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Defensive repertoire of *Xenodon dorbignyi* (Serpentes, Dipsadidae)

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Abstract: The ability of a species to defend itself against a predator is directly correlated with its survivorship. Thus, prey/predator interaction mechanisms are important elements of the natural history of species. In this study, we examined the defensive repertoire of the South-American hognose snake (*Xenodon dorbignyi*) through simulations of predator attacks in the field. Nine defensive displays were observed. The most frequently observed displays were erratic movements, body flattening, head triangulation and tail display. No differences were detected in the defensive strategies shown by males and females, regardless of their reproductive state. Our findings suggest that *X. dorbignyi* has the ability to evaluate the level of threat imposed by the aggressor, with cryptic behavior, body flattening and locomotor escape as the primary defensive strategies, with other displays used as secondary responses to a predator attack. Our results support the hypothesis that *X. dorbignyi* is a mimic of both *Micrurus* and *Bothrops*.

Keywords: defensive behavior, predation, snake, display.

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Resumo: A capacidade de uma espécie em defender-se da ação de um predador esta diretamente relacionada à sua sobrevivência. Nesse sentido, os mecanismos de interação presa/predador são elementos importantes da história natural das espécies. Neste estudo foi avaliado o repertório defensivo da cobra-nariguda (*Xenodon dorbignyi*), a partir da simulação de ataques predatórios na natureza. Foram observadas nove unidades comportamentais defensivas, sendo os movimentos erráticos, achatamento do corpo, triangulação da cabeça e *display* caudal os comportamentos mais frequentemente exibidos. Não foram detectadas diferenças na estratégia defensiva entre os sexos ou entre indivíduos em diferentes estados reprodutivos. Os resultados sugerem que *X. dorbignyi* possui a capacidade de avaliar o nível de ameaça imposto pelo agressor, sendo o comportamento críptico, o achatamento do corpo e a fuga as estratégias defensivas primárias, com os demais *displays* representando respostas secundárias ao ataque predatório. Os resultados reforçam a hipótese de que *X. dorbignyi* represente simultaneamente um mímico de *Micrurus* e *Bothrops*.

Palavras-chave: comportamento defensivo, predação, serpente, *display*.

Introduction

Predators play an important role in the population dynamics of their prey, affecting even demographic aspects of these populations (e.g., Sinclair & Arcese 1995, Lima 1998). The ability of a species to defend itself from a predator is intrinsically associated to its survivorship, increasing its capacity to exploit the environment as well as to obtain resources (Lima & Dill 1990, Downes 2001). Thus, antipredator mechanisms are important factors in the evolutionary processes of many animals (see Vermeij 1982, Lima & Dill 1990). In general, prey/predator interaction mechanisms are key elements of the natural history of species, and their understanding contributes to the development of evolutionary biology and ecological studies (Greene 1988).

Reptiles exhibit extremely varied antipredator mechanisms, including cryptic coloration and/or behavior, mimicry, aposematism, in addition to various ways of intimidating aggressors (Pough et al. 2004). Snakes are interesting models for studies on defense mechanism, as they have very elaborated behaviors and are potential preys of several animals, such as mammals, birds, other reptiles and invertebrates (Greene 1988). Because of their ectotherm physiology, snakes have their capacity of performing defensive behaviors influenced by environmental factors, such as level of solar exposure and air temperature, that directly affect their body temperature and metabolic levels (Duvall et al. 1985, Brodie & Russel 1999, Shine et al. 2000). Another important environmental element associated to antipredator strategies is habitat heterogeneity, which provides different possibilities for shelter (e.g. holes, burrows, vegetation; Shine et al. 2000). Shepard (2007) shows that the probability of attack to lizards models is higher in more open microhabitats.

