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Phylogeny and Ecology Determine Morphological Structure in a Snake Assemblage in the Central Brazilian Cerrado

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To investigate the role of ecological and historical factors in the organization of communities, we describe the ecomorphological structure of an assemblage of snakes (61 species in six families) in the Cerrado (a savanna-like grassland) of Distrito Federal, Brazil. These snakes vary in habits, with some being fossorial, cryptozoic, terrestrial, semi-aquatic, or arboreal. Periods of activity also vary. A multivariate analysis identified distinct morphological groups associated with patterns of resource use. We report higher niche diversification compared to snakes in the Caatinga (a semi-arid region in northeastern Brazil), with fossorial and cryptozoic species occupying morphological space that is not occupied in the Caatinga. Monte Carlo permutations from canonical phylogenetic ordination revealed a significant phylogenetic effect on morphology for Colubridae, Colubrinae, Viperidae, Elapidae, and Boidae indicating that morphological divergence occurred in the distant past. We conclude that phylogeny is the most important factor determining structure of this Neotropical assemblage. Nevertheless, our results also suggest a strong ecological component characterizes a peculiar snake fauna.

A central problem in assemblage ecology is to understand if and how assemblages are structured with respect to diversity, trophic relations, and use of space and time (Pianka, 1973; Ricklefs and Schluter, 1993). Processes underlying assemblage structure remain debatable. Comparative and experimental studies centered on competition and predation support the hypothesis that ecological interactions between species affect assemblage structure (Schoener, 1974; Cody and Diamond, 1975). More recently, studies have suggested that historical factors contribute to composition and structure of contemporary assemblages (Cadle and Greene, 1993; Vitt et al., 1999; Mesquita et al., 2006a). Taken together, these studies indicate that ignoring historical information could produce equivocal conclusions about determinants of assemblage structure (Losos, 1996). Despite an enormous effort to understand and make predictions about assemblages, most studies concentrate on limited descriptions of the number and the relative abundance of the species.

Ecomorphology links the functional design of organisms with their environment, and it is increasingly clear that a combination of recent ecological mechanisms and phylogenetic history determine organismal design (Losos, 1990; Wainwright, 1991). In spite of morphological restrictions associated with limblessness, snake morphology varies considerably, and is often tied to macrohabitat use (Guyer and Donnelly, 1990; Cadle and Greene, 1993; Martins et al., 2001). For example, morphological shifts associated with arboreality or fossoriality have occurred independently in phylogenetically unrelated species, suggesting an ecological origin, whereas occurrence of specific morphologies throughout particular clades suggests origin much deeper in the evolutionary history of a particular group (Savitzky, 1983; Lillywhite and Henderson, 1993; Martins et al., 2001). Morphological analyses are frequently used to describe and compare biological assemblages, based on the premise that morphological similarity is correlated with ecological similarity (Ricklefs and Travis, 1980; Ricklefs et al., 1981; Araújo, 1991; Mesquita et al., 2007).

Studies on snake assemblages in South America have been done in different biomes, such as Amazonia (Martins and Oliveira, 1998; Bernarde and Abe, 2006), Atlantic Forest (Marques and Sazima, 2004), Caatinga (Vitt and Vangilder, 1983), Chaco (Leynaud and Bucher, 2001), and Pantanal (Strüssmann and Sazima, 1993). Most have provided information on natural history of the species and discuss some factors that lead to the local structure. In Brazil, only Vitt and Vangilder (1983) studied the morphological structure of a Caatinga snake assemblage and concluded that snake morphology cannot be adequately interpreted in the absence of ecological data. Herein, we describe the snake assemblage from a Cerrado habitat near Brasília, using ecological, morphometrical, and phylogenetic data to examine the relative roles of history and ecology in determining structure of this assemblage.

MATERIALS AND METHODS

Study area.—The Distrito Federal (DF) is located in the nuclear portion of Cerrado biome, a spatially complex habitat varying greatly in vegetative structure, with habitats ranging from interfluvial open areas (campos and cerrados)

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to forest formations (gallery forests). Other typical formations of biome also found in the study area are the humid grasslands and veredas (Eiten, 1994; Oliveira-Filho and Ratter, 1995). For a recent review about Cerrado physiognomies see Oliveira and Marquis (2002). The Distrito Federal covers approximately 5,814 km^2, with altitudes ranging between 750 and 1,340 m. The region is drained by rivers representing three of the most important fluvial basins of Brazil: the basins of Paraná, São Francisco, and Tocantins Rivers (Pinto, 1994). The climate is type Aw in the Köppen classification, receiving annually 1500–2000 mm of a highly predictable and strongly seasonal precipitation, almost entirely restricted to October–April (Nimer, 1989). Average temperatures vary between 20 and 22°C in the winter and summer, respectively (Nimer, 1989).

Natural history.—We analyzed 1,012 snakes collected in Distrito Federal since 1957, mostly from 1993 to 2003. All individuals are deposited in the Coleção Herpetológica da Universidade de Brasília (CHUNB), Coleção Herpetológica do Instituto Butantan (IB), Museu Nacional do Rio de Janeiro (MNRJ), and Museu de Zoologia da Universidade de São Paulo (MZUSP). Additional data were obtained from Coleção Didática of Faculdade da Terra de Brasília (FTB) and the Brasilia Zoo serpentarium. All morphological measures were obtained from preserved individuals. Information on habitat utilization and activity period were obtained by authors from field studies in Distrito Federal since 1993. Feeding data were based on literature and the dissection of 1,012 preserved specimens from the study area.

Morphology.—For each individual, we measured snout–vent length, tail length, circumference around midbody, head length (tip of snout to posterior edge of mandible), head width (at posterior edge of mandible), head height (at its highest point), eye diameter, and distance between nostrils. We took all measurements with electronic calipers to the nearest 0.01 mm. We recorded mass with Pesola scales (10–1000 g), after draining excess preservative fluid through ventral incisions. We log-10 transformed all morphometric variables prior to analyses to meet requirements of normality, and univariate and multivariate outliers were detected and removed (Tabachnick and Fidell, 2001). We defined body size as an isometric size variable (Rohlf and Bookstein, 1987), following the procedure described by Somers (1986), which calculates an isometric eigenvector, defined *a priori* with values equal to $p^{-0.5}$, where p is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size, by post-multiplying the n by p matrix of log-transformed data, where n is the number of observations, by the p by 1 isometric eigenvector.

A principal component analysis (PCA) was performed on log-transformed morphological variables with the SPSS procedure Factor Analysis, following the same method described in Vitt and Vangilder (1983). We tested the occurrence of morphological similarity among species to determine whether structural differences in study areas were associated with differences in morphological space. To measure the niche breadth of snake species, we calculated the mean volume occupied by each species in the assemblage in the morphological space generated by the all-species data set (Ricklefs and Travis, 1980).

A second PCA was performed with the residuals from regressions of morphometric variables (dependent variables) on body size estimators (independent variables), thus adjusting for body size variation among species. With the exception of mass and snout–vent length, all variables were regressed with trunk length to avoid autocorrelation (trunk = snout–vent length − head length). Mass was regressed on total snake length (= snout–vent length + tail length). Principal components were extracted from the covariance matrix of the residuals. In both cases, principal component axes with eingenvalues greater than one were retained. All statistical analyses were performed with SPSS (v. 10.0). Means are presented ± SE.

To assess the role of history in structuring the assemblage, we used Canonical Phylogenetic Ordination–CPO (Giannini, 2003). CPO is a modification of Canonical Correspondence Analysis–CCA (Ter Braak, 1986), a constrained ordination method that promotes the ordination of a set of variables in such a way that its association with a second set of variables is maximized. The significance of the association is tested via randomization of one or both of the data sets. In our CPO, one of the matrices (Y) contained data (morphology) measured across all lizard species in the assemblage, whereas the second matrix (X) consisted of a tree matrix that contained all clades in the assemblage (Fig. 1), each coded separately as a binary variable. The analysis thus consisted of finding the subset of groups (columns of X) that best explained the variation in Y, using CCA coupled with Monte Carlo permutations. We performed CPO in CANOCO 4.5 for Windows, using the following parameters: symmetric scaling, biplot scaling, downweighting of rare species, manual selection of environmental variables (monophyletic groups), 9,999 permutations, and unrestricted permutations.

RESULTS

Natural history.—The snake assemblage of Distrito Federal is species-rich, composed of 61 species distributed across six families (Table 1). Colubridae is the richest family with 50 species, while Anomalepididae and Leptotyphlopidae have only one species each. The dominant colubrid lineage is the subfamily Xenodontinae (59% of total richness). Two tribes of the Xenodontinae, Xenodontini and Pseudoboini, each comprise 25% of the subfamily species.

The snakes show a diversity of natural history characteristics (Table 1). Twenty-seven species are strictly terrestrial, six are strictly fossorial, five are strictly cryptozoic, 14 use arboreal microhabitats, and six use aquatic habitats frequently. Segregation exists in the preference for riparian environments in gallery forest and vereda (23 species) and interfluvial habitats in cerrado and campo (34 species). Only four species are typically found in all Cerrado habitats (*Liotyphlops ternetzii*, *Mastigodryas bifossatus*, *Oxyrhopus guibei*, and *Waglerophis merremii*). A relationship between activity patterns and phylogeny is evident. Almost all species that belong to the same family (except Colubridae) are active during the same time period (Table 1). Within Colubridae, a relationship between activity patterns and phylogeny is evident at the tribe level (Table 1). Most snakes are diurnal (39%), many are nocturnal (33%), and some are active during both periods (28%; Table 1). Most snakes are strictly terrestrial or terrestrial and semi-arboreal (57%), and many are fossorial or cryptozoic (20%). Six species are found in aquatic environments and six are mainly arboreal (Table 1).

