ECOLOGICAL AND PHYLOGENETIC CORRELATES OF FEEDING HABITS IN NEOTROPICAL PITVIPERS OF THE GENUS *BOTHROPS*

Marcio Martins[1], Otavio A. V. Marques[2], and Ivan Sazima[3]

Abstract: The Neotropical pitviper genus *Bothrops* (lanceheads) occurs from Mexico to Argentina. Data on feeding habits of 22 species indicate that most are (1) diet generalists, and (2) show ontogenetic diet shifts (both characters plesiomorphic). Four species (three of them closely related), however, are mammal specialists, adults from one island species feed heavily on birds, and another island species is a specialist on ectothermic prey. Mammal specialization may be related to life history strategies, whereas the diet shifts observed in the two island species are a consequence of prey availability (there are no small, non-volant mammals on the islands). Ontogenetic diet shifts that may be a consequence of growth were lost in some diet generalists, especially the small forms. Species of *Bothrops* that have a generalist diet incorporate endotherms at a narrow range of sizes and eliminate ectotherms at variable ones. Longer and more slender species eliminate ectotherms from their diets later in ontogeny than shorter, stout species. Caudal luring (also plesiomorphic) is documented in seven species and may occur in juveniles of all diet generalists. Feeding frequency is relatively low in *Bothrops*, perhaps due to sedentary habits and other factors related to living in warmer climates. Mean relative prey size is moderate in *Bothrops*, but very large prey is occasionally eaten. Mammal specialists are stouter and feed on larger prey than generalists, and relative prey size decreases during ontogeny in some species of *Bothrops*. Sit-and-wait foraging is the main tactic in *Bothrops*, as in other viperids. A high diversity of microhabitat use occurs in *Bothrops* and highly arboreal species feed more frequently on anurans. The lancehead species of *Bothrops* occur in several types of forests and open habitats, and their diets seem to reflect local prey availability. Allometry seems to be an important factor in the feeding habits of lanceheads. Although apomorphies appeared in some taxa, in general feeding habits in *Bothrops* are conservative, as most characters we analysed were present in outgroup taxa. Our results indicate that early lanceheads were probably stout, terrestrial forest dwellers that fed on a variety of prey (juveniles fed mostly on ectotherms that they lured with pale tail tips, whereas adults preyed mostly on mammals). The generalist diet of early *Bothrops* may have facilitated some of the ecological shifts described here and the great diversification that occurred in the genus in South America.

Introduction

The Neotropical pitviper genus *Bothrops* (including *Bothriopsis*; see below) is a recent, apparently monophyletic assemblage of about 40 species (ca. 25% of the Crotalinae), occurring from Mexico to Argentina (Hoge and Romano, 1973; Hoge and Romano-Hoge, 1981a, b; Rage, 1987; Campbell and Lamar, 1989; Greene, 1992; McDiarmid et al., 1999). Most species of *Bothrops* inhabit forests, but some are found exclusively in more open vegetation types (Campbell and Lamar, 1989). The genus comprises exclusively terrestrial species (e.g., *B. alternatus* and *B. neuwiedi*), as well as several that use vegetation, such as the semi-arboreal *B. jararaca* (Sazima, 1992) to the highly arboreal *B. bilineatus* (Duellman, 1978; Dixon and Soini, 1986). An ontogenetic shift in microhabitat use occurs in some semi-arboreal species, with juveniles found more frequently on vegetation than adults (Sazima, 1992; Campbell, 1998; Martins and Oliveira, 1999). Published data on feeding habits of *Bothrops* (e.g., Amaral, 1921; Beebe, 1946; Neill, 1960; Greene and Campbell, 1972; Cunha and Nascimento, 1975, 1978, 1982, 1993; Picado, 1976; Duellman, 1978; Scott, 1983; Leloup, 1984; Dixon and Soini, 1986; Sazima, 1988, 1989, 1991, 1992; Martins and Gordo, 1993; Norman, 1994; Duarte et al., 1995; Egler et al., 1996; Campbell, 1998; Martins and Oliveira, 1999) indicate that most species are diet generalists, at least some show an ontogenetic diet shift (i.e., from ectothermic to endothermic prey), and most ambush prey from a coiled posture (but see Sazima, 1992; Egler et al., 1996). Caudal luring was described in four species of *Bothrops* (e.g., Neill, 1960; Greene and Campbell, 1972; Sazima, 1991) and was suggested for several others (Greene, 1992; Sazima, 1992).

Greene (1992) discussed that the natural history of *Bothrops* might be relatively homogeneous when compared to other crotalines such as *Trimeresurus*. The present scarcity of behavioral and ecological information (see references above), however, makes further generalization impossible. Several interesting questions may be addressed in comparative studies on monophyletic assemblages of snakes. Greene (1992) outlined the steps needed to reconstruct past phenotypes and adaptive scenarios. Steps of interest here are: (1) survey behavior and ecology across taxa, map characters onto a phylogenetic tree, and infer historical

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[1] Departamento de Ecologia, Instituto de Biociências, C. P. 11461, Universidade de São Paulo, 05422-970 São Paulo SP, Brazil
E-mail: jararaca@ibs.usp.br

[2] Laboratório de Herpetologia, Instituto Butantan, 05503-900 São Paulo SP, Brazil

[3] Departamento de Zoologia and Museu de História Natural, Instituto de Biologia, C. P. 6109, Universidade Estadual de Campinas, 13083-970 Campinas SP, Brazil.

changes; and (2) make comparisons to discover concordances of shifts in morphology, behavior, and ecology (see also Brooks and McLennan, 1991). Despite the existence of several phylogenetic hypotheses for diverse groups of snakes (e.g., several chapters in Campbell and Brodie, 1992), such comparative methods have rarely been undertaken for snakes (but see Greene and Burghardt, 1978; Greene, 1992; Shine, 1994; Schuett et al., 2001, this volume; Greene et al., this volume).

During the last few years we gathered natural history data on several species of *Bothrops*, mostly from Brazil, in an attempt to uncover patterns and processes involved in the evolution of morphological, ecological, and behavioral traits in this diverse genus. Here we describe the diversity of feeding habits in *Bothrops* and attempt to answer the following questions, using a phylogenetic hypothesis based on recent systematic studies (see below). (1) How diverse are feeding habits in *Bothrops*? (2) Is feeding biology related to body size and form? (3) Is feeding biology related to habitat and microhabitat? (4) How did feeding biology evolve in *Bothrops*? (5) How does the feeding biology of *Bothrops* differ from other pitvipers? (6) What are the reconstructed feeding habits of the ancestor of *Bothrops*?

Taxonomy and Systematics of *Bothrops*

Recently, the taxonomy of bothropoid snakes has undergone extensive revision (Campbell and Lamar, 1989; McDiarmid et al., 1999), mainly as a result of systematic studies (see below). After splitting of the genus *Bothrops* (*sensu lato*; e.g., Hoge and Romano, 1973; Hoge and Romano-Hoge, 1981a, b) into several genera (*Atropoides*, *Bothriechis*, *Bothriopsis*, *Cerrophidion*, *Ophryacus*, and *Porthidium*; see, Campbell and Lamar, 1989, 1992; McDiarmid et al., 1999), the genus now comprises about 40 species and includes those previously allocated to *Bothriopsis* (e.g., Gutberlet, 1998; Parkinson, 1999; Salomão et al., 1997, 1999; Vidal et al., 1999; but see McDiarmid et al., 1999). Some species of *Bothrops*, like most of those related to *B. atrox*, are probably conspecific (see Wüster et al., 1997, 1999), but several forms in the *B. neuwiedi* complex are, indeed, good species (Silva, 2000; Wüster et al., this volume). Thus, the taxonomy (and number of species) of *Bothrops* will change.

Recent systematic studies (Cadle, 1992; Gutberlet, 1998; Salomão et al., 1997, 1999; Werman, 1992; Wüster et al., 1996, 1997, 1999, this volume; Parkinson et al., this volume; H. Ferrarezzi, pers. comm.) indicate that species of *Bothrops* may compose at least seven primary clades (with the species treated herein in parentheses): the *alternatus* group (*B. alternatus*, *B. ammodytoides*, *B. cotiara*, *B. fonsecai*, and *B. itapetiningae*), the *atrox* group (*B. asper*, *B. atrox*, *B. leucurus*, *B. moojeni*), the *jararaca* group (*B. alcatraz*, *B. insularis*, and *B. jararaca*), the *jararacussu* group (*B. brazili* and *B. jararacussu*), the *microphthalmus* group (*Bothrops hyoprorus*), the *neuwiedi* group (*B. erythromelas*, *B. mattogrossensis*, *B. neuwiedi*, *B. pauloensis,* and *B. pubescens*), and the *taeniatus* group (*B. bilineatus* and *B. taeniatus*).

When the above mentioned systematic studies are considered jointly, it is possible to assess the relationships among the clades: (1) the *atrox* and *jararacussu* groups apparently form a monophyletic clade (Cadle, 1992; Werman, 1992; Wüster et al., 1997, this volume; Parkinson et al., this volume;), with the *taeniatus* group as sister to that clade (Werman, 1992; Kraus et al., 1996; Salomão et. al., 1997; C. Parkinson, pers. comm.; but see Gutberlet, 1998, Salomão et. al., 1999); (2) the *jararaca* and *neuwiedi* groups form a clade that is sister to the *atrox*-*jararacussu*-*taeniatus* clade (Parkinson et al., this volume; Wüster et al., this volume; but see below); (3) the *alternatus* group is sister to the clade formed by all groups above (Werman, 1992; Salomão et. al., 1997, 1999; Wüster et al., this volume; Parkinson et al., this volume; H. Ferrarezzi, pers. comm.); and the *microphthalmus* group is basal in the phylogeny of *Bothrops* (Gutberlet, 1998; Parkinson et al., this volume; Wüster et al., this volume). The relationship between the *jararaca* and *neuwiedi* groups remains controversial because morphological data indicate that the *neuwiedi* group is more closely related to the *alternatus* than to the *jararaca* group (Werman, 1992; H. Ferrarezzi, pers. comm.). Two recent systematic studies using DNA data (Parkinson et al., this volume; Wüster et al., this volume) indicate, however, that the *jararaca* and *neuwiedi* groups form a distinct clade. Also, the relationships within each species group of *Bothrops* are controversial. In our analysis, we adopt the resolution of Wüster et al. (this volume), except for the *neuwiedi* group, for which we follow Silva (2000). Nevertheless, eventual changes in the position of species within groups, as well as of the *jararaca* and *neuwiedi* groups within *Bothrops*, are unlikely to substantially change the results and ideas we present. Some of the relationships among genera of crotalines are controversial (see Kraus et al., 1996; Vidal et al., 1999; Werman, 1999), but comprehensive studies on the systematics of crotalines (Gutberlet, 1998a, b, Gutberlet and Harvey, this volume; Parkinson, 1999; Parkinson et al., this volume; see also Werman, 1992) indicate that the clade composed by *Atropoides*, *Cerrophidion* and *Porthidium* is sister to *Bothrops*.

Species identifications used here follow Campbell and Lamar (1989), except that we treat the population earlier assigned to *B. pradoi* as *B. leucurus* (see Wüster et al., 1997, 1999) and former subspecies of the *B. neuwiedi* complex as full species (*B. mattogrossensis*, *B. neuwiedi*, *B. pauloensis*, and *B. pubescens*; Silva, 2000). An newly described species (*B. alcatraz*) from Alcatrazes Island, southeastern Brazil, is also treated herein (see Marques et al., 2002).

METHODS

Dietary Data

The diet of 22 species of *Bothrops* was analyzed by examining the digestive tracts (DT) of approx. 3,000 preserved specimens, most of them in museum collections, but also of specimens obtained during fieldwork, resulting in a total of 1,055 prey or prey remains. Geographical data on the specimens examined are in Appendix I. Except for animals that were maintained in captivity for long periods after being collected in the field (over a week, for instance), in most collections the DT of every specimen was examined, regardless of evident stomach contents. In the case of *B. insularis*, prey was detected by palpation of live animals in the field. The DT of preserved specimens was examined through a series of short incisions. Each prey or its remains (e.g., hair, feathers, scales) was recorded, as well as insect remains (presumed prey contents). When only insect remains were found in the hindgut of diet generalists, we inferred that the prey was a frog (Martins and Gordo, 1993) because hair, feathers, and squamate scales are evident when present in the hindgut. No insects were found in the foregut of any *Bothrops*. Where possible, each intact prey item (or a reference specimen of comparable size; see Greene, 1989) was measured to the nearest 1.0 mm and weighed to the nearest 0.1 g with spring scales. We are aware that the proportion of different prey in the diets of those species that show ontogenetic shifts in prey type varies with varying ratios of juveniles to adults sampled. Unless stated otherwise, however, our samples have similar proportions of adults and juveniles. Museum specimens that contained prey were dried with blotting paper, weighed to the nearest 1.0 g with spring scales, and measured to the nearest 1.0 mm with a flexible rule. Length measurements were snout-to-vent (SVL), tail (TL), and head length (HL).

