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Intense Male-Male Ritual Combat in the *Micrurus ibiboboca* Complex (Elapidae) from Northeastern South America

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***Abstract.*—Snakes engaged in agonistic encounters may employ visual and tactile displays that sometimes culminate in ritual combat. Here, we describe novel male-male ritual combat behaviors in South American coral snakes in the *Micrurus ibiboboca* complex based on the largest observational dataset of ritual combat for any species of the genus *Micrurus*. The dataset includes 85 photographs and four videographs from six respective observation records of male snakes. We observed four of these fights during the daytime and two during the night. All observations were random encounters in different natural environments during transitional dry seasons (i.e., early dry season between April and June in the west, and the early wet season between August and September on the east coast). During each respective period, precipitation is < 100 mm and is accompanied with decreasing and increasing temperatures, respectively. The following behaviors were observed: recognition, ascent, and alignment. These were followed by orientation, entwining and twisting, rolling, and hovering; then, oblique display stances and topping (including lyre-shaped positioning and dorsal hyperextension). The topping attempts were from high oblique display positions with one male attempting to force the head of the other down. We also observed snapping, where snake opponents twist the heads of each other creating a quick snap-like sound. We suggest these complex ritual displays communicate dominance between snakes.**

Key Words.—coral snakes; dorsal hyperextension; lyre-shaped; nocturnal activity; snaps

***Resumo.*—Serpentes envolvidas em encontros agonísticos podem assumir manifestações visuais e tácteis por vezes culminando em combate ritual. Aqui, descrevemos combates rituais entre machos com novas posições dos oponentes durante as fases da luta a partir do complexo *Micrurus ibiboboca*, com base na compilação do maior conjunto de dados da natureza para qualquer espécie do genero *Micrurus*. O conjunto de dados é composto por 85 fotografias e quatro vídeos provenientes de seis respectivos registros de machos. O combate entre os machos foi observado em quatro dias e duas noites. As lutas foram registadas em encontros aleatórios, em diferentes ambientes naturais durante as estações secas, de transição (ou seja, início da estação seca entre Abril e Junho no oeste, e início da estação menos chuvosa entre Agosto e Setembro na costa leste). Durante cada respectivo período, a precipitação atingiu menos de 100 mm, concomitante com a diminuição e aumento da temperatura. Os seguintes comportamentos foram observados: reconhecimento, ascensão e alinhamento. Estes, foram seguidos por orientação, entrelaçamento e torção, rolagem e pausa; então, posição de exibição oblíqua e topping (incluindo posição em forma de lyra e hiperextensão dorsal). As tentativas de topping foram de uma posição de exibição oblíqua alta, com um macho tentando baixar a cabeça do outro. Foram também observadas pequenas pancadas entre as cabeças. Nós sugerimos que esta exibição comportamental é uma comunicação por dominância entre serpentes.**

Palavras-chave.—atividade noturna; estalos; forma de lira; hiperextensão dorsal; serpentes corais

Introduction

Among vertebrates, snakes form a specialized clade within the order Squamata and represent one the most successful limbless reptiles on the planet (Apesteguía and Zaher 2006; Zaher et al. 2009; Longrich et al. 2012). The loss of limbs, ears, and associated body elongation limit the ways snakes can communicate with other organisms in their environment. To compensate for these morphological constraints, snakes have evolved behavioral displays that are unique among vertebrates (Bogert and Roth 1966; Carpenter 1977; Carpenter and Ferguson 1977). Social interactions vary in snakes, and include a number of different body postures, movements, or tactile displays used for courtship and mating, parental care, or agonistic behaviors (Bogert and Roth 1966; Carpenter 1977). Agonistic behaviors represent some of the most complex social interactions in snakes, and sometimes may culminate in ritual combat, where two or more individuals fight for dominance.

Several studies have focused on the function of ritual combat in snakes (e.g., Bromley 1934; Davis 1936; Shine 1978, 1994; Almeida-Santos and Marques 2002). Ritual combat includes agonistic behaviors that may be elicited by factors such as predatory combat in feeding (Naulleau 1967; Almeida-Santos et al. 1999), territoriality (Almeida-Santos and Marques 2002; Pizzatto et al. 2006; Muniz-da-Silva and Almeida-Santos 2013), copulatory guarding (defense of a receptive female; Andrén 1986), tail wrestling (separation of couple; Shine et al. 1981) or gaining priority of access to females (Gillingham and Schuett 1989). Male-male ritual combat has been described in approximately 4% of the 430 recognized species of Brazilian snakes (e.g., Pizzatto et al. 2007; Muniz-da-Silva and Almeida-Santos 2013; Senter et al. 2014; Guedes et al. 2019; Costa et al. 2021). Because snakes are inconspicuous animals with secretive habits, we believe that this rate is underestimated.

