

DEFENSIVE BEHAVIOUR IN PIT VIPERS OF THE GENUS *BOTHROPS* (SERPENTES, VIPERIDAE)

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The genus *Bothrops* encompasses at least six evolutionary lineages that show a great diversification in macro and microhabitat use. We studied the defensive behaviour of one species of each of five lineages within the genus *Bothrops*: *B. alternatus*, *B. jararaca*, *B. jararacussu*, *B. moojeni* and *B. pauloensis*. Specifically, we investigated if this diversification in habitat use was accompanied by a similar divergence in the characters related to defensive behaviour in the genus. Eight behavioural categories were recorded, five of which may be classified as “threatening” (strike, tail vibration, head and neck elevation, dorsoventral body compression and body thrashing); two as “escape” (locomotor escape and cocking); and one as “cryptic” (head hiding). We observed significant differences in four behavioural categories. We also detected a significant difference in the way species elevated their head and neck. Tail vibration and strikes were the most common behaviours presented, and snakes that displayed their tails struck more frequently than those that did not display. A reconstruction of characters related to defensive behaviour on a phylogeny of *Bothrops* indicated an increase in the use of dorsoventral body compression in the groups *alternatus* and *neuwiedi*, which may be associated with the invasion of open areas by these lineages.

Key words: comparative method, Crotalinae, defensive tactics, evolution of behaviour

INTRODUCTION

Snakes are exposed to different kinds of predators in the various habitats they occupy (Greene, 1988), and, as a result, may differ in defensive behaviour. For example, snakes in open habitats may suffer a more intense predation pressure from highly mobile predators than in forested habitats (Greene, 1988). Microhabitat use in snakes (e.g. terrestrial, arboreal) may also be associated with defensive behaviours (Greene, 1979). For instance, an association between gaping behaviour and arboreality has been demonstrated in snakes (Greene, 1997). In the case of the genus *Bothrops*, the ways by which the habitat is used by snakes are diverse (Martins *et al.*, 2001). Within the genus, there are lineages of both open and forested areas and with varying degrees of arboreality (Martins *et al.*, 2002). These differences in use of microhabitat (terrestrial and arboreal) and macrohabitat (open and forested areas) may be associated with differences in defensive behaviour of the different lineages of *Bothrops*. In fact, with the exception of the studies on *B. jararaca* by Sazima (1988, 1992), there are no detailed studies of defensive behaviour in the genus *Bothrops*. Sazima (1992) suggested that comparative studies among some *Bothrops* species typical of forested areas and species of open areas could reveal similarities and differences related to their ecology and their phylogenetic relationships.

The genus *Bothrops* (including *Bothriopsis*; e.g., Wüster *et al.*, 2002) includes about 45 described species (Campbell & Lamar, 2004). The phylogenetic relationships within *Bothrops* have been explored in the last few years (e.g. Salomão *et al.*, 1997; Vidal *et al.* 1997; Wüster *et al.*, 2002). The genus encompasses at least six lineages, the groups *atrox*, *jararacussu*, *jararaca*, *alternatus*, *neuwiedi* and *taeniatus* (Wüster *et al.*, 2002).

Here we describe and compare the defensive behaviour of one species of each of five lineages within the genus *Bothrops*, namely *B. alternatus* (*alternatus* group), a terrestrial species which inhabits open areas; *B. jararaca* (*jararaca* group), a semi-arboreal forest dweller; *B. jararacussu* (*jararacussu* group), a terrestrial forest inhabitant; *B. moojeni* (*atrox* group), a semi-arboreal species found in open formations, but associated almost exclusively with riparian forests within these areas; and finally *B. pauloensis* (*neuwiedi* group), a terrestrial species exclusive to open areas (Table 1). We also explore the evolution of characters related to defensive behaviour in the genus *Bothrops* and speculate on possible associations between changes in defensive behaviour and changes in habitat use.

