

HOW TO BE ARBOREAL AND DIURNAL AND STILL STAY ALIVE: MICROHABITAT USE, TIME OF ACTIVITY, AND DEFENSE IN NEOTROPICAL FOREST SNAKES

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ABSTRACT. Previous studies indicate that (1) defensive displays are associated with habitat use in snakes, (2) visual defenses correlate better with habitat than with phylogeny, and (3) arboreal snakes are more exposed to predators than terrestrial species. We hypothesize that similar patterns exist for diurnal versus nocturnal snakes, and test these hypotheses against the occurrence of 13 defense types directed to visually oriented predators in 92 colubrids from two Neotropical assemblages, one from central Amazonia (26 genera, 41 species) and another from the Atlantic Forest (23 genera, 62 species). Arboreal species and genera displayed more visual defensive tactics than terrestrial ones. Frontal display, gaping, gular inflation, head elevation, neck S-coil, and, apparently, head triangulation, tended to be more frequent in arboreal species, whereas dorsoventral body depression and, apparently, polymorphism, were more frequent in terrestrial ones. Peculiarities of the arboreal microhabitat, such as the prevalence of a green background, a likely higher exposition to predators, and the variety of directions from which a predator would approach may have led to the evolution of peculiar visual defensive tactics in arboreal species. With regard to time of activity, the number of visual defensive tactics was not different between diurnal and nocturnal species or genera. However, frontal display, gaping, gular inflation, and crypsis were prevalent in diurnal snakes, whereas mimicry and, apparently, head triangulation were more frequent in nocturnal forms. Furthermore, green was significantly more frequent in diurnal species, whereas contrasting color patterns were more frequent in nocturnal species. A cluster analysis based on the occurrence of visual defenses resulted mostly in heterogeneous groups of genera regarding phylogenetic position (clade), preferred microhabitat and time of activity. In general, our analyses indicate that the way Neotropical snakes defend themselves from predators results from a complex interaction between ecological factors and phylogenetic constraints.

KEYWORDS. Defense; Habitat; Amazonia; Atlantic Forest; Brazil.

INTRODUCTION

Antipredator mechanisms in snakes are diverse and complex, and several defensive tactics supposedly are directed to visually oriented predators (review in Greene, 1988a). Some defensive displays are associated with the microhabitat used by the snake: tail and horizontal head displays were found mostly in terrestrial species whereas vertical head display occurred mainly in arboreal ones (Greene 1979). The visibility hypothesis (Senter, 1999) suggests that the advantages of these defensive displays are related to the line of vision of approaching predators. Defenses of terrestrial species would be directed to predators approaching from above, whereas those of arboreal snakes would be directed to predators coming from all sides (Senter, 1999).

Another common observation on the defensive tactics of tropical snakes is the repeated occurrence of green and brown color patterns in arboreal snakes from several lineages (Cott, 1940; Lillywhite and Henderson, 1993; see also several examples of green,

arboreal pitvipers and their putative mimics in Campbell and Lamar, 2004). Indeed, cryptic color patterns are widespread in Neotropical snakes, including many terrestrial species (see, e.g., Campbell, 1998; Dixon and Soini, 1986; Duellman, 1978; Marques *et al.*, 2004; Martins and Oliveira, 1998).

In their comprehensive review of characters related to arboreality in snakes, Lillywhite and Henderson (1993) hypothesized that arboreal species have more limited access to retreats and therefore are more exposed to visually oriented predators than terrestrial species, which can rely on various kinds of retreats like burrows, holes or crevices. They also suggested that a supposed high incidence of crypsis and absence of brightly contrasting color patterns in arboreal snakes were evidences supporting their hypothesis. Although information on intensity of predation on arboreal snakes is scarce, some studies indicate it may be intense in Neotropical forests, mainly by diurnal birds of prey (Braker and Greene, 1994; Greene, 1988b; Lillywhite and Henderson, 1993; Martins, 1996; Sazima, 1992). Indeed, the frequent occurrence

of cryptic patterns in Neotropical snakes corroborates the hypothesis that visually oriented predators are important in the evolution of coloration in these snakes (Lillywhite and Henderson, 1993).

If arboreal snakes are in fact more exposed to visually oriented predators as suggested by Lillywhite and Henderson (1993), it should be expected that, in general, they would be more “visually defensive” than terrestrials. Similarly, if visually oriented predators are so important in the evolution of defensive tactics in snakes, we hypothesize that diurnal snakes should be more visually defensive than the nocturnal ones.