Ritual combat involves body contact between at least two snakes, usually males, with pushes, flips, or entwinement between individuals attempting to achieve dominance (Carpenter and Ferguson 1977). In a review of male-male combat in snakes, Bogert and Roth (1966) recognized four distinct patterns, with later evidence pointing to intermediate patterns in Brazilian snakes (Pizzatto et al. 2007). The actions involve high vertical to horizontal display postures, with either male attempting to force the head of the other down (Carpenter 1977).

In elapid snakes, the general pattern of male-male ritual combat involves entwining and twisting of the mid-posterior region of the body and tail, with the anterior region, neck, and head in a vertical or oblique position, while each opponent swings and tries to entwine and force the head of the other down, elevating the anterior body as a sign of dominance (Carpenter 1977; Shine and Allen 1980). Several studies have described male-male ritual combat in African, Australian, and Asian elapids (see Carpenter 1986 for more details), but there have been few studies of combat in North and South American elapids, such as the coral snake genus *Micrurus* (Almeida-Santos et al. 1998; Marques et al. 2013; Missassi et al. 2017; Valencia et al. 2020; Mendes et al 2021).

Knowledge of the biology of *Micrurus* species in nature is limited and the few publications describing combat between males are restricted to members of the black ring triadal (hereafter BRT) clade (Marques et al. 2013; Jower et al. 2019), such as the Uruguayan Coral Snake (*M. altirostris*), Brazilian Ribbon Coral Snake (*M. lemniscatus carvalhoi*), Pacific Red-tailed Coral Snake (*M. mipartitus decussatus*), and Eastern Worm-eating Coral Snake (*M. hemprichii hemprichii*). The behaviors observed include horizontal alignment, twisting with intertwined bodies and tails with oblique heads slightly above the ground, and moving forward trying to maintain the head above the opponent in a probable expression of dominance (Almeida-Santos et al. 1998; Missassi et al. 2017). Furthermore, the elevation of the anterior trunk and the head was observed in captive and wild specimens of *M. altirostris* (Almeida-Santos et al. 1998; Marques et al. 2013) and *M. mipartitus decussatus* (Valencia et al. 2020), respectively. Additional details for other members of the genus are unavailable (Almeida-Santos et al. 1998; Marques et al. 2013; Missassi et al. 2017; Valencia et al. 2020; Mendes et al. 2021).

We contribute to the knowledge of agonistic behaviors in *Micrurus* by describing novel male-male ritual combat of the South American elapid coral snakes of the *Micrurus ibiboboca* complex. Over the last 14 y, we obtained six previously undocumented instances of male agonistic behavior in nature, the largest sequence of data on combat behavior for any elapid coral snake species. Using this dataset, we provide the first compilation of natural male-male ritual combat for *Micrurus* species, which allows us to summarily describe and reinterpret restrictions in previously published datasets. We report the occurrence of three hitherto undescribed postures for South American elapids during male-male combat, describe behaviors based on direct sequential photographic evidence and videos, compare these with pertinent literature, and provide the first descriptions of nocturnal male-male combat behavior in *Micrurus* species. We also discuss the phenology of these observations in comparison with a recently published model discussing reproductive trends in South American coral snakes (Almeida-Santos et al. 2021).

Table 1. Observations of male-male ritual combat in the *Micrurus ibiboboca* complex. The interacting males were found by different observers in six independent localities in Bahia (BA) and Rio Grande do Norte (RN) states, Brazil, always after the beginning of the combat.

Interaction	Municipality / State	Locality	Date of observation	Time of observation	Elapsed time
1 (84 photos)	Salvador / BA	Sapiranga Ecological Reserve	31 August 2009	1130	120 s
2 (2 videos)	Camaçari / BA	—	22 September 2010	2052	60 s
3 (video)	Palmeiras / BA	Estrada do Capão	4 June 2015	1656	46 s
4 (video)	— / BA	Chapada Diamantina, Vale do Pati	11 April 2016	Sunny period	108 s
5 (video)	Rio do Antonio / BA	—	06 May 2018	1200	60 s
6 (photo)	Tibau do Sul / RN	—	28 August 2020	2040	01 s