The defensive repertoire of the South-American hognose snake (*Xenodon dorbignyi*) makes it an interesting subject for studies on defense mechanisms against predators. *Xenodon dorbignyi* is a small semi-fossorial colubrid snake of the tribe Xenodontini (Cadle 1984) usually associated to open environments (e.g. grasslands) that occur in southern Brazil, Paraguay, Uruguay, and Argentina (Lema 1994, Oliveira 2005). The genus *Lystrophis* has been recently synonymized with *Xenodon*, according to results of a revised phylogeny and classification of Neotropical xenodontines (Zaher et al. 2009). Despite the relatively wide distribution of this species, field studies are scarce (Oliveira et al. 2001). In the present study, the defensive behavior of individuals from a population of *X. dorbignyi* was examined based on environmental and sexual variables through simulations of predator attacks in natural environment.

Material and Methods

Fieldwork was carried out in an area of coastal sand dunes (sampled area of approximately 333 ha; 30° 21' S and 50° 17' W; sea level), in the municipality of Pinhal, northern coast of Rio Grande do Sul State, Brazil. The area is characterized by coastal dunes with sparse vegetation consisted of shrubs and plants associated to a system of temporary lagoons (Waechter 1985). The climate is humid subtropical, according to the classification of Köppen (Vieira & Rangel 1998), with average annual temperature of 20 °C and uniform average annual precipitation of 1322.9 mm (Hasenack & Ferraro 1989). Individuals of *Xenodon dorbignyi* were found by non-systematic visual search between November and December of 2007, a period that includes the breeding season (Oliveira 2005). Searches were conducted by walking slowly while examining as many microhabitats as possible in the study area. Searches were carried out between between 7:00 and 12:00 AM and between 4:00 and 6:00 PM including the daily peak of activity of this species (Oliveira 2005). Immediately

session of predator attacks. The simulation consisted of five repeated movements of the experimenter's hand towards the snake's head. The snake was confronted with the experimenter's open hand at a constant speed (Figure 1) so that the time interval between the first and the fifth approach was not longer than 20 seconds. Despite this simple scheme, studies show that the approach of the human hand elicits the same types of response observed in a real predator attack on snakes and frogs (Herzog & Bailey 1987, Shine et al. 2000, Gibbons & Dorcas 2002, Toledo et al. 2005).

All defensive displays shown by individuals were classified according to Greene (1988). After each session of stimuli, individuals were measured (size and body mass) and ventral scales were permanently tattooed (Di-Bernardo et al. 2007). The sex of individuals was determined by everting the hemipenis and/or use of cloacal probing. Females were palpated to assess their reproductive status (e.g. presence of eggs of large follicles; Fitch 1987). Each snake was tested only once immediately after being found, and was released after the test.

The behavior of snakes, from the moment they were found until the examination and release was divided into three categories (treatments): 1 – response during first approach (defensive displays observed during the interval between the encounter of the animal and the beginning of the simulation); 2 – reaction during the session of stimuli (defensive displays observed during the simulation) and; 3 – reaction during handling (defensive displays observed during the manipulation process for marking and measurements). For each one of the three categories, the occurrence of each defensive display was recorded, rather than the number of times of each defensive display. For example, if an individual stroke once or several times during only one category (e.g. hand approach), only one record was made for this display; if the individual stroke once or several times in the three categories, three records were made, one for each category. Thus, it was possible to quantitatively compare displays of different natures without having to evaluate frequency (e.g. number of strikes) or the duration of the display (e.g. strike, body flatten) in the same session. Only displays recorded in at least 30% of the observations were considered.

Because of the predominance of exposed soil with little or no vegetation, snakes were visually located from an average distance of two meters, allowing the observation of the behavior of the animal before the effects of the disturbance caused by the approach of the experimenter. Only active animals (exposed) on the surface of the substrate were tested. The existence of correlations between the displays observed and substrate and air temperature was examined with the Spearman Rank Order Correlation tests, *r_s*. Comparisons between the obtained and expected values for each one of the displays were conducted with the chi-square test. Comparisons between treatments were conducted with G test (Fowler et al. 1998).