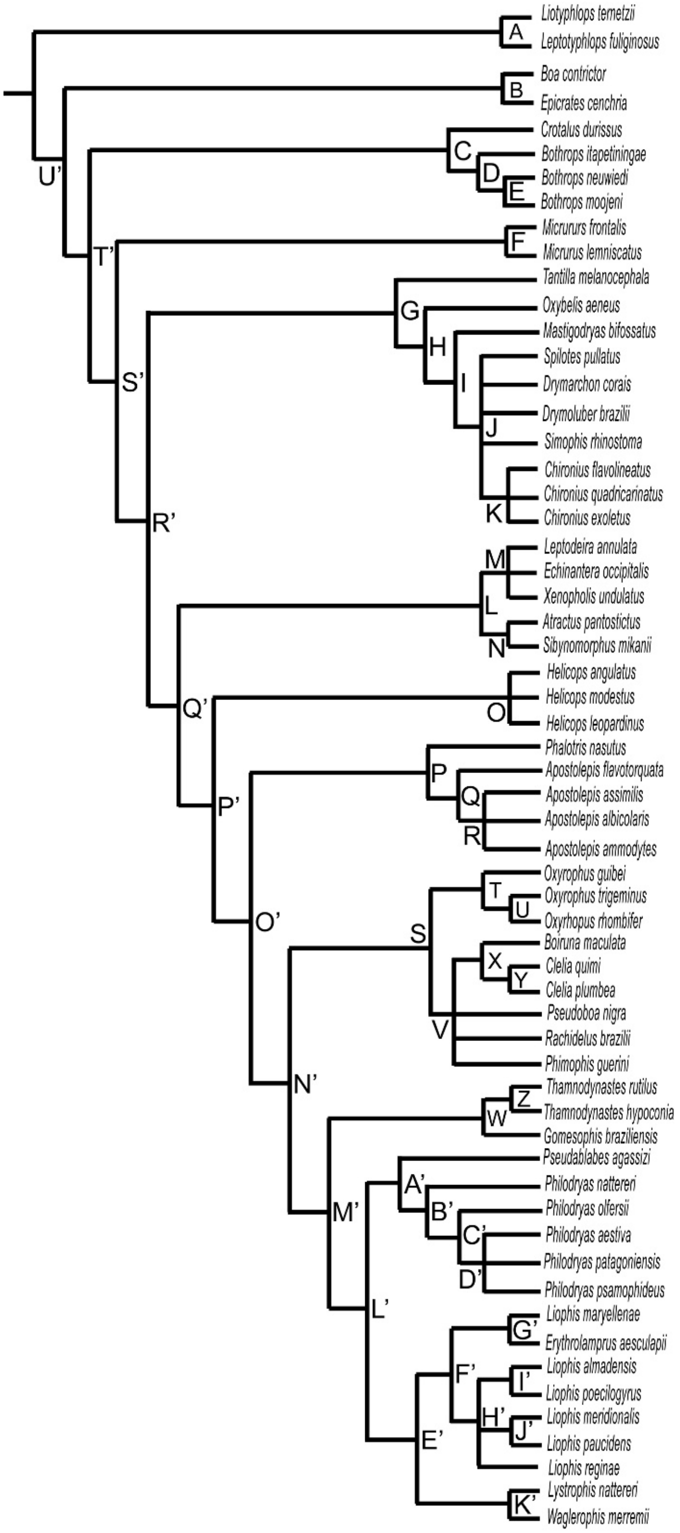

Fig. 1. Individual groups used in canonical phylogenetic ordination for microhabitat and diet data. Phylogeny based on Burbrink (2005); Cadle and Greene (1993); Dixon (1985); Ferrarezzi (1993, 1994); Ferrarezzi et al. (2005); Greene (1997); Lawson et al. (2005); Lobo and Scrocchi (1994); Martins et al. (2002); Vidal et al. (2000); Wüster et al. (2002); and Zaher (1999).

The 61 sympatric snakes feed on 13 prey categories, varying from invertebrate eggs to vertebrates (Tables 1, 2). Twenty-nine species are diet specialists, with diets restricted to one class of organisms. Nevertheless, the genera *Eunectes*, *Bothrops*, *Drymarchon*, and *Mastigodryas* feed on five or more classes. Mammals, amphibians, and lizards are the most common prey of snake species in Distrito Federal. Invertebrates are consumed by scolecophidians (insects), *Bothrops* (chilopods), Dipsadini (''goo-eaters''—slugs and snails), *Atractus pantostictus* and *Sibynomorphus mikanii* (earthworms and gastropods), *Gomesophis brasiliensis* (earthworms), *Pseudablabes agassizii* (arachnids), and *Tantilla melanocephala* (chilopods).

Morphology.—We measured 914 specimens. Only *Eunectes murinus*, the largest snake species of the region, was not measured because the single specimen collected from study area was poorly preserved and we were unable to take morphological measures accurately. Table 3 summarizes these data.

Two axes extracted by the PCA explain 96.3% of morphological variation. All nine variables were positively correlated with the first axis (87% of the variation; Table 4). This axis shows high loadings for head measures, trunk, and mass, representing variation along general body size gradient. The second axis (6% of the variation) was positively correlated with tail length and eye diameter, which are measures independent of the increase in body size.

Fossorial and cryptozoic species have low values for the two axes. The species with long and heavy bodies and big heads, such as boids and vipers, scored strongly positive on the first factor, whereas the species that have long tails and larger eye diameters, such as colubrine snakes, scored strongly positive on the second factor (Fig. 2). The morphological volume of the entire snake assemblage was 0.24, and the mean volume per species is 0.0041.

Two axes extracted from the PCA using regression residuals explained 85% of size-adjusted morphology (Table 5). The first axis (65% of the variation) describes a gradient based on three head measures and body circumference, and can be considered as an isometric axis. The second axis (19% of the variation) is highly and negatively influenced by the tail length and eye diameter and positively influenced by mass, and can be considered as an allometric axis. All variables that contributed most to the principal components were significantly correlated with their respective principal component ($P < 0.0001$).

It is evident that some morphologically similar species are similar in one or more natural history attributes (Fig. 3). In most cases these are closely related, congeneric snakes, such as those in the genera *Apostolepis*, *Bothrops*, *Chironius*, and *Helicops*, indicating the importance of phylogeny. However, some non-related snakes were morphologically similar in natural history attributes. The earthworm specialists *Atractus pantostictus* (Dipsadinae) and *Gomesophis brasiliensis* (Tachymenini) are clustered together, as are the semiarboreal, diurnal *Chironius* (Colubrinae) and *Philodryas* (Xenodontinae: Philodryadini; Fig. 3), indicating that both historical and ecological factors contribute to ecomorphology.

Monte Carlo permutations (based on 9,999 permutations) from the canonical ordination revealed a significant phylogenetic effect on morphological aspects of the snake assemblage of Central Brazilian Cerrado (Table 6). Colubridae (R′), Colubrinae (G), Colubrini (H), Viperidae (C), Elapidae (F), and Boidae (B) contributed most to morphological variation, all being statistically significant (Fig. 1; Table 6).

Table 1. Summary of the Information of Natural History of the Snakes in Distrito Federal. Abbreviations are: A = arboreal, C = cryptozoic, F = fossorial, T = terrestrial, SAB = semi-arboreal, SAQ = semi-aquatic, CA = Campo, CE = Cerrado, GF = Gallery Forest, VE = Vereda, N = nocturnal, D = diurnal, ND = nocturnal–diurnal, abn = amphisbaenian, amp = amphibian, ann = annelids, arn = aranae, bi = birds, chi = chilopoda, cro = crocodylians, fi = fish, gas = gastropode, ins = insecta, li = lizards, mam = mammals, sn = snakes. Capital letter means main habitats.