Materials and Methods

Data collection.—Our description and analyses of male-male ritual combat behavior are based on 85 photographic records and four videographs recorded in nature of six independent encounters with males of the *Micrurus ibiboboca* complex engaged in combat. All encounters happened after the males began combat, meaning we did not see the beginning of the rituals. We used these photographs and videographs to generate our dataset (Table 1). Records 1 to 5 were obtained in the State of Bahia (BA) and record 6 was obtained in the State of Rio Grande do Norte (RN), Brazil, between 2009 and 2020. Record 1 consisted of photographs obtained by the professional photographer Eduardo Moody at the Sapiranga Ecological Reserve. Record 2 was composed of two videographs obtained by Eric Paranaguá in Camaçari municipality at two localities near the Atlantic coast. Record 3 was provided by Andrew Kemp and obtained at Estrada do Capão, Palmeira municipality. Record 4 has an unknown author and was obtained in the Vale do Pati, Chapada Diamantina, approximately 330 km west of the Atlantic coast at an altitude at least 300 m above sea level. Record 5 was obtained by Paulo Rocha in Rio do Antonio municipality, roughly 717 km western from the Atlantic coast. Record 6 consisted of a photograph obtained by Marcelo Kokubum at Tibau do Sul municipality, Rio Grande do Norte State (Table 1). These localities are along the northeastern known distribution for the *M. ibiboboca* complex and were mapped using the open source software Qgis 3.4 Madeira (http://www.qgis.org; Fig. 1).

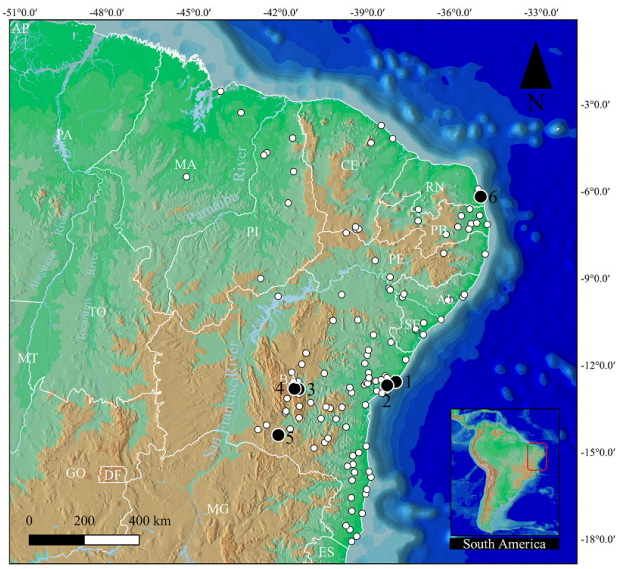

Figure 1. Geographic distribution of the *Micrurus ibiboboca* complex in Brazil, northeastern South America (inset, red rectangle). The type locality given by Merrem (1820) is in Brazil, whereas Wied (1825) specified it as "Mouth of Belmonte river, State of Bahia, Brazil" (not shown in map). White dots represent the known distribution of the species based on literature (Vangilder and Vitt 1983; Olmos 1988; Rocha and Santos 2004; Guedes 2006; Rocha 2007; Serafim et al. 2007; Santana et al. 2008; Farias 2009; Queissada 2009; Nunes et al. 2010; Marques et al. 2011; Morato et al. 2011; Rodrigues and Prudente 2011; Cavalcanti et al. 2012; Pires et al. 2014). The highlighted black dots represent the areas where the interacting males were observed. Legend: Brazil, Bahia (BA): (1) Sapiranga Ecological Reserve, Salvador municipality; (2) Camaçari municipality; (3) Estrada do Capão, Palmeiras municipality; (4) Chapada Diamantina, Vale do Pati locality; (5) Rio do Antonio municipality; Rio Grande do Norte (RN); (6) Tibau do Sul municipality.

We recorded precipitation and temperature for the combat period of occurrence, which we compared to the life history and reproductive patterns hypothesized for BRT-patterned *Micrurus* (Marques et al. 2013; Almeida-Santos et al. 2021). We used data from the National Meteorology Institute (https://bdmep.inmet.gov.br; Fig. 2), to locate weather stations near the localities or nearby in Brazil that provided data from 1984 to 2019 (35 y). We present the average monthly precipitation in millimeters (mm) and maximum, mean, and minimum monthly temperatures (ºC; Fig. 2). We split the areas into eastern and western regions (Fig. 2) in the State of Bahia due to different morphoclimatic domains and define dry months as those in which the precipitation in mm was less than twice the temperature in ºC (Cardoso et al. 2014). Characterization of the climatology of the area followed Koppen's classification (Alvares et al. 2013). As the east coast in Bahia State has a continuous rainy season, we classified the periods as more (rainy) or less (dry) rainy seasons (Santos et al. 2016).

