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Aggressive Behavior in Male Tiger Rat Snakes (*Spilotes pullatus*) During Ritual Combat

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***Abstract.*—Like many snakes, Tiger Rat Snakes (*Spilotes pullatus*) engage in male-male combat during the mating season. These combats involve ritualized dances, but aggressive behaviors that may cause physical injuries to the opponent have not been reported in the species so far. Here, we report the first cases of aggressive behavior (biting) during ritualized male-male combat in *S. pullatus* based on detailed field observations. Because male *S. pullatus* can engage in aggressive fights during the mating season, even in the absence of females, we argue that the motivation for these interactions extends beyond reproductive competition and that these disputes can escalate into aggressive interactions if dominance is not established during the ritual combats. Our observations contribute to a better understanding of the social behaviors and hierarchical structures in snakes, with implications for evolutionary studies of combat strategies and the associated fitness costs**

Key Words.—agonistic interactions; Brazil; dominance; male-male combat; snake behavior; territoriality.

Introduction

Many studies suggest that snakes can interact and exhibit social behaviors with conspecifics during combat rituals, courtship, mating, and parental care (Carpenter 1977, 1984; Barker et al. 1979; Gillingham 1987; Batista et al. 2021). For these social interactions to occur, snakes use individual recognition mechanisms, such as visual, olfactory, and tactile cues (Carpenter 1977). An individual snake can interact with conspecifics to compete for resources (e.g., mates, food, and territory) to ultimately establish dominance (Carpenter 1984; Batista et al. 2021). Clear criteria to define dominance are generally lacking in snakes. Carpenter (1984), however, defines dominance as an interaction between two individual snakes in which one performs certain behaviors that ultimately cause the other to avoid those behaviors. On some occasions, these interactions involve no physical contact between individuals, but on others, individuals engage in physical combat for access to resources.

Male-male combat has been described in several snake taxa (Shine 1978; Senter 2022), and this rivalry has been proposed to be associated with territoriality (Carpenter and Ferguson 1977). In many cases, male combats are ritualized, involving sequences of interactions between two male snakes that appear to be in a contest for superiority or dominance (Carpenter 1977). In other cases, bites can be employed by rival males, as reported in boids, elapids, and viperids (Andrén 1986; Williams 1992; Almeida-Santos et al. 1999; Webb et al. 2015; Santos et al. 2020), including many colubrids (for a comprehensive list, see Appendix Table). Aggressive behavior remains poorly understood in snakes; however, few reports have suggested territoriality in this group (Kennedy 1965; Huang et al. 2011; Webb et al. 2015).

Male Tiger Rat Snakes, *Spilotes pullatus* (Colubridae), have been reported to exhibit ritual combat between mid-winter and early spring (August-October) associated with the mating season, with sperm storage in the ductus deferens and peak of activity in the sexual segment of the kidney, but dissociated from spermiogenesis that occurs in austral autumn (late March to June; Muniz-da-Silva 2012; Muniz-da-Silva and Almeida-Santos 2013; Marques et al. 2014). Male *S. pullatus* may even interrupt a courtship event to chase away rivals from the area (Muniz-da-Silva and Almeida-Santos 2013). In one case, a male briefly exposed the hemipenis a few times during combat (Muniz-da-Silva and Almeida-Santos 2013). Despite the long duration of combat rituals (up to one hour), however, aggressive

behaviors that may cause physical injuries to the opponent have not been reported for the species so far. Faced with a predator or threat, male *S. pullatus* nod, bite, and inflate their necks, increasing their size to intimidate the opponent (Martins et al. 2008). No females were observed in some of the combat sites (Muniz-da-Silva and Almeida-Santos 2013; Marques et al. 2014), suggesting that male combat rituals in *S. pullatus* serve purposes other than access to females, such as dominance or territorial disputes (Muniz-da-Silva and Almeida-Santos 2013). Here, we report the first cases of aggressive behavior during male-male combat in *S. pullatus*. Because male *S. pullatus* can also aggressively fight during the mating season even without the presence of females, we consider the possibilities that males fight for dominance or territory regardless of the presence of females and that these disputes can escalate into aggressive interactions (with bites being delivered to the body of the rival) when dominance is not established.