MATERIALS AND METHODS

Test subjects were species of *Bothrops* from several localities of southeastern (*B. alternatus*, *B. jararaca*, *B. jararacussu*, *B. pauloensis* and *B. moojeni*) and central Brazil (*B. moojeni*) brought to the Instituto Butantan between April 1998 and February 1999. Ten

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TABLE 1. Habitat use, sizes (mm), captivity duration (days), and number of individuals of the five species of *Bothrops* studied. T: terrestrial; SA: semi-arboreal; O: open areas; F: forests; SVL: snout-vent length; SD: standard deviation; CD: captivity duration; n = number of individuals.

Species	Habitat use	Mean SVL	SD	Mean CD	SD	n
<i>B. alternatus</i>	T/O	708.6	160.35	4	4.8	10
<i>B. jararaca</i>	SA/F	803.2	169.86	1	1.3	10
<i>B. jararacussu</i>	T/F	611.1	187.13	8	9.6	10
<i>B. moojeni</i>	SA/F	946.5	137.48	5	3.6	10
<i>B. pauloensis</i>	T/O	608.0	126.23	5	2.8	10

individuals of each species were tested as they arrived at the Instituto Butantan (Table 1). Upon arrival, individuals were housed in a large plastic container (c. 100 × 70 × 60 cm high) with bark mulch as a substrate. Snakes were not manipulated until they were removed from the container, measured and individually put in small wood containers, and taken to a temperature-controlled laboratory (25±2°C) where the tests were conducted. The snakes were taken to the laboratory during daytime, approximately eight hours before the initiation of the tests, and the tests were carried out on the same day, always at night, from 1758 hr to 0002 hr. The snakes were tested 0–16 days after arrival at the Instituto Butantan, except for one individual of *B. jararacussu* that was kept for 33 days at the Instituto Butantan before tests were performed. Each individual snake was tested only once.

The tests were carried out in an arena set on the ground of the laboratory (Fig. 1). The laboratory wall formed one of the sides of the arena; the other three sides were made of wood and glass. One of the sides adjacent to the wall was opaque and the other two sides were transparent. During trials, we stayed behind the opaque side of the arena to minimize possible disturbance. Two Panasonic NVRJ PR VHS cameras were used, one over the arena set on a tripod and facing the ground, and the other on the ground, lateral to the arena and facing the wall. The ground was covered with a black plastic sheet; both the plastic sheet and the wall had gridlines of 1 and 2 cm, respectively, for distance estimates. The light sources were two 60 W bulbs set on the main axis of the arena, one at each side. Although rather artificial, the light sources were necessary for the recording of the trials on tape.

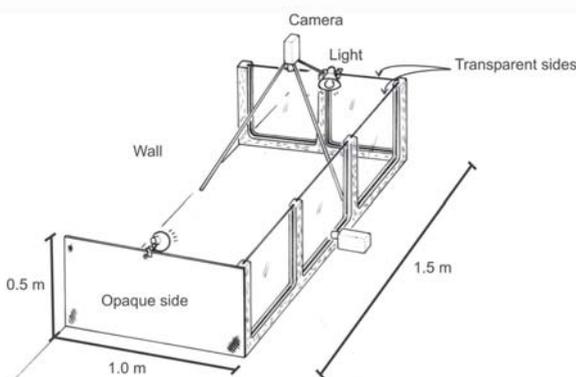


FIG. 1. Arena where the defensive behaviour of five species of *Bothrops* was elicited and filmed.