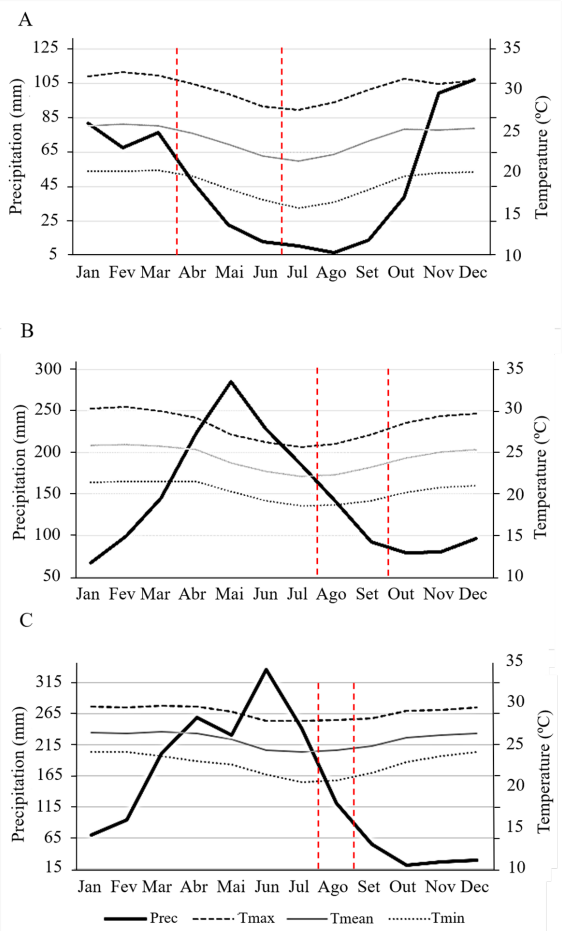

Figure 2. Thermopluviometric graph of the northeastern region in South America, respectively, in the Brazilian States of the Bahia: western region (A) Ituaçu (meteorological station 83292, m.s. hereafter) near Vale do Pati in Chapada Diamantina, and east coast (B) Salvador (m.s. 83229) near Reserva Sapiranga and Camaçarí; and Rio Grande do Norte: east coast (C) Natal (m.s. 82598). Precipitation and temperature correspond to the average of the last 35 y (1984–2019), obtained from dataset of the National Meteorology Institute (Inmet – Bdmep) in Brazil. Dashed red line delimits the period in which combat was recorded.

Identification of the combating males.—To refine inferences in combat behavior, we recognized each male specimen by natural marks on the dorsal, lateral, and ventral aspects of the head (*sensu* Sazima 1988), and named combatants as male 1 and male 2 in each record using the natural marks observed. We analyzed the high-resolution photographs and videographs frame by frame, comparing the data obtained to pertinent taxonomic literature (Merrem 1820; Amaral 1925, 1927; Pires et al. 2014; Silva et al. 2016). This procedure was useful for delineating our behavioral analysis, interpretation, and description of the combat, and allowed us to confirm the taxonomic identity of the competing males. All specimens could be easily assigned to the *M. ibiboboca* complex based on quantitative and qualitative characters observed (Merrem 1820; Pires et al. 2014), except the males from the *M. ibiboboca* 3 combat (Table 1), which presented an anomalous color pattern. We used all datasets to understand and describe the male-male ritual combat behavior of the species (records 1–6, Table 1), and rely particularly on the combat shown in *M. ibiboboca* 1 to illustrate the behavior because of the richness and quality of images.

Data processing.—We compared the data obtained from photographs and videographs to pertinent literature on snake behavior. We referred to previously determined descriptions and patterns to interpret sequences of postures and movements observed, and to interpret the behavioral significance of male-male combat in the *M. ibiboboca* complex (Bogert and Roth 1966; Carpenter et al. 1976; Carpenter 1977; Carpenter and Ferguson 1977). Additionally, we measured the angle of the anterior part of the interacting bodies of males with respect to the ground (Appendix Fig. 1). The position of the head and anterior body is important in determining the winner and loser of the ritual and is distinct among different types of fighting in snakes (e.g., Bogert 1966; Carpenter 1977; Pizzatto et al. 2006; Fig. 4). We selected 19 sequential photographs from *M. ibiboboca* 1 combat, all with at least one of the two males in combat in a lateral position (see Appendix Fig. 1) to avoid distortions. We then drew lines perpendicular to the length of the body, advancing in the anterior direction (Appendix Fig. 1) to determine the display and orientation of males (*sensu* Carpenter et al. 1976). The angle measurements were performed using the open source version of ImageJ v1.52d (Schneider et al. 2012). The results of angle

Figure 3. Nocturnal interaction of males of the *M. ibiboboca* complex. (Photograph courtesy of Marcelo Kokubum).

measurements were used as response variable and subjected to a *t*-test (for all selected images with at least one of the males in lateral position) and a paired *t*-test (for images in which both male 1 and 2 were measured in the same image) to verify whether the angle of the anterior region of the body was higher in the male 1 or male 2. Finally, we checked for normality of the data using a Shapiro-Wilk normality test, and data were normal. We used R v.3.5.1 (R Core Team 2018) for all statistical analyses with an $\alpha = 0.01$.

