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Repertoire of antipredator displays in the semifossorial snake *Ninia atrata* (Hallowell, 1845) (Serpentes: Dipsadidae)

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The semifossorial snake *Ninia atrata* is a widespread Neotropical species that ranges from western Panama, Colombia, Ecuador, Venezuela to Trinidad and Tobago, at altitudes between sea level and 1000 m a.s.l. (McCranie and Wilson, 1995; Savage, 2002; Angarita-Sierra, 2009; 2014). *Ninia atrata* inhabits leaf litter in almost all habitats, including the Amazonian and Chocoan rainforests, the evergreen forest of the main Andean rivers, the Orinoquian savannas, and the xerophitic forest at the Caribbean coast (Rangel-Ch, 2004; 2012; Angarita-Sierra, 2009; 2014). This species has a high tolerance to disturbed or transformed habitats such as oil palm plantations and annual crops. Recently, aspects of its hemipenial morphology, taxonomy, phylogeny and geographic variation have been studied (McCranie and Wilson, 1995; Ingrasci, 2011; Angarita-Sierra, 2009; 2014). Nevertheless, some of its basic biological features such as diet, reproductive cycle, antipredator behavior and ecological interactions remain unknown. Antipredator displays such as crouching, elevated body loops, and dorsoventral neck compression (Savage, 2002; Köhler, 2008) have been reported for only a few species of the genus [*N. celata* (McCranie and Wilson, 1995)*, N. hudsoni* (Parker, 1940)*, N. maculate* (Peters, 1861)*, N. psephota* (Cope, 1876), and *N. sebae* (Duméril, Bribon, and Duméril, 1854)].

As part of an ongoing study of population dynamics, antipredator behavior of individuals from a population of *N. atrata* was examined based on simulations of predator attacks in natural environment. Fieldwork was carried out in oil palm plantation of PALMASOL S.A. at Vereda La Castañeda, municipality of San Martin, department of Meta-Colombia (3°31´46, 6" N; 73°32´15, 3" W). The plantation is located on the piedmont forests of the eastern slopes of the Cordillera Oriental, as well as on high savanna plateaus. Annual rainfall at the site is 3,070 mm. Individuals of *N. atrata* were found by systematic search between August 2014 and January 2015. Searches were conducted by removing piles of palm leaves from 8:00h to 17:30h. Immediately after each encounter, individuals were put in cloth bags to be measured and marked. A session of predator attack simulations was performed the next morning before releasing the snakes at the same place where they were caught. The simulation procedure followed Tozetti et al. (2009) and consisted in eight repeated movements of the researcher's open hand towards the snake's head at a constant speed. The time to perform the eight approaches was not longer than 10 seconds. Exhibited antipredator displays were classified according to Arnold and Bennett (1984) and Greene (1988). A multidimensional scaling test was performed to assess if a behavioral pattern is associated with the stage of maturity or sex (see Parker & Plummer, 1987; Dorcas and Wilson, 2006). The measure used in multidimensional scaling test was "Kruskal´s stress" (**S**) (Fox et al., 2014), which is an average of the deviations between the end and the initial spatial distances normalized to take values between 0 and 1. Values near 1 indicate the worst fit, and values near 0 indicate the best fit. However, values between 0.025-0.05 are considered good values, < 0.025 are excellent, and values equal 0 are perfect (Guisande et al., 2014). This test was carried out using the software Rwizard version 1.0 (Guisande et al., 2014) and the MDS function of the vegan package (Oksanen et al., 2013). The function "scatterplot" of the car package was used to generate the biplot graphic (Fox et al., 2014).

