

Dominant and submissive behaviour in the rattlesnake *Crotalus durissus* under semi-natural conditions

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INTRODUCTION

Dominance behaviour can be described as interindividual interactions (physical or not) that induce one individual (subordinate) to avoid the other (dominant) (Carpenter, 1984). This behaviour has been more often related to reproductive events, such as combat, courtship, and copulation (Barker et al., 1979; Gillingham et al., 1983; Carpenter, 1984; Guedes et al., 2014). Dominance in snakes is rarely observed in the wild, probably because in most field studies there is a low encounter rate and in any case, monitoring may often be mistimed to observe this behaviour (Bennion & Parker, 1976). However, dominance has often been reported in captivity, an environment that seems to facilitate the formation of hierarchies (e.g., Carpenter et al., 1976; Carpenter & Gillingham, 1977; Carpenter, 1979; Barker et al., 1979; Gillingham et al., 1983; Carpenter, 1984; Guedes et al., 2014).

In snakes, dominant and submissive behaviours are relatively generalised (Carpenter, 1984). In combat rituals, a male tries to force his opponent down in at least two ways: (1) by quickly looping around his rival and toppling him over or (2) by lowering the head and anterior trunk on the anterior region of his opponent, forcing him down and pinning his anterior region to the substrate (Carpenter, 1984). The subordinate male assumes a submissive posture, including coiling, tail waving, hiding the head beneath the body, retreat, or flight (Carpenter, 1984).

In vipers, males typically raise the anterior trunk and position the head vertically to the ground while orienting themselves face to face or in the same direction. Their backs are usually in contact and sometimes partially intertwined (Carpenter & Ferguson, 1977). This pattern has been recorded in *Crotalus* (Langlada, 1975; Carpenter & Ferguson, 1977; Gillingham et al., 1983; Hayes, 1986; Almeida-Santos et al., 1990; Reed, 2003), *Bothrops* (Leloup, 1975; Almeida-Santos & Salomão, 2002; Almeida-Santos et al., 2017), and in species that perform dorsal tracking instead of trunk raising, such as *Vipera*, *Sistrurus*, and *Bitis* (Carpenter & Ferguson, 1977). Dominant and submissive behaviours among males may or may not occur before combat and courtship (Gillingham, 1983; Carpenter, 1984).

In the South American rattlesnake, *Crotalus durissus*, these rituals occur during the courtship/mating season in autumn (Almeida-Santos et al., 1990). Opponents raise and sometimes loosely intertwine their trunks in the posterior region while keeping their heads upright and oriented face to face or in the same direction. Both males swing the anterior trunk back and forth, pushing and pressing each other until they fall and restart a new bout (Langlada, 1975; Almeida-Santos et al., 1990). These rituals can last from a few minutes to several hours, and this variation may be related to environmental conditions or restrictions imposed by captivity (Almeida-Santos et al., 1990). Here, we report a sequence of interactions among captive male *C. durissus* that established a dominant-subordinate relationship during the mating season.

Behavioural observations were made at the serpentarium of the Instituto Butantan, municipality of São Paulo, state of São Paulo, south-eastern Brazil (23° 34' S; 46° 43' W). The serpentarium is a semi-natural outdoor enclosure (area = 183.22 m²) designed to keep snakes in a semi-extensive breeding system (Leloup, 1984). It contains a grassy area, circular concrete shelters, artificial concrete burrows, stones, trees, and an artificial river (Gomes & Almeida-Santos, 2012). Snakes were kept under ambient conditions of temperature, photoperiod, and humidity at the time of observations. Specimens of both sexes were kept in the same area, and all individuals had their rattles marked with nail polish so that they could be identified without any physical restraint. We observed dominant and submissive behaviours in three adult males, hereafter, Alpha (1060 mm snout-vent length [SVL] and 950 g), Beta (1040 mm SVL and 720 g), and Gamma (1090 mm SVL and 770 g). These individuals had lived together in captivity for 179 days before observations commenced. Our behavioural nomenclature follows Carpenter (1976, 1979, 1984).