Another important question in snake defensive biology is the role of ecology and phylogeny in the occurrence of defensive tactics in a given species or clade. Greene (1979) emphasized that defensive tactics correlate better with habitat than with phylogeny in snakes, calling attention to several putative examples of convergence in distantly related species. More recently, however, Martins (1996) suggested that phylogeny is a strong determinant factor in the occurrence of defensive tactics in Central Amazonian snakes of eight families, but also that shared potential predators may have led to some convergent defenses.

Snake communities in Neotropical rainforests are good subjects to address the questions above, since they encompass several species of various lineages, displaying a high diversity of defensive tactics (e.g., Duellman, 1978, 2005; Martins and Oliveira, 1998; Marques and Sazima, 2003; Marques *et al.*, 2004). Moreover these assemblages have a high proportion of arboreal species (only 14 out of 75 genera in Greene, 1979 were arboreal), as well as high proportions of diurnal and nocturnal species (see, e.g., Dixon and Soini, 1986; Duellman, 1978; Martins and Oliveira, 1998). Here we use two extensive databases on defensive tactics in two snake assemblages, one from Central Amazonia (Martins and Oliveira, 1998) and another from the Serra do Mar mountain range in the Atlantic Forest (Marques *et al.*, 2004; Marques and Sazima, 2003), to address the following questions regarding defensive strategies in Neotropical snakes: (1) Do arboreal snakes display more defensive tactics directed to visually oriented predators than terrestrial ones? (2) Do diurnal snakes exhibit more defensive tactics directed to visually oriented predators than nocturnal ones? (3) Are green color and crypsis more common in arboreal snakes? (4) Are contrasting color patterns less common in arboreal species than in terrestrial ones? And (5) do visual defensive tactics correlate better with ecology (microhabitat use and time of activity) than with phylogeny in Neotropical snakes?

METHODS

In Central Amazonia, data on defensive tactics were gathered from 1990 through 1995 during fieldwork at the Reserva Florestal Adolpho Ducke, a 100 km² tract of forest, mostly undisturbed, located ca. 25 km north of Manaus, Amazonas, Brazil, as well as at a few other localities in the Manaus region (see detailed descriptions of these areas in Martins and Oliveira, 1998). All defensive tactics displayed by snakes when approached, grasped, and handled were recorded (Martins and Oliveira, 1998). Data from the Atlantic Forest was gathered during the last 20 years during fieldwork in many localities throughout the Serra do Mar mountain range, southeastern Brazil (see Marques *et al.*, 2004), as well as during studies with captive snakes at the Instituto Butantan where many Atlantic Forest species are brought by lay people throughout the year.

We consider arboreal (similar to bush and tree inhabitants in Duellman, 1978) those snakes that regularly spend at least part of their activity time on the vegetation above the ground level; thus, this definition also includes semi arboreal species (see Martins and Oliveira, 1998). Fossorial and cryptozoic species are included in the terrestrial category (see Greene, 1979), since these snakes are collected on the ground and thus may face a similar suite of predators. Primarily aquatic species (e.g., *Helicops* spp.) were excluded from all analyses.

Only colubrids (26 genera, 41 species in Central Amazonia; 23 genera, 62 species in the Atlantic Forest) are considered here, since this group shows a high diversity of defensive tactics and is represented by several arboreal and terrestrial, as well as diurnal and nocturnal species in both assemblages (Martins and Oliveira, 1998; Marques *et al.*, 2004). Ten species occur in both assemblages (see Table 1). Based on gross external morphology, we consider the species we call *Liophis typhlus* in the Amazonian and the Atlantic Forest assemblages as different species; herein we call these taxa *Liophis typhlus* Amazon and *Liophis typhlus* Atlantic, respectively. Thus, our analyses included a total of 92 South American forest colubrids. *Rhinobothrium lentiginosum*, which occurs in Central Amazonia, was not included in our analyses for lack of field data. In the comparisons of the number of defensive tactics observed in arboreal and terrestrial species (hereafter arboreals and terrestrials) as well as in diurnal and nocturnal species (hereafter diurnals and nocturnals), we used both species and genera (see Greene, 1979, for the latter). In the comparisons of