We split videographs into step-by-step video frames and compared them with photographs to better understand their movements and account for a more accurate and detailed description of behaviors previously described in the genus, given the constraints of previous *Micrurus* datasets (Almeida-Santos et al. 1998; Marques et al. 2013; Missassi et al. 2017). Although we could not determine the sex of the interacting specimens, the sequences of their postures and durations of their behaviors differed significantly from those observed in interactions between male and female snakes (Pizzatto et al. 2006; Almeida-Santos et al. 2017). In a general snake pattern of copulation, the male approaches the female and keeps his head on her back, which keeps her close to the ground. In addition, entwining and twisting, rolling, and hovering are behaviors that have only been observed in fights between males (Davis 1936; Carpenter 1977; Shine 1978). In *Micrurus*, during copulation the individuals do not exhibit elevated postures of the heads and trunks, and both remain with their tails intertwined and bodies separated (Almeida-Santos et al. 2017). These observations, in addition to our experience and knowledge of the snake combat literature, convinces us that we observed male-male ritual combat events.

Figure 4. Sequence of events observed in male-male ritual combat from the *M. ibiboboca* complex: (A) ascent-alignment orientation; (B) entwining and twisting; (C) rolling; and (D) hovering behaviors, where in the latter, male 2 exhibits dominance with an oblique stance movement. The likely occurrence of an (E) form of lyre in combat can be seen in the lower photo. Note males 1 and 2 with the (B) trunk, bodies and tails entwined, in a (C) horizontal alignment position as previously described in the *Micrurus* literature. (Photographs courtesy of Eduardo Moody).

Results

Datasets.—The behavioral records lasted from 46 to 120 s (mean time = 65.8 ± 43 [standard deviation], n = 6). They represented six independent records in distinct localities from eastern Brazil (Fig. 1; Table 1). The six male-male ritual combats (photographs plus videographs) were recorded in the transitional dry season: April to June in the western region (early dry season), and August and September during the early what we called less rainy season in the eastern region. This season corresponds to a decrease in precipitation and increase in temperature (Fig. 2), although increased temperature was not observed in the eastern region (Fig. 2). The *M. ibiboboca* 1, 3, 4, and 5 combats were recorded during the day, while the *M. ibiboboca* 2 and 6 combats occurred at night (Fig. 3; Table 1; Appendix Videograph 1).

Identified males.—Most specimens (i.e., males 1 and 2) were easily identified as *M. ibiboboca* by quantitative and qualitative characters (Merrem 1820; Pires et al. 2014). The exception was males from *M. ibiboboca* 3 combat, which had anomalous color patterns but could still be recognized as this species (Appendix Fig. 3). In Record 3, the anomaly observed on male 1 was a pentad in the second triadal black rings, a rare condition found in *Micrurus* BRT species. Male 2 had a color pattern with black rings fused from the third anterior-most ring on the body, and white rings incomplete or absent in dorsal and lateral view. The triadal counts from both males were 9 + 2/3 + 1/3, assigning these specimens to *M. ibiboboca* complex. In male 2, the black cephalic cap position and white rostral and nostril region (Appendix Fig. 3) both refer it to the *M. ibiboboca* complex. The white rings, conspicuous in the ventral region (Appendix Fig. 3), also distinguish this specimen from *M. lemniscatus carvalhoi.* Furthermore, species of the *M. lemniscatus* complex have distinct cephalic caps and black rostral and nostril regions, rather than white, a variant condition observed in the *M. ibiboboca* complex (Lywouty Nascimento, pers. comm.). Thus, the first two qualitative characters, together with the known geographic range of both species, lead us to consider this specimen as an anomalous *M. ibiboboca* rather than an *M. lemniscatus* (see Pires et al. 2014 and Silva 2016 for more details). In the *M. ibiboboca* 1 combat, used to illustrate the behavior pattern, males could be recognized by the following character set: male 1 – entirely black internasals and posterior borders of the parietals black, black first supralabial and infralabials and white chinshields; male 2 – white internasals with black posterior borders and one small black blotch in the posterior suture of parietals; white first supralabial and red infralabials and chinshields, with a small white blotch in the anterior chinshield.

Description of combat.—The sequence of events that comprise male-male ritual combat in the *M. ibiboboca* complex consisted of the following: recognition, ascent, and alignment-orientation; entwining and twisting; rolling; hovering; and a lyre-shaped positioning of the anterior trunk region (Fig. 4). The hovering with lyre-shaped head positioning was followed by an oblique display stance and dorsal hyperextension of the head (Appendix Videograph 2), with the anterior trunk, neck, and head regions rising obliquely in a visual and tactile communication (Fig. 5). Topping occurs with one of the males interlacing its body with the body of the opponent (Fig. 6). Each male tried to inhibit the head ascension of the opponent by positioning its head above the opponent (Fig. 6) and resting its head and neck obliquely above the opponent. One of the males pushed the opponent to the ground and quickly overtook its head in upper position by topping (males entwine anteriorly and force opponent down; Table 2) for a short

Table 2. Interactive behaviors observed in males of the *Micrurus ibiboboca* complex based on six distinct records and localities with detailed descriptions of the comportment.