We observed two behavioural interactions in April 2014. At that time, five oestrous females and three males were kept in the serpentarium. The first interaction was observed on 10th April 2014, and was both videoed (BHS video, 2021) and photographed using a mobile phone. Alpha was found performing a solicitation display, pursuing, crawling over, and lying on Beta (Fig. 1A). Beta showed no interest in facing

Alpha, avoiding him and assuming a submissive posture. Alpha crawled over Beta toward the head while raising his anterior trunk. Beta retracted his body abruptly while waving his tail (Fig. 1B and C; BHS video). At the same time, Alpha raised his head and performed a vertical display while topping, forcing the anterior trunk and keeping his posterior trunk over the anterior portion of Beta's body, which was coiled with the head down (Fig. 1D and E). As soon as Alpha lowered his anterior trunk slightly, Beta fled (Fig. 1F). The following week, we observed Gamma exhibiting the same submissive behaviour (coiling and head down) to Alpha. Throughout

the 2014 mating season, only Alpha was observed courting different females and copulated with one. Beta and Gamma remained distant, always occupying microhabitats different from those occupied by Alpha.

We observed several visual and tactile communications between male rattlesnakes that may be significant in establishing dominant-submissive relationships. The observed behavioural patterns classify Alpha as the dominant male and Beta and Gamma as the submissive ones (Carpenter et al., 1976; Carpenter & Gillingham, 1977; Carpenter, 1979; Barker et al., 1979; Gillingham et al., 1983;