	Assemblage	Clade	Ac	Mh	Gr	Cc	Nvd	BA	BD	BI	CR	FD	GA	GI	HE	HT	MI	NC	PO	TD
<i>Liophis miliaris</i>	At	xen	d/n	t	0	0	3	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Liophis poecilogyrus</i>	At	xen	d/n	t	0	1	3	0	1	0	1	0	0	0	0	0	1	0	0	0
<i>Liophis reginae</i>	Am	xen	d	t	1	0	3	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Liophis schotti</i>	At	xen	d/n	t	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Liophis typhlus</i> (Atlantic)	At	xen	d	t	1	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Liophis typhlus</i> (Manaus)	Am	xen	d	t	1	0	4	0	1	1	1	0	0	0	0	0	0	0	1	0
<i>Mastigodryas</i> <i>bifossatus</i>	At	col	d	t	0	0	5	0	0	0	1	1	1	0	1	0	0	1	0	0
<i>Mastigodryas</i> <i>boddaerti</i>	Am	col	d	a	0	0	3	0	0	0	1	0	0	0	1	0	0	1	0	0
<i>Oxybelis aeneus</i>	Am/At	col	d	a	0	0	5	0	0	0	1	1	1	0	1	0	0	1	0	0
<i>Oxybelis fulgidus</i>	Am	col	d	a	1	0	5	0	0	0	1	1	0	0	1	1	0	1	0	0
<i>Oxyrhopus clathratus</i>	At	xen	n	t	0	1	2	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>Oxyrhopus formosus</i>	Am	xen	n	t	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Oxyrhopus</i> <i>melanogenys</i>	Am	xen	n	t	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Oxyrhopus petola</i>	At	xen	n	t	0	1	2	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>Philodryas aestivus</i>	At	xen	d	a	1	0	3	0	0	0	1	0	0	0	1	0	0	1	0	0
<i>Philodryas olfersii</i>	At	xen	d	a	1	0	5	0	0	0	1	1	1	0	1	0	0	1	0	0
<i>Philodryas</i> <i>patagoniensis</i>	At	xen	d	t	0	0	5	0	1	0	1	0	0	0	1	1	0	1	0	0
<i>Philodryas</i> <i>viridissimus</i>	Am	xen	d	a	1	0	6	0	0	0	1	1	1	0	1	1	0	1	0	0
<i>Pseudoboa haasi</i>	At	xen	n	t	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pseudoboa neuwiedi</i>	Am	xen	n	t	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pseudoboa serrana</i>	At	xen	n	t	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pseustes poecilonotus</i>	Am	col	d	a	0	0	6	0	0	0	1	1	1	1	1	0	0	1	0	0
<i>Pseustes sulphureus</i>	Am/At	col	d	a	0	0	6	0	0	1	1	1	0	1	1	0	0	1	0	0
<i>Sibynomorphus</i> <i>neuwiedii</i>	At	dip	n	a	0	0	6	0	0	0	1	0	0	0	1	1	1	1	1	0
<i>Siphlophis cervinus</i>	Am	xen	n	a	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Siphlophis compressus</i>	Am/At	xen	n	a	0	1	4	0	0	0	0	0	0	0	1	1	1	1	0	0
<i>Siphlophis</i> <i>longicaudatus</i>	At	xen	n	a	0	0	4	0	0	0	1	0	0	0	1	0	1	1	0	0
<i>Siphlophis pulcher</i>	At	xen	n	a	0	1	4	1	0	0	0	0	0	0	1	0	1	1	0	0
<i>Spilotes pullatus</i>	Am/At	col	d	a	0	1	5	0	0	1	0	1	0	1	1	0	0	1	0	0
<i>Taeniophallus</i> <i>breviceps</i>	Am	xen	d	t	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Taeniophallus nicagus</i>	Am	xen	d	t	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Tantilla</i> <i>melanocephala</i>	Am	col	d	t	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Thamnodynastes</i> <i>hypoconia</i>	At	xen	n	t	0	0	6	0	1	0	1	0	0	0	1	1	1	1	0	0
<i>Thamnodynastes</i> <i>longicaudus</i>	At	xen	n	a	0	0	3	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Thamnodynastes</i> <i>strigatus</i>	At	xen	n	t	0	0	6	0	1	0	1	0	0	0	1	1	1	1	0	0
<i>Thamnodynastes</i> sp.	At	xen	n	t	0	0	6	0	1	0	1	0	0	0	1	1	1	1	0	0
<i>Tomodon dorsatus</i>	At	xen	d	t	0	0	11	1	1	1	1	1	1	0	1	1	1	1	1	0
<i>Tropidodryas serra</i>	At	xen	d	a	0	0	5	0	0	0	1	1	0	0	1	0	1	1	0	0
<i>Tropidodryas</i> <i>striaticiceps</i>	At	xen	d	a	0	0	5	0	0	0	1	1	0	0	1	0	1	1	0	0
<i>Uromacerina</i> <i>ricardinii</i>	At	xen	d	a	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0
<i>Xenodon neuwiedi</i>	At	xen	d	t	0	0	7	0	1	0	1	0	0	0	1	1	1	1	1	0
<i>Xenodon</i> <i>rhabdocephalus</i>	Am	xen	d	t	0	0	4	0	1	0	0	0	0	0	1	1	1	1	0	0
<i>Xenopholis scalaris</i>	Am/At	dip	n	t	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Xenoxybelis argenteus</i>	Am	xen	d	a	0	0	2	0	0	0	1	0	0	0	0	0	0	1	0	0