Defensive behaviour was elicited with using a stimulus object, a plastic bottle (height 15 cm; diameter 10 cm; volume 0.5 l) covered with a 0.5 cm-thick sheet of soft black rubber to which a 1.5 m plastic pipe was attached at a 45° angle. The purpose of the rubber was to minimize injuries to the snakes' fangs during strikes. The bottle was filled with warm water (60°C) shortly before the tests to raise the temperature of the external surface of the rubber to about 37°C (mean±SD = 37.1±0.94°C; $n=17$; recorded immediately before trials by a Miller & Weber Inc. quick-reading thermometer with an accuracy of 0.1°C). The stimulus object was developed by us and was chosen, among several others, on the grounds that it immediately elicited typical defensive behaviours upon its introduction into the arena. We believe that the stimulus object simulated the head of a mammal approaching the snake horizontally and close to the ground.

Before each test, the internal surfaces of the arena as well as the stimulus object were cleaned with ethanol. The snake was then put in the centre of the arena and a transparent acrylic box (30 cm on each side and 15 cm high), with the open side facing down, was put over the snake using a hook. We used a transparent box to make sure that the snake could see its surrounding environment before the initiation of trials. The acrylic box was also cleaned with ethanol before the tests. The arena lights were on prior to introducing snakes into the arena. Snakes were left undisturbed for 10 minutes before the beginning of the tests. The 10 minute interval was selected arbitrarily, but we believe it was enough for the snakes to settle down before the initiation of trials.

Cameras were turned on by remote control and recorded at 30 frames/s. Trials began when the acrylic cover was removed with a hook and the stimulus object was introduced into the arena and moved towards the snake, parallel to the ground and about 1 cm above it, always by the same person. The stimulus object touched the snake's body and was withdrawn repeatedly, about once every two seconds, 30 times uninterruptedly for each snake. If the snake went out of the camera's field (time out; cf. Martin & Bateson, 1993), the stimulus object was removed from the arena and the snake was brought to its centre with a hook; this will hereafter be termed an intervention. The stimulus object was then reintroduced and the stimulation was resumed.

During trials, we never moved from behind the light bulb, even when the stimulation had to be interrupted

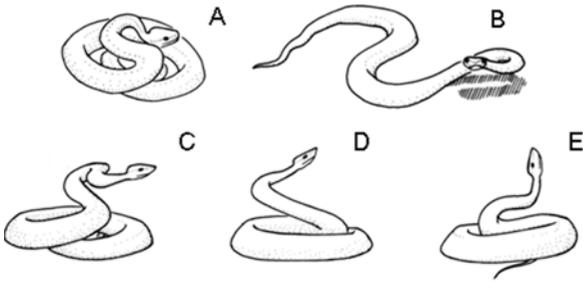


FIG. 2. Defensive behaviour of *Bothrops* spp. Defensive body posture, A: coiled; and B: loose. Head and neck elevation, C: horizontal; D: at angle of 45°; E: vertically.

and the snakes brought to the centre of the arena. Trials were later analysed frame-by-frame with a Panasonic NVSD475 PR VHS player. We measured the duration of each trial with the use of a digital chronometer; time-out periods were not considered in the estimates of time.

We used the continuous sampling method (cf. Martin & Bateson, 1993) and all the behaviours were recorded and quantified. Behavioural responses were categorized according to Greene (1988) and Sazima (1992), and were as follows: (1) strike: a rapid movement of the snake's head towards the stimulus object with its jaws wide open, as the lateral curves of its anterior body straightened, and the posterior part of the body remained stationary; (2) tail vibration: the tail was moved rapidly back and forth against the substrate, with production of sound; (3) head and neck elevation: the head and anterior part of the body were lifted from the substrate; this could be horizontal (Fig. 2C), at an angle of approximately 45° (Fig. 2D) or vertical (Fig. 2E); (4) dorsoventral body compression: the snake flattened its body dorsoventrally; (5) locomotor escape: a flight response in which snakes moved away quickly from the stimulus object; (6) cocking: the snake retreated backwards employing the posterior part of its body, while keeping the anterior portion of its body in an S-coil, and facing the stimulus object; (7) head hiding: the snake hid its head under one or more parts of its body; and (8) body thrashing: the snake made sudden and erratic movements.