We determined that a species is a diet specialist when a single prey type accounts for over 75% of all prey found. For diet generalists, we determined that a species showed an ontogenetic diet shift when the size of individuals that consumed endothermic prey was significantly larger than those that consumed ectotherms (Mann-Whitney test; see Rodriguez-Robles et al., 1999). To assess the importance of body size, head length, and stoutness in determining the size at which endotherms were incorporated and ectotherms were excluded from the diet of generalists, we ran correlation analyses on these variables. Feeding frequency (percent of individuals with stomach contents) was estimated for snake species represented by large, unbiased samples (those that did not include specimens kept in captivity). Observations on habitat, microhabitat, and foraging behavior of almost all species were made in the field in several localities in Brazil.

Snake Size and Morphology

For morphological analyses, we measured (SVL, TL, and HL) and obtained the mass of 28–35 individuals of each species except *B. ammodytoides* and *B. asper*. For *Bothrops alcatraz*, only 24 specimens were measured. All samples included similar numbers of males and females and the whole size range of each species, from newborns to full-grown adults, except for *Bothrops alcatraz*, for which no juveniles were available. In analyses using juvenile and adult size, we used the mean of the 10 lower and 10 higher values of these samples, respectively. To compensate for differences in body size (see Forsman, 1991), in analyses using snake mass and head length we used the residuals of simple regressions between these variables and SVL and trunk length (= SVL minus HL), respectively, including data for all species treated in each analysis. All variables were common log transformed. The means of these residuals are treated here as relative tail length and relative stoutness, respectively.

Prey-size/Snake-size Relationships

For each well preserved prey or a reference specimen of comparable size we calculated ingestion ratio (IR = prey width/snake head length) and mass ratio (MR = prey mass/snake mass; see Greene, 1983; Pough and Groves, 1983). We determined that a species showed ontogenetic shift in relative prey size when the slope of the regression line between prey

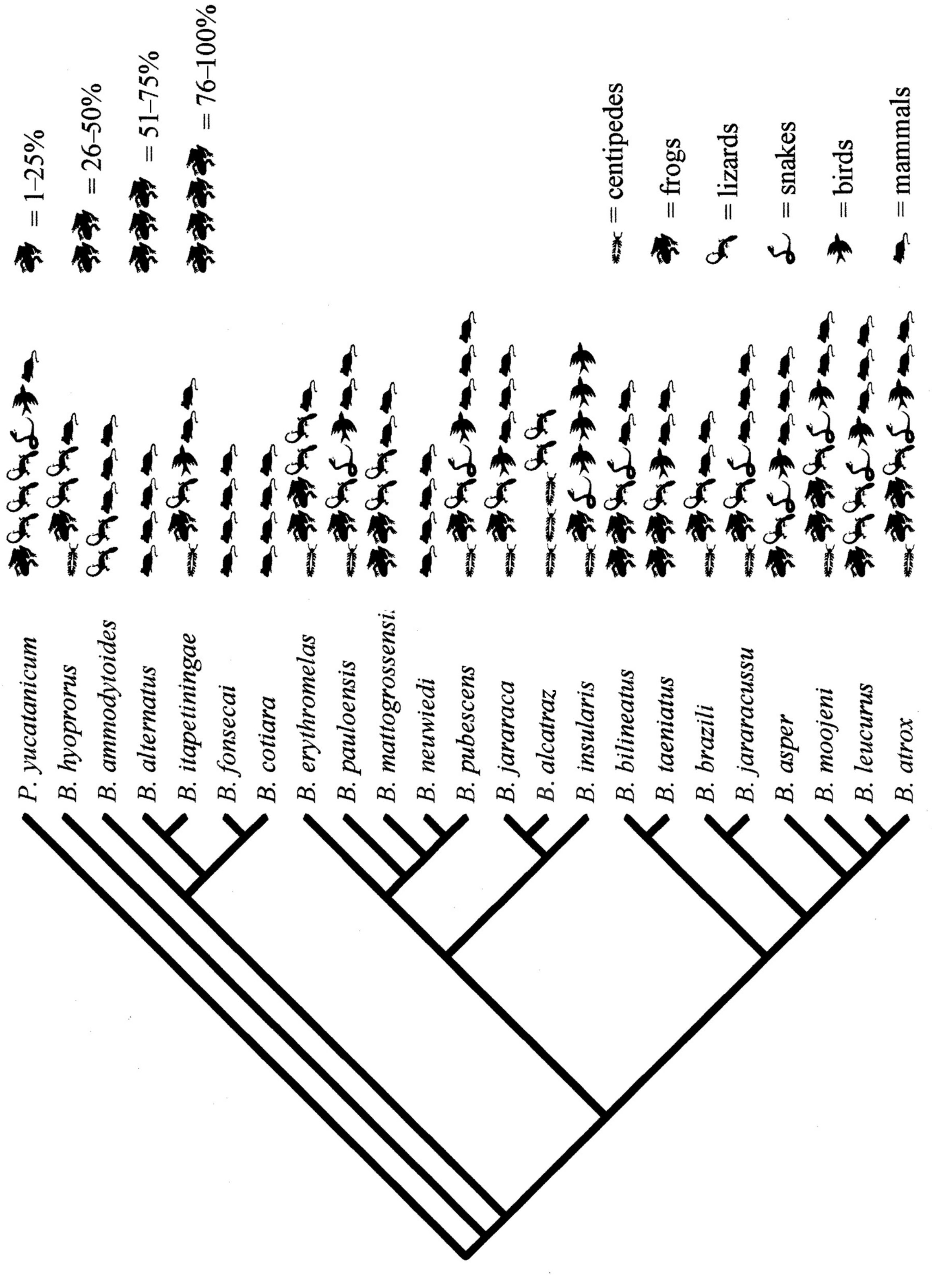

Fig. 1. Summary of diet composition in *Bothrops*, mapped onto a phylogenetic hypothesis of the species discussed (see Taxonomy and Systematics of *Bothrops*). Note that: (1) mammals, frogs, and lizards are the main prey types in most species of *Bothrops*, (2) tremendous variation in diet composition occurs within *Bothrops*, (3) mammal specialization is a synapomorphy of a subclade of the *alternatus* group and of *B. neuwiedi*, and (4) distinct diets are apomorphies of both island species.

size (width and mass separately) and snake size (SVL) was significantly different from one. To compare relative prey size (IR and MR) among snake species, we used Kruskal-Wallis median tests and post-hoc tests to detect differences between pairs of species. To compare prey mass and width among the three most common prey types consumed by *Bothrops* (mammals, frogs, and lizards), we used the residuals of simple regressions between these variables and prey length (body length in mammals and SVL in frogs and lizards), including data for all three prey types. All variables were common log transformed. Statistical analyses were performed using Statistica (StatSoft, 1998).

Character Reconstruction

Reconstruction of character states by linear parsimony analyses was accomplished using MacClade (Maddison and Maddison, 1992). The phylogeny used in our reconstructions was modified from Wüster et al. (this volume), by incorporating the outgroups (Gutberlet, 1998; Parkinson et al., this volume) and a different resolution within the *neuwiedi* group (Silva, 2000). Characters used in reconstructions were habitat (forests, open areas, gallery forests), microhabitat (terrestrial, semi-arboreal), and five characters related to feeding biology (character states in parentheses): (1) diet (generalist, mammal specialist, birds in adults, restricted to ectotherms); (2) ontogenetic shift in prey types (yes, no); (3) tail tip color in juveniles in relation to the remainder of the tail (different, same, or variable);(4) retention of modified tail tip in adults (yes, no); and (5) color of tail tip in relation to the remainder of the tail (paler, darker, same, or variable). In all analyses, a clade formed by *Porthidium nasutum* and *P. yucatanicum* was used as the outgroup. All characters were treated as unordered. Different results might appear in reconstructions based on alternative phylogenetic hypotheses (see Greene, 1992), but extensive exploration of our data with different phylogenies indicates that the general trends described below are generally insensitive to minor changes in tree topology, especially within-species groups.

RESULTS AND DISCUSSION

Dietary Variation

Detailed information on the feeding habits of *Bothrops* is available for very few species, mainly *B. asper* (e.g., Neill, 1960; Picado, 1976; Scott, 1983; Campbell, 1998), *B. atrox* (e.g., Beebe, 1946; Cunha and Nascimento, 1975, 1978, 1982, 1993; Duellman, 1978; Dixon and Soini, 1986; Martins and Gordo, 1993), and *B. jararaca* (Sazima, 1989, 1991, 1992). For some other species, only anecdotal information is available (e.g., *B. bilineatus*, Greene and Campbell, 1972; *B. insularis*, Duarte et al., 1995; *B. moojeni*, Leloup, 1984). Almost all species of *Bothrops* studied thus far are diet generalists, and feed primarily on mammals and ectotherms (frogs, lizards, and centipedes), although birds were also recorded for almost all species (see brief reviews in Greene, 1992; Sazima, 1992). Norman (1994) suggested that *B. alternatus* might feed primarily on mammals, whereas Yanosky et al. (1996) provided unconfirmed information that this species also feed on amphibians. Recently, a detailed account on the natural history of *B. neuwiedi pauloensis* (= *B. pauloensis*), including data on feeding habits, was provided by Valdujo et. al., 2002).

Data on the diet of 22 taxa of *Bothrops* are summarized in Figure 1 (percentages are in Appendix II). Almost all species of *Bothrops* treated herein are diet generalists (i. e., no prey type accounted for more than 75% of the diet), except for three species in the *alternatus* group and *B. neuwiedi* that are mammal specialists, and *B. insularis*, which is a bird specialist that inhabits an island where no non-volant mammals occur (M. Martins and O. Marques, unpublished). Considering the diet generalists, for which our sample sizes are moderate to large (over 10 prey; N = 14 species), small mammals are eaten by all, in proportions varying from 15–70% of the prey (Appendix II). Anurans and lizards are also important prey for diet generalists, occurring in all species in proportions varying from 8–50% and 6–33% of the diet, respectively. Birds, centipedes, and snakes are generally less important prey in generalists (< 10% of the prey found), although they occur in the diet of most species. Besides mammal specialists, and the bird specialist *B. insularis*, exceptions for this general pattern are *Bothrops alcatraz*, which seems to feed heavily on centipedes (nine of the 12 prey found), and *B. erythromelas* and *B. brazili*, whose juveniles feed on centipedes (23% and 18%, respectively, of the prey found). The absence of less important prey types (birds, centipedes, and snakes) in other species may be due to small sample sizes (this may be the case in most species for which our sample is lower than 30 prey). Besides the common prey types in Figure 1, some species of *Bothrops* may occasionally feed on odd prey, such as a freshwater eel found in *B. atrox* (M. Oliveira and M. Martins, unpublished) and lizard eggs in *B. pauloensis* (P. Valdujo, pers. comm.). Limited data on a few species of *Bothrops* indicate that geo-

Table 1. Summary of tests (Mann-Whitney) for ontogenetic shift in prey types (OSPT), tail tip color in juveniles (Ttc), mean adult total length (maTTL), relative head length (RHL), relative stoutness (RST), and macrohabitat use (Mac; proportion of individuals found on vegetation) in 22 species of *Bothrops*. Additional abbreviations are: d = distinct from the remainder of the tail; h = form that occurs in a higher proportion of juveniles; N_1 = number of specimens used to calculate RHL and RST; N_2 = number of individuals found in the field for macrohabitat characterization; s = similar to the remainder of the tail; SD = standard deviation.