FAMILY SUBFAMILY Species	Habits	Habitats	Activity	Diet	Reference
ANOMALEPIDIDAE					
Liotyphlops ternetzii	F	CA, CE, GF	N	Ins	This work
LEPTOTYPHLOPIDAE					
Leptotyphlops fuliginosus	F	CA, CE	N	Ins	Sawaya, 2003
BOIDAE					
Boa constrictor	T, SAB	GF, ce	ND	Mam, bi	Henderson et al., 1995
Epicrates cenchria	T, SAB	CE, ca	ND	Mam, bi, li	Henderson, 1993
Eunectes murinus	SAQ	GF, VE	ND	Mam, bi, fi, li, sn, cro	Strimple, 1993
VIPERIDAE					
Bothrops itapetiningae	T	CA, ce	ND	Mam, li, amp, bi, chi	Martins et al., 2002
Bothrops moojeni	T	GF, ve, ce	ND	Mam, li, amp, bi, sn, chi	Nogueira et al., 2003
Bothrops neuwiedi	T	CA, ce	ND	Mam, li, amp, bi, sn, chi	Valdujo et al., 2002
Crotalus durissus	T	CE, CA, gf	ND	Mam, bi	Salomão et al., 1995
ELAPIDAE					
Micrurus frontalis	C	CE, CA, gf	ND	Sn, abn	Roze, 1996
Micrurus lemniscatus	C	GF	N	Sn	Roze, 1996
COLUBRIDAE					
COLUBRINAE					
Chironius exoletus	A, T	GF	D	Amp, li, bi, mam	Dixon et al., 1993
Chironius flavolineatus	A, T	GF, ve, ce	D	Amp, li, bi, mam	Dixon et al., 1993
Chironius quadricarinatus	A, T	CE, ca	D	Amp, li, bi, mam	Dixon et al., 1993
Drymarchon corais	T, SAB	CE, gf	D	Mam, amp, li, bi, sn, abn	Cunha and Nascimento, 1978
Drymoluber brazili	T	CE	D	Li	Marques et al., 2005
Mastigodryas bifossatus	T	CE, GF, CA	D	Mam, amp, li, bi, sn, abn	Marques et al., 2005
Oxybelis aeneus	A, SAB	CE	D	Amp, li, bi, mam	Martins and Oliveira, 1998
Simophis rhinostoma	T	CE, CA	D	Amp	Bizerra et al., 1994
Spilotes pullatus	A, SAB	GF, ve, ce	D	Bi, mam	Martins and Oliveira, 1998
Tantilla melanocephala	F, C	CA, CE	N	Chi	Marques and Puorto, 1998
DIPSADINAE					
DIPSADINI					
Atractus pantostictus	C	GF, ce	N	Ann	Sawaya, 2003
Sibynomorphus mikanii	T, SAB	VE, GF, ce	N	Gás	Laporta-Ferreira et al., 1986
LEPTODERINI					
Echinantera occipitalis	T	CE, CA, gf	D	Li, amp	Scrocchi and Giraudo, 2005
Leptodeira annulata	A, SAB	GF, VE	N	Amp	Vitt, 1996
Xenopholis undulatus	C	GF	N	Amp	Cunha and Nascimento, 1993
XENODONTINAE					
ELAPOMORPHINI					
Apostolepis albicollaris	F	CE, CA	ND	Abn	Lema, 2001
Apostolepis ammodytes	F	CA	ND	Abn	Lema, 2001
Apostolepis assimilis	F	CE, CA, gf	ND	Abn	This work
Apostolepis flavotorquata	F	CE	ND	Abn	Lema, 2001
Phalotris nasutus	C, F	CA, CE	ND	Abn, Sn	This work
HYDROPSINI					
Helicops angulatus	SAQ	GF, VE	N	Fi, Amp	Martins and Oliveira, 1998
Helicops leopardinus	SAQ	GF	N	Fi, Amp	Scrocchi and Giraudo, 2005
Helicops modestus	SAQ	GF, VE	N	Fi, Amp	Sawaya, 2003
TACHYMENINI					
Gomesophis brasiliensis	SAQ	VE, gf	N	Ann	Oliveira et al., 2003
Thamnodynastes hypoconia	T, SAB	VE, gf	N	Amp	Sawaya, 2003
Thamnodynastes rutilus	T, SAQ	GF	N	Amp, fi	Vanzolini, 1948
PHILODRIADINI					
Philodryas aestiva	T	CA, ce	D	Mam, li	Scrocchi and Giraudo, 2005
Philodryas nattereri	T, SAB	CE, ca	D	Mam, amp, li, bi	Vitt, 1980
Philodryas olfersii	SAB, T	GF, ce	D	Mam, amp, li, bi	Hartmann and Marques, 2005

Table 1. Continued.

FAMILY SUBFAMILY Species	Habits	Habitats	Activity	Diet	Reference
Philodryas patagoniensis	T, SAB	CE, ca, ve	D	Mam, amp, li, bi	Hartmann and Marques, 2005
Philodryas psammophideus	T	CE	D	Li	Marques et al., 2005
Pseudablabes agassizii	T	CA, ce	D	Arn	Marques et al., 2006
PSEUDOBOINI					
Boiruna maculata	T	CE	N	Sn, mam	Pinto and Lema, 2002
Clelia plumbea	T	GF	N	Sn, li, mam	Pinto and Lema, 2002
Clelia quimi	T	GF, ce	N	Sn, mam	Pinto and Lema, 2002
Oxyrhopus guibei	T	GF, CE, CA	N	Li, mam	Andrade and Silvano, 1996
Oxyrhopus rhombifer	T	CA, CE, gf	N	Li, mam	França and Araújo, 2005
Oxyrhopus trigeminus	T	CE, CA	N	Li, mam	Vitt and Vangilder, 1983
Phimophis guerini	C	CE, CA	N	Li	Sawaya, 2003
Pseudoboa nigra	T	CE	N	Li	Vitt and Vangilder, 1983
Rhachidelus brazili	T	CE	N	Bi (eggs)	Marques and Oliveira, 2004
XENODONTINI					
Erythrolamprus aesculapii	T, C	GF	D	Sn, li	Marques and Puorto, 1994
Liophis almadensis	T	CE, CA, gf	D	Amp	Michaud and Dixon, 1989
Liophis maryellenae	T, SAQ	VE, gf	D	Fi, Amp	Cassimiro and Bertoluci, 2003
Liophis meridionalis	T	CE, CA, gf	D	Amp, li	Sawaya, 2003
Liophis paucidens	T	CE	D	Li	Michaud and Dixon, 1989
Liophis poecilogyrus	T	CE, CA, gf	D-N	Amp	Sawaya, 2003
Liophis reginae	T	GF	D-N	Amp	Michaud and Dixon, 1989
Lystrophis nattereri	T	CA, ce	D	Li (eggs)	Sawaya, 2003
Waglerophis merremii	T	CE, GF	D	Amp	Vitt, 1983

DISCUSSION

Natural history.—The snake fauna from the Distrito Federal is more diverse than other assemblages from Cerrado, including Pirassununga, São Paulo, with 22 species (Vanzolini, 1948) and Cuiabá, Mato Grosso, with 37 species (Carvalho and Nogueira, 1998) and with snake faunas from other South American biomes, including Atlantic forest, with 30 species in Juréia, São Paulo (Marques and Sazima, 2004), Caatinga, with 19 species in Exu, Pernambuco (Vitt and Vangilder, 1983), Chaco, with 21 species in Los Colorados, Salta, Argentina (Leynaud and Bucher, 2001), and Pantanal, with 26 species in Poconé, Mato Grosso (Strüssmann and Sazima, 1993). Only Amazonian snake assemblages have similar or higher richness than Distrito Federal: 66 species in Ducke reserve near Manaus, Amazonas (Martins and Oliveira, 1998), 62 in INPA-WWF reserve near Manaus, Amazonas (Zimmerman and Rodrigues, 1990), and 56 in Espigão do Oeste, Rondônia (Bernarde and Abe, 2006).

Habitat selection has been frequently reported as the primary factor maintaining species diversity and assemblage structure in sympatric snakes (Reinert, 1984, 2001; Borges and Araújo, 1998). In our study area, only *Liotyphlops ternetzii*, *Mastigodryas bifossatus*, *Oxyrhopus guibei*, and *Oxyrhopus rhombifer* are found in all Cerrado habitats. The remaining species were found in riparian (36% of 61 species) and interfluvial habitats (57%). Snake species are not randomly distributed across habitats in our study area. Two factors contribute to this pattern. First, the open interfluvial grasslands of Cerrado are dominant when compared with the riparian forests (Oliveira-Filho and Ratter, 1995). Second, phylogenetic lineages with high number of species in Cerrado, like the tribes Elapomorphini and Philodriadini, use interfluvial habitats preferentially. Habitat selection can also result from variation in foraging environments. All snakes are predators, and the location and distribution of their prey has undoubtedly played an important role in the evolution of habitat selection in snakes (Greene, 1983; Reinert, 2001; Martins et al., 2002). Most snake species in this assemblage feed on amphibians and are found in riparian habitats, where amphibians are abundant and diverse, whereas all snakes that prey on amphisbaenians select open interfluvial habitats.

Structure of Cerrado vegetation, dominated by open habitats that comprise approximately 75% of the domain (Eiten, 1994), may account for high diversity of terrestrial species. For example, in Distrito Federal, the Colubrinae subfamily, a lineage usually associated with arboreal habitats (Cadle and Greene, 1993), is represented by a high number of terrestrial species (40%). In central Amazonia the Colubrinae accounts for 21% of all snake species, 80% of which are arboreal (Martins and Oliveira, 1998). A similar pattern occurs in Dipsadinae snakes. Among the five species (five genera) in Distrito Federal, only *Leptodeira annulata* is primary arboreal. However, in Amazon rainforest near Manaus, three genera (*Dipsas*, *Imantodes*, and *Leptodeira*) are primary arboreal and live in forest (Martins and Oliveira, 1998).

Morphology, resource utilization, and historical effects.—All phylogenetic lineages present in Cerrado and Caatinga assemblages cover the same morphological space. The Boidae (*Boa constrictor* and *Epicrates cenchria*) and the viper *Crotalus durissus* form a cluster of heavy-body snakes and separate from arboreal snakes in both assemblages. Moreover, species with morphological characters associated with arboreality or rapid locomotion have high positive scores on factor 2 and mid-range scores on factor 1 in both

Table 2. Summary of Stomach Content Analysis for Snakes Sampled in Distrito Federal. Abbreviations are: SE = stomachs examined, SCF = stomachs containing food.