Depending on their type, behavioural categories were quantified as the frequency of occurrences during trials (strikes, head and neck elevation, locomotor escape, cocking and body thrashing) or as the proportion of the trial time during which the behaviour was exhibited, varying from 0 to 1 (tail vibration, dorsoventral body compression and head hiding). We carried out a two-factor analysis of covariance (ANCOVA) in order to compare the behaviours among snakes, and test the effects of sex, snake size, captivity duration and the number of interventions during trials on the snakes' behaviours. Factors were species and sex, whereas snake size, captivity duration and the number of interventions were covariates. We used snout-vent length (SVL) in mm as a measure of size. Captivity duration was measured in days from the arrival of a given specimen at the Instituto Butantan until the day of the trial, and the

number of interventions as the number of times we had to introduce the hook into the arena and pull the snake back to the camera's field during a trial. The frequency of the types of head and neck elevation were compared with a Pearson chi-square test. The number of strikes made by snakes that tail vibrated during tests and of those that did not tail vibrate was compared with a *t*-test. Because of the small number of individuals that did not tail vibrate, we pooled the data of all species in this latter analysis. Variables were all transformed to fulfil test assumptions. We did a ln transformation on snake size; square-root transformations on captivity duration, number of interventions and the behavioural variables strikes, head and neck elevation, locomotor escape, cocking and body thrashing (frequencies); and finally arcsine transformations on the behavioural variables tail vibration, dorsoventral body compression and head hiding (proportions; Zar, 1999). Due to the high degree of asymmetry in the distributions of the raw values of variables, we decided to use their medians, instead of the means, on the character optimization onto a phylogeny of the genus *Bothrops* (adapted from Wüster *et al.*, 2002) using Linear Parsimony Analysis with the use of MacClade 4.0 (Maddison & Maddison, 2000). We were not able to optimize the characters head hiding and body thrashing, because the median values for all five species were zero.

RESULTS

During trials the snakes remained with the anterior part of the body in an S-shape position either coiled (Fig. 2A) or in a loose posture (Fig. 2B), and could change from one position to the other. We were not able to record the penetration of the snake's fangs into the rubber of the stimulus object (bite) through the analysis of the videotapes. However, it certainly occurred, since the rubber always presented marks of perforation from which venom drained following the tests.

Strike and tail vibration were the most used defensive behaviours by the five species studied (Table 2). Frequency of head and neck elevation, dorsoventral body compression, locomotor escape and cocking varied among species, whereas head hiding and body thrashing were rarely used by all species (Table 2). The ANCOVA revealed significant differences among species in head and neck elevation, dorsoventral body compression, locomotor escape and cocking (Table 3). The differences were related to the prevalence of head and neck elevation and cocking in *B. moojeni* (Fig. 3), of dorsoventral body compression in *B. alternatus* and *B. pauloensis* (Fig. 3) and of locomotor escape in *B. jararacussu* (Fig. 3). There was no effect of sex on the variables, nor any interactions between the factors sex and species (Table 3). However, we found a significant effect of interventions on both locomotor escape and head and neck elevations, as well as an effect of captivity duration on head hiding (Table 3). We detected a significant difference in the frequency of horizontal and 45-degree angle head and neck elevations among spe-

TABLE 2. Number of individuals of each *Bothrops* sp. that displayed each of the defensive behaviours ($n=10$ of each species). Total: number of individuals of all species which displayed the behaviour; values in parentheses are percentages of the total number of individuals ($n=50$).