Species	OSPT (*Z*)	OSPT (*P*)	Ttc	maTTL	N_1	RHL ($\bar{x}$ ± SD)	RST ($\bar{x}$ ± SD)	Mac	N_2
B. hyoprorus	1.94	0.052	s/d	527	30	0.207 ± 0.112	0.495 ± 0.243	—	—
B. alternatus	—	—	s	1166	33	0.094 ± 0.110	0.286 ± 0.336	0.00	24
B. cotiara	—	—	s(h)/d	838	27	0.077 ± 0.067	0.364 ± 0.220	—	—
B. fonsecai	—	—	s/d	918	28	0.053 ± 0.055	0.515 ± 0.217	0.00	13
B. itapetiningae	0.85	0.397	d[1]	593	35	0.042 ± 0.065	0.125 ± 0.256	0.10	10
B. erythromelas	0.79	0.430	s/d(h)	626	30	– 0.061 ± 0.064	0.028 ± 0.268	—	
B. mattogrossensis	0.17	0.861	d	742	28	– 0.069 ± 0.055	– 0.145 ± 0.204	0.00	6
B. neuwiedi	—	—	d	803	29	0.003 ± 0.070	0.216 ± 0.217	0.09	11
B. pauloensis	3.44	< 0.001	d	735	34	– 0.031 ± 0.047	0.132 ± 0.223	0.00	50
B. pubescens	2.40	0.017	d	922	35	– 0.124 ± 0.090	0.151 ± 0.292	0.00	36
B. insularis	—	—	d[1]	823	30	0.036 ± 0.065	– 0.294 ± 0.305	0.32	273
B. jararaca	3.74	< 0.001	d	1061	29	– 0.003 ± 0.129	– 0.068 ± 0.548	0.13	64
B. alcatraz	—	—	s(h)/d[1]	490	24	– 0.033 ± 0.062	– 0.214 ± 0.266	—	—
B. bilineatus	2.73	0.006	d[1]	753	30	– 0.164 ± 0.073	– 0.718 ± 0.253	0.90	33
B. taeniatus	1.78	0.075	d	1088	30	– 0.092 ± 0.071	– 0.674 ± 0.222	0.50	10
B. asper	2.72	0.006	s/d	—	—	—	—	—	—
B. atrox	8.73	<< 0.001	d[2]	1163	28	– 0.031 ± 0.101	– 0.290 ± 0.220	0.39	79
B. leucurus	3.42	< 0.001	d	1233	33	– 0.053 ± 0.091	– 0.232 ± 0.259	0.15	20
B. moojeni	4.88	<< 0.001	d	1284	33	0.040 ± 0.092	– 0.022 ± 0.305	0.18	22
B. brazili	3.05	0.002	d	1044	32	0.079 ± 0.091	0.014 ± 0.325	0.00	11
B. jararacussu	3.39	< 0.001	d	1291	33	0.025 ± 0.131	0.171 ± 0.331	0.00	61

[1] Tail tip color present in adults. [2] Possibly sexually dimorphic (Burger and Smith, 1950).

graphic variation in diet is negligible, perhaps because prey availability is similar across species ranges (see Habitats and Prey Availability).

Our results agree with those already published for some *Bothrops* (e.g., Beebe, 1946; Neill, 1960; Greene and Campbell, 1972; Cunha and Nascimento, 1975, 1978, 1982, 1993; Picado, 1976; Duellman, 1978; Scott, 1983; Leloup, 1984; Dixon and Soini, 1986; Sazima, 1988, 1989, 1991, 1992; Martins and Gordo, 1993; Strüssmann and Sazima, 1993; Norman, 1994; Duarte et al., 1995; Campbell, 1998; Martins and Oliveira, 1999). Although our sample size is large (85 prey), we failed to find amphibians in the gut of *B. alternatus* as reported by Yanosky et al. (1996; Table 1).

Mammal specialization was noted in three species of the *alternatus* group and one in the *neuwiedi* group (Fig. 1); this also occurs in several other species of pitvipers (*Lachesis*, some species of *Crotalus*; e.g., Ernst, 1992; Martins and Oliveira, 1999), and apparently evolved independently in the *alternatus* and *neuwiedi* groups (see below). The venoms of juvenile *B. alternatus* and *B. cotiara* seem to be more toxic to mice than those of adults (Furtado et al., 1991; but see conflicting results for *B. alternatus* in Andrade and Abe, 1999), which indicates that mammal specialization could be associated with increased venom toxicity in juveniles. Higher venom toxicity in juveniles of mammal specialists may be a consequence of: (1) the need to immobilize relatively larger prey (mammals are, in general, larger than ectothermic prey; Andrade and Abe, 1999; see below); (2) the need to quickly immobilize relatively dangerous prey (small mammals are generally more prone to inflict potentially dangerous bites than ectotherms; I. Sazima, unpublished); (3) the need to digest large prey (Pough and Groves, 1983); and/or (4) the smaller amount of venom available in juveniles (see Furtado et al., 1991; Andrade and Abe, 1999).

Among the island species, *B. insularis* exploits migrant passerine birds (M. Martins, O. Marques, and I. Sazima, unpublished), and *Bothrops alcatraz* apparently evolved paedomorphic feeding habits in the sense that adults retain the diet of juveniles (and also the venom composition; M. Furtado, pers. comm.). Birds are a major food source in at least three species of insular pitvipers: *B. insularis* (this study), *Crotalus catalinensis* (Rubio, 1998), and *Gloydius sheddaoensis* (Jian-Li, 1995). In a study comparing Prairie Rattlesnakes (*C. v. viridis*) feeding on birds and mice, Hayes (1992; see Hayes et al., this volume) indicated that birds are more difficult to immobilize and kill than small mammals. Thus, bird specialization in pitvipers would be facilitated by increased venom toxicity. Indeed, the venom of *B. insularis* is about five times more toxic to neonatal chickens than that of the sister species *B. jararaca* (Cogo, 1991), which rarely feeds on birds (Fig. 1, Appendix II; see comments below on the possibility of adult *B. insularis* luring birds with their tail tips). Mammals and birds are present in the diet of most generalist *Bothrops* (Fig. 1), and were probably in the diet of the ancestors of the *alternatus*, *jararaca*, and *neuwiedi* groups (see below), which include four mammal specialists (*B. alternatus*, *B. cotiara*, *B. fonsecai*, and *B. neuwiedi*) and a bird specialist (*B. insularis*). Thus, birds and mammals are not novel prey in *Bothrops*, like perhaps orthopterans are in the diet of *Cerrophidion godmani* (Campbell and Solórzano, 1992).

Diet shifts observed in both of the insular species of *Bothrops* are probably related to prey availability, since small mammals are not available. The mammal specialization that appeared in a subclade of the *alternatus* group and in *B. neuwiedi*, however, does not seem related to prey availability, as ectothermic prey and birds are more abundant in the habitats occupied by these species than in those occupied by diet generalists (M. Martins, unpublished). Indeed, other diet generalist species of *Bothrops* (e.g., *B. itapetiningae*, *B. jararaca*, *B. neuwiedi*, *B. pauloensis*) occur in the same habitats occupied by the mammal specialists. Based on the present distribution of the mammal specialists and the availability of prey types in their habitats, it seems improbable that mammal specialization appeared as a response to differential availability of mammals in relation to other prey types.

Saint Girons and Naulleau (1981) observed that juveniles of some species of *Vipera* feed on ectotherms, and in those species litters are composed of many small offspring (in length and mass). In contrast, in those species of *Vipera* where juveniles feed on mammals, litters have fewer but larger offspring. A similar situation occurs in *Bothrops* (see Ontogenetic Shift in Prey Size). Perhaps the mammal specialists in *Bothrops* and *Vipera* (as well as *Lachesis*; Martins and Oliveira, 1999) adopted the strategy of investing more mass in fewer, larger newborns. The consequent shift in newborn stoutness (but not in length in *Bothrops*; Table 1), thus, facilitated the adoption of a juvenile diet based on mammals, which is perhaps more profitable energetically than an ecthothermic diet. Whatever the selective agent(s) that led to mammal specialization in some *Bothrops*, a diet composed exclusively of mammals would require a stout body, and the putative ancestors of the *alternatus* and *neuwiedi* groups were most probably stout species (Martins et al., 2001). Indeed, mammal specialization has not appeared in any semi-arboreal *Bothrops*, which are more slender than terrestrials (Martins et al., 2001).

The reconstruction (character mapping) of diet in *Bothrops* (Fig. 2a) indicates that: (1) a generalist diet is plesiomorphic, (2) mammal specialization is synapomorphic in a subclade of the *alternatus* group (*B. alternatus*, *B. cotiara*, and *B. fonsecai*) and autapomorphic for *B. neuwiedi*; (3) a diet based mostly on birds is autapomorphic for *B. insularis*; and (4) a diet apparently restricted to ectotherms is autapomorphic for *Bothrops alcatraz*.

Ontogenetic Shift in Prey Types

Snakes from several families show ontogenetic diet shifts (Greene, 1989; Shine and Slip, 1990), which are generally attributed to changes in body size and other behavioral, morphological, and physiological characteristics during ontogeny (Mushinsky, 1987). Ontogenetic diet shifts are widespread in crotalines and viperines (Greene, 1997; Holycross et al., this volume; see Comparisons with Other Crotalines). Descriptions of ontogenetic diet shifts are known in *Bothrops asper* (Campbell, 1998), *B. atrox* (Martins and Gordo, 1993; Martins and Oliveira, 1999; see Sexton, 1956-57), *B. jararaca* (Sazima, 1991, 1992), and *B. moojeni* (Andrade et al., 1996). In the latter two species, venom toxicity to frogs decreases during ontogeny, whereas venom toxicity to mice increases in *B. jararaca* (Andrade et al., 1996; Andrade and Abe, 1999). Andrade and Abe (1999) suggest that prey immobilization and death are the main roles of juvenile venom, whereas a digestive role becomes more important as snakes mature and their prey become larger.

Among the generalist species of *Bothrops* discussed herein, ontogenetic diet shifts occur in all but the small-bodied *B. erythromelas*, *B. itapetiningae*, and *B. mattogrossensis* (Table 1); the result for *B. taeniatus* ($P = 0.07$) may be due to inadequate sample

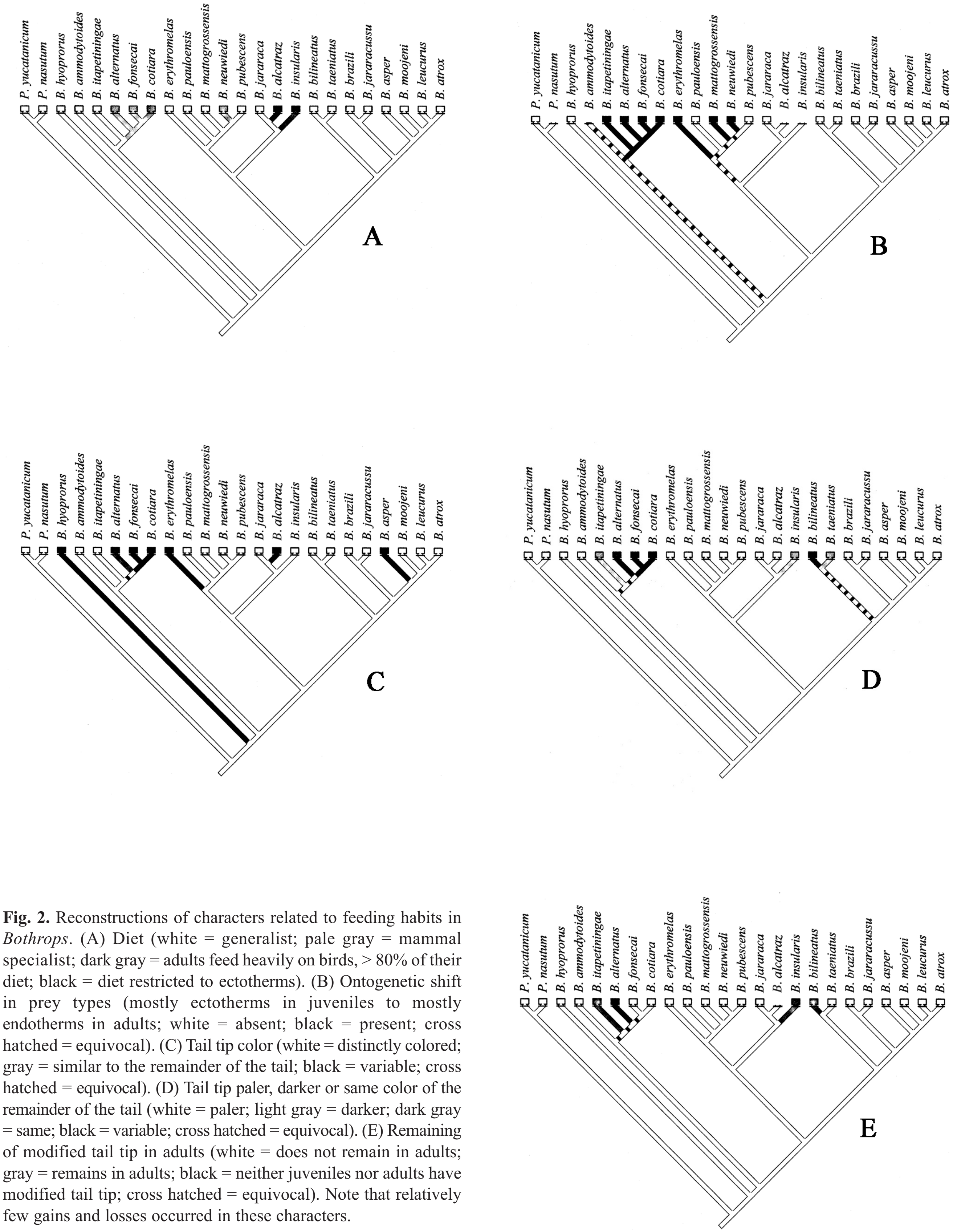

Fig. 2. Reconstructions of characters related to feeding habits in *Bothrops*. (A) Diet (white = generalist; pale gray = mammal specialist; dark gray = adults feed heavily on birds, > 80% of their diet; black = diet restricted to ectotherms). (B) Ontogenetic shift in prey types (mostly ectotherms in juveniles to mostly endotherms in adults; white = absent; black = present; cross hatched = equivocal). (C) Tail tip color (white = distinctly colored; gray = similar to the remainder of the tail; black = variable; cross hatched = equivocal). (D) Tail tip paler, darker or same color of the remainder of the tail (white = paler; light gray = darker; dark gray = same; black = variable; cross hatched = equivocal). (E) Remaining of modified tail tip in adults (white = does not remain in adults; gray = remains in adults; black = neither juveniles nor adults have modified tail tip; cross hatched = equivocal). Note that relatively few gains and losses occurred in these characters.

