

## The Snake Assemblage of the Pantanal at Poconé, Western Brazil: Faunal Composition and Ecological Summary

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The faunal composition and ecological features were studied in a snake assemblage in the Pantanal, an open and seasonally flooded area in western Brazil. Twenty six species of snakes in 19 genera and five families, and their use of habitat, substrate, time, and food were recorded. *Hydrodynastes gigas* and *Eunectes notaeus*, the two commonest and largest species, explore the widest range of habitats and food resources. Trends in use of substrate, time of activity and food were compared to those known for snake assemblages from two open and two forested areas in the neotropics. The comparisons indicate that features such as vertical distribution may be viewed essentially from an ecological perspective, while trends in food use benefit from the addition of a faunal perspective.

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### Introduction

Studies on neotropical snake faunas often indicate a high species richness and complex ecological interactions (Duellman, 1989, 1990; Cadle and Greene, 1992). Ecological trends within a given snake assemblage may be regarded as resulting strictly from ecological factors (e.g. Vitt and Vangilder, 1983) or may incorporate historical and faunal considerations (Duellman, 1989; Cadle and Greene, 1992). Despite a recent increase in the number of faunal and ecological studies on neotropical snakes (e.g. Vanzolini et al., 1980; Dixon and Soini, 1986; Zimmerman and Rodrigues, 1990; see revision and additional references in Cadle and Greene, 1992), data are still needed for comparisons between major formations, e.g. forested vs. open areas.

Here we present a brief faunal survey and an ecological summary of snakes in the northern part of the Pantanal, an open and seasonally flooded area in western Brazil. We used a number of basic data on natural history such as vertical distribution, activity, and food, to identify trends and to compare our results to

studies from both open and forested neotropical areas. From the comparison we found that some trends (e.g. use of substrate) may be viewed essentially from an ecological perspective, while others (e.g. food use) benefit from the addition of a faunal perspective.

### Study Site and Methods

Fieldwork was done in the Pantanal, a region with about 300,000 km<sup>2</sup> of flat to slightly undulating terrain in southwestern Brazil and adjacent countries (Prance and Schaller, 1982). Roughly a half of this area is annually flooded during the wet season (February-June) by the tributaries of the Paraguay river, and about a half of the year the same places suffer a severe drought (Adamoli, 1986). Annual temperature in 25°C on average, with the maxima (around 40°C) during the dry season (Tarifa, 1986). Temperature may drop abruptly several times between May and September, for two to four consecutive days.

We searched for snakes in the northern part of the Pantanal, and concentrated our efforts at the Santa Inês Ranch and along the Transpantaneira road, both sites near the town of Poconé (16°30'S, 56°45'W), Mato Grosso, Brazil (Fig. 1). At both sites we recognized three main categories of habitats where snakes were found: (1) seasonally flooded, open plains (which present distinct physiognomies and may harbor different snake sub-assemblages during dry and wet seasons); (2) forested areas, and (3) deforested areas. In the Pantanal at Poconé most areas are large, open plains covered by native grasses (lightly disturbed by cattle grazing) and low bushes during the dry season, and by aquatic vegetation during floods (Fig. 2a, see also Prance and Schaller, 1982). When flooded, water depth varies from a few centimeters in the open fields to more than a meter in adjacent permanent swamps, water channels and ponds, which provide year-round stable habitats for species closely associated to water. The forested formations are usually found in patches ("capões") or strips ("cordilheiras") of non-flooded higher ground, interspersed throughout the Pantanal lowlands (see Prance and Schaller, 1982). The semideciduous forest covering the "cordilheiras" is cleared out in some places for settlement of ranches, creating new open habitats (Fig. 2b), sometimes with orchards or a few groups of trees left in place.