Materials and Methods

We described three ritual combats between male *S. pullatus* based on the analysis of video footage and detailed notes taken during field research, whose main objective was to survey reptiles and amphibians in this region. The observations were made from 1–3 m away and the snakes appeared unaffected while observers recorded the event. We analyzed the videographs frame by frame and named combatants as male 1 and male 2 in each record using the natural marks observed on the dorsal or lateral aspects of the head and body. The snakes were not captured at any time and their body size was inferred from the knowledge of the researchers in the field (pers. obs.). Observations were made at Legado das Águas (24°03'12.0"S, 47°12'55.7"W; about 560 m elevation), in the state of São Paulo, southeastern Brazil. Legado das Águas (31,000 ha) is the largest private reserve of the Atlantic Forest, encompassing areas in the municipalities of Tapiraí, Miracatu, and Juquiá.

The observations of combats were made in Miracatu during the austral winters 2016–2018. The climate in this region is seasonal with an average annual temperature of 24.4º C, a maximum temperature of 34.2º C, and a minimum of 13.1º C. Warmer temperatures occur from spring (October-December) to summer (January-March), associated with higher rainfall between the months of January and February with an average of 2,000 to 3,000 mm. Lower temperatures occur from autumn (April-June) to winter (July-September), associated with lower rainfall between the months of July and September with an average of 1,609 mm (Mendonça and Danni-Oliveira 2007).

Results

Combat #1.—On 20 August 2016 (mid-winter), at 1719, two male *S. pullatus* were found on an open trail with their posterior trunks slightly entwined. The males were similar lengths and exhibited constant tongue flicking. Male #1 inspected the anterior trunk of Male #2 for 14 s as Male #2 slowly crawled toward the woods. Then, Male #1 bit and held the anterior trunk of Male #2 for 32 s (Fig 1). After a 3-s pause, Male #1 bit and held the posterior trunk of Male #2 near the tail for 17 s. During this time, Male #2 inspected the tail of Male #1. By that time, the snakes were no longer entwined. Fourteen seconds later, Male #2 slightly raised his anterior trunk and moved over the head of Male #1, following movements by Male #1 for 10 s. Both males stopped moving for 10 s and kept their heads apart (Fig 1). When they resumed movement, Male #2 raised his anterior trunk, and Male #1 promptly bit the head of its opponent for 18 s (Fig 1). After 5 s, Male #1 attacked Male #2 again, biting his anterior trunk for 20 s. When Male #1 released his bite, Male #2 attempted to bite the midbody of Male #1 but stopped as soon as he was bitten back by Male #1. Ten seconds later, Male #1 released his bite. Male #2 raised his anterior trunk and was immediately followed by Male #1. Both males kept their anterior trunks swaying from side to side, each attempting to attain a higher position. The ritual combat continued without any additional bites (Fig 1). During the combat, Male #1 bit Male #2 six times, whereas Male #2 bit Male #1 twice. We were unable to establish dominance between the males. In addition, no females were noted in the vicinity during the observation. The complete record of this combat is available in Supplemental Information Video S1.

Combat #2.—On 1 September 2017 (late winter), around 1030, two male *S. pullatus* with similar body size were spotted with their posterior trunks entwined. The combat occurred partly over low-lying vegetation and partly on terrestrial substrates. Both males repeatedly attempted to keep their anterior trunks raised above that of the opponent (Appendix Fig. 1). After 33 s, one of the males fled. The other male moved while keeping his head up and engaged