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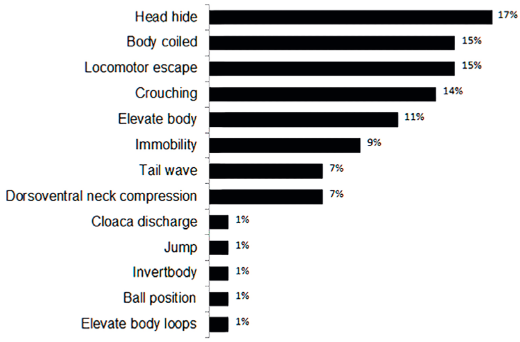

Figure 1. Frequencies of antipredator displays in *Ninia atrata.*

A total of 20 specimens of *N. atrata* were observed during the stimulatory sessions (12 females and 8 males) including five newborns, five juveniles and ten adults. As a result, 13 antipredator displays were recorded, as well as three combined antipredator displays and one social response. Among the 13 behaviors observed, the most frequent displays were head hide (17%), body coiled (15%), locomotor scape (15%) and crouching (14%). On the contrary, the least frequent displays were cloacal discharge (1%), jump (1%), invertbody (1%), ball position (1%), and elevate body loops (1%) (Fig. 1). The social response was recorded after putting together nine specimens of *N. atrata,* which were found under the same piles of palm leaves (one female and eight male), in the cloth bag. After 24 hours of cohabitation within limited space, the specimens organized themself into a spherical form (ball position) (Fig. 2A). Snakes maintained the spherical formation with heads in the center of the ball and tails on the outside during at least 12 to 15 minutes.

The first combined antipredator display resulted from the merge of elevation body, dorsoventral neck compression and invertbody behavior originating a remarkable defensive display (Fig. 2G). The second behavior merges head hide and crouching behavior (Fig. 2F and 2I) and the third combined behavior merges elevate body and dorsoventral neck compression resulting in a body posture similar to the observed in the King Cobra [*Ophiophagus hannah* (Cantor, 1836)] (Fig. 2H). One juvenile showed ball position with head exposed (Fig. 2O). This was a combined antipredator display resulted from the merge of ball position and head exposed displays. During fieldwork, snakes were handled carefully, however, manipulations frequently stress snakes. As a consequence of this stress, most of the specimens (70 of the 89 specimens observed during the sampling period) exhibited some of the 13 antipredator displays registered.

Antipredator behaviors observed in *N. atrata* follow a general pattern of hierarchical decision making (see Roth and Johnson, 2004): (1) if a predator stimuli is detected, the reaction is to retreat (escape behavior), (2) if the threatening stimulus persists, the reaction is to employ passive deterrents (head hide, body coiled, crouching, immobility, tail wave, elevated body loops, ball position), and (3) if the threat further escalates, the reaction is to engage in aggressive defense (dorsoventral neck compression, invertbody, elevated body, jump, cloaca discharge). Similar hierarchical responses have been reported in a wide variety of terrestrial snakes from temperate latitudes (Greene, 1979; Gibbons and Dorcas, 2002; Roth and Johnson, 2004). However, comparisons with South American snakes are not possible because this behavioral feature is unknown for related taxa.

Finally, the multidimensional scaling test showed high stress values (S), which means that behavioral patterns evaluated might not be associated with the stage of maturity (S=0.158) or sex (S=0.163) (Fig. 3). These results are not in agreement with the conclusions of other studies that have demonstrated that differences in sex or stage of maturity affect individual responses to predation risk (Clutton-Brock, 1991; Magurran and Nowak, 1991; Krause et al., 1998; Madsen and Shine, 2000; Shine et al., 2000; Roth and Johnson, 2004).

Perhaps antipredator response of *N. atrata* is more correlated to the phylogeny (Martins, 1996; Martins et al., 2008) or microhabitat use (Greene, 1979; Senter, 1999; Martins et al., 2008; Tozetti et al., 2009) rather than the intrinsically biological features such as body size, sex, or locomotor ability (Lima, 1998). The most frequent displays such as head hide, body coiled, locomotor scape, and crouching have been observed in *N. atrata* as well as a wide variety of terrestrial snakes that conform the Neotropical rainforests communities (Martins et al., 2008). These set of defensive behaviors has been suggested as characteristic of the Neotropical terrestrial species which have a related evolutionary history (Martins, 1996.)