The defensive repertoire of *X. dorbignyi* was compared to those of other species of the tribe Xenodontini. The comparison with species of the same tribe is justified, because despite the scarcity of phylogenetic studies on neotropical snakes, there are indications that species of South American Xenodontini form a monophyletic group (Vidal et al. 2000; Zaher et al. 2009). The comparison with other species was performed using the data reported by Marques et al. (2004), Carreira et al. (2005), Marques et al. (2005) and Sawaya et al. (2008). These studies were chosen because the procedures used to record defensive behaviors of snakes were similar to those of the present study. We compiled species data in a presence/absence matrix of each defensive display and perform a comparison among species with a cluster analysis (Sneath & Sokal 1973), using the Euclidian distance and the grouping method “weighted pair-group average” (WPGA; Sneath & Sokal 1973). Statistical analysis was performed using the

Defense in *Xenodon dorbignyi*

Figure 1. Some defensive displays shown by individuals of *Xenodon dorbignyi* during simulation of a predator attack. A = simulation of a predator attack and detail of the tail display (tail coiling); B = head triangulation; C = body flattening; and D = hide head.

Figura 1. Algumas das unidades comportamentais (displays) apresentadas por indivíduos de *Xenodon dorbignyi* durante a simulação de um ataque predatório. A = simulação de ataque predatório e detalhe do display caudal (exibição da cauda enrolada); B = triangulação da cabeça; C = achatamento do corpo; D = esconder a cabeça.

different sizes (variation on the number of displays observed in each species). We adopted the species nomenclature of Bérnils (2009). For all analyses, differences were considered significant when $p < 0.05$ (Zar 1999).

Results

We analysed a total of 31 adult individuals of *Xenodon dorbignyi*, including 15 males (average body size = $396.5 \text{ mm} \pm 102.3 \text{ mm}$; range = $138.0 \text{ mm} - 494.0 \text{ mm}$; average body mass = $29.4 \text{ g} \pm 12.0 \text{ g}$; range = $8.45 \text{ g} - 51.6 \text{ g}$) and 16 females (average body size = $386.6 \text{ mm} \pm 51.7 \text{ mm}$; range = $184.0 \text{ mm} - 484.0 \text{ mm}$; average body mass = $34.1 \text{ g} \pm 11.1 \text{ g}$; range = $10.8 \text{ g} - 56.4 \text{ g}$), of which six were gravid. Nine behavioral displays were characterized: (1) body flattening (dorsoventral body compression), (2) cloacal discharge (contents of the cloaca are expelled, including feces and urine), (3) erratic movements (body thrashing), (4) false strike (strike with closed mouth), (5) head triangulation, (6) hide head (the head is hidden under one or more parts of the body), (7) locomotor escape, (8) tail display (coiled tail is elevated; Figure 1) and (9) immobility (not evaluated during the handling).

A significant variation in the number of records of each behavioral display was observed ($\chi^2 = 68.0$; $df = 8$; $p < 0.001$). The most frequent behavioral display was body flattening (21.6%), followed by head triangulation (16.1%), tail display (12.9%), locomotor escape (12.9%), erratic movements (12.9%), false strike (9.7%), hide head (9.7%), cloacal discharge (9.7%), and immobility (9.7%).

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of records), flattened body (18.8% of records), head triangulation (16.1% of records) and tail display (14.0% of records; Table 1). A small number of records of false strikes (2.7% of records) and hiding the head (2.0% of records) was observed. Cloacal discharge was recorded exclusively during handling and false strikes never occurred during the first approach (Table 1).

The frequency of each defensive display varied significantly between first approach and the simulation of the predator attack ($G = 25.150$; $df = 14$; $p < 0.05$). When analyzed separately, the frequency of each display observed during the first approach did not vary significantly ($\chi^2 = 8.2$; $df = 5$; $p = 0.14$; Figure 2). However, this variation was significant during the simulation of the predator attack (hand approach; $\chi^2 = 41.2$; $df = 7$; $p < 0.001$; Figure 2), in which the most frequent displays were body flattening (22.0% of records), tail display (21.0% of records), erratic movements (20.0% of records), and head triangulation (16.0% of records; Figure 2). In 2.0% of the records, animals hid their heads during hand approach, and remained motionless in only 1.0% of records. The frequency of each defensive display varied significantly during snake handling ($\chi^2 = 37.5$; $df = 5$; $p < 0.001$; Figure 3). When handled, the most frequent displays were cloacal discharge (35.0% of records), erratic movements (35.0% of records) and head triangulation (21.0% of records).