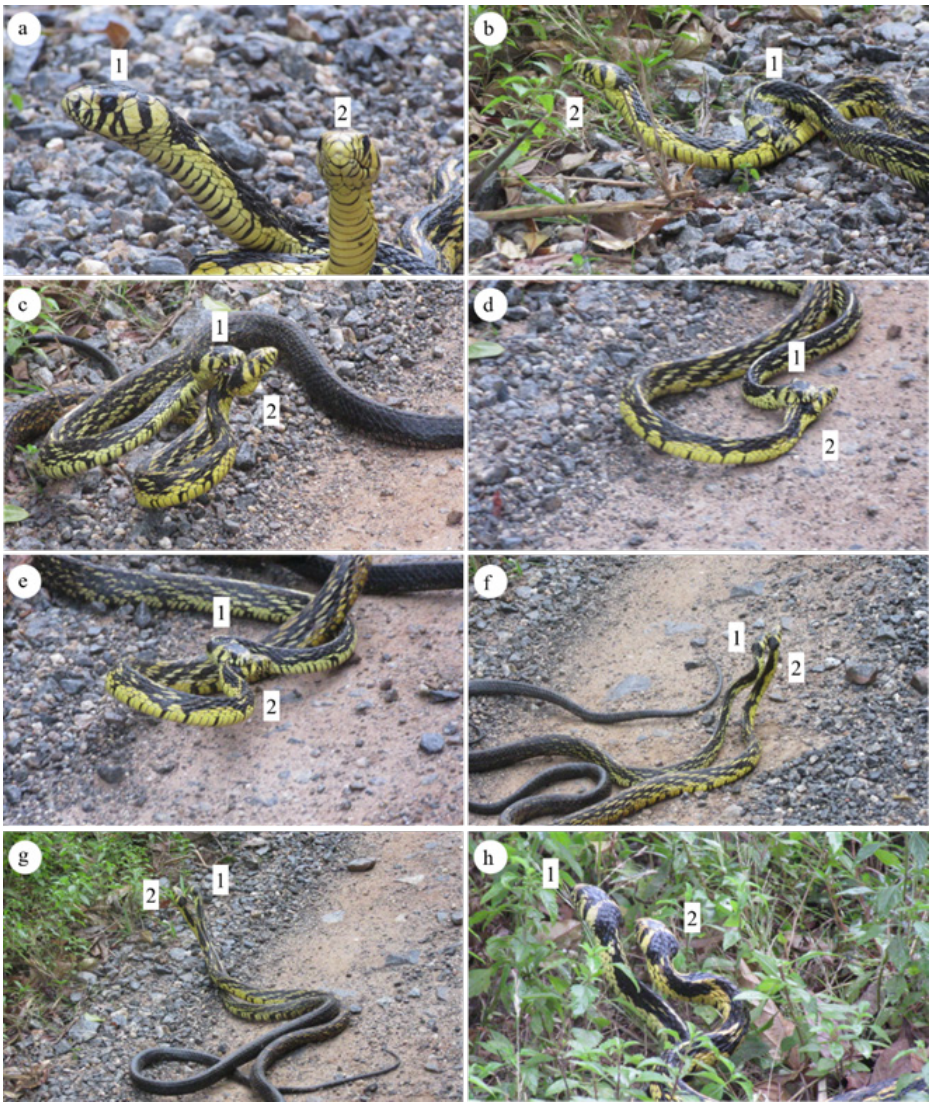

Figure 1. Male-male ritual combat in the Yellow Rat Snake (*Spilotes pullatus*) with aggressive behavior. (a) Vertical display (orientation). (b) Male #1 inspecting and biting the midbody of Male #2. (c) Male #2 lifting his head (while inflating the neck region) and raising the trunk and neck, followed by Male #1. (d, e) Male #1 biting the head of Male #2. (f) Vertical display (orientation). (g, h) Topping attempt. (Photographed by Miguel F. de Jesus).

in intense tongue-flicking towards the rival male. No bites were observed, and females were not witnessed in the vicinity during this combat.

Combat #3.—In September 2018, two male *S. pullatus* were found on the ground at the forest edge. The males were similar lengths and entwined with their bodies aligned (Appendix Fig. 2). Male #1 was inspecting the body of Male #2 while Male #2 had his mouth partially open and his head-neck region raised. Male #1 then bit the anterior trunk of Male #2 and released it after 2 s (Appendix Fig. 2). Male #1 returned to inspect the anterior trunk of Male #2 again. After 10 s, Male #1 vibrated his tail against the substrate while biting the anterior trunk of Male #2 for approximately 2 s. Male #2 remained motionless during this period. Male #1 resumed inspecting the anterior trunk of Male #2 once again. Male #2 then moved, and Male #1 moved over the head region of Male #2 (Appendix Fig. 2). Male #2 tongue-flicked frequently. Next, Male #1 came down on the head of his rival (Appendix Fig. 2). Shortly after, the observer moved, and Male #2 turned and crawled into the forest, followed by Male #1. Females were not

founded in the vicinity of the combat.