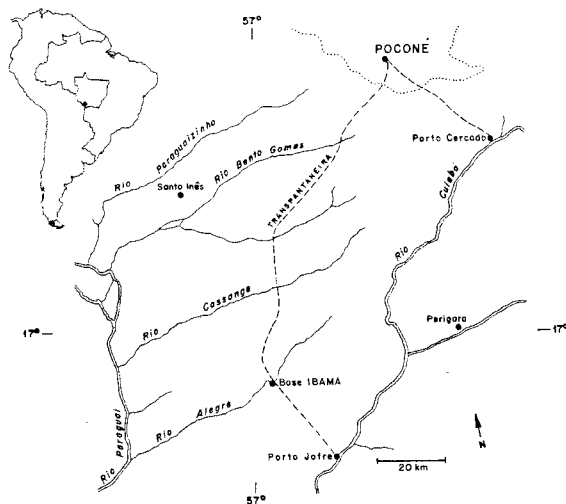


Fig. 1. Map of the northern part of the Pantanal, Mato Grosso, western Brazil, showing sites mentioned in the text. Dotted line represents approximate northeastern limit of the Pantanal wetlands; dashed lines represent the two main unpaved routes.

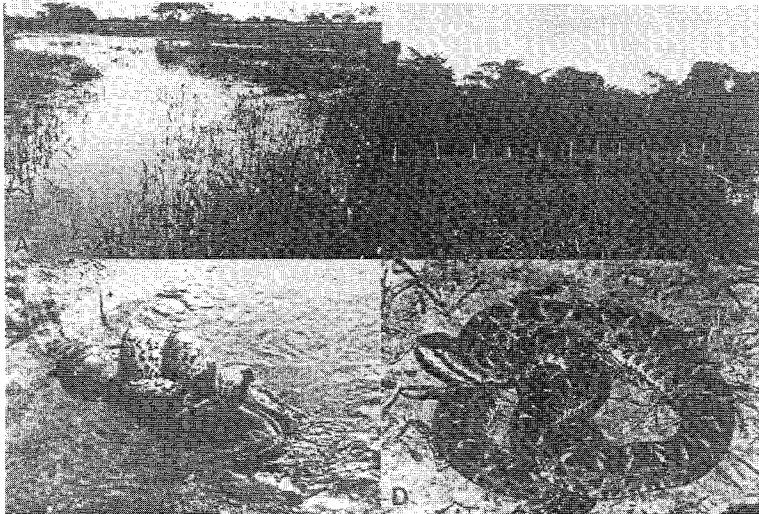


Fig. 2. Habitats and species of snakes from the Pantanal, western Brazil. (A) Seasonally flooded plain with forested patches in background. (B) Deforested area with adjacent forested strip in background (tree stumps and fallen logs habitually shelter several species of snakes). (C) An adult *Eunectes notaeus* (160 cm total length, TL), constricting an adult caiman, *Caiman crocodilus yacare* (120 cm TL) (photo M. Wendler). (D) Adult male *Bothrops neuwiedi*, a cause of cattle loss in the Pantanal (50 cm TL, specimen ZUEC 1208).

Snakes were searched for on the ground, under logs and debris, on bushes and low trees, on the water edge and in the water, during daytime and night. We spent about 810 h searching for snakes, and fieldwork was done mostly from March to October 1989, December 1989 to January 1990, March to July 1990 and June 1991. For each snake we recorded habitat, substrate (e.g. on the ground or perched), activity, and time. Most individuals were caught and examined for gut contents. A few snakes were killed and preserved as vouchers in the Museu de História Natural, Universidade Estadual de Campinas (ZUEC, see Fig. 3). We compared some of our snakes to type specimens and others housed in the Instituto Butantan collection in São Paulo (IB).

For the categories of vertical distribution (substrate) used in the table, we followed the general usage for fossorial, terrestrial and aquatic species (e.g. Duellman, 1989). We use "cryptozoic" in the sense of Cadle and Greene (1992), and define "semi-arboreal" for the snakes using both the ground and the vegetation, and "semi-aquatic" for those which are at ease both in the water and on the ground.