frequency of specific defensive tactics (e.g., crypsis), we used only species.

Only defensive tactics supposedly directed at visually oriented predators ($n = 13$) are considered here. Definitions of defensive tactics follow Greene (1988a; see also Martins and Oliveira, 1998). We consider that a species has a brightly contrasting color pattern when it bears contrasting combinations of red, orange, yellow, white, and/or black, anywhere on its body. We follow Endler (1986) in considering as cryptic a color pattern that resembles a random sample of the background. Besides being considered as cryptic, patterns with conspicuous brown or gray blotches or other marks on a lighter ground (e.g., those of *Leptodeira annulata* and *Xenodon rhabdocephalus*) were also considered as mimic of sympatric pitvipers, since there are evidences that viper color patterns may be aposematic (e.g., Wüster *et al.*, 2004; Niskanen and Mappes, 2005; see also similar results in Andrén and Nilson, 1981). Furthermore, even patterns that vaguely resemble dangerous models may be avoided by predators (Endler and Mappes, 2004). Juvenile *Chironius scurrulus* is considered a mimic of *Philodryas viridissimus*, and juvenile *C. laevicollis* is considered a mimic of *P. aestivus* and *P. olfersii* (see Martins and Oliveira, 1998; Marques and Sazima, 2003). A single species was included in more than one category in the following cases: (1) it shows ontogenetic shifts from one category to the other (e.g., contrasting pattern to crypsis in *Clelia clelia*; mimicry to crypsis in *Chironius scurrulus* and *C. laevicollis*); or (2) different parts of the body fall in different categories (e.g., a cryptic dorsum and a brightly contrasting venter in *Liophis breviceps*; dorsum brightly contrasting anteriorly in *Drepanoides anomalus*). In the analyses involving time of activity, species for which no defined time of activity occurs (e.g., *Atractus* spp., see Martins and Oliveira, 1998) or those for which this character is unknown were excluded.

To compare the number of visual defensive tactics found in ecological categories (terrestrial, arboreal, diurnal, nocturnal) we used Mann-Whitney *U*-tests. The number of visual defensive tactics was compared among colubrid main clades (colubrines, dipsadines, and xenodontines; see, e.g., Zaher, 1999, Vidal *et al.*, 2000) with a Kruskal-Wallis analysis of variance. To compare the frequency of particular visual defensive tactics between ecological groups, we performed chi-square tests. The effect of phylogeny and ecology (microhabitat use and time of activity) in the occurrence of visual defensive tactics was explored through a cluster analysis using percent disagreement

as the distance measure and complete linkage as the amalgamation rule. All analyses were performed with Statistica (StatSoft, 2003). Results were considered significant when $p < 0.05$ and marginally non-significant when $0.05 < p < 0.10$.

RESULTS

Terrestrial and arboreal colubrids comprised 64.1% and 35.9%, respectively, of our sample of 92 species from Central Amazonia and the Atlantic Forest (Table 1). Arboreal colubrids displayed significantly more defensive tactics directed to visually oriented predators than the terrestrial ones (medians 5.0 and 2.0, ranges 1-6 and 1-11, respectively; $z = 4.55$, $p < 0.001$; Table 1); the same trend was recorded for arboreal genera in relation to terrestrial ones, although marginally non-significant (medians 5.0 and 3.0, ranges 1-7 and 1-11 respectively; $z = 1.73$, $p = 0.079$). Regarding time of activity, diurnal and nocturnal colubrids comprised 64.1% and 35.9%, respectively, of our sample of 92 species from Central Amazonia and the Atlantic Forest. The number of visual defensive tactics was not significantly different between diurnal and nocturnal species (medians 5.0 and 4.0 ranges 1-11 and 1-6, respectively; $z = 0.83$, $p = 0.405$) or genera (medians 4.5 and 3.5 ranges 1-11 and 1-6, respectively; $z = 1.68$, $p = 0.092$).