Behavior	Description	Reference
Ascent-alignment-orientation	The male-male ritual combat in which *M. ibiboboca* tend to assume horizontal alignment, with the trunk and tail regions entwined.	Bogert and Roth 1966; Almeida-Santos et al. 1998; Missassi et al. 2017
Entwining and twisting	Involves tight entwining and twisting of the mid to posterior trunk regions and tail.	Carpenter et al. 1976
Rolling	During the combat the entwined bodies of both snakes roll completely over.	Bogert and Roth 1966
Hovering	Actions contributing to a less intertwined anterior portion of the body and a possibly lyre-shaped position of the trunk.	Bogert and Roth 1966; Carpenter 1977
Oblique display stance	High oblique stance with entwining that makes possible a dorsal hyperextension of the heads.	Carpenter et al. 1976; Carpenter 1977
Topping	Entwine anteriorly and force opponent down.	Carpenter et al. 1976
Snap the heads	Opponents snapped their heads several times during the oblique display stance and topping.	Shine and Allen 1980

Figure 5. Sequence of events observed in male-male ritual combat from the *M. ibiboboca* complex: (A) hovering with lyre-shape position of the heads; (B) male 2 expressing oblique dominance display with dorsal hyperextension of the head; and (C) oblique stance display with entwined body, in a visual and tactile communication. (Photographs courtesy of Eduardo Moody).

period (Fig. 6). Then the combat was initiated again. Several times, the males snapped their heads for a short time during the topping, then returned to combat (Table 2, Appendix Videograph 3). The extent of interlacing between the bodies and tails varied from time to time, but snakes were continually intertwined throughout the observation. Sometimes the two snakes had the anterior portions of their bodies free. Both snakes entirely rolled over (Appendix Videographs 1–3).

Angulation during combat.—In the *M. ibiboboca* 1 combat, male 1 (mean angle = 47° ± 26°, n = 16) and male 2 (49° ± 25°, n= 11) presented similar average anterior body angulations in the topping, although male 1 presented a higher angulation position during combat (male 1 range, 26–100º; male 2 range, 25–69º). The mean angles were not significantly different, however (t = -0.265, df = 23, P = 0.793; paired t = -0.795, df = 6, P = 0.457). The predominance of male 1 over its opponent, however, was evident when we examined the raw data. This male also remained in the topping position for a longer time than its opponent, with the head of male 1 being observed 42 times over the head of male 2, compared to 21 times for the head of male 2 being over the head of male 1. In this way, male 1 could be considered the Displayer, whereas male 2 could be consider the Orientor (*sensu* Carpenter et al. 1976).

Discussion

Our recorded data of male-male combat in the *Micrurus ibiboboca* complex are a first step in understanding the reproductive strategies of this species. Although male-male combat may occur in other environmental contexts, it is clearly a part of the life-history strategies employed by elapid coral snakes. The BRT species group has reproductive cycles in which vitellogenesis begins in autumn and the peak of sperm production is observed in the winter, with courtship (and consequently, male-male combat) occurring during this period (Almeida-Santos et al. 2021). Although northeastern South America does not have four marked seasons, a dry (or less rainy) condition is commonly observed during periods when *Micrurus* male-male