FAMILY				
SUBFAMILY			Stomach contents	
Species	SE	SCF	Prey classes	Identification
ANOMALEPIDIDAE				
Liotyphlops ternetzii	20	2	Isoptera	*Nasutitermes* sp. and eggs
BOIDAE				
Boa constrictor	9	2	Mammals	Muridae
			Lizards	*Ameiva ameiva*
Epicrates cenchria	10	3	Mammals	Muridae and unidentified
			Lizards	*Ameiva ameiva*
VIPERIDAE				
Bothrops itapetiningae	9	4	Lizards	*Tropidurus* sp. and Gymnophthalmidae
			Mammals	*Bolomys lasiurus* and unidentified
Bothrops moojeni	30	22	Anurans	*Leptodactylus fuscus* and *Hyla albopunctata* (2)
			Chilopode	*Otostygmus* sp.
			Lizards	*Ameiva ameiva*, *Tropidurus* sp., and unidentified (3)
			Mammals	*Bolomys lasiurus* (3), *Oligoryzomes* sp., and unidentified (13)
Bothrops neuwiedi	15	10	Anurans	*Scinax fuscovarius* and *Scinax* sp. (2)
			Chilopode	*Otostygmus* sp.
			Lizards	*Cercosaura ocellata*
			Mammals	Muridae, *Calomys tener*, and unidentified (4)
Crotalus durissus	30	14	Mammals	Muridae (2), *Bolomys lasiurus*, and unidentified (11)
ELAPIDAE				
Micrurus frontalis	9	2	Snakes	Colubridae (2)
Micrurus lemniscatus	7	1	Snakes	*Sibynomorphus mikanii*
COLUBRIDAE				
COLUBRINAE				
Chironius exoletus	2	1	Anurans	*Hyla albopunctata*
Chironius flavolineatus	7	2	Anurans	*Hyla* sp. (2) and unidentified
Chironius quadricarinatus	8	4	Anurans	*Hyla* sp. (2), *Scinax fuscovarius*, and *Physalaemus cuvieri*
Drymarchon corais	10	4	Amphisbaenians	*Amphisbaena alba*
			Anurans	Unidentified and *Bufo paracnemis* (2)
			Snakes	*Erythrolamprus aesculapii*
			Mammals	Muridae and unidentified
Drymoluber brazili	2	1	Lizards	Gymnophthalmidae
Mastigodryas bifossatus	11	4	Amphisbaenians	*Amphisbaena vermicularis*
			Anurans	*Hyla albopunctata* (2)
			Lizards	*Mabuya nigropunctata* and *Tropidurus itambere*
Oxybelis aeneus	3	2	Lizards	*Micrablepharus atticolus*
			Anurans	Hylidae
Simophis rhinostoma	5	1	Anurans	Unidentified
Spilotes pullatus	7	2	Mammals	Unidentified (2)
			Birds	Unidentified
Tantilla melanocephala	10	4	Chilopode	*Otostygmus* sp. (4)
DIPSADINAE				
Atractus pantostictus	3	1	Annelids	Unidentified
Echinantera occipitalis	7	1	Lizards	Gymnophthalmidae
Sibynomorphus mikanii	24	4	Molluscs	Unidentified (11)
Leptodeira annulata	1	1	Anurans	Hylidae
XENODONTINAE				
Apostolepis assimilis	4	1	Amphisbaenians	*Bronia* sp. (2)
Phalotris nasutus	4	1	Amphisbaenians	*Amphisbaena alba*
Helicops modestus	5	1	Fish	Unidentified
Philodryas aestiva	7	2	Mammals	Unidentified
			Lizards	*Ameiva ameiva*
Philodryas nattereri	30	18	Mammals	Echimidae and unidentified (12)
			Lizards	*Mabuya* sp., *Tropidurus itambere*, and *T. torquatus* (4)
			Anurans	Unidentified
			Birds	*Volatinia jacarina* (1), unidentified
			Birds	

Table 2. Continued.

FAMILY SUBFAMILY			Stomach contents	
Species	SE	SCF	Prey classes	Identification
Philodryas olfersii	22	8	Mammals	Unidentified (2)
			Lizards	*Ameiva ameiva* and *Enyalius* sp.
			Anurans	Hylidae (3)
			Birds	*Gnorimopzar chopi* (2)
Philodryas patagoniensis	34	17	Mammals	Unidentified (8)
			Lizards	*Ameiva ameiva*, *Mabuya* sp. (2), *Tropidurus* sp., and *Micrablepharus atticolus*
			Snakes	Colubridae
			Anurans	Hylidae
			Birds	Unidentified
Pseudablabes agassizii	12	2	Aranae	Lycosidae (3)
Boiruna maculata	3	1	Snakes	*Liophis poecilogyrus*
Oxyrhopus guibei	24	7	Lizards	*Ameiva ameiva*, *Tropidurus torquatus* (2), and *Pantodactylus scherbersii* (2)
			Mammals	Muridae and unidentified
Oxyrhopus rhombifer	34	16	Lizards	*Anolis meridionalis*, *Mabuya nigropunctata*, *Tropidurus itambere*, *T. torquatus* (3), *Micrabepharus atticolus* (2), *Colobosaura modesta*, and *Ameiva ameiva* (3)
			Mammals	Unidentified (2)
Oxyrhopus trigeminus	12	7	Lizards	*Tropidurus* sp. and *Ameiva ameiva*
			Mammals	Unidentified (3)
Phimophis guerini	1	1	Lizards	Gymnophthalmidae
Pseudoboa nigra	2	1	Lizards	*Tropidurus torquatus*
Rhachidelus brazili	3	1	Birds	Eggs
Thamnodynastes hypoconia	6	1	Anurans	Hylidae
Erythrolamprus aesculapii	20	4	Snakes	Colubridae, *Atractus pantostictus*, *Sibynomorphus mikanii* (2), and *Xenopholis undulates*
Liophis almadensis	8	2	Anurans	*Leptodactylus* sp. and Leptodactylidae
Liophis maryellenae	2	1	Fish	Unidentified
Liophis meridionalis	10	1	Lizards	Gymnophthalmidae
Liophis paucidens	1	1	Lizards	*Cnemidophorus ocellifer* (2)
Liophis poecilogyrus	43	9	Anurans	*Physalaemus centralis*, *Hyla* sp. (2), *Bufo paracnemis* (2), and unidentified (12)
Liophis reginae	18	4	Anurans	*Leptodactylus* sp. (2) and *Hyla* sp. (2)
Waglerophis merremii	20	7	Anurans	*Bufo schneideri* (5) and *Leptodactylus* sp. (2)

assemblages, which suggests high influence of phylogeny; the same lineages in drastically different environments show the same ecological traits (Brooks and McLennan, 1993; Losos, 1996).

The morphological space of the Distrito Federal snake assemblage is more tightly packed than the Exu assemblage, due the presence of snakes with ecological attributes not represented in Caatinga. For example, the fossorial and cryptozoic snakes (*Apostolepis*, *Leptotyphlops*, *Liotyphlops*, *Micrurus*, and *Phalotris*), which have low scores on factors 1 and 2, have relatively small heads with small eyes, short tails and elongated bodies. In Caatinga only *Micrurus ibiboboca* is cryptozoic and also has low scores on both factors. In ecomorphological analysis of assemblage structure, the degree of species packing into niche space is estimated by morphological distances between nearest neighbors or by the average morphological volume occupied per species (Ricklefs and Travis, 1980). Although Vitt and Vangilder (1983) did not provide the measure of the morphological volume occupied by the Caatinga assemblage, morphological volume of Cerrado assemblage would most likely be higher mainly due the presence of fossorial and cryptozoic species. In the absence of data on the morphological space occupied by snake assemblages from other South American habitats, further comparisons cannot be made.

In snakes, habitat use and prey type often correlate with morphology (Pough and Groves, 1983; Cadle and Greene, 1993; Vitt, 2001). The PCA of regression residuals of morphological variables of Cerrado snakes reveals some interesting ecological and phylogenetic associations. Fossorial and cryptozoic snakes (*Apostolepis*, *Leptotyphlops*, *Liotyphlops*, *Micrurus*, and *Phalotris*) have low scores on factor 1 revealing relatively small heads with small eyes and short tails. These morphological features are recognized as adaptations for these secretive habits (Savitzky, 1983; Greene, 1997). Examining morphological similarity of species with these features, we can distinguish a phylogenetically similar group as the basal scolecophidian and another group, the Elapomorphini *Apostolepis*, both both of which consist entirely of fossorial species. However, the similar morphology of *Phalotris nasutus* and the two coralsnakes (family Elapidae), *Micrurus frontalis* and *M. leminisca-*

Table 3. Morphological Measurements of Species of Snakes, Reported as Mean ± SE. All measurements in mm unless otherwise indicated. Abbreviations are: SVL = snout–vent length, TL = tail length, CIR = circumference around midbody, HL = head length, HW = head width, HH = head height, ED = eye diameter, BN = between nostrils. *n* = Sample sizes. For abbreviations see Table 1.