The frequency of five defensive tactics supposedly directed to visually oriented predators (frontal display, gaping, gular inflation, head elevation, and neck S-coil) was significantly higher in arboreal species than in the terrestrial ones; additionally, head triangulation was also higher in arboreal species than in the terrestrial ones, although the result was marginally non-significant (Table 2). On the other hand, the frequency of body depression was significantly higher in terrestrial species; the frequency of polymorphism was also higher in terrestrial species, but the result was marginally non-significant (Table 2). Contrasting color patterns were more frequent in terrestrial species than in the arboreal ones, but the result was marginally non-significant (Table 2). Regarding time of activity, the frequency of frontal display, gaping and gular inflation was significantly higher in diurnal species than in nocturnal ones, whereas the frequency of mimicry was significantly higher in the latter (Table 2). The frequency of head triangulation was also higher in nocturnal species, but the result was marginally non-significant (Table 2). Green was significantly more frequent in diurnal species, whereas

TABLE 2. Occurrence of defensive tactics supposedly directed to visually oriented predators and of green and brightly contrasting color patterns in forest colubrids from Central Amazonia (original data from Martins and Oliveira, 1998) and the Atlantic Forest (original data from Marques *et al.* 2004 and unpublished). Number of species in each category in brackets. Only tactics that occurred in more than five species are included. Abbreviations are: n = number of species that display a given defensive tactic; p = significance level of Fisher exact test. Significant results ($p < 0.050$) are indicated in boldface and marginally non-significant results ($0.050 < p < 0.100$) in italics.

	Terrestrials (59)		Arboreals (33)		p	Diurnals (44)		Nocturnals (30)		
	n	%	n	%		n	%	n	%	p
Body depression	30	50.8	1	3.0	<0.001	15	34.1	5	16.7	0.155
Crypsis	46	78.0	28	84.8	0.460	40	90.9	17	56.7	0.139
Frontal display	3	5.1	15	45.5	<0.001	17	38.6	1	3.3	0.003
Gaping	3	5.1	9	27.3	0.011	12	27.3	0	0.0	0.004
Gular inflation	1	1.7	8	24.2	0.003	9	20.5	0	0.0	0.013
Head elevation	16	27.1	30	90.9	0.001	29	65.9	16	53.3	0.365
Head triangulation	8	13.6	11	33.3	<i>0.064</i>	7	15.9	12	40.0	<i>0.066</i>
Mimicry	27	45.8	15	45.5	0.573	10	22.7	26	86.7	0.002
Neck S-coil	10	16.9	29	87.9	<0.001	25	56.8	14	46.7	0.392
Polymorphism	10	16.9	1	3.0	<i>0.067</i>	4	9.1	3	10.0	0.602
Green color	7	11.9	9	27.3	0.104	16	36.4	0	0.0	<0.001
Contrasting colors	18	30.5	4	12.1	<i>0.087</i>	4	9.1	13	43.3	0.007

contrasting color patterns were more frequent in nocturnal species (Table 2).

Snake lineages differed significantly in the number of visual defensive tactics displayed (colubrids, median 5, range 1-7, $n = 17$; dipsadines, median 4, range 1-6 $n = 21$; xenodontines, median 2, range 1-11, $n = 54$; $H_{[2,92]} = 15.78$, $p < 0.001$). Post-hoc tests indicated that all pairs of clades differed significantly, except for the pair colubrids-dipsadines.

Among dipsadines, arboreal species displayed significantly more defensive tactics than terrestrial ones (medians 5.0 and 2.0, ranges 4-6 and 1-4, respectively, $z = 3.55$, $p < 0.001$). In xenodontines, arboreal species also displayed more defensive tactics than terrestrial, although the result was marginally non-significant (medians 4.0 and 2.0, ranges 1-6 and 1-11, respectively; $z = 1.66$, $p = 0.097$). Among colubrids, the frequency of visual defensive displays was not significantly different between arboreal and terrestrial species (medians 6.0 and 3.0, ranges 3-6 and 1-7, respectively, $z = 1.46$, $p = 0.140$). With regard to time of activity, there was no difference in number of visual defensive tactics between diurnal and nocturnal xenodontines (medians 2 and 2, ranges 1-9 and 1-5, respectively; $z = 1.56$, $p = 0.118$); sample size precluded the analysis for colubrids (no nocturnal species) and dipsadines (no exclusively diurnal species).