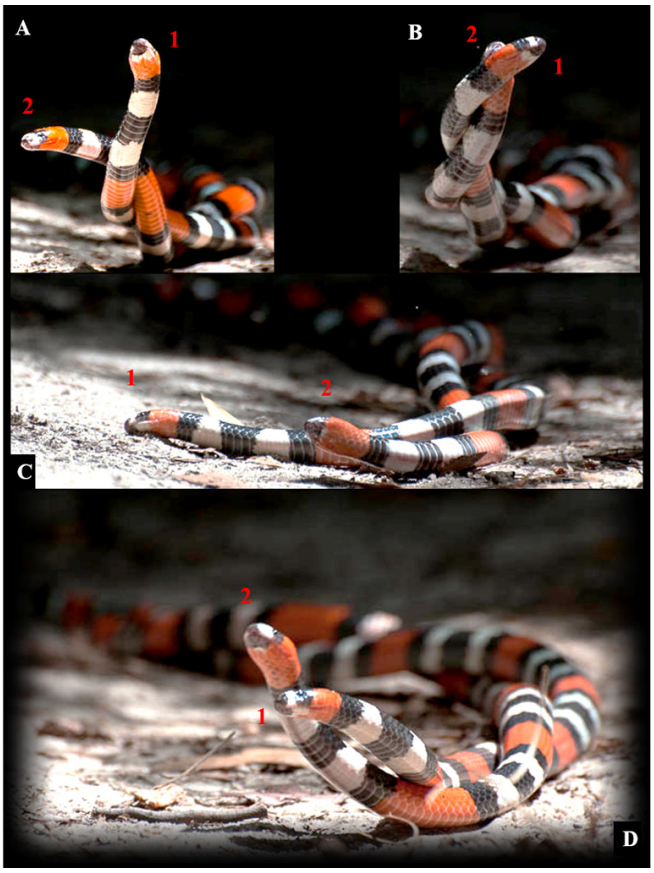

Figure 6. Topping sequence observed in male-male ritual combat from the *M. ibiboboca* complex, where (A) male 1 is in oblique display stance, with the anterior trunk, neck and head regions raised; (B) male 2 is in oblique display stance with the head above male 1 applying it to topping; (C) male 2 and male 1 fall and try to compose themselves to continue the fight; and (D) the moment in which male 2 assumes the topping dominance position. (Photographs courtesy of Eduardo Moody).

combats are observed. This idea is reinforced by male-male combats observed in the cold-and-dry autumn and winter climates in Brazilian subtropical areas (Almeida-Santos et al. 2021).

We observed *M. ibiboboca* males in combat in the early dry season (April to June in the west) and the less rainy season (August to September in the east) when there is a decrease in the precipitation and temperature (Cardoso et al. 2014; Santos et al. 2016). The number of distinct *M. ibiboboca* males in combat observed during this dry season in Bahia and Rio Grande do Norte states of Brazil reinforces the idea that this behavior occurs synchronously across different regions, presenting a climate-related pattern (Mathies 2011; Almeida-Santos et al. 2021). Thus, it is likely that male-male combat in elapid coral snakes of the BRT group is a key aspect of the reproductive or mating period of this species.

In our *M. ibiboboca* 3 combat observations, male 1 with fused black rings presents an anomalous condition rarely observed in BRT coral snakes. We have identified the anomalous male 2 as *M. ibiboboca*, based on current taxonomic literature and keys. The absence of preserved specimens, however, prevented us from establishing whether other *M. ibiboboca* share these anomalous color traits. In black ring monadal (hereafter BRM) species, specimens rarely present reduction of the number or absence of black rings and a predominance of red rings in the body, which is a condition known in Painted Coral Snake (*M. corallinus*; Grantsau 2013; pers. obs.) and Pará Coral Snake (*M. paraensis*; Feitosa et al. 2007; pers. obs.). Although intergeneric or interspecific combat has been previously recorded in some species, it is not frequently observed in wild snakes (Carpenter 1977). Besides being rare, it may result from captive males maintained in the same cage or arena (Wagner 1962; Carpenter 1977).

In most BRT species of *Micrurus*, males are larger than females (Marques et al. 2013), a characteristic frequently associated with snake species in which males engage in combat. Although males of this species have more ventral scales than females (Pires et al. 2014; Silva 2016), this is a condition known for several snakes (e.g., some Imantodini and Tachymenini) and does not necessarily mean males are larger than females (Myers

1982; Missassi 2014; Trevine 2017). Furthermore, it is still unknown whether *M. ibiboboca* exhibits size-based sexual dimorphism similar to other members of the BRT *Micrurus* group. Thus, our results could not corroborate the sexual dimorphism index in which larger males engage in combat (Shine 1994), and males being larger than females is not a general rule in snakes (Santos-Costa and Prudente 2005; Pizzatto et al. 2006, 2007), including at least one species of *Micrurus* in which females are larger than males (Missassi et al. 2017).

Several studies have described male-male ritual combat in African, Australian, and Asian elapids, including in the genera *Austrelaps*, *Bungarus*, *Dendroaspis*, *Hemiaspis*, *Naja*, *Notechis, Ophiophagus*, *Oxyuranus, Pseudechis*, and *Pseudonaja* (see Carpenter 1986 for more details). According to our results, the *M. ibiboboca* complex can be recognized as Pattern 2, described by Bogert and Roth (1966), where competing males entwine their bodies and raise their heads horizontally above the ground. These observations are similar to combat observed in other elapid species, such as Black Mambas (*Dendroaspis polylepis*), which attain an upright position when entwining their bodies (Grant 1956). A few male colubrids may also lift their heads high above the substrate when engaged in ritual combat (Almeida-Santos and Marques 2002). Additionally, many viperids and crotalids raise the head by lifting the anterior or posterior third of the body to an almost vertical position (Bogert and Roth 1966).

We provide the first example in a *Micrurus* species of head dorsal hyperextension (Carpenter et al. 1976) during the oblique display stance movement. Our observation, added to the heads slightly raised posture described for the Pacific Red-tailed Coral Snake (*M. mipartitus decussatus*), changes our understanding of male-male combat in the genus, which has been previously understood to exhibit what is termed horizontal fighting (Almeida-Santos et al. 1998; Missassi et al. 2017) due to limited sampling in earlier datasets. We can now reinterpret these observations as what we call high oblique stance based on our results. This posture observed in the male-male combat rituals of Brazilian *Micrurus* resemble the combat behavior of other elapids (Grant 1956; Shine and Allen 1980). Snaps, a behavior previously observed in the Australian Copperhead (*Austrelaps superbus*) by Shine and Allen (1980) are also described for the first time in the genus.