## Results

**Species composition and taxonomic comments.** – Representatives of 26 species in 19 genera and five families were found in the Pantanal snake assemblage (Table 1).

We are unable to assign our female specimen of *Chironius* (Fig. 3b) to any recognized species. It will key out as *C. carinatus* (L.) in Peters and Orejas-Miranda (1970), Wiest (1978) and Cunha and Nascimento (1983) but differs in dorsal color pattern and its subcaudals are immaculate instead of being outlined in

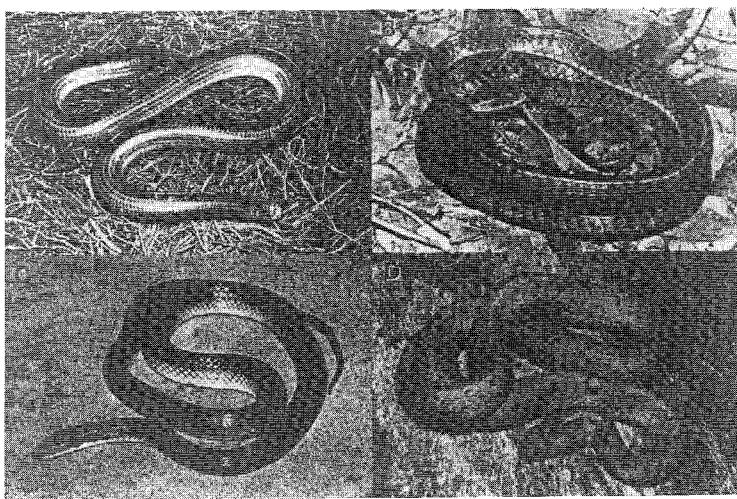


Fig. 3. Species of snakes from the Pantanal, western Brazil. (A) Adult *Typhlops brongersmianus* found inside a fallen, decaying trunk of a palm (28 cm TL, specimen ZUEC 1151). (B) Adult female *Chironius* sp. (aff. *multiventris*) (172 cm TL, ZUEC 1163). (C) Adult male *Clelia bicolor* (56 cm TL, ZUEC 1187). (D) Adult female *Thamnodynastes* sp. flattening head in defense (51 cm TL, ZUEC 1204).

black or dark brown. It approaches better what is regarded as the polymorphic *C. multiventris* Schmidt et Walker (Wiest, 1978) but differs in its bicolored dorsal pattern in life (the two anterior thirds of body are smoke gray, and the rest including the tail is buff orange), besides having low ventral counts (155, subcaudals incomplete).

The specimens we assigned to *Clelia bicolor* (Fig. 3c) differ from the original description (Peracca, 1904) in having a single anal plate (vs. divided in the male described by Peracca, maybe an anomaly or a flaw?). Our three males have slightly higher number of ventrals (163-170 vs. 157) and lower number of subcaudals (67-68 vs. 70). (See also an account on *C. bicolor* in Scrocchi and Viñas, 1990). We doubt the occurrence of *C. bicolor* in Peru (Dixon and Soini, 1986; Vanzolini, 1986) based on the very high ventral and subcaudal counts of the only male (188 and 93, respectively), dorsum bright coral red, venter pinkish yellow to red, and yellow and black head of the snakes referred by Dixon and Soini (1986). The description of Peracca (1904) clearly mentions dorsum violaceous brown and venter yellow, which fits well our specimens.

We use the name "*Liophis*" *joberti* (Peters and Orejas-Miranda, 1970; Hoge et al., 1975) for the snake figured as *Liophis genimaculatus* by Amaral (1977) and treated as "incertae sedis" by Dixon (1980). *Liophis poecilogyrus* is currently a difficult taxon, probably a composite (Vanzolini et al., 1980; Dixon, 1989; pers. obs.) and our specimens may be assigned to the taxon currently called *L. poecilogyrus intermedius* (Peters and Orejas-Miranda, 1970), possibly a junior synonym of *L. p. reticulatus* (see Amaral, 1944 and Parker, 1931 respectively for descriptions). We tentatively assign our juvenile specimen (210 mm SVL) of

Table 1. Twenty six species of snakes of the Pantanal at Poconé and data on their natural history.

