Behavioural Processes 97 (2013) 11–17

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Inter-individual variation and temperature-dependent antipredator behavior in the snake *Tomodon dorsatus* (Dipsadidae)

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ARTICLE INFO

Article history:
Received 1 February 2013
Accepted 14 March 2013

Keywords:
Temperature
Antipredator behavior
Individuality
Snakes
Tomodon dorsatus

ABSTRACT

Although many studies assessed the influence of temperature on the behavior of ectotermic vertebrates, little attention has been given to interindividual variation in the defensive responses of reptiles. In the present study we investigated the defensive behavior of the snake *Tomodon dorsatus*, in order to test the hypotheses that (1) individuals differ in their antipredator behavior consistently with the concept of behavioral syndromes, (2) temperature influences the defensive behavior, and (3) these two factors interact with each other. There was significant interindividual variation in defensive behavior, as well as consistently aggressive, passive or evasive behaviors. Temperature influenced aggressiveness, which was slightly higher when body temperature was lower, but this trend was only evident in animals with aggressive disposition. Our results corroborate the hypothesis of interaction between individuality of behavior and temperature-dependent defensive behavior in *T. dorsatus*. These results, together with results from previous studies, suggest that the evolution of temperature-dependent defensive behavior differs among lineages of ectothermic tetrapods.

This article is part of a Special Issue entitled: insert SI title.

1. Introduction

Ambient temperature has a large influence on the defensive behavior of ectothermic tetrapods (Rand, 1964; Arnold and Bennett, 1984; Schieffelin and de Queiroz, 1991). This influence has been primarily investigated through two approaches, one related to the effects of body temperature on the type of defensive behavior expressed by an animal (Hertz et al., 1982; Bulova, 1994) and another related to the impact of body temperature on behavioral performance (Cooper, 2000; Barros et al., 2010). These approaches are conceptually related because behavioral diversity in a species may be favored if the most efficient defensive behavior varies within the range of ecologically relevant temperatures for that species (Hertz et al., 1982; Crowley and Pietruszka, 1983; Mori and Burghardt, 2001). In turn, this premise is related to behavioral and physiological performance, since in terms of mechanisms the maximum expression of some behaviors, such as locomotion, is affected by temperature via thermal dependence of the underlying physiological processes (Brattstrom, 1963; Avery, 1982; Huey, 1982). For example, studies with different species of ectothermic tetrapods show an optimal temperature range for locomotor performance (Huey and Kingsolver, 1993; Angilletta et al., 2002), contraction speed of isolated skeletal muscles (James et al., 2007), and performance of muscular fibers (Jayne et al., 1990).

From an optimization perspective, one would expect that in ectothermic tetrapods the type of behavior favored under particular temperature conditions would minimize the effects of temperature on behavioral performance. This problem has been mainly studied from the perspective of thermal dependence of qualitative behavioral responses (type of behavior) and of the underlying functions supporting these responses. For example, in snakes the number of strikes and their speed increase with body temperature (Greenwald, 1974; Schieffelin and de Queiroz, 1991), and individuals with high body temperature are able to attack faster and more precisely (Webb and Shine, 1998). Besides, fast movements associated with escape may be limited at low temperatures; hence, aggressive responses could be a more feasible alternative under these conditions (Schieffelin and de Queiroz, 1991). Hertz et al. (1982), studying lizards, observed that escape is more frequent at high temperatures when the animals are faster, whereas aggression to the potential predator increases at low temperatures. Later, Herrel et al. (2007) complemented the ideas of Hertz et al. (1982) by showing that bite force in lizards does not change with temperature, evidencing that the aggressive capacity is preserved when thermal conditions are less favorable for escape.

According to the current evidence, an evolutionary scenario that favors variation in type of behavior with temperature is supported, and this variation is consistent with thermal dependence of the

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http://dx.doi.org/10.1016/j.beproc.2013.03.008

underlying physiological processes. However, other studies with ectothermic tetrapods report intrapopulation differences in behavior, which may not be attributed to typical ontogenetic, seasonal, or otherwise predictable variation. This individual variation has been considered analogous to personality (Dall et al., 2012) and may be compatible with the concepts of individuality, and possibly, of behavioral syndromes. These syndromes are behavioral tendencies that characterize part of the individuals of a population, and that tend to be expressed and preserved in these individuals across different contexts (Sih et al., 2004). Individuality in defensive behavior has been reported in salamanders (Brodie Jr. et al., 1991), anuran amphibians (Gomes et al., 2002), lizards (Rand, 1964; Hertz et al., 1982), and snakes (Fitch, 1965; Arnold and Bennett, 1984; Mori and Burghardt, 2001). Hence, in contexts such as defense, both individuality and thermal dependence of behavior are expressed in ectothermic vertebrates. This situation raises questions that have been poorly studied. Although among ectothermic tetrapods the evidence of individuality in behavior is stronger in defensive contexts, possibly behavioral syndromes exist in some taxa. However, the concept of individuality in behavior contrasts with the premise of behavioral plasticity expressed as a function of body temperature, although these two phenomena are not necessarily mutually exclusive. For example, body temperature could modulate the magnitude of expression of individual behavioral tendencies.