FAMILY SUBFAMILY Tribe Species	SVL	TL	CIR	HL	HW	HH	ED	BN	Mass (g)
ANOMALEPIDIDAE									
L. ternetzii (30)	239 ± 61 (93–319)	4 ± 1 (1.85–6.35)	14 ± 4 (6–20)	5.09 ± 0.93 (2.34–6.94)	2.91 ± 0.48 (1.88–3.63)	2.41 ± 0.51 (1.52–2.89)	0.00	1.65 ± 0.38 (0.91–2.5)	3 ± 3 (1–5)
LEPTOTYPHLOPIDAE									
L. fuliginosus (1)	165	17	18	6.51	3.65	3.39	0.00	1.65	3
BOIDAE									
B. constrictor (14)	599 ± 268 (263–1028)	78 ± 40 (34.1–121)	92 ± 45 (51–170)	38.00 ± 11.86 (25.03–63.02)	24.00 ± 9.09 (14.12–42.22)	15.27 ± 5.01 (9.75–23.61)	3.81 ± 0.50 (3.17–4.77)	5.54 ± 1.33 (4.12–7.38)	463 ± 540 (37–1500)
E. cenchria (21)	521 ± 261 (233–1097)	67 ± 35 (28–139)	71 ± 35 (31–136)	29.31 ± 11.07 (17.43–50.13)	16.74 ± 6.51 (9.65–28.12)	12.01 ± 4.64 (7.52–20.32)	3.45 ± 0.91 (2.44–5.76)	4.36 ± 1.48 (2.79–8.35)	279 ± 380 (17–1100)
VIPERIDAE									
B. itapetiningae (13)	304 ± 117 (180–511)	39 ± 13 (27–63)	45 ± 14 (30–75)	20.11 ± 4.97 (14.7–26.66)	11.63 ± 3.71 (8.6–18.64)	8.83 ± 1.97 (7.24–13.13)	2.89 ± 0.41 (2.7–3.45)	4.63 ± 0.84 (3.89–6.15)	38 ± 40 (9–125)
B. moojeni (45)	618 ± 320 (200–1461)	101 ± 48 (42–181)	65 ± 32 (31–135)	32.77 ± 14.10 (16.65–61.57)	20.80 ± 9.63 (10.8–43.08)	13.37 ± 5.37 (7.38–25.08)	4.29 ± 1.24 (2.88–6.67)	5.75 ± 1.91 (3.07–9.91)	217 ± 284 (7–1200)
B. neuwiedi (26)	413 ± 145 (160–615)	60 ± 21 (26–88)	41 ± 12 (24–69)	22.89 ± 5.30 (15.25–32.33)	13.90 ± 3.48 (6.88–21.46)	9.52 ± 1.95 (5.48–13.97)	3.43 ± 0.55 (2.49–4.45)	4.39 ± 0.79 (2.84–5.6)	43 ± 30 (8–113)
C. durissus (50)	755 ± 263 (300–1167)	69 ± 32 (20–129)	106 ± 42 (32–170)	39.18 ± 10.30 (19.57–53.95)	26.26 ± 7.58 (12.37–36.25)	17.45 ± 5.50 (7.63–26.93)	4.49 ± 0.89 (3.1–5.77)	6.89 ± 1.35 (4.69–8.61)	613 ± 487 (20–1650)
ELAPIDAE									
M. frontalis (17)	650 ± 234 (350–1123)	42 ± 14 (23–68)	40 ± 15 (21–83)	18.86 ± 5.66 (11.08–26.08)	11.61 ± 3.55 (6.13–18.85)	7.59 ± 2.29 (4.15–12.95)	1.76 ± 0.50 (1.17–3.02)	5.13 ± 1.20 (3.22–7.68)	80 ± 94 (12–390)
M. lemniscatus (8)	603 ± 312 (283–1227)	43 ± 20 (23–85)	38 ± 19 (20–78)	18.64 ± 7.98 (11.52–34.9)	10.50 ± 4.45 (6.32–19.85)	7.51 ± 3.54 (4.11–14.83)	1.27 ± 0.48 (0.9–1.93)	4.47 ± 1.69 (2.97–7.94)	84 ± 139 (7–420)
COLUBRIDAE									
COLUBRINAE									
C. exoletus (4)	807 ± 96 (670–890)	469 ± 51 (405–529)	54 ± 6 (45–60)	32.10 ± 3.54 (27.35–35.9)	16.88 ± 2.32 (13.67–19.21)	11.54 ± 1.44 (9.66–13.17)	6.37 ± 0.67 (5.67–7.03)	6.60 ± 0.66 (5.74–7.2)	147 ± 57 (77–200)
C. flavolineatus (13)	675 ± 119 (288–749)	441 ± 91 (164–515)	44 ± 11 (18–57)	26.94 ± 9.40 (13.93–27.36)	11.82 ± 2.08 (6.28–14.94)	8.59 ± 1.35 (4.32–9.64)	4.99 ± 0.70 (3.13–5.54)	5.22 ± 0.88 (2.54–5.86)	89 ± 30 (5–120)
C. quadricarinatus (15)	599 ± 81 (386–738)	360 ± 57 (232–435)	42 ± 7 (27–50)	25.09 ± 3.11 (17.3–30.65)	11.23 ± 1.59 (7.28–12.69)	8.53 ± 1.21 (5.32–10.38)	4.63 ± 0.48 (3.64–5.21)	5.18 ± 0.55 (3.85–5.89)	58 ± 22 (15–95)
D. corais (16)	1249 ± 297 (387–1585)	304 ± 85 (89–343)	108 ± 31 (40–175)	47.68 ± 9.25 (22.85–59.55)	28.81 ± 6.65 (13.37–38.66)	20.83 ± 4.87 (7.99–26.11)	6.41 ± 0.89 (4.11–7.38)	9.22 ± 2.18 (4.29–11.76)	829 ± 460 (28–1750)
D. brazili (4)	493 ± 188 (270–983)	129 ± 49 (94–210)	45 ± 20 (21–73)	20.07 ± 6.43 (17.7–35.89)	10.47 ± 2.76 (7.61–17.32)	7.96 ± 1.91 (5.61–12.01)	2.27 ± 0.58 (3.69–5.86)	3.55 ± 0.86 (3.19–6.87)	89 ± 104 (5–290)

Table 3. Continued.