Discussion

The three male combats reported here occurred during the late austral winter, coinciding with the timing of mating and ritual combat (but without biting) previously described in the species (Muniz-da-Silva and Almeida-Santos 2013; Marques et al. 2014). In combats #1 and #3, the males exhibited aggressive behavior by biting heads and bodies of each other. On the other hand, in combat #2, one of the males fled, suggesting that dominance was established (Carpenter 1984; Gillingham 1987), as recorded in the South American Rattlesnake, *Crotalus durissus* (Batista et al. 2021). Body size, however, is not necessarily related to victory in combat (Glaudas et al. 2020). Other fights between male *S. pullatus* with frequent bites have been observed in Chapada dos Guimarães, Mato Grosso (central Brazil), and this behavior is apparently common during the reproductive period (Renan Costa, pers. comm.). Because no bites were reported in *S. pullatus* before in the literature, our observations bring new information about this behavior, although it appeared in Colubridae much earlier (Senter 2022; see Appendix Table). It is worth noting that no females were noted near the combat sites during the observations, suggesting that males are reactive and fight with other males regardless of the presence of females, thus reinforcing the idea that males fight for dominance or territory.

Territoriality is interpreted as a form of relative dominance (Kaufmann 1983). Snakes are dominant within certain spatial boundaries (territories) but tend to be relatively subordinate outside of these territories (Gillingham 1987). Therefore, male *S. pullatus* might be stimulated to engage in disputes for dominance and chase away other males that enter their territory. We suggest that if dominance is not established during the ritual combats, these disputes may escalate to aggressive interactions, with bites being delivered to the body and head of rivals. In Indian Rock Pythons (*Python molurus*,) biting is usually used by the dominant male to prevent the subordinate snake from escaping (Barker et al. 1979).

Capula and Luiselli (1997) tentatively classified the behavioral types of male combats exhibited by snakes on the Italian Peninsula, subdividing them into four groups: (1) Type 1 (highly ritualized dances without biting); (2) Type 2 (vigorous biting); (3) Type 3 (vigorous biting and tail wrestling); and (4) Type 4 (ritualized dances with occasional biting). Therefore, although it is impossible to draw strong conclusions from only three observations, *S. pullatus* seems to exhibit combat Type 4, which also occurs in many colubrids, including phylogenetically related taxa (Appendix Table; see also Senter 2022). Additional data on other colubrids are needed not only to test whether male-male combat with biting is an ancestral trait but also to reconstruct the evolutionary history of male combat behavioral types.

Biting during male combat has been observed in non-venomous smooth snakes (*Coronella* spp.), false smooth snakes (*Macroprotodon* spp.), and rat snakes (*Elaphe* spp.; see Capula and Luiselli 1997) and venomous snake species, such as Sidewinders (*Crotalus cerastes*; Lowe 1942; Lowe and Norris 1950) and Eastern Small-eyed Snakes (*Cryptophis nigrescens*; Webb et al. 2015). Bites delivered to the head and body during combat bouts may inflict severe damage on individual males (Araújo et al. 2022). In the colubrid Formosa Kukri (*Oligodon formosanus*), tail injuries have been attributed to intraspecific agonistic encounters for territorial defense (Huang et al. 2011). Therefore, employing this aggressive behavior during male combat is expected to have high fitness costs for male *S. pullatus* and other snakes.

Our observations and discussion raise further questions for future studies. These questions can be tested experimentally; for example, by keeping male and female *S. pullatus* together in captivity and observing their social interactions. Future studies could manipulate combat between males of different sizes in captivity to test whether this behavior is exclusive to gaining access to females and whether the intermittent biting described here reflects the absence of established dominance through ritual combat.