Snake species	Habitat	Substrate	Activity	Food
<b>TYPHLOPIDAE</b>				
<i>Typhlops brongersmianus</i> Vanzolini	DA, fa <sup>1</sup>	FO	?	IN
<b>BOIDAE</b>				
<i>Boa constrictor</i> L.	fa, da	TE	n, d	(MA, BI)
<i>Eunectes notaeus</i> Cope	SFW, da, fa	SA	N, d	BI, ve, fi, ca
<b>COLUBRIDAE</b>				
<i>Chironius quadricarinatus</i> (Boie)	FA	SB	D	(FR)
<i>Chironius</i> sp.	fa	sb	d	fr
<i>Clelia bicolor</i> (Peracca)	DA, sfd	TE	N	fr, li, sn
<i>Clelia clelia</i> (Daudin)	da	te	(N)	(SN, LI)
<i>Drymarchon corais</i> (Boie)	FA	TE	D	fr, sn, (VE)
<i>Helicops leopardinus</i> (Schlegel)	SFW	AQ	N, d	FI, fr
<i>Hydrodynastes gigas</i> (D., B. et D.)	UB	SA	D	FI, FR, ma, ca
<i>Leptophis ahaetulla</i> (L.)	FA, da	SB	D	fr, (FR, li)
<i>Liophis almadensis</i> (Wagler)	da	te	d	fr, (FR)
" <i>Liophis</i> " <i>joberti</i> (Sauvage)	FA, da	SB	D	fr, li
<i>Liophis poecilogyrus</i> (Wied)	DA, sfd, fa	TE	D, n	FR
<i>Liophis reginae</i> (L.)	sfw	te	d	fr, (FR)
<i>Mastigodryas bifossatus</i> (Raddi)	FA, da	TE	D	FR, li, (ma)
<i>Oxyrhopus</i> sp.	da	te	n	(LI, MA)
<i>Pseudoboa nigra</i> (D., B. et D.)	DA, fa	TE	N	li, (LI)
<i>Pseudoeryx plicatilis</i> (L.)	sfw	aq	d	(FI)
<i>Thamnodynastes cf. strigilis</i> (Thunberg)	DA, fa, sfw	SB	N, d	FR
<i>Thamnodynastes</i> sp.	da, fa	SB	N	fr
<i>Xenopholis cf. undulatus</i> (Jensen)	da	cr	?	fr
<b>ELAPIDAE</b>				
<i>Micrurus tricolor</i> Hoge	da	te <sup>2</sup>	n	sn
<b>VIPERIDAE</b>				
<i>Bothrops moojeni</i> Hoge	sfw	te	d <sup>3</sup>	sn, (VE)
<i>Bothrops neuwiedi</i> Wagler	DA, fa	TE	N	MA, fr
<i>Crotalus durissus</i> L.	fa, da	TE	(N)	(MA)

<sup>1</sup> Minor letters denote single observation or minor importance within a category, and brackets indicate literature data: Cunha and Nascimento, 1978; Leloup, 1984; Vanzolini, 1948; Vitt and Vangilder, 1983; Wiest, 1978; Zimmerman and Rodrigues, 1990.

<sup>2</sup> The single specimen was found crawling on the ground but *Micrurus* is regarded as fossorial.

<sup>3</sup> The single specimen was found feeding by day but *B. moojeni* is mainly nocturnal.

ABBREVIATIONS - AM: amphisbaenians; AQ: aquatic; BI: birds; CA: carrion (fish, frog); CR: cryptozoic; D: diurnal; DA: deforested areas; FA: forested areas; FI: fishes; FO: fossorial; FR: frogs; IN: insects; LI: lizards; MA: mammals; N: nocturnal; SA: semi-aquatic; SB: semi-arboreal; SFD: seasonally flooded areas, dry season; SFW: seasonally flooded areas, wet season; SN: snakes; TE: terrestrial; UB: ubiquitous; VE: vertebrate major groups other than fish.