FAMILY SUBFAMILY Tribe Species	SVL	TL	CIR	HL	HW	HH	ED	BN	Mass (g)
M. bifossatus (11)	1017 ± 383 (445–1560)	393 ± 138 (158–536)	86 ± 37 (37–150)	45.65 ± 14.71 (23.45–67.57)	24.71 ± 9.45 (12.19–44.65)	16.11 ± 5.33 (9.02–23.95)	6.91 ± 1.67 (4.99–9.13)	7.25 ± 2.12 (4.19–9.47)	523 ± 415 (40–1150)
O. aeneus (3)	749 ± 48 (695–785)	469 ± 32 (445–505)	31 ± 1 (30–32)	29.07 ± 1.60 (27.34–30.51)	7.45 ± 0.99 (6.61–8.54)	8.43 ± 0.72 (7.71–9.14)	3.56 ± 0.39 (3.17–3.95)	2.82 ± 0.43 (2.51–2.63)	44 ± 8 (35–51)
S. rhinostoma (11)	449 ± 105 (265–575)	116 ± 27 (66–150)	34 ± 7 (21–45)	19.43 ± 2.59 (13.97–22.47)	9.88 ± 1.25 (7.04–11.42)	7.10 ± 1.10 (4.98–8.2)	2.87 ± 0.37 (2.11–3.46)	4.34 ± 0.35 (3.62–4.69)	32 ± 20 (8–67)
S. pullatus (9)	1299 ± 298 (710–1608)	432 ± 114 (213–557)	93 ± 22 (50–121)	40.63 ± 6.48 (28.01–46.86)	22.73 ± 3.81 (14.93–27.45)	17.91 ± 3.63 (10.16–21.58)	6.13 ± 0.63 (4.84–6.73)	8.96 ± 1.55 (6.11–10.67)	670 ± 318 (95–1005)
T. melanocephala (15)	228 ± 62 (123–380)	73 ± 22 (35–115)	21 ± 6 (12–35)	9.44 ± 1.41 (6.98–11.77)	4.90 ± 1.15 (3.51–7.91)	3.65 ± 0.71 (2.5–5.34)	1.18 ± 0.28 (0.73–1.54)	2.25 ± 0.55 (1.7–3.41)	7 ± 6 (1.5–28)
DIPSADINAE									
Dipsadini									
A. pantostictus (10)	269 ± 95 (122–420)	31 ± 11 (12–46)	28 ± 9 (15–37)	12.13 ± 2.33 (9.87–15.03)	6.78 ± 1.34 (4.61–8.4)	5.28 ± 1.11 (3.51–7.35)	1.35 ± 0.16 (1.21–1.57)	2.19 ± 0.51 (1.6–2.94)	15 ± 10 (5–34)
S. mikanii (36)	270 ± 108 (122–465)	62 ± 26 (27–111)	26 ± 8 (17–42)	12.59 ± 2.28 (8.87–17.02)	6.90 ± 1.52 (4.78–10.53)	5.48 ± 1.21 (4–7.63)	1.84 ± 0.28 (1.41–2.52)	3.29 ± 0.57 (2.73–4.58)	12 ± 11 (2–38)
Leptoderini									
L. annulata (5)	478 ± 101 (372–601)	167 ± 28 (143–200)	39 ± 9 (31–49)	19.85 ± 3.26 (16.36–23.36)	12.60 ± 2.48 (10.18–16.36)	8.61 ± 1.51 (7.18–10.48)	3.28 ± 0.45 (3.01–3.77)	4.23 ± 0.48 (4.08–4.76)	41 ± 27 (16–82)
E. occipitalis (12)	323 ± 69 (147–414)	107 ± 25 (46–142)	23 ± 4 (17–30)	12.83 ± 1.57 (9.42–14.86)	6.24 ± 1.13 (4.39–8.16)	4.65 ± 0.59 (3.16–5.08)	2.22 ± 0.37 (1.54–2.62)	2.44 ± 0.41 (1.49–3.07)	10 ± 4 (3–17)
X. undulatus (8)	268 ± 66 (172–352)	48 ± 12 (29–64)	23 ± 5 (14–30)	12.68 ± 2.43 (10.02–16.25)	6.03 ± 1.12 (5.33–7.7)	8.15 ± 6.81 (3.65–19.15)	1.17 ± 0.19 (1.01–1.4)	2.53 ± 0.49 (1.85–3.16)	10 ± 5 (3.5–17)
XENODONTINAE									
Elapomorphini									
A. albicolaris (9)	267 ± 73 (155–400)	30 ± 10 (17–50)	17 ± 3 (13–21)	8.33 ± 1.17 (6.71–10.55)	4.14 ± 0.64 (3.41–5.26)	3.07 ± 0.46 (2.61–3.7)	0.90 ± 0.15 (0.74–1.15)	1.88 ± 0.22 (1.69–2.25)	4 ± 2 (1–7)
A. ammodytes (5)	232 ± 34 (197–275)	27 ± 4 (20–30)	13 ± 2 (11–16)	6.29 ± 0.54 (5.85–6.99)	3.00 ± 0.33 (2.74–3.54)	2.22 ± 0.22 (2.15–2.55)	0.68 ± 0.15 (0.77–0.81)	1.59 ± 0.18 (1.69–1.85)	2 ± 1 (2–4)
A. assimilis (10)	228 ± 72 (160–346)	23 ± 12 (10–44)	14 ± 5 (10–24)	7.47 ± 1.02 (6.5–9.68)	3.87 ± 0.70 (3.02–5.27)	2.81 ± 0.53 (2.56–3.57)	0.68 ± 0.17 (0.45–1.01)	1.87 ± 0.35 (1.44–2.68)	4 ± 3 (2–11)
A. flavotorquata (2)	460 ± 45 (428–491)	42 ± 2 (40–43)	25 ± 4 (22–27)	12.04 ± 0.06 (10.55–12.08)	6.18 ± 0.45 (4.72–5.26)	4.24 ± 0.45 (3.04–3.64)	1.13 ± 0.23 (0.92–1.15)	2.89 ± 0.29 (1.87–2.08)	20 ± 11 (4–7)
P. nasutus (10)	518 ± 160 (307–854)	58 ± 14 (40–81)	38 ± 11 (26–65)	16.96 ± 5.73 (11.6–32)	9.99 ± 4.57 (6.45–22.42)	6.87 ± 2.31 (4.59–13)	1.46 ± 0.33 (1.07–2.2)	3.83 ± 1.15 (2.96–6.84)	58 ± 62 (14–220)
Hydropsini									
H. angulatus (4)	395 ± 144 (186–496)	187 ± 76 (76–245)	56 ± 21 (25–70)	25.11 ± 8.28 (13.23–32.51)	15.08 ± 4.98 (8.45–20.29)	10.58 ± 3.19 (5.81–12.39)	2.37 ± 0.49 (1.68–2.74)	3.65 ± 0.91 (2.46–4.61)	93 ± 60 (8–140)
H. leopardinus (1)	240	120	41	17.38	9.05	7.29	2.16	2.04	24

Table 3. Continued.

FAMILY									
SUBFAMILY									
Tribe									
Species	SVL	TL	CIR	HL	HW	HH	ED	BN	Mass (g)
H. modestus (18)	285 ± 106 (129–490)	93 ± 31 (39–150)	40 ± 15 (22–70)	18.16 ± 5.68 (11.6–31.49)	10.00 ± 4.22 (6.24–20.16)	7.33 ± 2.38 (4.48–12.02)	1.98 ± 0.48 (1.29–2.91)	2.26 ± 0.58 (1.43–3.34)	35 ± 36 (3–126)
Philodriadini									
P. aestiva (14)	504 ± 157 (265–869)	214 ± 63 (104–301)	36 ± 11 (19–56)	19.94 ± 3.55 (14.42–26.7)	8.85 ± 1.74 (6.06–11.44)	7.38 ± 1.42 (5.21–10.49)	3.20 ± 0.30 (2.83–3.74)	3.22 ± 0.65 (2.49–4.1)	47 ± 43 (4–172)
P. nattereri (35)	697 ± 278 (275–1160)	278 ± 121 (93–467)	58 ± 22 (22–96)	28.21 ± 8.50 (16.05–46.05)	14.97 ± 5.33 (7.05–28.2)	10.69 ± 3.50 (5.73–17.78)	4.67 ± 1.01 (2.84–6.47)	4.89 ± 1.42 (2.7–7.66)	179 ± 171 (8–575)
P. olfersii (22)	648 ± 208 (269–964)	261 ± 83 (112–388)	44 ± 14 (19–71)	24.23 ± 5.64 (13.85–34.54)	12.07 ± 3.50 (7.19–19.3)	9.05 ± 2.26 (4.87–14.26)	4.32 ± 0.76 (3.02–5.36)	4.88 ± 1.06 (2.87–6.9)	90 ± 80 (4–360)
P. patagoniensis (46)	677 ± 251 (215–1088)	252 ± 87 (74–380)	55 ± 21 (20–94)	27.77 ± 7.52 (14.11–39.72)	13.87 ± 4.05 (6.55–21.11)	10.95 ± 3.23 (5.18–18.37)	4.68 ± 0.98 (2.54–6.41)	4.55 ± 1.06 (2.59–6.72)	168 ± 158 (4–610)
P. psammophideus (2)	454 ± 87 (392–515)	156 ± 43 (125–186)	38 ± 4 (35–40)	19.24 ± 0.56 (18.84–19.63)	9.35 ± 1.48 (8.3–10.4)	7.62 ± 1.48 (6.57–8.67)	3.60 ± 0.84 (3–4.19)	3.46 ± 0.05 (3.42–3.49)	50 ± 8 (44–55)
P. agassizii (21)	261 ± 75 (130–401)	85 ± 24 (34–125)	29 ± 7 (17–40)	14.11 ± 2.64 (9.61–18.22)	7.10 ± 1.62 (4.68–10.71)	5.96 ± 1.17 (4.08–7.28)	2.03 ± 0.34 (1.73–2.48)	2.84 ± 0.55 (2.05–3.6)	16 ± 11 (4–45)
Pseudoboini									
B. maculata (3)	458 ± 132 (323–586)	94 ± 18 (76–111)	37 ± 6 (30–40)	20.99 ± 4.49 (15.82–23.94)	11.13 ± 1.28 (9.70–12.19)	8.39 ± 1.69 (6.48–9.70)	2.54 ± 0.18 (2.35–2.70)	4.42 ± 0.58 (4.09–5.09)	42 ± 21 (20–62)
C. plumbea (1)	1401	315	95	45.12	27.71	18.87	5.16	9.25	600
C. quimi (7)	493 ± 188 (221–749)	129 ± 49 (56–197)	45 ± 20 (20–80)	20.07 ± 6.43 (11.73–30.1)	10.47 ± 2.76 (5.93–13.5)	7.96 ± 1.91 (5.11–10)	2.27 ± 0.58 (1.55–2.85)	3.55 ± 0.86 (2.45–4.6)	89 ± 104 (8–310)
O. trigeminus (11)	501 ± 136 (323–743)	128 ± 29 (90–156)	41 ± 11 (25–59)	18.89 ± 3.77 (13.72–24.36)	10.09 ± 2.25 (7.43–14.75)	7.10 ± 1.79 (5.26–10.65)	2.30 ± 0.37 (1.78–2.81)	3.41 ± 0.83 (2.21–4.12)	53 ± 42 (10–130)
O. guibei (34)	439 ± 194 (195–817)	117 ± 55 (41–199)	35 ± 14 (15–69)	16.45 ± 5.10 (9.73–25.24)	8.87 ± 2.79 (4.9–14.44)	6.25 ± 1.90 (3.25–10.32)	2.00 ± 0.52 (1.25–2.9)	3.18 ± 0.85 (2.01–5.28)	43 ± 43 (4–145)
O. rhombifer (40)	312 ± 136 (146–609)	77 ± 36 (30–154)	31 ± 13 (17–65)	14.04 ± 4.27 (9.33–26.52)	7.48 ± 2.43 (4.92–14.23)	5.52 ± 1.80 (3.59–11.09)	1.75 ± 0.52 (1.09–2.72)	3.37 ± 3.73 (1.78–4.6)	21 ± 26 (2–100)
P. guerini (4)	476 ± 223 (255–784)	131 ± 66 (66–215)	42 ± 18 (23–65)	18.84 ± 5.58 (13.81–25.55)	10.83 ± 3.44 (7.74–15.49)	7.91 ± 2.64 (5.38–11.36)	2.19 ± 0.42 (1.84–2.78)	4.14 ± 0.94 (3.33–5.33)	87 ± 109 (8–265)
P. nigra (7)	544 ± 238 (264–779)	181 ± 85 (89–281)	52 ± 21 (24–79)	22.25 ± 6.70 (15.06–30.91)	12.78 ± 4.23 (7.89–17.15)	8.76 ± 2.66 (5.35–12.24)	2.77 ± 0.62 (1.93–3.39)	4.52 ± 1.25 (3–5.81)	108 ± 89 (9–195)
R. brazili (6)	786 ± 316 (435–1200)	213 ± 104 (105–329)	92 ± 30 (51–123)	35.25 ± 7.91 (26.71–46.54)	21.34 ± 5.49 (13.78–28.1)	14.91 ± 4.23 (9.17–20.4)	3.48 ± 0.89 (2.1–4.78)	6.74 ± 1.68 (4.69–8.75)	561 ± 437 (67–1100)
Tachymenini									
G. brasiliensis (4)	289 ± 44 (249–336)	70 ± 32 (86–90)	38 ± 3 (35–40)	14.27 ± 1.30 (14.95–15.08)	7.23 ± 0.72 (6.93–8.05)	6.08 ± 0.49 (6.15–6.54)	2.06 ± 0.16 (1.91–2.23)	2.12 ± 0.26 (1.95–2.42)	23 ± 6 (18–29)
T. hypoconia (9)	323 ± 57 (232–403)	114 ± 23 (75–146)	29 ± 8 (19–38)	16.42 ± 1.93 (13.7–18.58)	7.88 ± 1.46 (6.21–9.81)	6.23 ± 0.74 (5.6–7.18)	2.66 ± 0.33 (2.51–3.22)	2.68 ± 0.20 (2.51–3.05)	16 ± 8 (7–25)