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Supplemental Information: https://vimeo.com/1079244192

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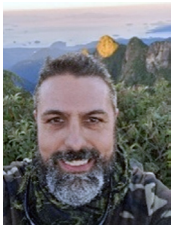

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Appendices

Appendix Figure 1. Male-male combat in the Yellow Rat Snake (*Spilotes pullatus*). (a) Topping attempt (red arrows indicate the heads of the males). (b) Vertical display with dorsal hyperextension (red arrows indicate the heads of the males). (c) One of the males fleeing (orange arrow) while the other male keeps his head up with intense tongue-flicking (yellow arrow), apparently attempting to locate the rival male. (Photographed by Rafaella Jurkfitz).

Appendix Figure 2. Male-male ritual combat in the Yellow Rat Snake (*Spilotes pullatus*). (a) Male #1 inspecting the body of Male #2. (b) Male #1 biting the midbody of Male #2. (c, d) Topping. (Photographed by Miguel F. de Jesus).

Appendix Table. Social interactions involving biting and chasing recorded in the family Colubridae.

Species	Reproductive behavior	Bite	Presence of female	Site	Reference
Trans-Pecos Rat Snake (*Bogertophis subocularis*)	Combat	Yes	-	-	Rehak 1990
Smooth Snake (*Coronella austriaca*)	Combat	Yes	Yes / No	Nature	Capula and Luiselli 1997
Southern Smooth Snake (*Coronella girondica*)	Combat	Yes	-	Nature	Capula and Luiselli 1997
Eastern Small-eyed Snakes (*Cryptophis nigrescens*)	Combat	Yes	No	Captivity	Webb et al. 2015
Blacktail Cribo (*Drymarchon melanurus*)	Combat	Yes	-	-	Rehak 1990
Japanese Ratsnake (*Elaphe climacophora*)	Combat	Yes	-	-	Rehak 1990
Four-lined snake (*Elaphe quatuorlineata*)	Combat	Yes	-	Nature	Capula and Luiselli 1997
Grey-banded Kingsnake (*Lampropeltis alterna*)	Combat	Yes	Yes	Captivity	Murphy et al. 1978
California Kingsnake (*Lampropeltis californiae*)	Combat	Yes	-	-	Rehak 1990
Common Kingsnake (*Lampropeltis getula*)	Combat	Yes	-	-	Krysko et al. 1998
Mexican Kingsnake (*Lampropeltis mexicana*)	Combat	Yes	-	Captivity	Secor 1990
Atlantic Central American Milksnake (*Lampropeltis polyzona*)	Combat	Yes	-	-	Rehak 1990
Arizona Mountain Kingsnake (*Lampropeltis pyromelana*)	Combat	Yes	-	-	Martin 1976
Giant Parrot Snake (*Leptophis ahaetulla*)	Combat	Yes	Yes	Nature	Mattos et al. 2017
False Smooth Snake (*Macroprotodon cucullatus*)	Combat	Yes	No	Captivity	Capula and Luiselli 1997
Eastern Coachwhip (*Masticophis flagellum*)	Combat	Yes	No	Nature	Schuett and West 2020
Striped Racer (*Masticophis lateralis*)	Combat	Yes	Yes	Captivity	Hammerson 1978
Striped Whipsnake (*Masticophis taeniatus*)	Combat	Yes	No	Nature	Bennion and Parker 1976
Brown vinesnake (*Oxybelis aeneus*)	Combat	Yes	Yes	Nature	Araújo et al. 2022
Red Cornsnake (*Pantherophis guttatus*)	Combat	Yes	-	-	Rehak 1990
Eastern Rat Snake (*Pantherophis alleghaniensis*)	Combat	Yes	-	Nature	Stickel et al. 1980
Eastern Pine Snake (*Pituophis melanoleucus*)	Combat	Yes	-	Captivity	Shaw 1951
Black-banded Snake (*Scolecophis atrocinctus*)	Combat	Yes	No	Nature	Chernov et al. 2020
Ground Snake (*Sonora episcopa*)	Combat	Yes	-	-	Kroll 1971
Tiger Rat Snake (*Spilotes pullatus*)	Combat	Yes	No	Nature	This study
Leopard ratsnake (*Zamenis situla*)	Combat	Yes	Yes	Captivity	Capula and Luiselli 1997