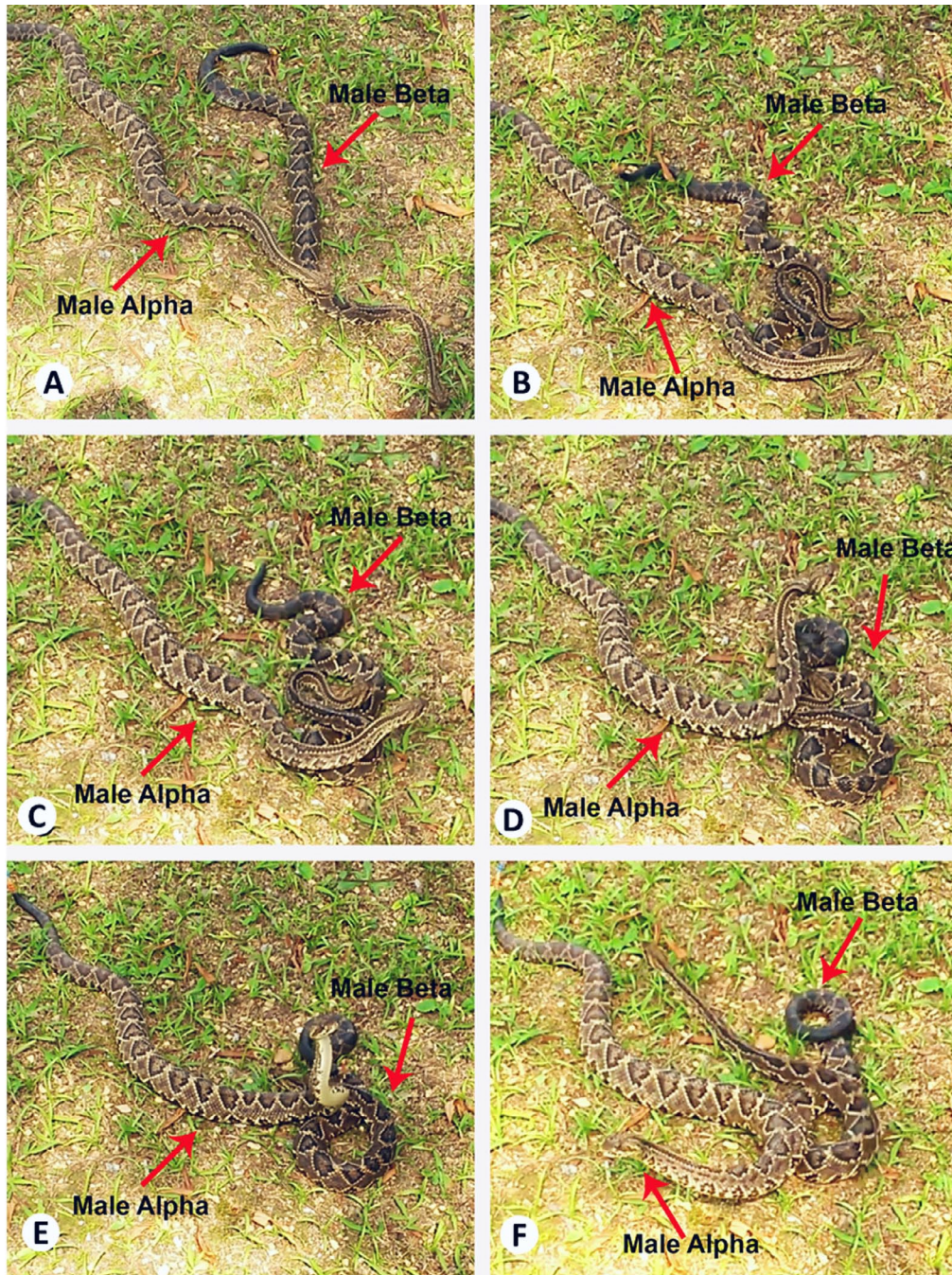


Figure 1. Behavioural sequence for establishing dominance and submission in captive male *Crotalus durissus*- **A.** Alpha approaches Beta and initiates contact by crawling over, **B.** Alpha approaches Beta, which coils, **C.** Alpha crawls over and lies on Beta, **D.** Alpha raises his head and anterior trunk and keeps his posterior trunk over Beta's anterior trunk and Beta shows a submissive posture (coiled and head down), **E.** Alpha crawls over Beta, which assumes a submissive posture, note the vertical display of Alpha (dominant male), and **F.** Alpha lies on Beta, which tries to flee

Carpenter, 1984). The tactile signs exhibited by the dominant male included crawling over, topping, and lying on, whereas the visual signs included vertical display, approach, pursuit, and solicitation display. The tactile and visual signs exhibited by the subordinate males included avoidance, flight (retreat), thrashing, tail waving, coiling, head down, and submissive posture (Fig. 1).

Snakes are seen as animals with little or no social behaviour (Wilson, 1975). However, individual recognition apparently occurs in aggregation behaviours (Clark, 2004; Skinner & Miller, 2020), as well as in the formation of a stable linear social hierarchy among captive male *Python molurus* (Barker et al., 1979). In our observations, the dominant male always pursued and remained over the subordinate males, exerting the classic dominance observed in male-male combat which prevented the subordinates from assuming any dominance posture. In turn, the subordinate males avoided the dominant male throughout the austral autumn. Furthermore, the subordinate males were never seen courting captive females, even days after the observed dominance actions. Indeed, subordinate males are believed to be sexually inhibited even days after the male-male combat, due to stress hormones levels, and their reproductive performance is probably reduced (Schuett, 1996; Schuett & Grober, 2000). On the other hand, in atypical situations of coexistence, such as in captivity, there may be some chemical or visual recognition in which subordinate male snakes recognise and avoid dominant ones, thus establishing social hierarchies (Barker et al., 1979; Clark, 2004; Skinner & Miller, 2020).

In some situations, body size may not be the main factor determining male reproductive success or establishing dominance (Barker et al., 1979; Muniz-da-Silva & Almeida-Santos, 2013; Glaudas et al., 2020a; Glaudas et al., 2020b). Nevertheless, body size does play an important role in determining dominance and subordination in snakes, as both our data and the literature show that dominant males are slightly larger and/or heavier than subordinate males (Carpenter, 1984; Guedes et al., 2014). Male-biased sexual size dimorphism is common in species that exhibit male-male combat, including *Crotalus* (Almeida-Santos et al., 1990; Shine, 1994; Senter et al., 2014) and, consequently, body size is under strong sexual selection (Shine, 1994). In our observations, the dominant male was the stoutest (not the longest) male in the serpentarium emphasising the importance of body weight rather than just length.

Because most observations on dominance in snakes have been made in captivity, it is likely that this environment favours the emergence of this hierarchical social relationship. Thus, the captive environment provides valuable opportunities to study behaviours that are difficult to observe in the wild (Carpenter et al., 1976; Carpenter & Gillingham, 1977; Carpenter, 1979; Barker et al., 1979; Gillingham et al., 1983; Carpenter, 1984; Guedes et al., 2014). Although male-male predatory combat (i.e. snakes fighting over food) and dominance/subordination behaviour have already been reported in captive *C. durissus* (Almeida-Santos et al., 1999), our report is the first detailing observations in semi-natural conditions (semi-extensive captivity) using video to enable a more detailed description (spatially and temporally) of these behaviours in a reproductive context.

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