The cluster analysis based on the occurrence of visual defenses ($n = 13$) resulted mostly in heterogeneous groups of genera regarding phylogenetic position (clade), preferred microhabitat, and time of activity (Fig. 1).

DISCUSSION

Our results strongly indicate that arboreal colubrids are more “visually defensive” than the terrestrial ones in Neotropical rainforests. This result strengthens Lillywhite and Henderson’s (1993) hypothesis that arboreal species are more exposed to visually oriented predators than terrestrial ones. Furthermore, there seems to be a suite of visual defenses typical of arboreal snakes in the Neotropics, which includes frontal display, gaping, gular inflation, head elevation, neck S-coil, and, apparently, head triangulation. All these behaviors are apparently associated with threatening displays. Crypsis seems to be an important visual defense for both arboreal and terrestrial colubrids (see discussion below). A green pattern seems also to be more frequent in arboreal species. On the other hand, dorsoventral body depression is typical of terrestrial species, as predicted by Greene (1979), and our results indicate that polymorphism and contrasting colors may also be prevalent in terrestrial species. Some peculiarities of the arboreal microhabitat, such as the prevalence of a green background, a likely higher exposition to predators (Lillywhite and Henderson, 1993; this study), and the diversity of directions from which a predator can approach (in contrast to almost always from above in terrestrial species; see Senter, 1999), may have led to the evolution of the peculiar visual defensive tactics in arboreal species.

With regard to time of activity, frontal display, gaping and gular inflation were more frequent in diurnal species and the same result was found for green color. On the other hand, mimicry and contrasting

colors (the latter perhaps a consequence of the former in many species) were more frequent in nocturnal snakes. Furthermore, head triangulation seems to be prevalent in nocturnal species. These results support our hypothesis that diurnal snakes are more visually defensive than nocturnal ones.

Part of the trends we found indicates that our results may be strongly influenced by phylogeny. For instance, the prevalence of gular display in arboreals and diurnals may be a consequence of the fact that this tactic is typical of colubrids, which are all diurnal and generally arboreal. The prevalence of mimicry in nocturnals (a seemingly contradictory result) may be due to the fact that dipsadines and pseudoboines are almost all nocturnal species and many of them are putative mimics of pitvipers and coral snakes, respectively (e.g., Campbell and Lamar, 2004; Greene

and McDiarmid, 2005). At the family level, Martins (1996) suggests that defensive tactics seem to correlate better with phylogeny than at lower taxonomic levels (Martins, 1996: Fig. 1), based on an analysis of the occurrence of 33 defensive tactics in the same central Amazonian assemblage dealt with here. On the other hand, shared potential predators may have led to convergent defense types (Martins, 1996) such as dorsoventral body depression, which occur both in dipsadines (*Atractus* and *Xenopholis*) and xenodontines (*Erythrolamprus*, *Liophis*, and *Xenodon*). Thus, as also indicated by our cluster analyses, both phylogeny and ecology seem to affect the way Neotropical snakes defend themselves from predators. In any case, defense seems to be less conservative than other aspects of the ecology of Neotropical snakes (e.g., feeding habits, habitat use, and reproduction;