*Oxyrhopus* to the *petola* group (sensu Peters and Orejas-Miranda, 1970), but this may prove incorrect since "*petola*" is a notoriously difficult assembly.

The confusing genus *Thamnodynastes* is currently under revision by R. Thomas (M.T. Rodrigues, pers. comm.) and no name can be assigned with confidence to most Brazilian species (see Vitt and Vangilder, 1983; Vanzolini, 1986). Individuals of our *T. cf. strigilis* show variable colors in life (drab gray, beige, ochraceous, or ferruginous), have keeled dorsals in 19-19-15 rows, ventrals 143-154, caudals 58-69, and supraoculars large and roughly triangular. The possibility exists that we are dealing with more than one highly variable species, but for the purpose of this study we prefer the treatment given above. Our other species of *Thamnodynastes* (Fig. 3d) also has keeled dorsals and presents similar counts, but its color in life approaches orange yellow, and it has supraoculars narrower and roughly rectangular, besides seeming less irritable than *T. cf. strigilis*.

We compared our specimen of *Xenopholis* to a series identified as *X. undulatus* by Hoge and Federsoni (1975) in the IB collection. The Pantanal snake differs from this series mainly by its color pattern in life: dorsum uniformly violaceous brown, the scales in 4th and 5th rows with orange center, appearing as an irregular lateral stripe; venter and first two dorsal scale rows yellowish (see Hoge and Federsoni, 1975 and Amaral, 1977 for the color pattern of *X. undulatus*). Additionally, our specimen (a male) has frontal scale shorter than the distance from its anterior margin to the snout tip, and 161 ventrals (169-178 in nine males studied by Hoge and Federsoni, 1975).

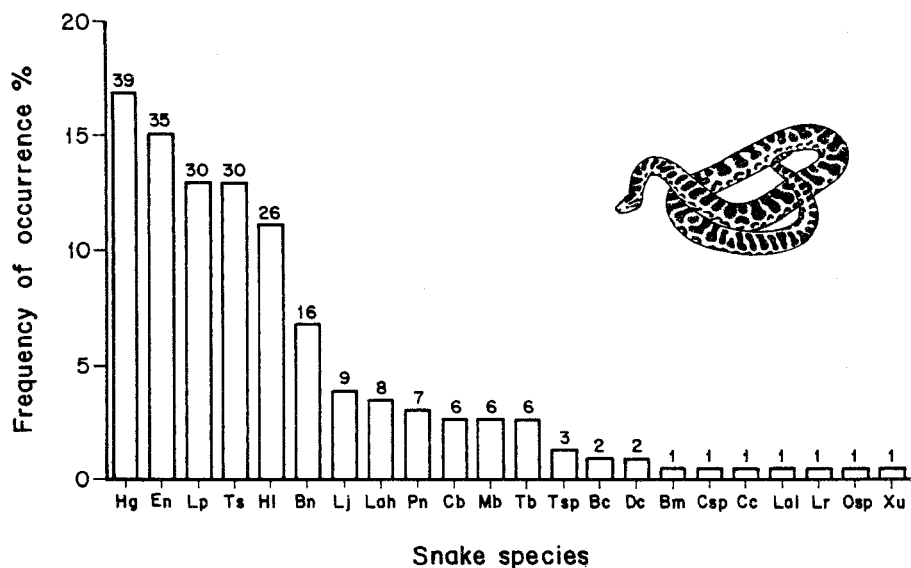


Fig. 4. Relative abundance of 22 species of snakes in the northern part of the Pantanal, western Brazil. Values on top of columns represent number of individuals (n) for each species. Abbreviations represent the first letter of generic and specific names respectively (Table. 1).

