head and anterior body part, and this combat

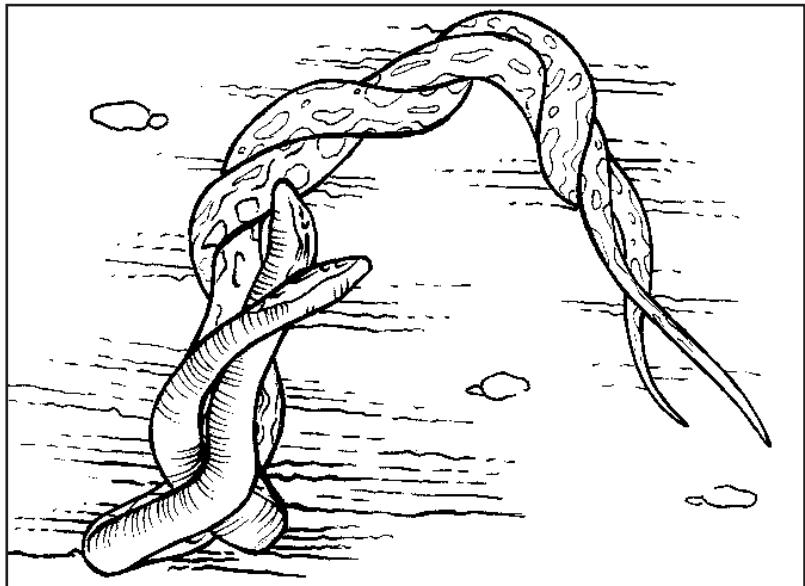
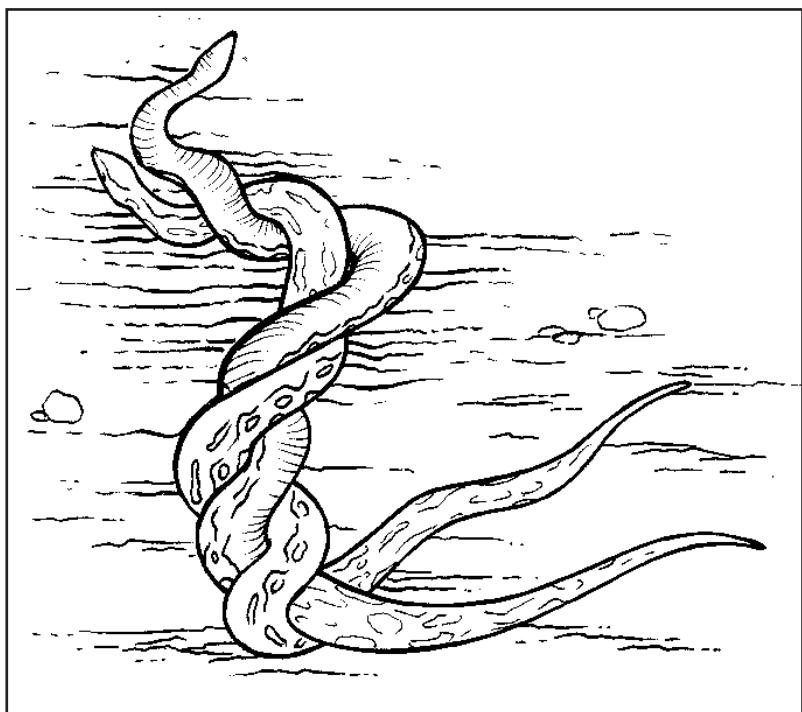


Figure 1 (above). Topping phase in *Epicrates c. crassus* showing males with 1/3 anterior trunk elevated, heads in vertical position and the posterior trunks firmly entwined. Dominant males maintain head more elevated.

Figure 2 (below). Topping phase in *E. c. crassus* showing males completely entwined, spinning and constricting each other vigorously (subordinate male is beneath dominant).



behaviour is synchronized with mating (Barker *et al.*, 1979; Schuett & Schuett, 1995). In addition, constriction during entwining is another component of boid combat behaviour, at least in *P. molurus* and *Corallus caninus* (Barker *et al.*, 1979; Osborne, 1984), and we also observed this behaviour in our study. Spur use has been recorded in courtship and combat in boine and pythonine snakes. However, we never observed this behaviour in the present work or in *E. c. cenchria* combat (Schuett & Schuett, 1995). There are at least two possibilities for this: spur use occurs but the captive conditions and small size of spurs in this species did not permit its observation, or it does not occur in this species.

Within *Epicrates*, male competition for females during the reproductive season can occur, at least in two forms: the ritualized combat, as described here, or an intense aggression which includes biting and other kinds of injury (Tolson, 1992).