When analyzed separately, no significant differences were found in the number of records of each display in gravid females ($\chi^2 = 11.0$; $df = 8$; $p = 0.20$; Table 1). However, differences were significant for non-gravid females ($\chi^2 = 25.7$; $df = 8$; $p < 0.001$) and males ($\chi^2 = 38.9$; $df = 8$; $p < 0.001$; Table 1). The most frequently observed displays were erratic movements (20.4% of records of non-gravid females and 21.6% of records of males), body flattening (18.5% of records of non-gravid females and 20.6% of records of males), followed by tail display in non-gravid females (18.5% of records) and locomotor escape in males (14.4% of records; Table 1). A significant positive correlation was observed between the number of displays and substrate temperature ($r_s = 0.36$; $p = 0.047$; $N = 30$). However, no significant correlations were found between the number of displays observed and body temperature ($r_s = 0.16$; $p = 0.38$; $N = 30$) or air temperature ($r_s = 0.34$; $P = 0.065$; $N = 30$).

The comparison with other species of the tribe Xenodontini revealed two large clusters, one grouping most of the species of *Xenodon* compared and another group consisted mostly of species of the genus *Liophis* (Figure 4). Among the species of *Xenodon*

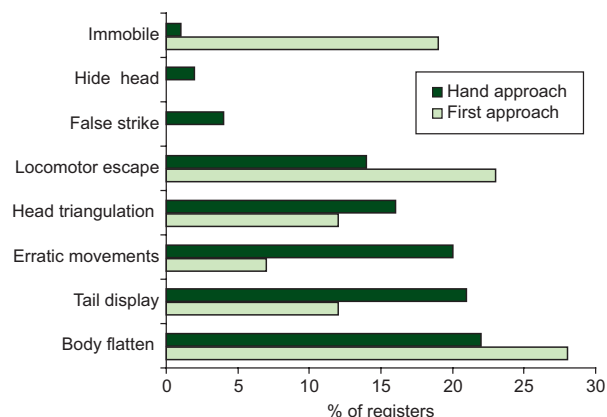


Figure 2. Records of different defensive displays shown by males and females of *Xenodon dorbignyi* during human approach and during simulation of a predator attack (see methods for simulation details).

Figura 2. Registros de diferentes unidades comportamentais exibidas por machos e fêmeas de *Xenodon dorbignyi* durante a aproximação humana e durante a simulação do ataque de um predador (veja nos métodos os detalhes da simulação).

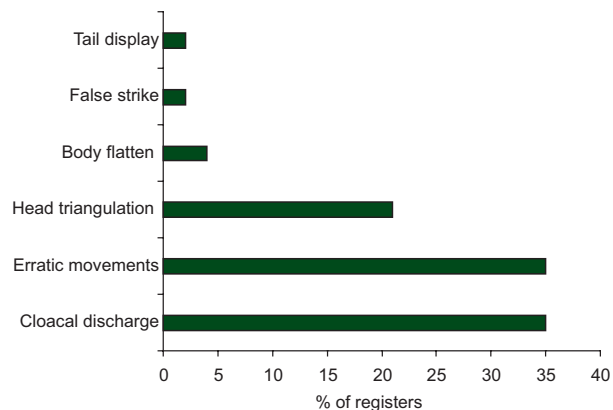


Figure 3. Records of defensive displays shown by males and females of *Xenodon dorbignyi* during handling (see methods for details).

Figura 3. Registros de diferentes unidades comportamentais exibidas por machos e fêmeas de *Xenodon dorbignyi* durante o manuseio (veja nos métodos os detalhes).