We refer our specimen of *Micrurus* to *M. tricolor*, regarded as a subspecies of *M. frontalis* by Roze (1983) and Campbell and Lamar (1989), and treated as a junior synonym of *M. pyrrhocryptus* by Hoge and Romano-Hoge (1981) and Scrocchi (1990). Indeed, our specimen fits well the type series used by Hoge (1957) for the original description of *M. tricolor*, which differs markedly from the other supposedly related species. *Bothrops neuwiedi* is another difficult taxon (Peters and Orejas-Miranda, 1970; Fernandes and Abe, 1991), but our specimens (Fig. 2d) fit well the type series of what is currently known as *B. neuwiedi mato Grossoensis* (Amaral, 1925).

Ecological data. — Comparable data on relative abundance are available for 232 individuals of 22 species in the Pantanal snake assemblage (Fig. 4). The additional four species (*C. quadricarinatus*, *P. plicatilis*, *M. tricolor* and *C. durissus*) were added to our list (Table 1) based on specimens obtained by other collectors or prior to the beginning of the present field study.

Seasonal incidence may be evaluated from data gathered in the first year of our study, when 60% of the individuals here analyzed were found. Monthly abundance of snakes decreased with the onset of the dry season (Fig. 5), an apparently common trend among neotropical snakes (see Reynolds, 1982).

The commonest species in the Pantanal were the boid *E. notaeus* (Fig. 2c), the colubrids *Hy. gigas*, *He. leopardinus*, *L. poecilogyrus*, *T. cf. strigilis*, and the viperid *B. neuwiedi*. These six species represented 76% of individuals in our sample (Fig. 4). For this reason these are the snakes we have the best set of natural history data (Table 1). On the other hand, it seems difficult to obtain additional, comparable ecological data for the scarcely represented and apparently rare colubrids *P. plicatilis* and *X. cf. undulatus*, and the elapid *M. tricolor*.

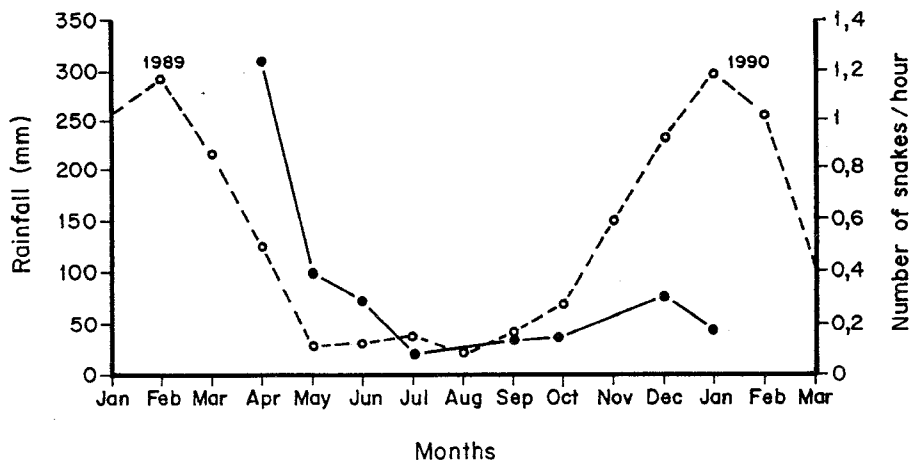


Fig. 5. Mean monthly rainfall (dotted line) and number of active snakes found per hour of fieldwork (solid line) in the northern part of Pantanal, Mato Grosso, western Brazil. Rainfall data obtained at the Perigara site (see Fig. 1).

## Discussion

Ecological attributes are notoriously difficult to ascribe to snakes (see Cadle and Greene, 1992 for a relevant discussion) due to these reptiles' secretiveness, fortuitous finding and thus a general lack of information on their basic activities (use of time, substrate, food). Moreover, the same snake species may present different patterns of resource use (e.g. substrate or food) over its area of occurrence (Cadle and Greene, 1992), especially those taxa widely distributed. For instance, *Leptophis ahaetulla* is regarded as an arboreal snake (e.g. Duellman, 1989; Rodriguez and Cadle, 1990) but we consider it as semi-arboreal in the Pantanal based on its habit of foraging on both the ground and low bushes (see also Cunha and Nascimento, 1978). Moreover, the actual possibility of dealing with complexes of related species and/or misidentifications should be borne in mind when making comparisons between snake assemblages.