The main objective of the present study was to investigate the relationship between individual behavioral tendencies and temperature-dependent defensive behavior in ectothermic vertebrates. As a model, we selected the snake *Tomodon dorsatus* because it has a rich range of defensive behaviors that can be qualitatively distinguished (Bizerra, 1998). Besides, preliminary behavioral observations suggested interindividual variation in aggressiveness. Regarding temperature, individuals of this species are naturally exposed to significant thermal variation, given its extended period of annual activity in subtropical climates (Marques, 1998). We tested the hypotheses that (i) *T. dorsatus* shows consistent interindividual variation in defensive behavior, and (ii) temperature affects the type of defensive behavior expressed. From a perspective of behavior optimization, we expected that individuals exposed to low body temperatures would exhibit comparatively more aggressive or passive responses, whereas escape would characterize individuals exposed to higher temperatures. Finally, we tested the hypothesis that (iii) the influence of body temperature on defensive behavior may be constrained by interindividual variation in behavior. We expected strike and escape speeds to be higher at warmer temperatures, and made also a preliminary test of this hypothesis.

2. Material and methods

2.1. Study species

T. dorsatus belongs to the family Dipsadidae (previously Colubridae), which is found in center-southern South America and occurs in Brazil, Paraguay, Uruguay, and Argentina. It lives in humid tropical forests, including riparian forests in open vegetation, and can be found even in disturbed areas (Bizerra, 1998). It is a terricolous snake, but may use vegetation as a resting place, and has a predominantly diurnal activity.

We analyzed 49 adult individuals: 21 females (average snout-vent length = 46.54 ± 6.5 cm; average body mass = 38.78 ± 19.05 g) and 28 males (average snout-vent length = 46.91 ± 6.5 cm; average body mass = 39.54 ± 19.31 g) at four experimental temperatures. All individuals used in the present study came from donations to the Butantan Institute (state of São Paulo, Brazil) and were borrowed from this institute. All individuals came from the state of São Paulo, southeastern Brazil. We carried out behavioral tests from September 2009 to May 2010. The time between collection and arrival of the snakes at the Butantan Institute could not be controlled, because the snakes came from private donations. However, this time was usually shorter than four days (JMC, personal communication). The time between borrowing snakes and the beginning of tests varied from one to three days. We maintained the animals in the Ectothermic Animals Facility of the Department of Physiology of the Biosciences Institute, University of São Paulo. Snakes were individually maintained in 45 cm × 35 cm × 20 cm transparent plastic boxes provided with twigs and leaves, water *ad libitum*, and a resting place. We kept the boxes with animals in a room, whose temperature varied from 20 °C to 28 °C, with a photoperiod of 12:12 h (dark-light). Snakes were offered slugs to feed only after the tests and then were returned to the Butantan Institute. During the experimental period, snakes were handled as little as possible and always with a snake hook.

2.2. Behavioral tests

Before a behavioral test, and to avoid any sequence effect, we selected randomly (for each individual) one of the four experimental temperatures of 20 °C, 25 °C, 30 °C, and 35 °C. The chosen temperature was programmed in a walk-in climatic chamber. When the target temperature was reached, we transported the individual to be tested to the chamber in its maintenance box, where it remained without being disturbed for 1 h, before being subject to the test. We tested each specimen once for each temperature and allowed for one resting day between experimental rounds to minimize handling effects. The same procedure was repeated randomizing the next temperature tested for each individual, and so on until completing all four experimental temperatures.

Contact with animals was kept to a minimum; therefore, we did not measure the body temperature of experimental animals. We assumed that the individuals reached temperatures close to the target temperatures programmed in the chamber. This premise was corroborated by measurements taken from animals not used for data collection, but exposed to identical protocols. These tests indicated that the actual temperature of animals ($n = 8$) for each target temperature (average and standard deviation) was: 20 °C: 21.3 ± 1.4; 25 °C: 26.5 ± 1.1; 30 °C: 29.6 ± 0.9; and 35 °C: 34.4 ± 1.4.

For the tests, we removed the snakes from the plastic box with a snake hook and placed them in the center of an especially prepared experimental arena. The arena was rectangular (110 cm in length × 70 cm in width) and had three sides of wood and one side of glass, in which we placed a camcorder. We covered the arena's floor with brown graph paper provided of a 2 cm × 2 cm grid, in order to calculate the distances of the movements caused by a stimulus. Based on the results of various preliminary tests we opted for using as an experimental stimulus a low-pressure wooden cloth-clamp applied the tail of the snake about 3 cm before the tip. The cloth-clamp did not harm the animals in any way, but unequivocally elicited a reaction from snakes. We filmed individual reactions to tests with two cameras, the one placed on the glass side and a second camera placed on the top of the arena. To avoid possible behavioral alteration caused by eventually secreted chemicals, we changed the substrate after each test and cleaned the snake hook with alcohol 90%. We considered only the behaviors observed during the first 60 s after the application of the stimulus. The typical total amount of time under experimental manipulation (release from maintenance case and back) was 3 min. The quantification of behaviors involved annotating sequentially the behaviors elicited by the stimulus. This was straightforward because the protocol encompassed all possible defensive behaviors reported for