Defensive behaviour	<i>B. alternatus</i>	<i>B. jararaca</i>	<i>B. jararacussu</i>	<i>B. moojeni</i>	<i>B. pauloensis</i>	Total
Strike	10	10	9	10	8	47 (94)
Tail vibration	10	7	10	10	8	45 (90)
Head and neck elevation	5	9	5	10	7	36 (72)
Dorsoventral body compression	10	4	6	6	7	33 (66)
Locomotor escape	5	7	9	5	5	31 (62)
Cocking	3	10	4	9	5	31 (62)
Head hiding	4	2	4	1	3	14 (28)
Body thrashing	3	2	3	0	2	10 (20)

cies ($\chi^2=64.6$; $df=4$; $P<0.0001$): *Bothrops alternatus* and *B. pauloensis* elevated the head and neck parallel to the ground in most cases (Fig. 2; Table 4), *Bothrops jararacussu* showed horizontal and 45° elevation in similar proportions, whereas *B. jararaca* and *B. moojeni* elevated the head and neck at 45° more frequently (Table 4). Additionally, *B. moojeni* was the only species to elevate the head and neck vertically (Table 4). Snakes that vibrated their tails during tests struck more than those that did not vibrate their tails ($t_{48}=2.3$; $P=0.026$).

In the character optimization, *B. alternatus* did not show any change in relation to the ancestor of the genus in the median occurrence of any of the behaviours (Fig. 3). On the other hand, *B. pauloensis*, *B. jararaca* and *B. jararacussu* showed four changes each, and *B. moojeni* presented five changes (Fig. 3).

TABLE 3. F -values and levels of significance of a two-factor analysis of covariance (ANCOVA) on the defensive behaviour of *Bothrops alternatus*, *B. jararaca*, *B. jararacussu*, *B. moojeni* and *B. newwiedi* ($n=10$ of each species). Factors are species and sex; covariates are size, captivity and interventions. Species \times sex is the interaction between the two factors. See text for details of the quantification of variables. *Variables where significant differences among species were found.

Dependent variables	Factors and covariates					
	Species	Sex	Species \times sex	Size	Captivity duration	Interventions
Strike	$F_{4,45}=1.18$ $P=0.34$	$F_{1,45}=1.44$ $P=0.24$	$F_{4,45}=0.45$ $P=0.77$	$F_{1,45}=0.03$ $P=0.69$	$F_{1,45}=0.16$ $P=0.87$	$F_{1,45}=2.73$ $P=0.11$
Tail vibration	$F_{4,45}=2.01$ $P=0.11$	$F_{1,45}=1.05$ $P=0.31$	$F_{4,45}=0.38$ $P=0.82$	$F_{1,45}=0.26$ $P=0.62$	$F_{1,45}=0.00$ $P=0.95$	$F_{1,45}=2.3$ $P=0.14$
Head and neck elevation*	$F_{4,45}=8.08$ $P<0.0001$	$F_{1,45}=0.29$ $P=0.59$	$F_{4,45}=0.70$ $P=0.60$	$F_{1,45}=1.45$ $P=0.24$	$F_{1,45}=0.13$ $P=0.72$	$F_{1,45}=4.57$ $P=0.039$
Dorsoventral body compression*	$F_{4,45}=6.38$ $P=0.001$	$F_{4,45}=2.02$ $P=0.16$	$F_{4,45}=0.78$ $P=0.55$	$F_{1,45}=0.22$ $P=0.64$	$F_{1,45}=0.65$ $P=0.42$	$F_{1,45}=0.92$ $P=0.34$
Locomotor escape*	$F_{4,45}=2.64$ $P=0.05$	$F_{4,45}=3.53$ $P=0.07$	$F_{4,45}=0.23$ $P=0.92$	$F_{1,45}=1.05$ $P=0.31$	$F_{1,45}=1.34$ $P=0.26$	$F_{1,45}=55.91$ $P<0.0001$
Cocking*	$F_{4,45}=5.16$ $P=0.002$	$F_{4,45}=0.17$ $P=0.68$	$F_{4,45}=0.15$ $P=0.96$	$F_{1,45}=0.43$ $P=0.52$	$F_{1,45}=0.24$ $P=0.63$	$F_{1,45}=0.50$ $P=0.49$
Head-hiding	$F_{4,45}=0.67$ $P=0.61$	$F_{4,45}=0.85$ $P=0.36$	$F_{4,45}=0.16$ $P=0.96$	$F_{1,45}=0.26$ $P=0.62$	$F_{1,45}=5.90$ $P=0.02$	$F_{1,45}=2.38$ $P=0.13$
Body thrashing	$F_{4,45}=0.92$ $P=0.46$	$F_{4,45}=0.58$ $P=0.45$	$F_{4,45}=0.82$ $P=0.52$	$F_{1,45}=0.07$ $P=0.79$	$F_{1,45}=0.05$ $P=0.83$	$F_{1,45}=0.52$ $P=0.47$