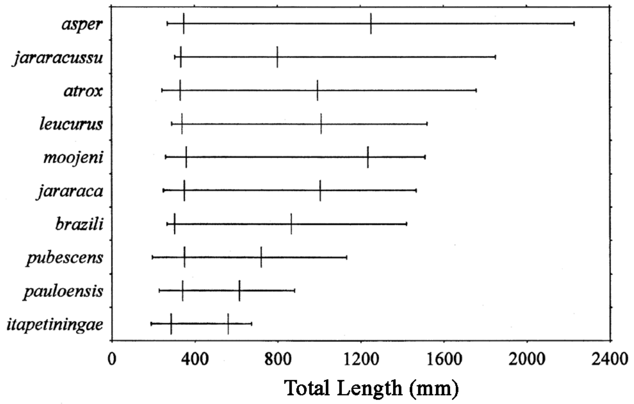

Fig. 3. Total length range (horizontal lines), length at which endotherms are included in the diet (left vertical bars), and length at which ectotherms are excluded from the diet (right vertical bars) for 10 species of *Bothrops* for which large samples of prey are available. Sample sizes are in Table 1.

size, and our sample of *B. ammodytoides* is likely too small to detect a possible ontogenetic shift. The generalist species for which we have sufficient samples of prey incorporate endotherms in their diets at 285 to 360 mm total length (TTL) (= 334 ± 23 mm) and drop ectotherms from their diets at 560 to 1251 mm (= 905 ± 237 mm; Fig. 3). There is no apparent relationship between the size at which generalists (N = 9) incorporate endotherms in their diets and either mean adult TTL (r = 0.538, P = 0.135), relative stoutness (r = 0.214, P = 0.580), or relative head length (r = 0.571, P = 0.108), but the size at which they eliminate ectotherms from their diets is positively correlated with mean adult TTL (r = 0.825, P = 0.006) and negatively correlated with relative stoutness (r = – 0.699, P = 0.036; Fig. 4). Thus, the larger and more slender the species, the later it excludes ectotherms from its diet (Fig. 4). There was no relationship between the size at which generalists exclude ectotherms from their diets and relative head length (r = 0.034, P = 0.930).

The proportion of mammals in the diet of *Bothrops* is highly variable (15–100%; N = 18 species; excluding *B. ammodytoides*, *B. asper*, and the two island species; Appendix II), and significantly correlated with relative stoutness (r = 0.511, P = 0.036), but not with relative head length (r = 0.265, P = 0.303) and mean adult TTL (r = 0.240, P = 0.354). Thus, the stouter the species, the greater the frequency of mammals consumed. Shine (1994) found a strong relationship between mean body length and proportion of mammals in the diet of Australian snakes (100 species from four families). Snakes are gape-limited predators (e.g., Greene, 1983, 1997; Pough and Groves, 1983; Arnold, 1993; Rodriguez-Robles et al., 1999), and vipers are characterized by a large gape that allows the consumption of relatively large prey (Greene, 1992; Cundall and Greene, 2000; Cundall, this volume; see Prey-size/snake-size relationships). Other morphological characters in *Bothrops*, however, such as stoutness, may also be important for consuming large prey.

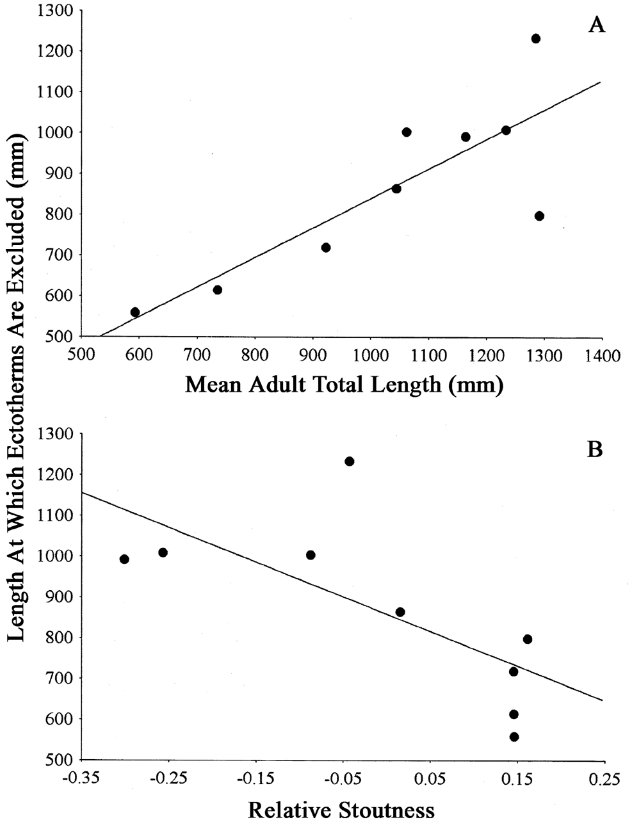

Fig. 4. Relationships between the length at which ectotherms are excluded from the diet and (A) mean adult total length (r = 0.825, P = 0.006 and relative stoutness) and (B) (r = – 0.699, P = 0.036).

Mammals are generally larger prey than anurans and lizards (see Prey-size/Snake-size Relationships), and ontogenetic diet shifts may be largely a consequence of changing body size (length and stoutness; see, Shine, 1994). Thus, the size constraints may prevent the consumption of mammals by the small, slender juveniles of most species of *Bothrops*. Not surprisingly, juveniles of mammal specialists are stouter than those of generalists ($F_{1,190}$ = 19.9, P < 0.001; N = 19 species; see similar result in Saint Girons and Naulleau, 1981), besides having a relatively larger head ($\mathrm{F}_{1,190}$ = 39.2, P < 0.001). Furthermore, three of the smallest species of *Bothrops* discussed here (*B. erythromelas*, *B. itapetiningae*, and *B. mattogrossensis*) do not show ontogenetic diet shifts. Our results indicate that allometry is important in the feeding biology of *Bothrops* (see Shine, 1994, for Australian snakes). The phylogenetic reconstruction of ontogenetic diet shifts (Fig. 2b) indicates that this character was already present in the sister group of *Bothrops*, and was lost in the *alternatus* group and at least once in the *neuwiedi* group.

Caudal Luring

Caudal luring in snakes occurs in species of at least five families, including several species of pitvipers (Strimple, 1995; Greene, 1997; R. Reiserer and G. Schuett, unpublished; Table 4). This behavior is frequently associated with feeding on ectothermic prey, especially anurans (e.g., Burger and Smith, 1950; Neill, 1960; Greene and Campbell, 1972; Schuett et al., 1984; Sazima, 1991, 1992; Greene, 1992; Martins and Gordo, 1993). For *Bothrops*, caudal luring is known to occur in *B. atrox*, *B. bilineatus*, *B. jararaca*, *B. jararacussu*, and *B. moojeni* (Andrade et al., 1996; Greene and Campbell, 1972; Sazima, 1991, 1992), and suggested for *B. asper*, *B. leucurus*, and *B. neuwiedi* based on the possession of a distinctly colored tail tip in juveniles (Greene, 1992; Sazima, 1991, 1992).

In addition to the abovementioned species, caudal luring occurs in *B. leucurus* and *B. taeniatus* (M. Martins, O. Marques, and I. Sazima, unpublished). Postures of foraging in free-living animals (with the tail tip exposed, lying over body coils, and close to the head; Plates 7f, 8a, c) indicate that caudal luring probably occurs in *B. insularis*, *B. pauloensis*, and *B. pubescens* (M. Martins, O. Marques, and I. Sazima, unpublished). Thus, caudal luring may occur in most species of *Bothrops* that are diet generalists (but see below). Juveniles of most diet generalists treated here bear a distinctly colored tail tip (Table 1), generally paler than the remainder of the tail, but darker in *B. itapetiningae*, *B. insularis*, and *B. taeniatus*, as well as some individuals of *B. bilineatus*, *B. jararaca*, and *B. moojeni*. Juveniles of the generalist *B. hyoprorus* are variable: some bear a pale tail tip while others lack it. Among mammal specialists, juveniles of *B. alternatus* lack a distinctly colored tail tip. This character is variable in *B. cotiara* and *B. fonsecai*, but all juveniles of *B. neuwiedi* bear pale tail tips. The complete loss of a modified tail tip in *B. alternatus* may be a consequence of mammal specialization. However, despite their diets being almost restricted to mammals, *B. cotiara*, *B. fonsecai*, and *B. neuwiedi* may have retained the distinctly colored tail tip from a generalist ancestor that used caudal luring. Caudal luring has not been recorded for the latter three species. The possession of a modified tail tip is also variable in four diet generalists (*B. alcatraz*, *B. asper*, *B. erythromelas*, and *B. hyoprorus*). Perhaps these species lost caudal luring behavior, as suggested for *B. asper* (Burger and Smith, 1950), or caudal luring in these species does not necessarily require a modified tail tip.

Observations on captive *B. moojeni* (D. Andrade, pers. comm.) and *B. taeniatus* indicate that caudal luring behavior is different in these two species when compared to the descriptions by Sazima (1991) for *B. jararaca* and *B. jararacussu*. For example, *B. moojeni* adopts the erect tail posture described for *Agkistrodon bilineatus* (Neill, 1960), and the tail of *B. taeniatus* reaches larger distance than those recorded for *B. jararaca* and *B. jararacussu*. Further observations on caudal luring in additional species of *Bothrops* would probably reveal additional differences between species and the factors responsible for such variation (e.g., prey types, microhabitat, phylogeny).

Adults of *B. insularis*, *B. itapetiningae*, and *B. bilineatus* retain the distinctly colored tail tip of juveniles (and probably caudal luring behavior; see Greene and Campbell, 1972), which may be associated with a high proportion of ectotherms in the diet of adults of all but *B. insularis*. Greene (1992) considered that *B. bilineatus* is paedomorphic in that adults retain the diet and caudal luring behavior of juveniles (although ontogenetic diet shift seems to occur in this species; Table 1). This may also be the case for *B. itapetiningae*, which does not exhibit an ontogenetic diet shift. Retention of a modified tail tip in adult *B. insularis* may indicate that they lure birds with their dark tail tip (all bird prey are primarily insectivorous).

The reconstruction of presence/absence of distinctly colored tail tips in juvenile *Bothrops* indicates that: (1) this character was already present in the ancestor of *Bothrops*; (2) variation in this character (some juveniles bear a distinct tail tip while some lack it) appeared in five species, three of them mammal specialists; and (3) the complete loss of a distinctly colored tail tip is autapomorphic for the mammal specialist *B. alternatus* (Fig. 2c). Reconstructions of tail tip color (paler or darker than the remaining of the tail; Fig. 2d) and presence/absence of distinct tail tip color in adults (i. e., whether adults retain a distinctly colored tail tip; Fig. 2e) indicate that a pale tail tip and its restriction to juveniles characterized the ancestor of the clade formed by *Bothrops* and its sister group (Table 1).

Table 2. Mean, range, and ontogenetic shift (OS) of ingestion ratio (IR) and mass ratio (MR) in nine selected species of *Bothrops* (see Methods for details). A significant *P* for ontogenetic shift in these characters indicates that they decrease during ontogeny (see Methods). Abbreviations are: N = sample size; ns = regression not significant.

Species	IR ($\bar{x}$)	N	Range	OS (*P*)	MR (m)	N	Range	OS (*P*)
B. alternatus	0.774	7	0.477–1.207	ns	0.293	9	0.045–0.925	0.044
B. fonsecai	—	—	—	—	0.355	4	0.076–0.882	—
B. pubescens	0.779	16	0.509–1.157	ns	0.163	28	0.002–0.627	ns
B. insularis	—	—	—	—	0.201[1]	31	0.024–0.482	—
B. jararaca	—	—	—	ns	0.209	10	0.096–0.421	0.008
B. atrox	0.959	87	0.357–2.000	ns	0.203	78	0.009–0.824	0.001
B. moojeni	0.613	10	0.241–0.920	ns	0.257	10	0.008–0.889	0.004
B. brazili	—	—	—	—	0.290	5	0.114–0.504	—
B. jararacussu	—	—	—	—	0.109	14	0.012–0.395	ns

[1] Almost all prey were detected through palpation; thus, results may be biased toward larger prey.