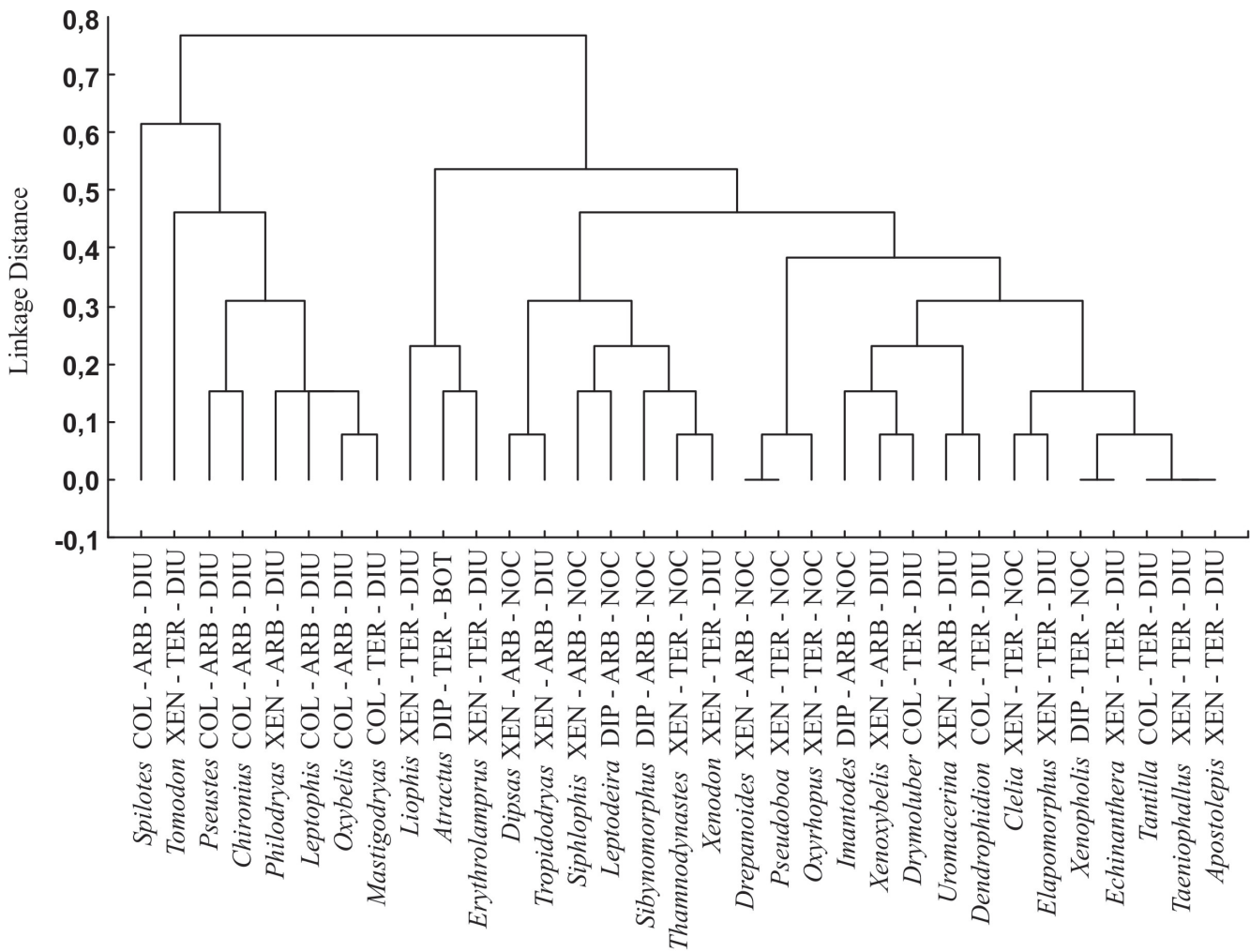


FIGURE 1. Cluster analysis (percent disagreement, complete linkage) of defensive tactics directed to visually oriented predators in colubrid genera from Central Amazonia and the Serra do Mar range in the Atlantic Forest, using presence/absence data from Table 1. ARB = arboreal; BOT = both diurnal and nocturnal; COL = colubrine; DIP = dipsadine; DIU = diurnal; NOC = nocturnal; TER = terrestrial; XEN = xenodontine.

see Martins and Oliveira, 1998; Martins *et al.*, 2002; Marques *et al.*, 2004), which indicates that predation is an important selective agent in the life history of these snakes.

Alternatively to being more exposed to visually oriented predators, arboreals and diurnals may be more defensive simply because they face a wider suite of predators than terrestrials and nocturnals. As pointed out by Lillywhite and Henderson (1993), it is unknown whether the intensity of aerial, avian predation pressure is higher in the arboreal microhabitat than on the ground level. The same holds true for the intensity of predation during daytime and at night. Greene (1988a) suggests that birds and mammals are the main predators of reptiles in Neotropical forests, calling attention to the occurrence of numerous birds of prey that potentially prey on snakes in these forests (see also Braker and Greene, 1994; DuVal *et al.*, 2006; Greene, 1988b; Sazima, 1992; Lillywhite and Henderson, 1993; Martins, 1996). Experiments on predation on coral snakes using plasticine models also indicate that birds are by far the most important predators of snakes in the Neotropics (e.g., Brodie, 1993; Brodie and Janzen, 1995). In Central Amazonia, for instance, there are several birds of prey that prey occasionally or frequently on snakes (e.g., *Buteo*, *Falco*, *Harpyhaliaetus*, *Herpetotheres*, *Leucopternis*, *Micrastur*, *Spizaretus*; Karr *et al.*, 1990), and many of them capture prey both on the ground and on the vegetation (Sick, 1984); the same holds true for carnivorous mammals (e.g., *Nasua*, *Eira*, *Leopardus*, *Panthera*, *Puma*, *Speothos*; Malcolm, 1990; Emmons, 1990). In the Atlantic Forest the same may apply, as the predators are mostly the same (our pers. obs.). In case predation pressure by visually oriented predators is higher on vegetation than on the ground, the differences in diversity of visual defensive tactics in arboreal and terrestrial snakes might be due to a higher exposition of arboreals, as suggested by Lillywhite and Henderson (1993). However, if predation pressure by visually oriented predators is similar on vegetation and on the ground, arboreal snakes might be more defensive simply because of the higher diversity of directions from which a predator would approach (cf. Senter, 1999).