According to the Optimality Theory, the behavioral response of an individual to a predator is influenced by the risk of predation (Ydenberg and Dill, 1986; Lima and Dill, 1990; Cooper and Vitt, 2002; Roth and Johnson, 2004). Hence, the advantage of the defensive tactic is

Figure 2. Repertoire of antipredator displays in *Ninia atrata*. A – Social response; B – Tail wave; C – Elevated body loops; D –Ball position; E – Body coiled; F – Crouching; G – Combined antipredator display (elevated body, dorsoventral neck compression and invertbody behavior); H – Dorsoventral neck compression; I – Head hide; J – Immobility; K – Elevated body, Tail; L – Elevated body, Head; M – Invert body; N – Locomotor escape; O – Ball position with head exposed.

related to the line of vision of approaching predators (Senter, 1999). *Ninia atrata,* as other species that inhabit on terrestrial microhabitats, have high risk of predation when the predator approaches from above and obtains a dorsal view of the snake. The analyzed individuals of *N. atrata* exhibited an elaborated antipredator repertoire

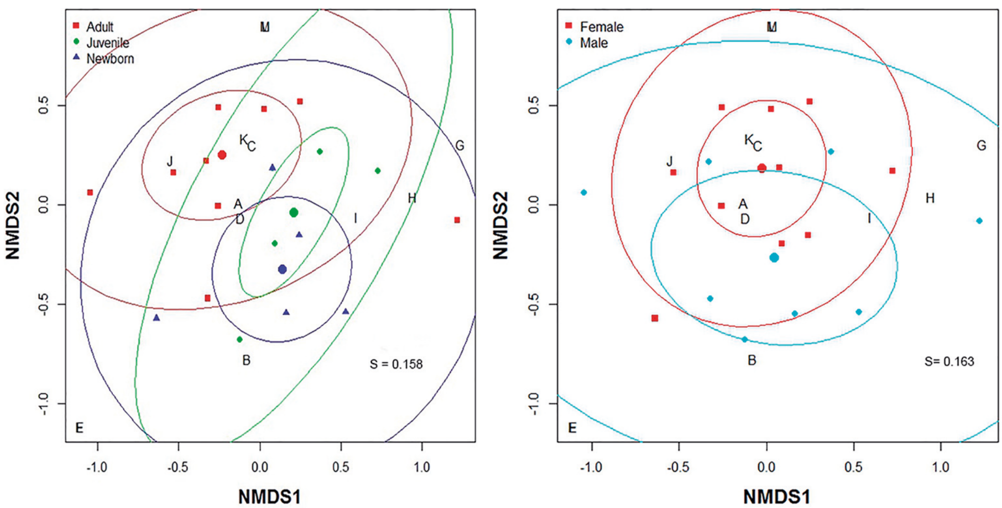

Figure 3. Multidimensional scaling test of antipredator displays in *Ninia atrata*: Inner ellipse represent 0.5 of significance; outer ellipse represent 0.95 of significance. Left: Stage of maturity. Right: Gender comparation. Defensive plays: A – Head hide; B – Immobility; C – Crouching; D – Locomotor scape; E – Elevate body; F – Ball position; G – Invertbody; H – Dorsoventral neck compression; I – Elevated body; J – Tail wave; K – Body coiled; L – Jump; M – Cloacal discharge.

comprising a diverse set of defensive displays, in which the snakes usually achieved a horizontal body expansion that maximizes their visible areas in dorsal view. These displays might intimidate a predator approaching from above. The most frequent displays observed (head hide, body coiled, locomotor scape, and crouching) are often associated with defense against visually oriented predators (Greene, 1988; Sazima and Martins, 1990; Oliveira et al., 2001; Oliveira, 2005; Martins et al., 2008; Tozetti et al., 2009). Also, less frequent displays observed such as ball position, elevated body loops and tail wave have been reported as behaviors that minimize injury to the head during predatory attack in terrestrial snakes (Arnold and Bennett, 1984). All these defensive displays have been categorized as typical in fossorial or terrestrial species (Greene, 1979; Martins et al., 2008) against attacks of predators that approach from above (Arnold and Bennett, 1984; Senter, 1999).

Complementary field and laboratory studies are needed to understand the behavioral responses patterns related with body size and sex as well as behavioral convergence between related taxa that inhabit the same biogeographic units. Moreover, more attention should be given to the diverse selective processes caused by the action of different type of predators and environments.

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