Feeding Frequency

The proportion of snakes with prey in their stomachs is low in six species for which we have large, unbiased samples: *B. alternatus* (0.18, N = 33), *B. atrox* (0.18, N = 205), *B. jararaca* (0.29, N = 76), *B. jararacussu* (0.23, N = 74), *B. moojeni* (0.15, N = 176), and *B. pauloensis* (0.16, N = 83). Shine (1986) found a mean proportion of 0.57 for eight species of viperids, 0.51 for colubrids, and 0.45 for elapids. The low proportion of recently-fed individuals in *Bothrops* may reflect: (1) under-representation of recently-fed individuals in the samples due to more sedentary and/or secretive habits during the first days after prey ingestion (Shine, 1986; Lillywhite, 1987); (2) a higher digestive ability in snakes inhabiting warmer climates (e.g., Lillywhite, 1987; Peterson et al., 1993); and (3) a low feeding frequency due to more sedentary habits and lower energy needs (Shine, 1986). Perhaps species from temperate climates [all vipers and most colubrids used in the review of Shine (1986) are from temperate areas] have a higher feeding rate than tropical species, because the active season of the former is shorter. Accordingly, all seven tropical colubrids used in Shine (1986) have lower feeding rates than the mean rate for viperids.

Prey-size/Snake-size Relationships

Vipers are capable of ingesting prey of relatively high ingestion ratio (IR; herein prey width divided by snake head length) and mass ratio (MR; prey mass divided by snake mass; e.g., Pough and Groves, 1983; Greene, 1992), and species of *Bothrops* seem to be typical vipers in this regard: Sazima (1992) reported on relatively high MRs (= 0.21 and 0.44 for juveniles and adults, respectively) for *B. jararaca* and Greene (1992) illustrated two examples of large prey for *B. asper* and *B. atrox* (MR 0.65 and 1.60, respectively). Allometric constraints, however, are known to have a strong effect on prey consumption by snakes (e.g., Pough and Groves, 1983; Shine, 1991; see above). Thus, the considerable variation in size and stoutness that occurs in *Bothrops* (Table 1; Greene, 1992; Martins et al., 2001) may have led to considerable variation in prey-size/snake-size relationships in this genus.

Mean IR and MR are low to moderate in adequately sampled species of *Bothrops* (IR = 0.61–0.96, N = 4, and MR = 0.11–0.35, N = 9; Table 2). However, these snakes can swallow very large prey, up to IR 2.00 in *B. atrox* and MR 0.92 in *B. alternatus* (Table 2). There is also a MR record of 1.46 for *B. jararaca* (I. Sazima, unpublished). High MRs in *B. alternatus* and *B. fonsecai* (= 0.29 and = 0.35, respectively; Table 2) may be associated with mammal specialization and/or a stouter body (see Table 2). We see no obvious reason why *B. jararacussu* should feed on relatively small prey (MR = 0.11), but this result is perhaps due to small sample size.

Mass ratio approaches significance among different species ($H_{8,194} = 15.4$, $P = 0.052$), but IR is highly significant ($H_{3,116} = 14.8$, $P = 0.002$), and a post hoc test indicates that *B. atrox* feeds on significantly higher IR prey than *B. moojeni*. Besides the consequences of specializing on larger prey, as suggested above for *B. alternatus* and *B. fonsecai*, further variations in MR and IR among species perhaps reflect differential availability of prey of different size and shape in the habitats where these snakes occur.

Arnold (1993) suggested optimal foraging strategies for snakes (mostly aquatic piscivorous species) that eliminate small prey from their diets during ontogeny. In all six adequately sampled species of *Bothrops*, adults do not eliminate small MR prey from their diets (*B. alternatus*, *B. insularis*, *B. jararaca*, *B. jararacussu*, *B. moojeni*, and *B. pubescens*). Perhaps small prey remain valuable in large individuals of *Bothrops* due to low costs of predation (e.g., Cruz-Neto et al., 1999).

In general, because mammals are larger prey than ectotherms (see below), it might be expected that relative prey size would increase during ontogeny in diet generalists, as a consequence of the ontogenetic diet shift. However, MR decreases during ontogeny in three generalists (*B. atrox*, *B. jararaca*, and *B. moojeni*), as well as in one mammal specialist (*B. alternatus*), while no trend is apparent in two other generalists (*B. jararacussu* and *B. pubescens*). Thus, although mammal prey tends to be larger than ectotherms consumed, we found no positive allometric trend in prey size. Juveniles of several snakes are known to occasionally attack relatively large prey when compared to adults (e.g., Sazima and Martins, 1991; Greene, 1992), which results in an ontogenetic decrease in relative prey size as described here for several species of *Bothrops* and recorded in other snake taxa (Shine et al., 1998). This decrease in MR may also be a consequence of the parallel decrease in relative head size during ontogeny, which occurs in all species of *Bothrops* treated here. Ingestion ratio remains constant in all four species that were adequately sampled (Table 2), indicating that gape is an important limitation in feeding ontogeny (Pough and Groves, 1983; Cruz-Neto et al., 1999).

Relative mass and width are significantly different among the three most common prey types consumed by *Bothrops* (mammals, frogs, and lizards; for mass $F_{2,\,120} = 5.29$, $P = 0.006$; for width $F_{2,\,119} = 4.82$, $P = 0.010$). In post hoc tests, anurans and lizards are significantly different in relative mass, whereas mammals and lizards are significantly different in relative width. Although poorly explored (see Greene, 1983; Cruz-Neto et al., 1999), these differences in prey shape and mass are probably important in determining patterns and constraints in the feeding habits of snakes (see putative examples above).

Feeding and Foraging Behavior

Few published accounts of feeding behavior are available for species of *Bothrops*. Sazima (1989, 1992) described in detail the feeding behavior of *B. jararaca* in southeastern Brazil, based on staged encounters between snakes and mammal prey (mice and rats) in the field. The feeding behavior of this snake on small mammals may be characterized by six components: orientation towards prey, approach, strike (with bite and release), trailing, inspection, and swallowing (see details and figures in Sazima, 1989, 1992). The feeding behavior described by Sazima (1989) for *B. jararaca* is similar to those described for several other pitvipers (see reviews in Sazima, 1989, 1992). Egler et al. (1996) described an instance of predation on a snake (*Atractus torquatus*) by *B. atrox* (Plate 7c); in this case, the snake prey was held until apparently dead. A few staged encounters made in the field indicate that *B. atrox* always retains frogs after the strike (M. Martins, unpublished), and a *B. jararaca* juvenile observed in the field showed the same behavior (Sazima, 1992). In captivity, the feeding behavior of *B. atrox* on mice (M. Martins and M. Oliveira, unpublished) is similar to that described by Sazima (1989) for *B. jararaca* in the field. Limited observations in the field (e.g., Plate 7c–e) and laboratory on several species of *Bothrops* indicate that all prey types except mammals (rodents), are held from strike through ingestion (M. Martins, I. Sazima, and O. Marques, unpublished).

Releasing rodent prey is thought to reduce the risk of handling dangerous prey (Chiszar et al., 1982; Kardong, 1986; Sazima, 1992; Stiles et al., this volume), and may be regarded as a secondarily acquired trait. When held after a strike, birds may also inflict potentially dangerous bites. Even so, *B. insularis* holds birds until swallowing (Amaral, 1921; O. Marques, unpublished), perhaps due to its extremely toxic venom that immobilizes them very quickly (Cogo, 1991). Birds flee by flying or jumping after being struck, leaving no adequate trail for the snake to find them after the strike, and the same may hold true for frogs. Thus, holding prey until swallowing may also relate to the chance of finding prey after post-strike.

Ambush hunting is typical of vipers (Greene, 1992, 1997), and the main tactic used by *Bothrops* (Plate 7a–b). Observations of two radiotracked *B. atrox* followed for eight and 16 months (M. Martins, unpublished) indicate that this species is a typical “mobile ambusher” that searches for good foraging sites to spend a few days to several weeks hunting by ambush (Greene, 1992). Some species of *Bothrops*, however, may occasionally forage actively. Egler et al. (1996) found a *B. atrox* foraging actively and eating a snake by day, and Sazima and Strüssmann (1990) and Sazima (1992) described scavenging in *B. jararaca*;

Table 3. Summary of macrohabitat (see Table 2) and microhabitat of 21 species of *Bothrops* described herein (see also Campbell and Lamar, 1989). S = semi-arboreal; T = terrestrial.

Species	Macrohabitat	Microhabitat
B. alternatus	T[1]	Open formations and swamps
B. cotiara	T	Open areas and edges of moderate to montane broadleaf and Araucaria forests
B. fonsecai	T	Open areas and edges of moderate to montane broadleaf and Araucaria forests
B. itapetiningae	T[1]	Cerrados
B. ammodytoides	T	Deciduous open shrublands in low elevations to montane, temperate broadleaf forests
B. erythromelas	T[1]	Dry to wet habitats in caatinga vegetation
B. mattogrossensis	T	Open areas adjacent to semidecidual forests in seasonally flooded open plains
B. neuwiedi	T[1]	Rocky outcrops and adjacent grassy fields and gallery forests in mountains
B. pauloensis	T	Cerrados
B. pubescens	T	Broadleaf forests
B. insularis	S[2]	Atlantic forest at Queimada Grande Island
B. jararaca	S	Atlantic forests
B. alcatraz	S	Atlantic forest at Alcatrazes Island
B. bilineatus	S	Lowland rainforests throughout Amazonia, and Atlantic forests
B. taeniatus	S	Lowland rainforests
B. atrox	S	Lowland rainforests
B. leucurus	S	Lowland to moderate elevation Atlantic forests
B. moojeni	S	Gallery forests and swamps in cerrados
B. asper	T	Forests
B. brazili	T	Lowland rainforests
B. jararacussu	T	Lowland to moderate elevation Atlantic forests

[1] Juveniles are occasionally found on low-lying plants (up to 50 cm above the ground). [2] Individuals may be found on higher locations of vegetation (up to 8 m; M. Martins and O. Marques, unpublished) than other species of the *jararaca* group.

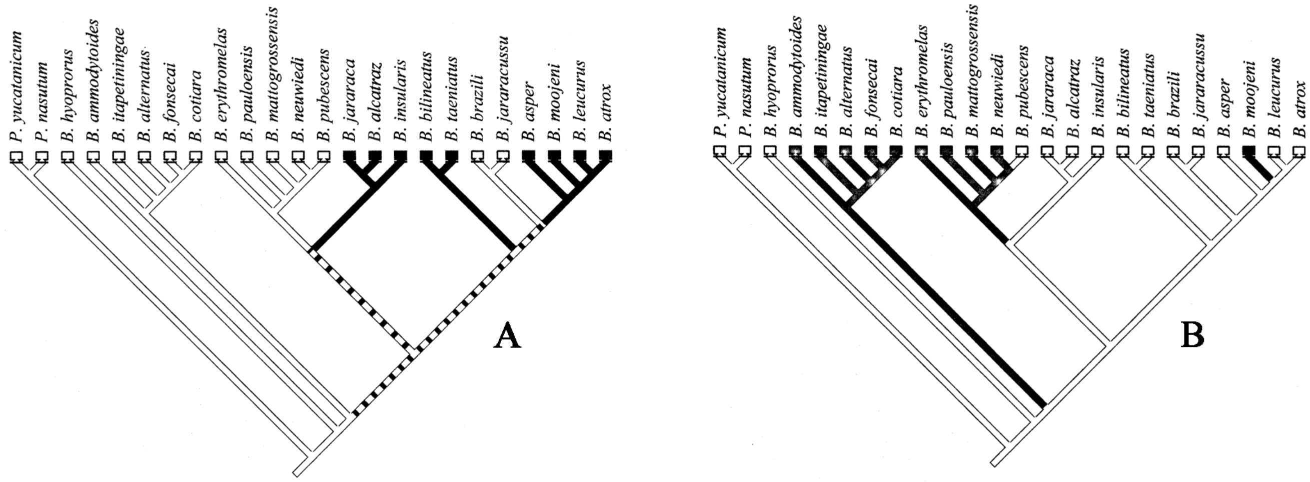

Fig. 5. Reconstructions of microhabitat (A) white = terrestrial; black = semi-arboreal; cross-hatched = equivocal; and habitat (B) white = forests; gray = open areas; black = gallery forests and nearby swamps in cerrados, in *Bothrops*. Note that: (1) early *Bothrops* were terrestrial forest inhabitants, (2) semi-arboreal habits appeared one to three times in the genus (Table 1), and (3) invasion of open areas occurred in two clades (the *alternatus* and *neuwiedi* groups).