Table 1. Number of records of each defensive display shown by adult individuals of *Xenodon dorbignyi*. In parenthesis, stimuli in which each defensive display was observed. Legend: fa = first approach; h = handling; ha = hand approach.

Tabela 1. Número de registros de cada unidade comportamental exibida por indivíduos adultos de *Xenodon dorbignyi*. Entre parênteses estão os estímulos em que cada unidade comportamental foi observada. Legenda: fa = primeira aproximação; h = manuseio; ha = aproximação da mão.

Display	# responses				% of responses			
	Gravid	Non gravid	Male	Total	Gravid	Non gravid	Male	Total
Erratic movements	7 (ha/h)	11 (fa/ha/h)	21 (fa/ha/h)	39	20.0	20.4	21.6	21.0
Body flattening	5 (fa/ha)	10 (fa/ha/h)	20 (fa/ha/h)	35	14.3	18.5	20.6	18.8
Head triangulation	5 (ha/h)	10 (fa/ha/h)	15 (fa/ha/h)	30	14.3	18.5	15.5	16.1
Tail display	5 (fa/ha)	10 (fa/ha/h)	11 (fa/ha)	26	14.3	18.5	11.3	14.0
Locomotor escape	3 (fa)	6 (fa/ha)	14 (fa/ha)	23	8.6	11.1	14.4	12.4
Cloacal discharge	6 (h)	4 (h)	7 (h)	17	17.1	7.4	7.2	9.1
Immobile	3 (fa/ha)	2 (fa)	4 (fa)	9	8.6	3.7	4.1	4.8
False strike	0 (none)	1 (ha)	4 (ha/h)	5	0.0	1.9	4.1	2.7
Hide head	1 (ha)	0 (none)	1 (ha)	2	2.9	0.0	1.0	1.1

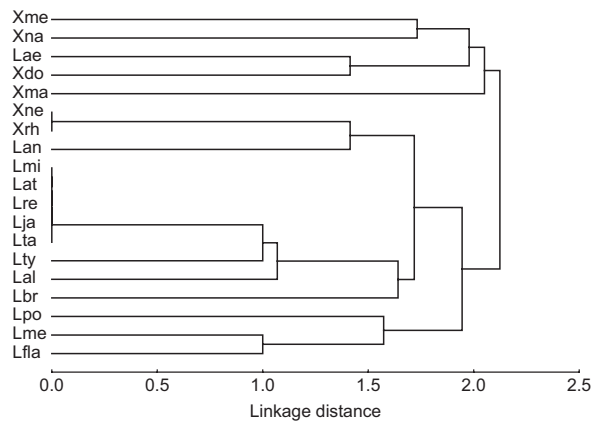


Figure 4. Dendrogram for the cluster analysis of defensive displays observed for snakes in Xenodontini. Cluster analysis using “WPGA”. Compared displays: lateral flattening, dorsoventral flattening, strike (false or not), cloacal discharge, tail display, mouth gaping, hide head, erratic movements, head triangulation, and tail vibration. Compared species: Lae = *Liophis aesculapii* (Linnaeus, 1766); Lal = *Liophis almadensis* (Wagler, 1824); Lan = *Lygophis anomalus* (Günther, 1858); Lat = *Liophis atraventer* (Dixon & Thomas, 1985); Lbr = *Liophis breviceps* (Cope, 1860); Lfla = *Lygophis flavifrenatus* (Cope, 1862); Lja = *Liophis jaegeri* (Günther, 1858); Lme = *Lygophis meridionalis* (Schenkel, 1901); Lmi = *Liophis miliaris* (Linnaeus, 1758); Lpo = *Liophis poecilogyrus* (Wied, 1825); Lre = *Liophis reginae* (Linnaeus, 1758); Lta = *Liophis taeniogaster* (Jan, 1863); Lty = *Liophis typhlus* (Linnaeus, 1758); Xdo = *Xenodon dorbignyi* (Duméril, Bibron & Duméril, 1854); Xma = *Xenodon matogrossensis* (Scrocchi & Cruz, 1993); Xme = *Xenodon merremii* (Wagler, 1824); Xna = *Xenodon nattereri* (Steindachner, 1867); Xne = *Xenodon newwedii* (Günther, 1863); Xrh = *Xenodon rhabdocephalus* (Wied, 1824).