DISCUSSION

In the present study, the escalation of the defensive sequence reported for *B. jararaca* (Sazima, 1988) and *C. viridis* (Duvall *et al.*, 1985) was obviously not observed, since the snakes were already in a restrained situation at the beginning of observations. This experimental constraint may be responsible for the generally high tendency of snakes to strike during trials, as reported for *B. jararaca* when constrained in the field (Sazima, 1988). Our observations support the suggestions made by Duvall *et al.* (1985) and Sazima (1988) that pit vipers are able to evaluate their chances of escape during an encounter with a potential predator and make a decision on which defensive tactic to adopt, which was also suggested in relation to another viperid, *Agkistrodon piscivorus* (Gibbons & Dorcas, 2002).

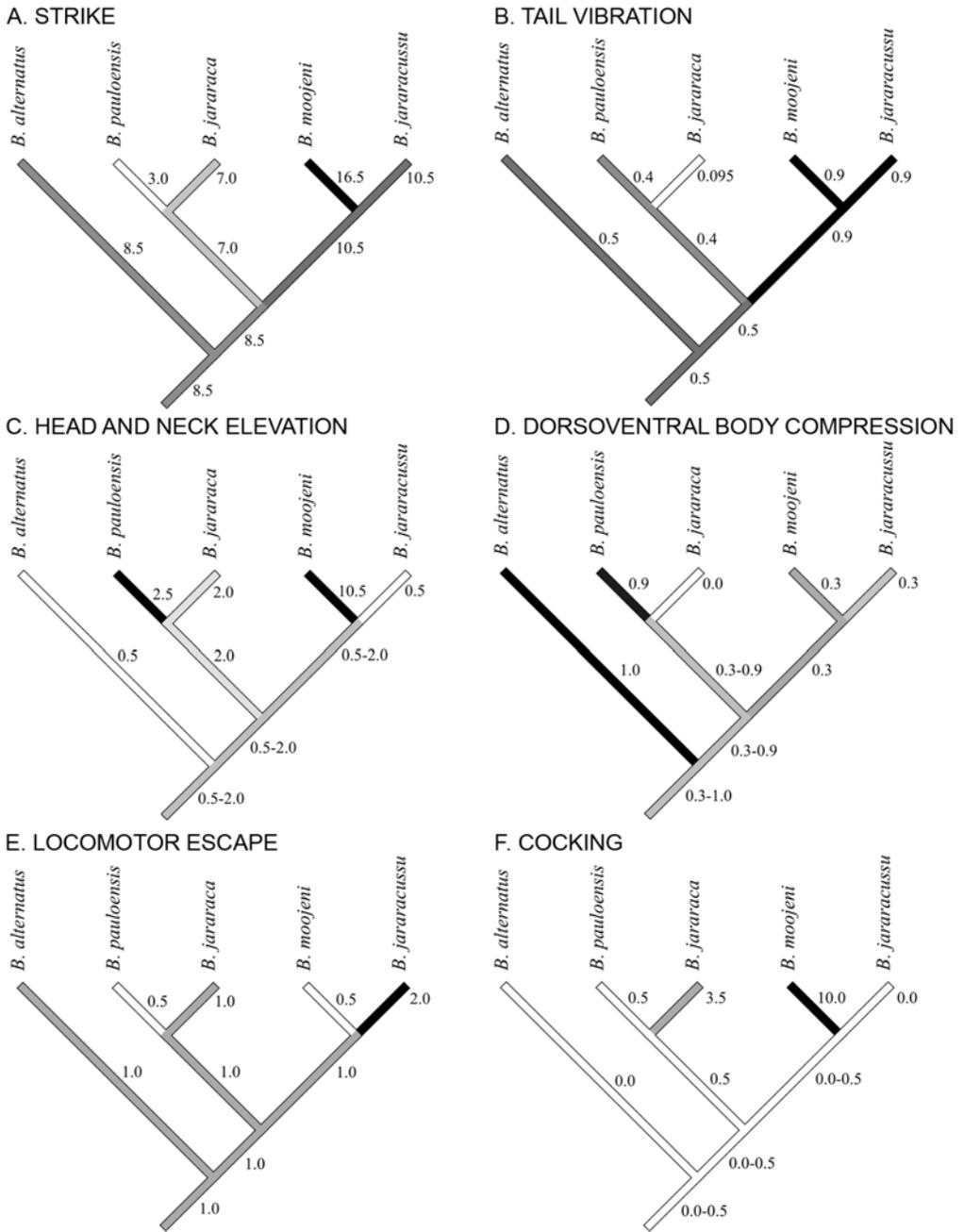


FIG. 3. Optimization using linear parsimony of defensive behaviours on a phylogenetic hypothesis for the species of *Bothrops* treated herein (adapted from Wüster *et al.*, 2002). The values for each species are medians. Tail vibration and dorsoventral body compression were quantified as the proportion of time they were exhibited by snakes during trials (varying from 0 to 1), the remaining characters as the frequency of occurrence during trials. A: strike; B: tail vibration; C: head and neck elevation; D: dorsoventral body compression; E: locomotor escape; F: cocking.

TABLE 4. Types of head and neck elevation in *Bothrops* spp. shown as percentages in relation to the total number of head and neck elevations in each species. Values in parentheses are the number of elevations.

Species	Horizontal	Angle of 45°	Vertical
<i>B. alternatus</i>	88.9 (8)	11.1 (1)	0
<i>B. jararaca</i>	26.9 (7)	73.1 (19)	0
<i>B. jararacussu</i>	44.4 (4)	55.6 (5)	0
<i>B. moojeni</i>	8.0 (9)	91.1 (102)	0.9 (1)