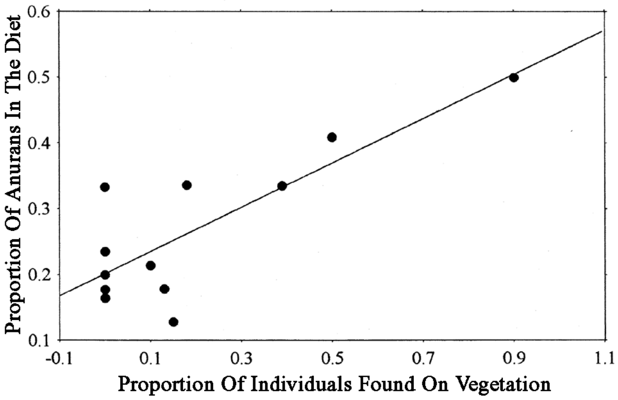

Fig. 6. Relationship between proportion of anurans in the diet and arboreality (proportion of individuals found on vegetation) in 12 species of *Bothrops* ($r = 0.815$, $P = 0.001$).

and Sazima (1992) inferred that two moving individuals of *B. jararaca* were foraging actively, and that another individual containing a nestling passerine bird in the DT found this prey by active foraging (but see Greene, 1997:261). Lizard eggs found in the DT of *B. pauloensis* (P. Valdujo, unpublished) were most likely found by active foraging. Sazima (1992) suggested that slender species of crotalines are more prone to forage actively than the stouter ones, a hypothesis that remains untested.

Microhabitat Use and Feeding Biology

Although early pitvipers were probably terrestrial (Greene, 1992; Martins et al., 2001), arboreality evolved several times within this group (Greene, 1992, 1997). The genus *Bothrops* shows a relatively high diversity of microhabitat use within the crotalines (Table 3), encompassing exclusively terrestrial species as well as several species that use vegetation, from the sporadically arboreal *B. jararaca* (Sazima, 1992) to the almost completely arboreal *B. bilineatus* (Dixon and Soini, 1986; Duellman, 1978; this paper). In at least some of the semi-arboreal species, an ontogenetic shift in microhabitat use also occurs, with juveniles found more frequently on the vegetation than adults (e.g., *B. asper*, Campbell, 1998; *B. atrox*, Duellman, 1978; Martins and Oliveira, 1999; *B. jararaca*, Sazima, 1992).

The phylogenetic reconstruction of microhabitat use in *Bothrops* provided equivocal results. Semi-arboreal habits may have appeared up to three times in the genus (Fig. 5a). Visual comparisons of this reconstruction with the characters related to feeding habits in Figure 2a–c indicate that there is no association between microhabitat use and any of these characters. There is, however, a strong positive correlation between the proportion of anurans in the diet and that of individuals found on vegetation in *Bothrops* (Fig. 6; N = 12 species, mammal specialists, island species, *B. ammodytoides*, *B. asper*, and *B. erythromelas* excluded; $r = 0.815$, $P = 0.001$). This result may reflect the relatively high abundance of arboreal frogs (hylids, and the leptodactylid *Eleutherodactylus*) in the tropical forests inhabited by most semi-arboreal species. On the other hand, there seems to be no relationship between the proportion of mammals and lizards in the diet and the intensity of use of vegetation ($r = -0.326$, $P = 0.300$, and $r = -0.333$, $P = 0.291$, respectively).

Habitats and Prey Availability

Besides proximate factors (e.g., head morphology and kinetics, sensory mediated preferences), the diet of many snakes may be determined also by ultimate factors, such as the relative availability of different prey types in the habitats they occupy (e.g., Wallace and Diller, 1990), rather than by cognitive decisions to capture or ignore a particular prey species (Greene, 1997). *Bothrops* species inhabit several types of open areas and forests in Central and South America (Table 3; Plate 8d–f; see Campbell and Lamar, 1989), and this diversification in habitat use could have been associated with a similar diversification in feeding biology, mainly if prey availability differs within habitats. However, this does not seem to be the case when Figure 5b is compared to Figure 2a–c.

The main prey types consumed by *Bothrops*, mammals, lizards, and frogs, as well as less important prey (centipedes, snakes, and birds), are relatively abundant in all kinds of habitats used by the species treated herein (Table 3), although frogs may be highly seasonal in drier and/or colder habitats. However, more localized differences in the abundance of certain prey may occur. For instance, in the cerrados, *B. itapetiningae* and *B. pauloensis* occur in dry interfluvial areas where lizards are relatively common and frogs tend to be rare, whereas *B. moojeni* occurs in gallery forests and swamps, wet habitats where frogs are relatively abundant and lizards are generally rare. Indeed, *B. itapetiningae* and *B. pauloensis* apparently feed more frequently on lizards (24% and 23% of prey found in the gut, respectively) and less frequently on frogs (20% and 21%) than *B. moojeni* (16% of lizards and 34% of frogs; Appendix II). Thus, perhaps most variations observed in the proportion of different prey types in the species of *Bothrops* treated here simply reflect differential prey availability in the habitats and

Table 4. Main habitat, macrohabitat, and prey types, as well as presence/absence of modified tail tip (and caudal luring behavior) in extant crotaline genera (data from Pope, 1935; Klauber, 1972; Mori et al., 1989; Moriguchi, 1989; Gloyd and Conant, 1990; Campbell and Solórzano, 1992; Ernst, 1992; David and Vogel, 1996; McDiarmid et al., 1999). Forests include woodlands. M = mammals, F = frogs, and L = lizards.

Genus	Main habitat	Main macrohabitat	Main prey types	Distinctly colored tail tip
Agkistrodon	Forests, open areas	Terrestrial	M, F, L	Yes
Gloydius	Forests, open areas	Terrestrial	M, F, L	Yes
Deinagkistrodon	Forests	Terrestrial	M, F, L	Yes
Tropidolaemus	Forests	Arboreal	M, F, L	Yes
Protobothrops	Forests, open areas	Terrestrial, arboreal	M, F, L	No
Ovophis	Forests, open areas	Terrestrial	M, F, L	Yes
Hypnale	Forests	Terrestrial	M, F, L	Yes
Calloselasma	Forests, open areas	Terrestrial	M, F, L	Yes
Trimeresurus	Forests, open areas	Terrestrial, arboreal	M, F, L	Yes
Lachesis	Forests	Terrestrial	M	No
Porthidium	Forests	Terrestrial	M, F, L	Yes
Atropoides	Forests	Terrestrial	M, F, L	Yes
Cerrophidion	Forests	Terrestrial	M, F, L	Yes
Ophryacus	Forests, open areas	Arboreal	?	Yes
Bothriechis	Forests	Arboreal	M, F, L	Yes
Bothrops (and *Bothriopsis*)	Forests, open areas	Terrestrial, arboreal	M, F, L	Yes
Crotalus	Open areas	Terrestrial	M, L	Yes
Azemiops	Forests	Terrestrial	M?	No

microhabitats they use, as suggested by Greene (1997) for snakes in general (see Shine, 1994).

Comparisons with Other Crotalines

Although most *Bothrops* studied are diet generalists, there seems to be considerable variation in the relative importance of each prey type among species (Fig. 1, Appendix II), a situation similar to that recorded for other pitviper genera (e.g., *Agkistrodon*, *Crotalus*, *Gloydius*, *Trimeresurus*; see Pope, 1935; Klauber, 1972; Mori et al., 1989; Gloyd and Conant 1990; Ernst, 1992; David and Vogel, 1996). However, for most species of *Bothrops* that are diet generalists, mammals, frogs, and lizards are very important prey, and together represent over 80% of the diet of most species (except for the bird specialist *B. insularis*). Besides mammals, frogs, and lizards, pitvipers of several genera also consume, at least occasionally, centipedes, birds, and snakes (e.g., Klauber, 1972; Mori and Moriguchi, 1988; Moriguchi, 1989; Gloyd and Conant, 1990; Campbell and Solorzano, 1992; Ernst, 1992; Taylor, 2001; Holycross et al., this volume).

Several characters analysed herein occur in most crotalines and are apparently plesiomorphic in the subfamily (Table 4). Phylogenetic reconstructions of the characters in Table 4, using the crotaline phylogeny of Parkinson (1999), indicate that at least terrestriality, a generalist diet, and the presence of a modified tail tip were already present in the earliest pitvipers (Fig. 7). Furthermore, most of these characters occur in several viperines (Greene, 1992), and thus may be plesiomorphic in the Viperidae. Besides the four characters in Table 4, diets based on relatively large prey (i. e., prey with high IR and MR), ambush foraging tactics, and ontogenetic diet shifts occur in most pitvipers and may be plesiomorphic characters in crotalines and other viperids (Greene, 1992). Thus, although a few apomorphies appeared in some species of *Bothrops*, in general the feeding habits in the genus are conservative, as suggested by Greene (1992). Similar studies on other viperid genera would show whether the several patterns we described for *Bothrops* are widespread in pitvipers.

CONCLUSIONS AND FUTURE RESEARCH

Our results indicate that early lancehead bothropoid species were likely stout, terrestrial forest dwellers that fed on a variety of prey types. Juveniles fed mostly on ectotherms that they lured with pale tail tips, whereas adults preyed mostly on mammals. This

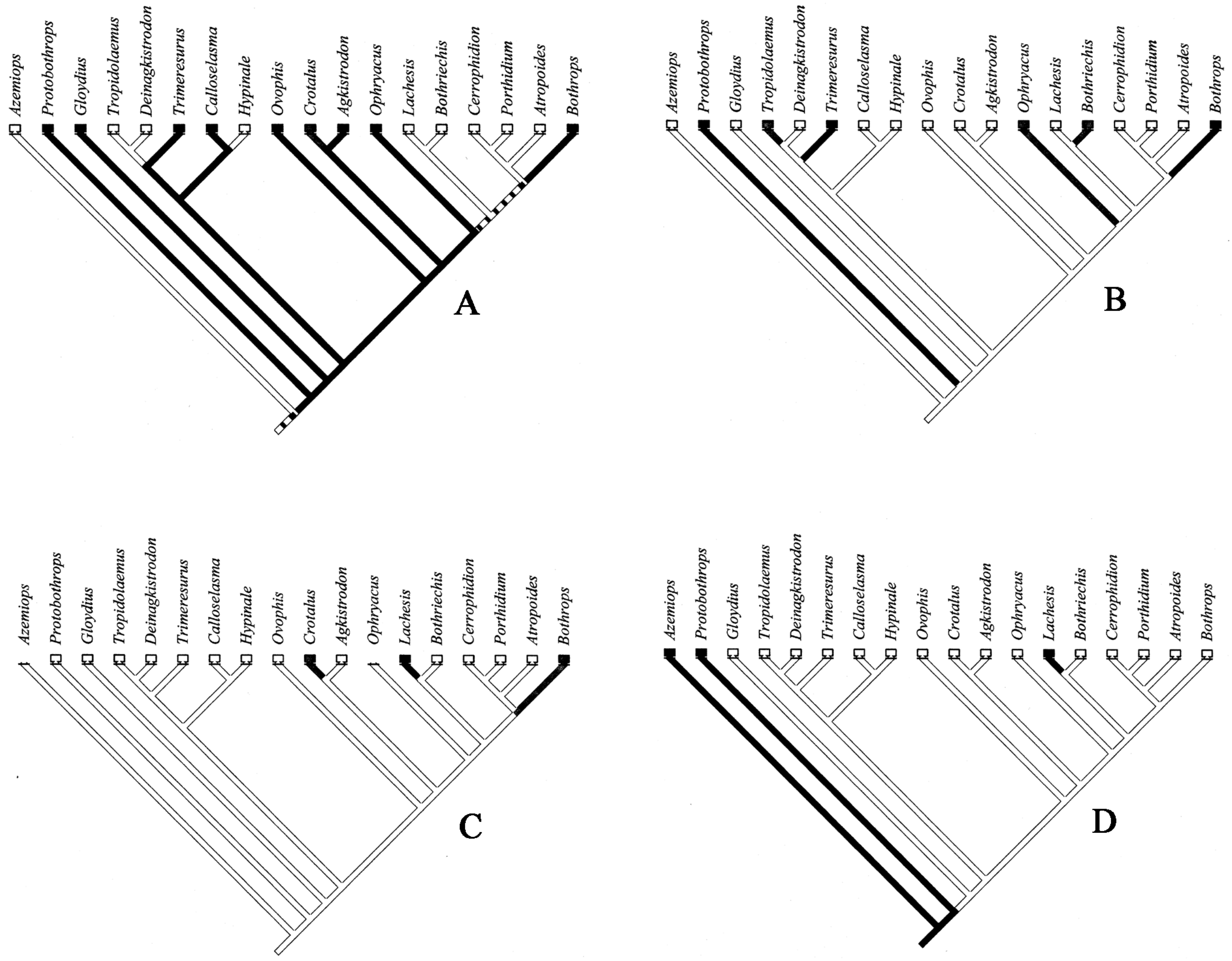

Fig. 7. Reconstruction of (A) habitat: white = forests; gray = open areas; black = variable; cross hatched = equivocal. Reconstruction of (B) macrohabitat: white = terrestrial; gray = arboreal; black = variable). Reconstruction of (C) diet: white = generalist; gray = variable; black = mammal specialist. Reconstruction of (D) presence/absence of a modified tail tip in juveniles (and probably caudal luring): white = present; black = absent, on a phylogeny of the Crotalinae (phylogeny from Parkinson, 1999: Fig. 3b). Note that terrestrial habits, a generalist diet, and the presence of a modified tail tip are likely plesiomorphic characters in pitvipers.

lifestyle is widespread among modern *Bothrops*, though incompletely conserved. Invasions of open areas occurred more than once in the genus *Bothrops*, although with no evident consequence to feeding biology, since prey availability is in general similar among habitats. However, changes toward arboreality in some clades led to considerable variation of stoutness and to a larger representation of frogs in lancehead diets. Body size apparently had a considerable effect in dietary variation, prey-size/snake-size relationships, and ontogenetic diet shifts by constraining the consumption of large prey (especially mammals) in small, slender species and/or individuals. Differential prey availability, namely the absence of small, non-volant mammals (an important prey for most *Bothrops*), was probably an important selective agent in the evolution of feeding habits in both island species. Specialization of mammal prey evolved in at least two clades, but the selective agent(s) involved are unclear and require future studies.