Table 3. Continued.

FAMILY									
SUBFAMILY									
Tribe									
Species	SVL	TL	CIR	HL	HW	HH	ED	BN	Mass (g)
T. rutilus (3)	275 ± 105 (155–350)	109 ± 4460–145)	39 ± 11 (29–50)	17.63 ± 3.77 (13.28–19.96)	8.16 ± 2.14 (6.1–10.37)	6.58 ± 1.62 (4.94–8.17)	2.61 ± 0.68 (1.84–3.14)	2.40 ± 0.60 (1.84–3.040)	21 ± 15 (6–36)
Xenodontini									
E. aesculapii (34)	426 ± 136 (206–590)	59 ± 22 (20–86)	37 ± 11 (22–58)	16.29 ± 3.26 (11.3–23.08)	10.12 ± 2.39 (6.01–14.89)	7.35 ± 1.72 (5.09–10.45)	2.57 ± 0.58 (1.86–3.29)	4.34 ± 0.81 (2.98–5.85)	40 ± 28 (5–95)
L. almadensis (9)	285 ± 88 (170–412)	90 ± 30 (47–127)	29 ± 8 (19–39)	15.10 ± 3.60 (10.99–21.25)	7.65 ± 1.84 (5.46–9.6)	5.68 ± 1.29 (4.2–7.68)	2.68 ± 0.45 (2.01–3.38)	2.72 ± 0.50 (2.3–3.38)	14 ± 11 (3–32)
L. maryellenae (13)	305 ± 112 (114–404)	94 ± 34 (36–125)	33 ± 12 (15–45)	14.93 ± 3.63 (9.06–19.27)	7.57 ± 2.21 (4.37–10.44)	6.28 ± 1.83 (3.3–8.15)	2.31 ± 0.53 (1.22–3.06)	2.78 ± 0.82 (1.53–4.12)	23 ± 16 (1–46)
L. meridionalis (11)	444 ± 120 (138–571)	167 ± 50 (41–224)	33 ± 7 (20–45)	17.55 ± 3.32 (9.29–21.49)	7.76 ± 1.42 (5–9.7)	6.40 ± 1.19 (3.98–7.61)	3.48 ± 0.71 (1.77–4.6)	2.86 ± 0.49 (1.84–3.61)	26 ± 15 (2–48)
L. paucidens (1)	369	127	30	16.93	8.41	5.93	3.09	3.17	20
L. poecilogyrus (56)	369 ± 129 (146–605)	87 ± 33 (30–162)	37 ± 11 (17–59)	19.96 ± 5.46 (10.6–36.12)	11.43 ± 3.47 (5.15–17.86)	7.67 ± 2.34 (3.91–13.15)	2.87 ± 0.56 (1.85–4.26)	3.94 ± 0.93 (2.25–5.59)	35 ± 30 (2–130)
L. reginae (19)	417 ± 100 (190–597)	159 ± 49 (75–228)	39 ± 9 (20–50)	20.43 ± 3.64 (11.71–26.89)	11.50 ± 2.86 (6.21–17.28)	7.98 ± 1.77 (4.18–11.76)	3.52 ± 0.60 (2.43–4.81)	3.78 ± 0.77 (1.9–4.81)	38 ± 23 (4–78
L. nattereri (7)	245 ± 76 (140–350)	44 ± 16 (18–65)	33 ± 9 (21–45)	13.93 ± 2.59 (10.08–16.73)	8.05 ± 1.42 (6.28–9.55)	6.93 ± 1.30 (4.98–8.35)	2.25 ± 0.37 (1.9–2.69)	3.36 ± 0.70 (2.67–4.3)	14 ± 10 (3–29)
W. merremii (46)	561 ± 215 (189–1127)	98 ± 39 (26–181)	64 ± 23 (25–124)	32.87 ± 10.38 (15.78–60.48)	20.31 ± 7.16 (7.97–35.94)	13.83 ± 5.03 (7.2–31.1)	4.72 ± 0.97 (2.84–7.09)	5.96 ± 1.82 (2.85–10.98)	163 ± 192 (6–940)

Table 4. Factor Loadings of Each Variable on the First Two Principal Components and Proportion of the Variance Explained by Each Component Following the Procedures in Vitt and Vangilder (1983).

Variable	Principal component factor loadings	
	Factor I	Factor II
Snout–vent length	0.911	0.000
Tail length	0.772	0.631
Circumference around midbody	0.962	−0.184
Head length	0.984	0.032
Head width	0.966	−0.157
Head height	0.961	−0.100
Eye diameter	0.887	0.254
Between nostrils	0.923	−0.132
Mass	0.982	−0.171
Eigenvalue	0.748	0.080
Variance explained		
Percent	86.977	9.286
Cumulative	86.977	96.263

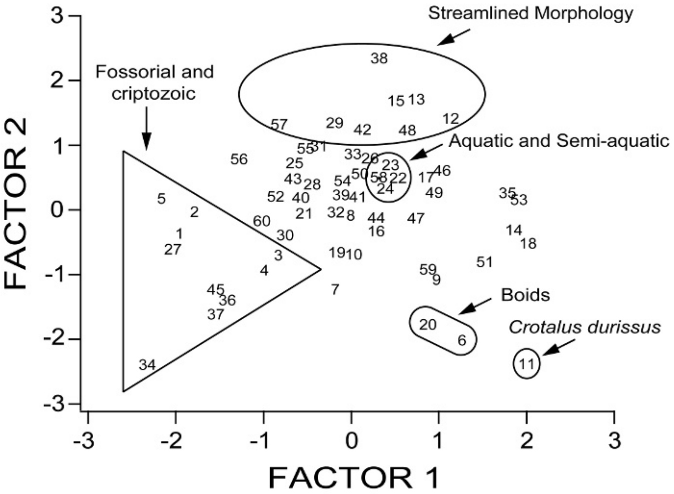

Fig. 2. Plot of factor scores from principal components for 60 species of Distrito Federal snakes. The PCA follows the model used by Vitt and Vangilder (1983). The species are: 1–*Apostolepis assimilis*; 2–*A. albicollaris* ; 3–*A. flavotorquata*; 4–*Atractus pantostictus*; 5–*Apostolepis ammodytes*; 6–*Boa constrictor*; 7–*Bothrops itapetiningae*; 8–*Boiruna maculata*; 9–*Bothrops moojeni*; 10–*Bothrops neuwiedi*; 11–*Crotalus durissus*; 12–*Chironius exoletus*; 13–*C. flavolineatus*; 14–*Clelia plumbea*; 15–*Chironius quadricarinatus*; 16–*Clelia quimi*; 17–*Drymoluber brazili*; 18–*Drymarchon corais*; 19–*Erythrolamprus aesculapii*; 20–*Epicrates cenchria*; 21–*Gomesophis brasiliensis*; 22–*Helicops angulatus*; 23–*H. leopardinus*; 24–*H. modestus*; 25–*Liophis almadensis*; 26–*Leptodeira annulata*; 27–*Leptotyphlops fuliginosus*; 28–*Liophis maryellenae*; 29–*Liophis meridionalis*; 30–*Lystrophis nattereri*; 31–*Liophis paucidens*; 32–*Liophis poecilogyrus*; 33–*Liophis reginae*; 34–*Liotyphlops ternetzii*; 35–*Mastigodryas bifossatus*; 36–*Micrurus frontalis*; 37–*M. lemniscatus*; 38–*Oxybelis aeneus*; 39–*Oxyrhopus guibei*; 40–*O. rhombifer*; 41–*O. trigeminus*; 42–*Philodryas aestiva*; 43–*Pseudablabes agassizii*; 44–*Phimophis guerini*; 45–*Phalotris nasutus*; 46–*Philodryas nattereri*; 47–*Pseudoboa nigra*; 48–*Philodryas olfersii*; 49–*P. patagoniensis*; 50–*P. psammophideus*; 51–*Rhachidelus brazili*; 52–*Sibynomorphus mikanii*; 53–*Spilotes pullatus*; 54–*Simophis rhinostoma*; 55–*Thamnodynastes hypoconia*; 56–*Tantilla melanocephala*; 57–*Echinantera occipitalis*; 58–*Thamnodynastes rutilus*; 59–*Waglerophis merremii*; 60–*Xenopholis undulatus*.