Combat bouts in *Epicrates c. crassus* were always recorded during Autumn. It coincides with gonadal size increase (L. Pizzatto, *umpubl. data*) which reflects testes activity (Volsøe, 1944; Fox, 1952; Shine, 1977). Testosterone is produced during spermatogenesis and the level of this hormone is related to agonistic behaviour

in males *Epicrates striatus* (Teubner; in Tolson, 1992). Larger males of *E. striatus* have higher testosterone levels and deter smaller ones, frequently being dominant in combat bouts. In addition, testosterone levels of subordinates increase after the dominant's courtship and mating (Teubner; in Tolson, 1992). Thus, it is possible that large dominant males delay gonadal recrudescence in smaller and less aggressive males (Tolson, 1992). In our study, the two largest males (1 and 3) were indeed competitive. Their hierarchical rank varied among years, while the smallest (male 2) always showed a submissive behaviour. Therefore, it is possible that males 1 and 3 had higher levels of testosterone than unchained combat behaviour and repressed male 2.

Our observations point out that chemical cues play an important role in initiating combat behaviour in *Epicrates c. crassus*. Pheromones may be a mediator of this behaviour, since males were not in visual contact before the combat. Many studies have recorded combat occurring in the presence of females (Carpenter *et al.*, 1978; Osborne, 1984; Schuett & Schuett, 1995) but it is apparently not essential in *E. c. crassus*, since no females were held captive in the same room.

There are four patterns of combat described for snakes (Bogert & Roth, 1966; Carpenter & Ferguson, 1977). The observed combat in *E. c. crassus* has characteristics of two; patterns four (viperids) and one (colubrids). The main characteristic of pattern four is that males are oriented in the same direction, upraise and intertwine loosely their anterior trunks and maintain heads tilted or in a vertical position. However, they frequently entwine most of their body, specifically the posterior ends, and keep their heads close together, barely raised from the ground (pattern one) (Bogert & Roth, 1966; Carpenter & Ferguson, 1977).

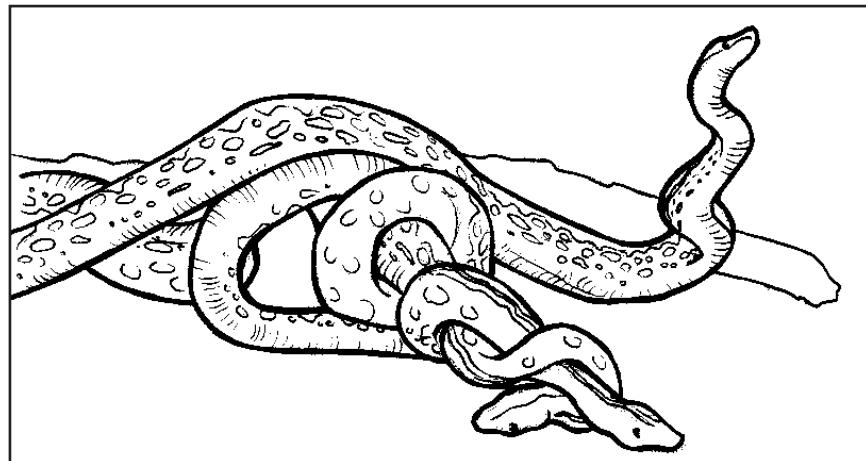


Figure 3. Topping phase in *Epicrates c. crassus* showing males with anterior trunk firmly entwined and posterior trunk loosely entwined. Dominant male is pressing the head of the subordinate male on the ground. The elevated male (male 2) is fleeing from the others and never engaged in combat.

Detailed descriptions of boid combat are scarce and current records include only four species: *Corallus caninus* (Osborne, 1984), *Epicrates c. cenchria* (Schuett & Schuett, 1995), *Epicrates angulifer* (Tolson & Henderson, 1993) and *Sanzinia madagascariensis* (Carpenter *et al.*, 1978). The latter species seems to present special adaptations of combat behaviour to the arboreal lifestyle which can not be a common pattern in this family (Carpenter *et al.*, 1978). The present work shows that *Epicrates c. crassus* combat is very similar to that of *Python molurus*, showing an anterior trunk and head elevation but lacking the spur use and biting (Barker *et al.*, 1979). *Epicrates angulifer* combatants also entwine their bodies and elevate part of the anterior trunk (see pictures in Tolson & Henderson, 1993). In conclusion, boid combat seems to be a mixed type that includes the vertical component of the anterior bodies and heads, and the entwinement of most portions of bodies with heads low to the ground and strong constriction and spinning. Mixed type of combat behaviour also occurs in the Neotropical colubrid *Chironius bicarinatus* (Almeida-Santos & Marques, 2002) and more studies can elucidate if it is common among less studied groups, such as the boids and colubrids.

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