<i>B. pauloensis</i>	67.9 (19)	32.1 (9)	0

Although not a primary goal of this study, our data suggest that the defensive behaviours of the studied species may be altered by captivity duration and manipulation of the snakes, which has already been reported for other viperid snakes (Glaudas, 2004). These undesired effects constitute an important caveat of our study and may be taken as a warning by investigators who are designing and conducting behavioural studies on snakes in captivity.

The behavioural categories we observed were the same as those described by Sazima (1988, 1992) for *B.*

jararaca in field conditions. Moreover, in field conditions, individuals of *B. jararaca* showed an increase in the frequency of strikes (90% of the individuals struck at the observer) when they did not have access to escape routes (Sazima, 1988), a percentage very similar to that observed in our study, considering *B. jararaca* alone (100%, Table 2) or all species pooled (94%, Table 2). It seems reasonable, therefore, that the defensive behaviour observed in our study can be interpreted as that of a cornered individual in the field. In spite of the caveats previously mentioned, we believe that behavioural data obtained in captivity are indeed reliable, at least for some types of behaviour (e.g. defensive), contrary to the suggestion of Shine *et al.* (2002) that responses of captive animals do not provide a viable alternative to behavioural field studies. In fact, there are a high number of behavioural studies with snakes housed in captivity (Ford, 1995). Furthermore, encounters with lanceheads of the genus *Bothrops* in the field are generally rare (see Nogueira *et al.*, 2003) and depend on long-term studies, which are time-consuming and costly. Studies in captivity, therefore, may be useful and necessary in such cases.