Figura 4. Dendrograma da análise de agrupamento das unidades comportamentais observadas em serpentes da tribo Xenodontini. Na análise foi utilizado o método “WPGA”. Foram comparadas as seguintes unidades comportamentais: achatamento lateral do corpo, achatamento dorsoventral, bote (falso ou não), descarga cloacal, display caudal, escancarar a boca, esconder a cabeça, movimentos erráticos, triangulação da cabeça e vibrar a cauda. Espécies comparadas: Lae = *Liophis aesculapii* (Linnaeus, 1766); Lal = *Liophis almadensis* (Wagler, 1824); Lan = *Lygophis anomalus* (Günther, 1858); Lat = *Liophis atraventer* (Dixon & Thomas, 1985); Lbr = *Liophis breviceps* (Cope, 1860); Lfla = *Lygophis flavifrenatus* (Cope, 1862); Lja = *Liophis jaegeri* (Günther, 1858); Lme = *Lygophis meridionalis* (Schenkel, 1901); Lmi = *Liophis miliaris* (Linnaeus, 1758); Lpo = *Liophis poecilogyrus* (Wied, 1825); Lre = *Liophis reginae* (Linnaeus, 1758); Lta = *Liophis taeniogaster* (Jan, 1863); Lty = *Liophis typhlus* (Linnaeus, 1758); Xdo = *Xenodon dorbignyi* (Duméril, Bibron & Duméril, 1854); Xma = *Xenodon matogrossensis* (Scrocchi & Cruz, 1993); Xme = *Xenodon merremii* (Wagler, 1824); Xna = *Xenodon nattereri* (Steindachner, 1867); Xne = *Xenodon newwedii* (Günther, 1863); Xrh = *Xenodon rhabdocephalus* (Wied, 1824).

compared, *X. nattereri* was most similar to *X. dorbignyi*, which was also similar to *L. aesculapii*.

Discussion

Tested individuals of *Xenodon dorbignyi* exhibited an elaborated defensive repertoire comprised of a diverse set of defensive displays. *Xenodon dorbignyi* actively forages on the substrate surface (Oliveira et al. 2001, Oliveira 2005), is diurnal and associated with open habitats (e.g. fields and sand dunes), favoring the action of visually oriented predators (e.g. birds of prey and/or mammals; Oliveira et al. 2004). This hypothesis is reinforced by the fact that the most frequent displays observed in the tested individuals (body flattening, tail

visually oriented predators. Body flattening and head triangulation, for example, may create the illusion that *X. dorbignyi* is larger than it is, inducing the predator to misjudge its capacity to subdue its prey. Erratic movements might be a way to demonstrate physical vigor, which would require a considerable energetic cost to the predator. This tactic may be especially important against predators with limited capacity to manipulate snakes, due to small size or inexperience (Sazima & Martins 1990). In addition, erratic movements can reduce the precision of the predator attack as most attacks (e.g. pecking) are directed to the snake’s head (see Buasso et al. 2006). Thus, erratic movements might be more efficient to protect the head than simply hide it under the body, which had few records. Also, by hiding the head, the ability of the snake to show other displays, such as false strikes or head triangulation, is limited.

Although diversified, the repertoire of displays of *X. dorbignyi* is not completely efficient, as indicated by the frequent presence of carcasses of *X. dorbignyi* near nests of burrowing-owls (*Athene cucularia*) in the study area. However, Oliveira et al. (2004) suggest that smaller individuals of *X. dorbignyi* may be preferentially preyed by *A. cucularia*, supporting the importance of antipredator displays that create the illusion that the snake is larger than it is. In this case, showing these displays might be extremely important during the breeding season, a period of extended daily activity on the surface (e.g. males searching for females; Oliveira 2005, Wilgers & Horne 2007).