Regarding time of activity, diurnal snakes might be more visually defensive than nocturnal ones due to the apparent prevalence of diurnal snake predators in the Neotropical forests (Braker and Greene, 1994; Greene, 1988b; Lillywhite and Henderson, 1993; Martins, 1996).

Lillywhite and Henderson (1993) suggest that the high incidence of crypsis and absence of brightly contrasting color patterns in arboreals support their hypothesis of higher exposition of snakes that dwell on vegetation. However, our results indicate that crypsis is not prevalent in arboreal species in Neotropical rainforests. Thus, crypsis seems to be as effective on the ground as on the vegetation. Finally, in our study, the frequency of contrasting color patterns was higher in terrestrials than in arboreals (as predicted by Lillywhite and Henderson, 1993), as well as higher in nocturnals than in diurnals. Although the latter result is apparently contradictory, both results show a strong phylogenetic effect: most species with contrasting colors in our sample are xenodontines of the tribe Pseudoboini (*Clelia*, *Drepanoides*, *Oxyrhopus*, *Pseudoboa* and *Siphlophis*), most of them terrestrial and all of them nocturnal.

This study and that of Martins (1996) indicate that by associating ecological and phylogenetic information it is possible to predict with a rather high degree of confidence the set of defensive tactics a snake would display, provided one knows its ecology and phylogenetic position (see also Greene, 1988a; Martins and Oliveira, 1998). By the same token, it seems possible to predict the ecology and the phylogenetic relations of a snake knowing the defensive tactics it displays. Additional studies would show whether the results herein reflect real trends for snakes in general, and help understand some of the factors involved in the evolution of defensive strategies in snakes.

RESUMO

Estudos anteriores indicam que (1) as exibições defensivas das serpentes estão associadas com o modo de uso do hábitat, (2) as defesas visuais estão mais correlacionadas com o hábitat do que com a filogenia e (3) serpentes arborícolas estão mais expostas a predadores do que serpentes terrestres. Examinamos aqui a hipótese de que padrões semelhantes devem existir para serpentes diurnas em relação às noturnas e testamos essas hipóteses por meio da ocorrência de 13 táticas defensivas dirigidas a predadores visuais em duas taxocenoses de colubrídeos neotropicais, uma na Amazônia central (26 gêneros, 41 espécies) e outra na Mata Atlântica (23 gêneros, 62 espécies). Espécies e gêneros arborícolas exibiram um maior número de defesas visuais do que os terrestres. Exibição frontal, abertura da boca, inflação da região gular, elevação da cabeça, curvatura sigmóide da parte ante-

rior e, aparentemente, triangulação da cabeça tenderam a ser mais freqüentes em espécies arborícolas, ao passo que depressão dorso-ventral e, aparentemente, polimorfismo foram mais freqüentes em espécies terrestres. Peculiaridades do microhabitat arbóreo, como a prevalência de fundo (substrato) verde, a provável maior exposição a predadores visuais e a diversidade de direções pelas quais um predador pode se aproximar podem ter influenciado a evolução de táticas defensivas peculiares em serpentes arborícolas. Com relação ao horário de atividade, o número de táticas defensivas visuais utilizadas por serpentes diurnas e noturnas não foi diferente. Entretanto, exibição frontal, abertura da boca, inflação da região gular e camuflagem foram prevalentes em espécies diurnas, ao passo que o mimetismo e, aparentemente, a triangulação da cabeça foram mais freqüentes em espécies noturnas. Além disso, a cor verde foi mais frequente em formas diurnas e os padrões contrastantes foram mais freqüentes nas espécies noturnas. A análise de agrupamento baseada na ocorrência de táticas defensivas visuais resultou principalmente em grupos heterogêneos de gêneros com relação à posição filogenética, microhabitat preferencial e horário de atividade. Em geral, nossas análises indicam que a forma como as serpentes neotropicais se defendem de seus predadores é o resultado de uma complexa interação entre fatores ecológicos e limitações filogenéticas.

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