Following the functional definitions of Mori & Burghardt (2004), of the eight behavioural categories observed herein five may be classified as “threatening” (strike, tail vibration, head and neck elevation, dorsoventral body compression and body thrashing), two as “escape” (locomotor escape and cocking) and one as “cryptic” (head hiding). When cornered, snakes of the genus *Bothrops* will readily defend themselves with strikes; however, they also rely on warning signals such as tail vibration to warn potential predators of their willingness to defend themselves. As observed in the viperid *Gloydus shedaoensis* (Shine *et al.*, 2002), tail vibration was also associated with striking in the species of *Bothrops* we studied. This may indicate that in the genus *Bothrops*, tail vibration provides a warning of an individual’s likelihood to strike. Our results, however, must be interpreted with caution, because of the fact that we pooled all species in this analysis.

The differences in the types of head and neck elevation (Table 4) may be associated with microhabitat use in the studied species. The terrestrial *B. alternatus* and *B. neuwiedi* (Martins *et al.*, 2001) tended to use horizontal head and neck displays, whereas the semi-arboreal *B. jararaca* and *B. moojeni* tended to position the head and neck at a 45-degree angle. *Bothrops jararacussu*, which belongs to a terrestrial lineage that descends from a semi-arboreal ancestor (Martins *et al.*, 2001), used both head elevation patterns at the same frequency.

The defensive behaviour of the five species studied was qualitatively very similar, since all species presented all types of behaviour, the only exception being the absence of body thrashing in *B. moojeni*. However, we observed quantitative differences in four behavioural categories (head and neck elevation, dorsoventral body compression, locomotor escape and cocking),

which is in accordance with the idea that behavioural differences in snakes, at the generic or specific levels, are mainly quantitative instead of qualitative (Arnold & Bennett, 1984).

Bothrops alternatus was the most and *B. moojeni* the least conservative lineage in relation to the ancestor of the genus (Fig. 3). There seems not to be a clear pattern relating the evolution of overall defensive behaviour (Fig. 3) and the great divergence of size, shape and habitat use in the genus *Bothrops* (see Martins *et al.*, 2001, 2002). Nevertheless, we believe that there is an association between habitat use and one of the observed behaviours, namely dorsoventral body compression. *Bothrops alternatus* and *B. pauloensis* showed a high prevalence of dorsoventral body compression (Fig. 3D). *Bothrops itapetiningae*, a species related to *B. alternatus* (Wüster *et al.*, 2002), also flattens the body frequently (M. Martins, personal observation), as does *B. mattogrossensis* (I. Sazima, unpublished data), of the *neuwiedi* group, which further indicates the prevalence of this behaviour in the groups *alternatus* and *neuwiedi*. The ancestor of *Bothrops* was most likely a forest species (Martins *et al.*, 2001, 2002) that subsequently invaded open areas, giving rise to the *alternatus* and *neuwiedi* groups. We believe that there was an increase in the use of this behaviour in these groups in relation to their ancestors (Fig. 3D), and that this increase is associated with the invasion of open habitats by these lineages. Perhaps the common occurrence of dorsoventral body compression in *B. alternatus* and *B. pauloensis* is an adaptation to a habitat where the predation pressure by birds of prey is higher than in the forests inhabited by the other species of *Bothrops*. Indeed, four predation attempts by the owl *Athene cunicularia* on *B. alternatus* were recently described (Valdujo & Nogueira, 2000; Martins *et al.*, 2003). An additional possibility is that the efficiency of body flattening may be increased in open habitats relative to forested habitats because snakes are possibly more visible to predators in the former. These two factors combined may account for the higher occurrence of this behaviour in the open habitat species. This hypothesis could be further explored by searching for convergent behaviours in other snake lineages that are also known to have invaded open areas.

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