We regard the mainly semi-aquatic *Hydrodynastes gigas*, a large colubrid (up to 2.5 m in total length), as ubiquitous since it uses extensively all habitats even during the dry season, when this snake switches to food resources other than fish and frogs (Strussmann and Sazima, 1990; pers. obs.). On the other hand, the also large boid (up to 4.0 m TL) *Eunectes notaeus* spends most of the dry season near permanent bodies of water, thus seeming restricted to the swampy or permanently flooded terrain.

Except for *E. notaeus* (probably restricted to the Pantanal wetlands), all other species in our list may be found also in drier and higher places peripheral to the Pantanal plains, including open vegetational formations such as the "cerrado" (Hoge et al., 1975; pers. obs.). The Pantanal snake assemblage, when compared to two other assemblages from open areas studied in Brazil, the cerrado (23 species – Vanzolini, 1948) and the "caatinga" (19 species – Vitt and Vangilder, 1983) obviously shows the highest proportion of aquatic and semi-aquatic species (Fig. 6). Additionally, *E. notaeus* and *H. gigas*, two mainly semi-aquatic species (Strussmann and Sazima, 1990; Strussmann, 1992), comprise 34% of the individuals in our total sample (Fig. 4).

Fossorial species (Fig. 3a) seem scarcer in the Pantanal and in the caatinga than in the cerrado (Fig. 6). The proportion of fossorial snakes in the latter area approaches those found in two Amazonian forested areas: Manaus, Brazil (Zimmerman and Rodrigues, 1990) and Iquitos, Peru (Dixon and Soini, 1986). These two latter areas harbor 62 and 88 species respectively (Fig. 6). Presently we are unable to explain the scarcity of fossorial snakes in the Pantanal and caatinga, but both undercollecting and limiting features such as soil structure may be evoked (see Vanzolini, 1971, for comments on the cerrado soil structure and associated fauna). The presence of two fossorial, leptotyphlopoid snakes in the comprehensive faunal survey of the caatinga region (Vanzolini et al., 1980), which are lacking in the assemblage studied by Vitt and Vangilder (1983), indicate undercollecting as one real possibility. In the Pantanal, periodic drastic changes in soil hydric conditions (due to annual floods) may be a limiting factor for subterranean life<sup>1</sup>.

Snake assemblages from the three open areas (the Pantanal, the cerrado and the caatinga) showed in common an evident predominance of terrestrial species, which contrasts with snake assemblages from the two Amazonian forested areas