Table 5. Factor Loadings of Each Variable on the First Two Principal Components and Proportion of the Variance Explained by Each Component Using the Residuals of the Regression between Morphological Variable with Body Size.

Variable (Regressions)	Principal component factor loadings	
	Factor I	Factor II
Tail length	0.079	−0.916
Circumference around midbody	0.906	0.037
Head length	0.921	−0.375
Head width	0.965	−0.116
Head height	0.961	−0.176
Eye diameter	0.646	−0.659
Between nostrils	0.800	−0.123
Mass	0.790	0.443
Eigenvalue	5.238	1.545
Variance explained		
Percent	65.471	19.318
Cumulative	65.471	84.789

tus, represent morphometric convergence due to ecological similarities among species.

Phylogeny has been considered the most important factor influencing structure of reptile assemblages (Cadle and Greene, 1993; Vitt et al., 1999; Mesquita et al., 2006a, 2006b). Nevertheless, ecological factors are often important as well. For example, three species of morphologically similar water-snakes in the genus *Helicops* (historically similar) are morphologically and ecologically similar to the unrelated snake *Thamnodynastes rutilus* (Tachymenini). Both taxa have low scores on factor 1, mid scores on factor 2, and share similar ecological attributes, including diet and habitat use. Similarly, the arboreal Colubrinae snakes *Chironius* and *Oxybelis* have low scores on factor 1 and 2. Their morphology (large eyes, elongate head, light body, long tail, and low mass) are usually associated with arboreality (Lillywhite and Henderson, 2001). These features are shared by the xenodontine snake *Philodryas olfersii*, which is more similar to *Chironius* species than other

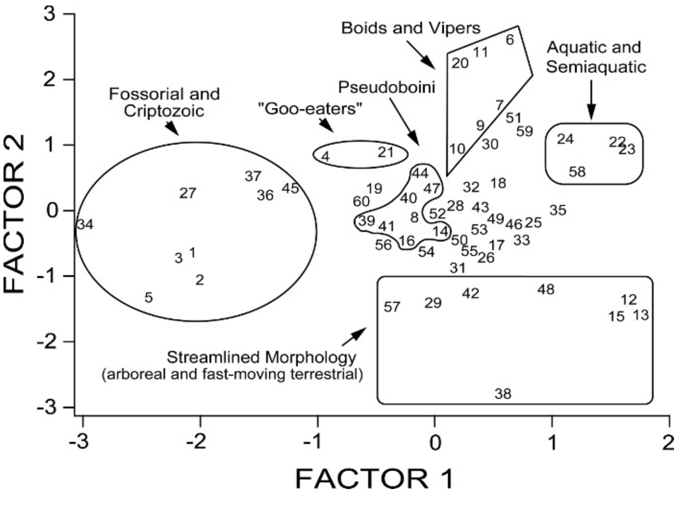

Fig. 3. Plot of factor scores from principal components for 60 species of Distrito Federal snakes. The PCA used residuals of the regression between morphological variables and the estimating variable for body size. For snake species, see legend of Figure 2.

Table 6. **Historical Effects on the Morphology of Snakes of Cerrado from Distrito Federal. Results of Monte Carlo permutation tests of individual groups (defined as in Fig. 1) for the Y matrices of morphology.** Percentage of the variation explained (relative to total unconstrained variation) and *F*- and *P*-values for each variable are given (9,999 permutations were used) for each main matrix. Note that no groups used for selection of variables yielded individual $P \leq 0.05$.

Group(s)	Variation	Variation %	*F*	*P*
R′	0.013	30.95	23.163	0.0001
K	0.011	26.19	17.608	0.0003
S′	0.010	23.81	15.318	0.0001
G	0.009	21.43	13.345	0.0002
H	0.009	21.43	13.511	0.0002
C	0.005	11.90	7.218	0.0053
F	0.004	9.52	6.135	0.0085
I	0.004	9.52	5.252	0.0160
P	0.004	9.52	4.884	0.0203
T′	0.004	9.52	5.387	0.0174
B	0.003	7.14	4.539	0.0283
J	0.003	7.14	4.563	0.0287
K	0.003	7.14	3.439	0.0532
D	0.002	4.76	2.652	0.0912
O	0.002	4.76	2.986	0.0741
X	0.002	4.76	2.729	0.0903
Y	0.002	4.76	2.827	0.867
A′	0.002	4.76	3.212	0.0605
B′	0.002	4.76	3.064	0.0719
C′	0.002	4.76	2.444	0.1025
L′	0.002	4.76	2.294	0.1167
M′	0.002	4.76	3.130	0.0662
A/U′	0.001	2.38	1.497	0.2150
E	0.001	2.38	1.738	0.1758
R	0.001	2.38	1.648	0.1954
S	0.001	2.38	1.249	0.2547
V	0.001	2.38	1.592	0.2081
Z	0.001	2.38	0.788	0.3869
D′	0.001	2.38	1.555	0.2058
H′	0.001	2.38	1.058	0.3060
J′	0.001	2.38	0.829	0.3758
K′	0.001	2.38	1.217	0.2605
L	0.000	0.00	0.083	0.9049
M	0.000	0.00	0.333	0.6378
N	0.000	0.00	0.230	0.7189
T	0.000	0.00	0.110	0.8701
U	0.000	0.00	0.046	0.9523
W	0.000	0.00	0.628	0.4669
E′	0.000	0.00	0.195	0.7913
F′	0.000	0.00	0.522	0.5317
G	0.000	0.00	0.122	0.8384
I′	0.000	0.00	0.081	0.8974
N′	0.000	0.00	0.412	0.6046
O′	0.000	0.00	0.329	0.6642
P′	0.000	0.00	0.208	0.7740
Q′	0.000	0.00	0.329	0.6633

Philodryas. In Distrito Federal region, *P. olfersii* occupies more forested areas and is more arboreal than all other sympatric *Philodryas*. Finally, *Waglerophis merremii* and *Lystrophis nattereri* (Xenodontini) are most similar morphologically to *Bothrops* (Viperidae). Morphological similarity (phenotypic resemblance) of the two non-venomous species, *Waglerophis* and *Lystrophis*, results from mimicry of the highly venomous *Bothrops* (Campbell and Lamar, 2004). All three of these examples point to the importance of ecological factors in driving some morphological divergence.

The results from CPO corroborate indirect evidence from the PCA. The Boidae, Colubrinae, *Chironius*, *Apostolepis*, and *Micrurus* among others show significant phylogenetic effects on morphology. The boids from Distrito Federal are very similar, ecologically and morphologically (Vanzolini et al., 1980; Greene, 1997; Martins and Oliveira, 1998), as are Colubrinae (Cadle and Greene, 1993), *Apostolepis* (Ferrarezzi, 1993; Ferrarezzi et al., 2005), *Chironius*, and *Micrurus*, which, despite their wide distributions, occur in drastically different biomes but exhibit similar morphology and ecology (Dixon et al., 1993; Roze, 1996). However, some results were not corroborated by the CPO, such as the *Helicops* clade. *Helicops* species are very similar morphologically and ecologically (Ford and Ford, 2002; Sawaya, 2003; Aguiar and Di-Bernardo, 2004); however, in the PCA they were clustered together with *Thamnodynastes rutilus*, which shows similar ecology (Araújo et al., 1998). Probably, the non-significant results of CPO were influenced by *Thamnodynastes rutilus*, which belong to a completely different clade but show similar ecology.

Our results suggest that both ecology and phylogeny are important determinants of the structure of snake assemblages as reported by others (Guyer and Donnelly, 1990; Martins et al., 2001, 2002; Mesquita et al., 2007). Although morphology often reflects phylogeny, morphological divergence can also occur in response to ecological factors such as habitat use and diet. Ecological factors account for some morphological variation among snake species in the Distrito Federal assemblage, but, similar to most studied Neotropical assemblages, the history of species accounts for most of the variation (Cadle and Greene, 1993; Vitt et al., 1999; Mesquita et al., 2006b). Although comparative methods can identify historical effects in assemblage structure, possible causes of the observed patterns are complex (Webb et al., 2002). Different taxa should have different responses to ecological variation, resulting in dissimilarly of the potential for diversification among various clades. Ecological data on coexisting species and comparisons among different assemblages in an historical context are essential if we are to understand the relative contributions of ecological and historical factors to structure of present-day assemblages.

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