The generalist habits of early *Bothrops* may have facilitated the shifts described here (including the diet shifts observed in island species), and may be one of the factors responsible for the relatively high abundance observed for *Bothrops* in most habitats (Duellman, 1978; Strüssmann and Sazima, 1993; Guyer, 1994; Sazima and Manzani, 1995; Martins and Oliveira, 1999). Similarly, generalist habits in early pitvipers may have facilitated the great diversification that occurred in the crotalines in tropical and subtropical regions of Asia and the Americas (e.g., Pope, 1935; Klauber, 1972; Campbell and Lamar, 1989; Gloyd and Conant, 1990; Ernst, 1992; David and Vogel, 1996).

Despite the omissions due to rarity in collections (e.g., *B. iglesiasi* and *B. pirajai*), the 22 species we studied represent a reasonably comprehensive treatment of the genus *Bothrops*. However, many important questions remain to be answered on the feeding biology of *Bothrops* (see Greene, 1992; Sazima, 1992): (1) Are the known patterns of feeding behavior typical for all *Bothrops*? (2) How does feeding behavior vary with different prey types? (Hayes, 1992); (3) How toxic are *Bothrops* venoms for different prey types and how do they vary ontogenetically? (see Andrade et al., 1996; Andrade and Abe, 1999); (4) Do common prey types vary in quality? (caloric and/or nutrient content; see Arnold, 1993); (5) Do costs of foraging and feeding vary among different prey types? (see Hayes, 1992; Cruz-Neto et al., 1999); (6) Which prey and predator characters are most important in determining prey size-snake size relationships?; (7) What is the relationship between feeding biology and other life history traits, especially reproduction (see Shine, 1994)?; (8) Do *Bothrops* diets precisely reflect prey availability in the habitats they use? and (9) Are there further relationships between microhabitat use and feeding biology in *Bothrops*? Answers to the above questions will require additional data on the ecology and natural history of *Bothrops*. A particularly promising research program would incorporate field studies with work on animals in the laboratory.

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LITERATURE CITED

AMARAL, A. 1921. Contribuição para o conhecimento dos ophidios do Brasil. A. Parte II. Biologia da nova espécie, *Lachesis insularis*. Anex. Mem. Inst. Butantan 1:39–44.

ANDRADE, D. V., AND A. S. ABE. 1999. Relationships of venom ontogeny and diet in *Bothrops*. Herpetologica 55:200–204.

———, ———, AND, M. C. DOS SANTOS. 1996. Is the venom related to diet and tail color during *Bothrops moojeni* ontogeny? J. Herpetol. 30:285–288.

ARNOLD, S. J. 1993. Foraging theory and prey-size—predator-size relations in snakes. Pp. 87–115 *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York.

BEEBE, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Zoologica 31:11–52.

BROOKS, D. R., AND D. A. MCLENNAN. 1991. Phylogeny, Ecology, and Behavior. The University of Chicago Press, Chicago.

BURGER, W. L., AND P. W. SMITH. 1950. The coloration of the tail tip of young fer-de-lances: sexual dimorphism rather than adaptive coloration. Science 112:431–433.

CADLE, J. E. 1992. Phylogenetic relationships among vipers: immunological evidence. Pp. 41–48 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

CAMPBELL, J. A. 1998. Amphibians and reptiles of northern Guatemala, the Yucatán, and Belize. Oklahoma University Press, Norman.

———, AND E. D. BRODIE, JR. (Eds.) 1992. Biology of the Pitvipers. Selva, Tyler, Texas.

———, AND W. W. LAMAR. 1989. The Venomous Reptiles of Latin America. Cornell University Press, Ithaca, New York.

———, AND W. W. LAMAR. 1992. Taxonomic status of miscellaneous Neotropical viperids, with the description of a new genus. Occ. Pap. Mus. Texas Tech. Univ. 153:1–32.

———, AND A. SOLÓRZANO. 1992. The distribution, variation, and natural history of the Middle American montane pitviper, *Porthidium godmani*. Pp. 223–250 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

CHISZAR, D., C. ANDREN, G. NILSON, B. O'CONNELL, J. S. MESTAS, JR., AND H. M. SMITH. 1982. Strike-induced chemosensory search in Old World vipers and New World pitvipers. Anim. Learn. Behav. 10:121–125.

COGO, J. C. 1991. Estudo dos efeitos da peçonha de *Bothrops insularis* (jararaca ilhôa) sobre o músculo de camondongo e pintainho. Unpublished M.Sc. dissertation, Universidade Estadual de Campinas, Campinas, Brazil.

CRUZ-NETO, A. P., D. V. ANDRADE, AND A. S. ABE. 1999. Energetic cost of predation: aerobic metabolism during prey ingestion by juvenile rattlesnakes, *Crotalus durissus*. J. Herpetol. 33:229–234.

CUNDALL, D., AND H. W. GREENE. 2000. Feeding in snakes. Pp. 293–333 *In* K. Schwenk (Ed.), Feeding: Form, Function, and Evolution in Tetrapod Vertebrates. Academic Press, San Diego.

CUNHA, O. R., AND F. P. NASCIMENTO. 1975. Ofídios da Amazônia VII - As serpents peçonhentas do gênero *Bothrops* (jararacas) e *Lachesis* (surucucu) da região leste do Pará (Ophidia, Viperidae). Bol. Mus. Par. Emílio Goeldi (n. s.) 83:1–42.

———, AND ———. 1978. Ofídios da Amazônia X - As cobras da região leste do Pará.Publ. Avul. Mus. Par. Emílio Goeldi 31:1–218.

———, AND ———. 1982. Ofídios da Amazônia XIV - As espécies de *Micrurus*, *Bothrops*, *Lachesis* e *Crotalus* do sul do Pará e oeste do Maranhão, incluindo áreas de cerrado deste estado. (Ophidia: Elapidae e Viperidae). Bol. Mus. Par. Emílio Goeldi 112:1–58.

———, AND ———. 1993. Ofídios da Amazônia. As cobras da região leste do Pará. Bol. Mus. Par. Emílio Goeldi sér. Zool. 9:1–191.

DAVID, P., AND G. VOGEL. 1996. The Snakes of Sumatra: An Annotated Checklist and Key with Natural History Notes. Edition Chimaira, Frankfurt.

DIXON, J. R. AND P. SOINI. 1986. The Reptiles of the Upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee.

DUARTE, M. R., G. PUORTO, AND F. L. FRANCO. 1995. A biological survey of the pitviper *Bothrops insularis* Amaral (Serpentes, Viperidae): an endemic and threatened offshore island snake of southeastern Brazil. Stud. Neotr. Fauna Environ. 30:1–13.

DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 65:1–352.

EGLER, S. G., OLIVEIRA, M. E., AND M. MARTINS. 1996. *Bothrops atrox* (Common Lancehead). Foraging behavior and ophiophagy. Herpetol. Rev. 27:22–23.

ERNST, C. H. 1992. Venomous Reptiles of North America. Smithsonian Institution Press, Washington.

FORSMAN, A. 1991. Adaptive variation in head size in *Vipera berus* L. populations. Biol. J. Linn. Soc. 43:281–296.

FURTADO, M. F. D., M. MARUYAMA, A. S. KAMIGUTI, AND L. C. ANTONIO. 1991. Comparative study of nine *Bothrops* snake venoms from adult female snakes and their offspring. Toxicon 29:219–226.

GLOYD, H. K., AND R. CONANT. 1990. Snakes of the *Agkistrodon* Complex: A Monographic Review. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology 6. Oxford, Ohio.

GREENE, H. W. 1983. Dietary correlates of the orgin and radiation of snakes. Amer. Zool. 23:431–441.

———. 1989. Ecological, evolutionary and conservation implications of feeding biology of Old World cat snakes, genus *Boiga* (Colubridae). Proc. California Acad. Sci. 46:193–207.

———. 1992. The ecological and behavioral context of pitviper evolution. Pp. 107–117 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

———. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley and Los Angeles.

———, AND G. M. BURGHARDT. 1978. Behavior and phylogeny: constriction in ancient and modern snakes. Science 200:74–77.

———, AND J. A. CAMPBELL. 1972. Notes on the use of caudal lures by arboreal green pitvipers. Herpetologica 28:32–34.

GUTBERLET, R. L., JR. 1998. Phylogenetic relationships of New World pitvipers (Squamata: Crotalinae) as inferred from gross anatomy, epidermal microstructure, and mitochondrial DNA. Unpublished Ph.D. dissertation. The University of Texas at Arlington.

GUYER, C. 1994. The reptile fauna: diversity and ecology. Pp. 210–216 *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.), La Selva: Ecology and Natural History of a Neotropical Rainforest. The University of Chicago Press, Chicago.

HAYES, W. K. 1992. Prey-handling and envenomation strategies of prairie rattlesnakes (*Crotalus v. viridis*) feeding on mice and sparrows. J. Herpetol. 26:496–499.

HOGE, A. R., AND S. A. R. W. D. L. ROMANO. 1973 (dated 1972). Sinopse das serpentes peçonhentas do Brasil. Serpentes, Elapidae e Viperidae. Mem. Inst. Butantan 36:109–207.

———, AND S. A. R. W. D. L. ROMANO-HOGE. 1981a (dated 1978/79). Poisonous snakes of the world. Part 1: Checklist of the pit vipers, Viperoidea, Viperidae, Crotalinae. Mem. Inst. Butantan 42/43:179–309.

———, AND ———. 1981b (dated 1978/79). Sinopse das serpentes peçonhentas do Brasil. Mem. Inst. Butantan 42/43:373–496.

JIAN-LI, L. 1995. China Snake Island. Herpetological series (7). Liaoning Science & Technology Press.

KARDONG, K. V. 1986. Predatory strike behavior of the rattlesnake, *Crotalus viridis oreganus*. J. Comp. Psychol. 100:304–314.

KLAUBER, L. M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. 2 Vols., 2nd ed. University of California Press, Berkeley and Los Angeles.

KRAUS, F., D. G. MINK, AND W. M. BROWN. 1996. Crotaline intergeneric relationships based on mitochondrial DNA sequence data. Copeia 1996:763–773.

LELOUP, P. 1984. Various aspects of venomous snake breeding on a large scale. Acta Zool. Pathol. Antverp. 78:177–198.

LILLYWHITE, H. B. 1987. Temperature, energetics, and physiological ecology. Pp. 422–477, *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade. Analysis of Phylogeny and Character Evolution, ver. 3.07. Sinauer Associates, Sunderland, Massachusetts.

MARQUES, O. A. V., M. MARTINS, AND I. SAZIMA. 2002. A new insular species of pitviper from Brazil, with comments on evolutionary biology and conservation of the *Bothrops jararaca* group (Serpentes, Viperidae) 58:303–312.

MARTINS, M., AND M. GORDO. 1993. *Bothrops atrox* (Common Lancehead). Diet. Herpetol.Rev. 24:151–152.

———, M. S. ARAÚJO, R. J. SAWAYA, and R. NUNES. (2001). Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). J. Zool. 254:529–538.

———, AND M. E. OLIVEIRA. 1999 (dated 1998). Natural history of snakes in forests of the Manaus Region, Central Amazonia, Brazil. Herpetol. Nat. Hist. 6:78–150.

MCDIARMID, R. W., J. A. CAMPBELL, AND T. A. TOURÉ. 1999. Snake Species of the World: A Taxonomic and Geographic Reference. The Herpetologists' League, Washington, D.C.

MORI, A. AND H. MORIGUCHI. 1988. Food habits of the snakes in Japan: a critical review. The Snake 20:98–113.

