Male-male combat in free-ranging Falcón Indigo Snakes, Drymarchon caudomaculatus Wüster et al., 2001, in Guajira, Colombia

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In snakes, reproductive behaviour can be complex and possibly involve numerous behaviours related to courtship, and combat rituals before mating (Almeida-Santos and Marques, 2002; Almeida-Santos et al., 2024). During these events, confrontations may occur between males, in which the two adversaries attempt to overpower each other through physical exertion (Batista et al., 2021; Araújo et al., 2024a). While there are variations in combat behaviour, all of it is agonistic and some of it may be aggressive, to the extent that it causes injury to the combatants (Senter et al., 2014).

Snake combat is a frequently observed behaviour, sometimes mistaken for copulation by the observer due to the intertwining bodies. However, while the posture appears to be similar, the purpose is different. In combat, males struggle to subdue their opponent to establish dominance (Almeida-Santos and Marques, 2002). This ritualistic behaviour is mainly characterised as a form of intrasexual selection, where males compete for females (Greene, 1997; Pizzatto et al., 2006).

The genus *Drymarchon* comprises large, nonvenomous snakes with generalist and terrestrial habits that inhabit tropical and subtropical environments in South America, Central America, and the southeastern United States (Wüster et al., 2001; Prudente et al., 2014). The genus is composed of five species (Uetz et al., 2024), and we here focus on *D. caudomaculatus*, a species found in Venezuela and Colombia. It is characterised by the absence of an obvious change of

hue along the dorsal colour pattern, having a brown dorsal colouration, with cream-coloured scales that form irregular patches along the dorsum. These snakes also present a dark pigmentation on the anterior portion of their venter, with some darkly pigmented subcaudal scales on an otherwise pale tail. *Drymarchon caudomaculatus* does not have distinctive oblique black bars on the side of the neck, no distinctive black supralabial borders, and 61–65 subcaudals (Wüster et al., 2001).

Details of reproduction in *Drymarchon* are scarce and mostly restricted to observations on captive individuals (Prudente et al., 2014). Male-male ritualistic combat was reported for *D. couperi* (Stevenson, 2003) and *D. melanurus* (Broussard et al., 2021). Here we describe combat behaviour in two free-ranging males of *D. caudomaculatus* for the first time.

At 11:16 h on 8 December 2007 (late dry season), two adult male D. caudomaculatus were seen engaged in combat on a trail in Guajira, Colombia (11.3795°N, 73.0894°W). Following the nomenclature proposed by Senter et al. (2014), the males performed coiling, head raising (Type 1), and downward pushing. First, we observed the alignment between the two males, where Male 1 positioned itself above the other. During the entire observation, both males were intertwined, each forming two coils around its opponent (Fig. 1A). They took turns trying to subdue each other by pushing the opponent downwards (Senter et al., 2014). Then, they laterally flattened their gular region, a visual sign to look bigger and intimidate the opponent (Fig. 1B). Simultaneously, both snakes raised a small portion of their anterior and alternately tried to elevate their heads higher while pushing the opponent downwards, a process they repeated a few times (Fig. 1C, D). We observed no violent behaviour during the interaction, and no female was seen nearby. This event was also caught on a video that can be accessed at https://youtu. be/5jee3GyhD5M?si=TQtwMNktBFkUTxR6.

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Figure 1. Male-male combat in free-ranging *Drymarchon caudomaculatus* in Guajira, Colombia. Red arrow: Male 1; blue arrow: Male 2. (A) Post-alignment, Male 2 on top of Male 1, with snakes coiling and raising their heads. (B) Male 1 flattening the gular region while trying to rise again. (C) Male 1 rising on top of his opponent. (D) Heads turned vertically and Male 1 forcing Male 2 downwards. Photos by Carl Downing.

Observing behaviours in free-ranging snakes is uncommon since these animals are usually elusive and difficult to spot (Greene, 1997; Steen, 2010; Batista et al., 2021). Though single observations only allow for generalized descriptions, they are important for forming a framework of knowledge (Batista et al., 2021; Maritz et al., 2021) and eventually help gain a better understanding of the biology of a given species.

Once known only for species of Europe, North America, and Australia (Almeida-Santos and Marques, 2002; Pizzatto et al., 2006), reports of male-to-male combat behaviour have been reported for several species over the years, and this type of behaviour is seemingly widespread in multiple families (Shine, 1978, 1994; Pizzatto et al., 2006), including in the Colubridae (*Chironius bicarinatus* – Almeida-Santos and Marques, 2002; *Drymarchon couperi* – Stevenson, 2003; *D. melanurus* – Broussard et al., 2021; *Oxybelis aeneus* – Araújo et al., 2024b; *Spilotes pullatus* – Muniz-

da-Silva and Almeida-Santos, 2013; S. sulphureus — Araújo et al., 2024a), Boidae (Chilabothrus angulifer — Tolson and Henderson, 1993; Corallus caninus — Osborne, 1984; Epicrates assisi — Guedes et al., 2019; E. cenchria — Schuett and Schuett, 1995; E. crassus — Pizzatto et al., 2006; Almeida-Santos et al., 2024; Sanzinia madagascariensis — Carpentes et al., 1978), Elapidae (Micrurus altirostris — Marques et al., 2013; M. lemniscatus — Missassi et al., 2017; M. mipartitus — Valencia et al., 2020), and Viperidae (Bothrops moojeni — Nogueira et al., 2003; Crotalus durissus — Batista et al., 2021). Two more comprehensive lists can be found in Senter et al. (2014) and Lock et al. (2023).

The sequence of events in the male-male combat observed in *D. caudomaculatus* is similar to what was previously described in other species of the genus by Stevenson (2003) and Broussard et al. (2021). Our study appears to indicate that intraspecific combat may be a behaviour common to all *Drymarchon* species.

So far, the exceptions are the widespread South American *D. corais* and the island-endemic *D. margaritae*, for which natural history data, including combat, remain unknown (Roze, 1959).

Male-male combat can often act as an evolutionary driver of sexual dimorphism, typically resulting in males being larger and heavier than females, or at least reaching similar sizes (Shine, 1978). While there is no sexual size dimorphism in *D. corais* (Prudente et al., 2014), *D. couperi* males are larger than females (Chandler et al., 2023). Data on sexual dimorphism in *D. caudomaculatus*, *D. margaritae*, and *D. melanurus* are currently insufficient to determine whether a male-biased size difference exists, which highlights the need for further research on these species and their characteristics.

It has been suggested that male-male combat may be associated with resource competition or territoriality in a given area (Araújo et al., 2024b), or with sexual selection (Shine, 1978, 1994; Pizzatto et al., 2006; Batista et al., 2021). Therefore, such observations could shed light on the reproductive period of a species. We suggest that observers pay close attention to the subtle details and differences between the behaviours displayed by different species because they might be informative for making interspecific comparisons. We hope this information will be used in the future to compose robust studies about the behaviour of snakes.

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