Apparently, a useful defense strategy of *X. dorbignyi* is to take advantage of its cryptic coloration or move far from the opponent. The more diverse kinds of displays were observed as secondary responses when a predator attack is imminent. This hypothesis is supported by the high number of animals that remained motionless or flattened the body during the first approach, compared to low frequency of these displays during hand approach. Both these behaviors do not increase visual cues to the predators. In other hand, during the first approach, a high number of animals have tried locomotor escape, avoiding proximity with predators. In general, snakes showed more displays during the hand approach or handling than when first approached. Thus, disruptive coloration and cryptic behaviors associated with semi-fossorial habits may limit the detection by predators. These results suggest that *X. dorbignyi* is capable of evaluating the level of threat imposed by the aggressor. Strikes, for example, are responses restricted to situations of extreme danger, as they were never observed during the first approaches. In addition, cloacal discharges were recorded only during handling, possibly as an extreme defense mechanism, when the snake tries to discourage its ingestion by the predator.

In some snakes, gravid females show a more aggressive behavior than males or non-gravid females (Shine 1993). This, however, was not observed for *X. dorbignyi*. Instead, the lower number of displays by gravid females revealed a lower tendency to exhibit defensive displays compared to males or non-gravid females. The presence of eggs may prevent the snake from showing some displays, such as body flattening and tail displays. However, it is possible that embryos of some females were not detected during handling, making the comparison between gravid and non-gravid females difficult. Males, on the other hand, had a higher tendency to flee, which might be associated to a lower mobility of females in advanced phases of vitellogenesis.

As metabolic rates of ectotherms are dependent on environmental temperature, so is their capacity to react to stimuli (Goode & Durvall 1989, Keogh & Deserto 1994). Thus, during colder days, cryptic behavior (immobility) might be more frequent than other displays (see Shine et al. 2000). In this study, no significant correlations

air temperature. A positive correlation found between the number of displays shown by animals and substrate temperature would reflect high metabolic rates at the warmer hours of the day.

The general aspect of individuals of *X. dorbignyi* of the study area is similar to that of *Bothrops*, as reported by Yanosky & Chani (1988). These authors suggest that *X. dorbignyi* is a mimic of *Bothrops*, not only due to its visual similarity, but also due to behavioral convergence (head triangulation and false strikes). These authors also suggest that *X. dorbignyi* is a mimic of *Micrurus* coral snakes, because of its caudal display, exhibiting red ventral scales, which, if effective, should reduce the risk of predation due to avoidance of snakes with coral-like pattern (Sazima & Abe 1991, Marques 2002, Buasso et al. 2006). Similarly, *Xenodon nattereri*, in southeastern Brazil, exhibits a color pattern similar to that of sympatric and syntopic *Bothrops itapetiningae*, and when handled, strikes (Sawaya et al. 2008). A similar behavior is observed in *Xenodon neuwiedii*, a supposed mimic of *Bothrops jararaca* (F. Barbo, personal communication).

If the mimicry hypothesis is valid, the defensive repertoire of *X. dorbignyi* should be associated to those of species that are also mimics of venomous snakes, regardless of phylogenetic factors (see Marques 2001). The cluster analysis supports this hypothesis, as *X. dorbignyi* was grouped with *Liophis aesculapii* (mimic species of the coral snake; Marques & Puerto 1991), closer than with other *Xenodon* species. Although a speculation, it is plausible that *X. dorbignyi* might be a mimic of *Micrurus* and *Bothrops* simultaneously. It should be pointed out that despite significant sampling and the systematic studies conducted in recent years, there are no records of *Micrurus* in the coastline of the southernmost region of Brazil (Oliveira 2005, Borges-Martins et al. 2007). However, historic factors might play an important role in the selection of elements of the defensive repertoire, and discussions based only on current predators have a limited scope (Greene 1988). It is possible that the complex repertoire of *X. dorbignyi* was shaped through diverse selective processes by the action of different types of predators or environments with different levels of exposure of snakes.

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