The *Micrurus ibiboboca* complex has both diurnal and nocturnal habits (Vangilder and Vitt 1983), which is consistent with our observations of combat seen in the day and at night. It is also important to highlight that most coral snake species are semifossorial and subterranean and require specific humidity and temperature conditions to become surface active (Roze 1996). Nocturnal combat would favor such environmental restrictions and probably increase performance and energy saving. We do not know if the males engage in ritual combat during the entire mating season, but the first two records of nocturnal male-male fights support the hypothesis of an intense period of combat during parts of this season.

Snakes are secretive and inconspicuous animals, and observations of male-male combat in nature are rare. As an example, we can take the six encounters described here, which were observed over the span of 12 y. This highlights the importance of videographic records and, in the absence or impossibility of obtaining these records, the need for more detailed collection of ethological data. In this work, we propose for the first time a simple and replicable methodology to assess dominance during combat between male snakes. We encourage future studies and observations of snake male ritual combat to employ these methodologies and improve our understanding of the agonistic behaviors these animals possess.

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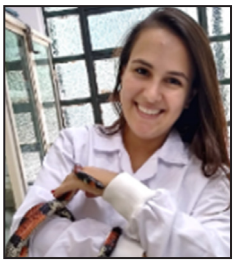

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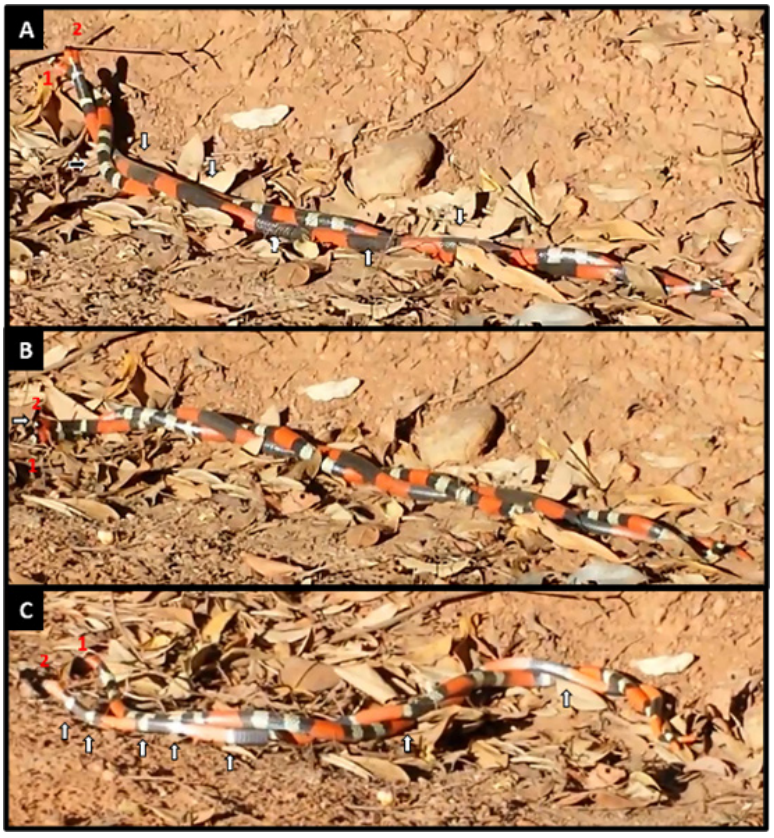
Appendices

Appendix Videograph 1. Struggler males of *M. ibiboboca* complex in nocturnal activity, Camaçari municipality, Bahia State, Brazil. https://figshare.com/s/157b88521d892101e6f4

Appendix Videograph 2. Oblique display stance and dorsal hyperextension of the head during the combat in struggler males of *M. ibiboboca* complex. https://figshare.com/s/d149a94beb6264eb4b62

Appendix Videograph 3. Snap in the heads behavior observed in struggler males of *M. ibiboboca* complex. https://figshare.com/s/be3532dade125f9dfc42

Appendix Figure 1. Angle measurement of the trunk anterior region during topping behavior, aiming detect the win male in the *M. ibiboboca* 1 combat. Angle for the male 2 in the small highlight. Observe the males in a high oblique stance position, in a visual and tactile communication. (Photograph courtesy of Eduardo Moody).



Appendix Figure 2. Anomalous males from *Micrurus ibiboboca* 3 combat: (A) male 1 with second triad in pentad (black arrow) and male 2 with fusionated black rings (white arrow); (B) white rostral and nostril region in the male 2 (white arrow); and (C) white rings in the ventral region in male 2 (white arrows). (Photographed by Andrew Kemp).