———, D. JI, H. MORIGUCHI, AND M. HASEGAWA. 1989. Food habits of snakes in East Asia: a biogeographical approach to resource partitioning. Pp. 433–436 *In* M. Matsui, T. Hikida and R. C. Goris (Eds.), Current Herpetology in East Asia: Proceedings of the Second Japan-China Herpetological Symposium, Kyoto, July 1988. Herpetological Society of Japan, Kyoto.

MORIGUCHI, H. 1989. Preliminary observation on *Trimeresurus okinavensis* in the field. Pp. 393–400 *In* M. Matsui, T. Hikida and R.C. Goris (Eds.), Current Herpetology in East Asia: Proceedings of the Second Japan-China Herpetological Symposium, Kyoto, July 1988. Herpetological Society of Japan, Kyoto.

MUSHINSKY, H. R. 1987. Foraging ecology. Pp. 302–334 *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), Snakes: Ecology and Evolutionary Biology. Macmillan, New York.

NEILL, W. T. 1960. The caudal lure of various juvenile snakes. Quart. J. Florida Acad. Sci. 23:173–200.

NORMAN, D. R. 1994. Anfibios y Reptiles del Chaco Paraguayo, Tomo 1; Amphibians and Reptiles of the Paraguayan Chaco, Vol. 1. Private printing, San José, Costa Rica.

PARKINSON, C. L. 1999. Molecular systematics and biogeographical history of pitvipers as determined by mitochondrial ribosomal DNA sequences. Copeia 1999:576–586.

PETERSON, C. R., A. R. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. Pp. 241–314 *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York.

PICADO, T. C. 1976. Serpientes Venenosas de Costa Rica. 2nd ed. Facsimile reprint (originally published in 1931) Editorial Universidad de Costa Rica, Editorial Costa Rica, San José.

POPE, C. H. 1935. The Reptiles of China. Amer. Mus. Nat. Hist., New York.

POUGH, F. H., AND J. D. GROVES. 1983. Specialization of the body form and food habits of snakes. Amer. Zool. 23:443–454.

RAGE, J. -C. 1987. Fossil history. Pp. 51–76 *In* R. A. Seigel, J. T. Collins, and S. S. Novak(Eds.), Snakes: Ecology and Evolutionary Biology. MacMillan, New York.

RODRIGUEZ-ROBLES, J. A., C. J. BELL, AND H. W. GREENE. 1999. Gape size and evolution of diet in snakes: feeding ecology of erycine boas. J. Zool., 248:49–58.

RUBIO, M. 1998. Rattlesnake: Portrait of a Predator. Smithsonian Institution Press, Washington and London.

SAINT GIRONS, H. AND G. NAULLEAU. 1981. Poids des nouveau-nes et strategies reprodutrices des vipères Européenes. Terre Vie 35:597–616.

SALOMÃO, M. G., W. WÜSTER, R. S. THORPE, AND BBBSP. 1999. MtDNA phylogeny of Neotropical pitvipers of the genus *Bothrops* (Squamata: Serpentes:Viperidae). Kaupia 8:127–134.

———, ———, ———, J.-M. TOUZET, AND BBBSP. 1997. DNA evolution of South American pitvipers of the genus *Bothrops* (Reptilia: Serpentes: Viperidae). Symp. Zool. Soc. Lond. 70:89–98.

SAZIMA, I. 1988. Um estudo de biologia comportamental da jararaca, *Bothrops jararaca*, com uso de marcas naturais. Mem. Inst. Butantan 50:83–89.

———. 1989. Comportamento alimentar da jararaca, *Bothrops jararaca*: encontros provocados na natureza. Ciênc. Cult. 41:500–505.

———. 1991. Caudal luring in two Neotropical pitvipers, *Bothrops jararaca* and *B. jararacussu*. Copeia 1991:245–248.

———. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in southeastern Brazil. Pp. 199–216 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

———, AND P. R. MANZANI. 1995. As cobras que vivem numa reserva florestal urbana. Pp. 78–82 *In* P. C. Morellato and H. F. Leitão-Filho (Eds.), Ecologia e Preservação de uma Floresta Tropical Urbana: Reserva de Santa Genebra. Editora da Unicamp, Campinas, Brazil.

———, AND M. MARTINS. 1991 (dated 1990). Presas grandes e serpentes jovens: quando os olhos são maiores que a boca. Mem. Inst. Butantan 52:73–79.

———, AND C. STRÜSSMANN. 1990. Necrofagia em serpentes brasileiras: exemplos e previsões. Rev. Brasil. Biol. 50:463–468.

SCHUETT, G. W., D. L. CLARK, AND F. KRAUS. 1984. Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. Anim. Behav. 32:625–626.

———, E. W. A. GERGUS, AND F. KRAUS. 2001. Phylogenetic correlation between male-male fighting and mode of prey subjugation in snakes. Acta Ethol. 4:31–49.

SCOTT, N. J. 1983. *Bothrops asper* (Terciopelo, Fer-de-lance). Pp. 383–384 *In* D. H. Janzen (Ed.) Costa Rican Natural History. The University of Chicago Press, Chicago and London.

SEXTON, O. 1956-57. The distribution of *Bothrops atrox* in relation to food supply. Bol. Mus. Cienc. Nat. 2-3:47–54.

Shine, R. 1986. Ecology of a low energy specialist: food habits and reproductive biology of the arafura filesnake (Acrochordidae). Copeia 1986:424–437.

———. 1991. Why do larger snakes eat larger prey items? Func. Ecol. 5:493–502.

———. 1994. Allometric patterns in the ecology of Australian snakes. Copeia 1994:851–867.

———, W. R. Branch, P. S. Harlow, and J. K. Webb. 1998. Reproductive biology and food habits of horned adders, *Bitis caudalis* (Viperidae), from southern Africa. Copeia 1998:391–401.

———, and D. J. Slip. 1990. Biological aspects of the adaptive radiation of Australian pythons (Serpentes: Boidae). Herpetologica 46:283–290.

Silva, V. X. 2000. Revisão sistemática do complexo *Bothrops neuwiedi* (Serpentes, Viperidae, Crotalinae). Unpublished Ph.D. dissertation. Universidade de São Paulo, São Paulo.

StatSoft. 1998. Statistica for Windows, Release 5.1. StatSoft, Inc., Tulsa, Oklahoma.

Strimple, P. 1995. Comments on caudal luring in snakes with observations on this behaviour in two subspecies of cantils, *Agkistrodon bilineatus* ssp. Litteratura Serpentium 15:74–77.

Strüssmann, C., and I. Sazima. 1993. The snake assemblage of the Pantanal at Poconé, western Brazil: faunal composition and ecological summary. Stud. Neotr. Fauna Environ. 28:157–168.

Taylor, E. N. 2001. Diet of the Baja California rattlesnake, *Crotalus enyo* (Viperidae). Copeia 2001:553–555.

Valdujo, P. H., C Nogueira, and M. Martins. 2002. Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Brazilian Cerrado. J. Herpetol. 36:169–176.

Vidal, N., G. Lecointre, J. Christophe and, J. P. Gasc. 1999. What can mitochrondrial gene sequences tell us about intergeneric relationships of pitvipers? Kaupia 8:107–112.

Wallace, R. L., and L. V. Diller. 1990. Feeding ecology of the rattlesnake, *Crotalus viridis oreganus* in northern Idaho. J. Herpetol. 24:246–253.

Werman, S. D. 1992. Phylogenetic relationships of Central and South American pitvipers of the genus *Bothrops* (*sensu lato*): cladistic analyses of biochemical and anatomical characters. Pp. 21–40 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

———. 1999. Molecular phylogenetics and morphological evolution in Neotropical pitvipers: an evaluation of mitochondrial DNA sequence information and the comparative morphology of the cranium and palatomaxillary arch. Kaupia 8:113–126.

Wüster, W., M. G. Salomão, G. J. Duckett, R. S. Thorpe, and BBBSP. 1999. Mitochondrial DNA phylogeny of the *Bothrops atrox* species complex (Squamata: Serpentes: Viperidae). Kaupia 8:135–144.

———, ———, R. S. Thorpe, G. Puorto, M. F. D. Furtado, S. A. Hoge, R. D. G. Theakston, and D. A. Warrel. 1997. Systematics of the *Bothrops atrox* complex: new insights from multivariate analysis and mitochondrial DNA sequence information. Symp. Zool. Soc. Lond. 70:99–113.

———, R. S. Thorpe, G. Puorto, and BBBSP. 1996. Systematics of the *Bothrops atrox* complex (Reptilia: Serpentes: Viperidae) in Brazil: a multivariate analysis. Herpetologica 52:263–271.

Yanosky, A. A., J. R. Dixon, and C. Mercolli. 1996. Ecology of the snake community at El Bagual ecological reserve, northeastern Argentina. Herpetol. Nat. Hist. 4:97–110.

APPENDIX I

Data on feeding habits, habitat, and microhabitat were collected from populations from the following states in Brazil, from south to north: *B. alternatus* from Rio Grande do Sul, Santa Catarina, São Paulo, Minas Gerais, and Goiás; *B. cotiara* from Rio Grande do Sul, Santa Catarina, and Paraná; *B. fonsecai* from São Paulo, Rio de Janeiro, and Minas Gerais; *B. itapetiningae* from São Paulo, Minas Gerais, Mato Grosso do Sul, Distrito Federal, and Goiás; *B. erythromelas* from several states in northeastern Brazil; *B. mattogrossensis* from Mato Grosso; *B. neuwiedi* from Minas Gerais and São Paulo; *B. pauloensis* from São Paulo, Minas Gerais, Distrito Federal, and Goiás; *B. pubescens* from Rio Grande do Sul; *B. jararaca* from Rio Grande do Sul, Santa Catarina, Paraná, and São Paulo; *B. insularis* from Queimada Grande Island in São Paulo; *Bothrops alcatraz* from Alcatrazes Island in

São Paulo; *B. bilineatus* from Espírito Santo, Minas Gerais, Pará, Amazonas, and Rondônia (as well as one individual from Leticia, Colombia); *B. taeniatus* from Pará, Maranhão, and Roraima (as well as two individuals from Leticia, Colombia); *B. atrox* from Pará, Maranhão, Amazonas, and Rondônia; *B. leucurus* from Espírito Santo; *B. moojeni* from São Paulo, Minas Gerais, Distrito Federal, Goiás, and Mato Grosso; *B. brazili* from Maranhão, Pará, and Rondônia; *B. jararacussu* from São Paulo, Rio de Janeiro, Paraná, and Santa Catarina.

Data for *B. ammodytoides* are from Argentina; for *B. asper* from Mexico, Belize, Guatemala, Honduras, Costa Rica, Panama, Colombia, and Ecuador; and for *B. hyoprorus* from Amazonian Peru, Ecuador, and Brazil.

APPENDIX II

Diet of 21 species of *Bothrops* and "*Porthidium*" *hyoprora* (see Appendix I; Plate 8b); N = number of prey found in the gut. Data for *B. mattogrossensis* include four records from Strüssman and Sazima (1993); those for *B. brazili* include one record from Dixon and Soini (1986).

Taxon	N	Centipedes	Anurans	Lizards	Snakes	Birds	Mammals
B. hyoprorus	12	8.3	25.0	41.7	0.0	0.0	25.0
B. alternatus	85	0.0	0.0	0.0	0.0	0.0	100.0
B. cotiara	18	0.0	0.0	0.0	0.0	0.0	100.0
B. fonsecai	41	0.0	0.0	0.0	0.0	0.0	100.0
B. itapetiningae	42	9.5	21.4	23.8	0.0	2.4	42.8
B. ammodytoides	5	0.0	0.0	40.0	0.0	0.0	60.0
B. erythromelas	13	23.1	30.8	30.8	0.0	0.0	15.4
B. mattogrossensis	27	0.0	33.3	33.3	0.0	0.0	33.3
B. neuwiedi	29	0.0	0.0	6.9	0.0	0.0	93.1
B. pauloensis	65	10.8	20.0	23.1	7.7	3.1	35.4
B. pubescens	79	2.5	17.7	6.3	7.6	7.6	58.2
B. insularis	36	5.5	8.3	0.0	2.8	83.3	0.0
B. jararaca	45	2.2	17.8	2.2	0.0	6.7	71.1
B. alcatraz	12	66.7	0.0	33.3	0.0	0.0	0.0
B. bilineatus	14	0.0	50.0	7.1	7.1	0.0	35.7
B. taeniatus	22	0.0	40.9	13.6	0.0	4.5	40.9
B. asper	32	0.0	18.7	6.2	12.5	3.1	59.4
B. atrox	233	1.7	33.5	14.2	2.1	2.6	45.5
B. leucurus	39	0.0	12.8	25.6	2.6	2.6	56.4
B. moojeni	107	0.9	33.6	15.9	4.7	2.8	42.1
B. brazili	34	17.6	23.5	14.7	0.0	0.0	44.1
B. jararacussu	67	1.5	16.4	10.4	1.5	0.0	70.1