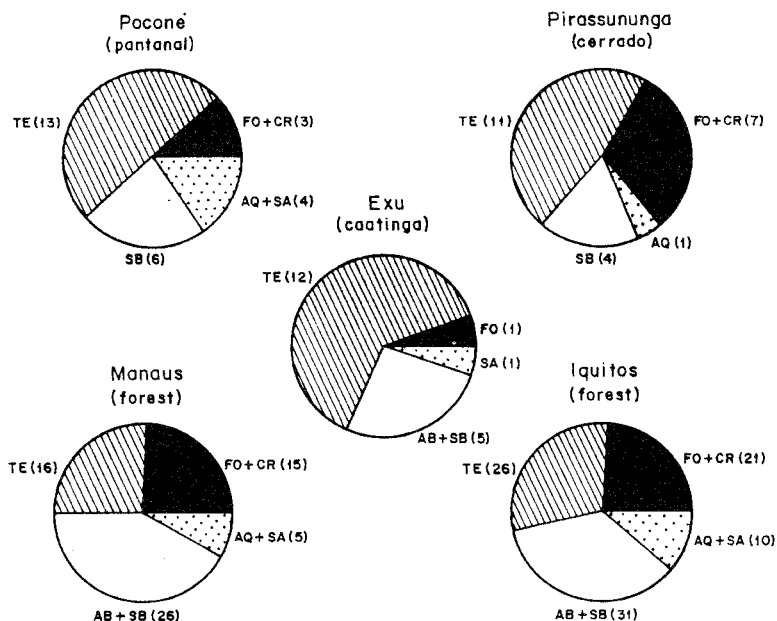


Fig. 6. Diagrams comparing substrate use by snakes in three open (Pantanal, cerrado, and caatinga) and two forested areas (Manaus and Iquitos) in the neotropics. Abbreviations follow Table 1, plus AB = arboreal. Values indicate number of species within each category.

(Fig. 6). Moreover, the ratio of terrestrial relative to arboreal and semi-arboreal snakes is from 2.2 to 3.0 in the three open areas, and 0.61 and 0.84 in the two forests, a difference which may be viewed essentially from an ecological perspective: a forest offers much more substrate and associated resources for the establishment of an arboreal fauna than an open area does (e.g. Duellman, 1989). The same idea applies to the available aquatic resources in the Pantanal and the relatively rich aquatic or semi-aquatic snake fauna.

We found that the forested areas and the cerrado harbor similar proportions of snakes using frogs as main food (26 to 29% of the total snake fauna) and that the caatinga and the Pantanal have the highest number of these frog-eaters (37 and 42% respectively). We think that considerations about this difference in food use may benefit from the addition of a faunal perspective (see Cadle and Greene, 1992 for an approach). The two latter open areas also harbor the highest number of xenodontine snakes (54 and 63% from total snake fauna in the Pantanal and the caatinga fauna respectively). About 25% of South American xenodontine genera (cf. Cadle and Greene, 1992) are composed of primarily frog-eating species, especially the huge genera *Liophis*, *Rhadinaea* and *Thamnodynastes*, and the specialized frog-eaters *Waglerophis* and *Xendodon*. Most species of *Liophis* and *Thamnodynastes* are common inhabitants of open areas and may skew the ratio towards frog-eating snakes at a given site. The ratio of *Liophis* + *Thamnodynastes* species relative to the total snake fauna is 0.13 for the cerrado, 0.23 for the Pantanal and 0.31 for the caatinga. In the two forested areas this ratio is consid-

erably lower, 0.08 (no *Thamnodynastes* is listed for Manaus).

The abundance of individuals should also be considered: in our Pantanal sample, snakes such as *H. gigas*, *L. poecilogyrus* and *T. cf. strigilis* (all of them relying heavily on frogs) represent 43% of the total number of individuals (Fig. 4).

The ratio of nocturnal relative to diurnal species is from 0.80 to 1.83 in the open areas and from 0.95 to 1.27 in the forest (we excluded fossorial snakes from this particular analysis since data on their activity are deficient and difficult to evaluate). We found no clear ecological or faunal basis for this roughly similar variation of nocturnal versus diurnal species in open and forested areas. Perhaps snake activity involves additional, complex features still undetected by the methods used thus far.

Ideally, sites should be compared on basis of similarly or proportionally sized areas and similarly collected snake faunas (see Duellman, 1989 and Cadle and Greene, 1992 for approaches). Moreover, it should be stressed when information is based on one or few observations or on a larger and more reliable set of data; original and literature data should also be clearly indicated (as in our Table 1). As with all faunal surveys we expect findings of additional taxa, especially among nocturnal, arboreal species (at the Pantanal, forested patches are scant and thus we did not spend much collecting effort there). We expect new records from the gallery forests, which may serve as faunal corridors to species coming from along the Pantanal borders (see Fig. 1).

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### Note

1. In February 1993 an adult female of the colubrid snake *Elapomorphus tricolor* D., B. et B. was caught at the Santa Inês site crawling on the ground at ca. 19.00 h. This snake raises to three the number of fossorial species in our study.

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