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The Lizards of Balbina, Central Amazonia, Brazil: A Qualitative Analysis of Resource Utilization

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Twenty one species of lizards (four families) were found in the region of Balbina Hydroelectric Station, Uatumã river, 60 km east of Presidente Figueiredo, Amazonas State, Brazil. Most lizards are exclusive forest dwellers exploring horizontal, vertical, or both spaces. Twenty species are diurnal and one is nocturnal; no marked seasonal difference in activity was observed. Except for the known food specialists *Iguana iguana* (leaves) and *Plica umbra* (ants), and the omnivorous *Tupinambis nigropunctatus*, all other species seem to be arthropod generalists. Three guilds with widely overlapping resource utilization are evident. These patterns are very similar to those found in other localities in the Amazon Basin, probably because of the similarity among their herpetofaunas and structural habitats. A brief review of the hypothesis that tries to explain how the members of these complex assemblages coexist shows that, although some authors suggest that competition is weak or inexists in these assemblages, there is no published study demonstrating the role of competition and/or predation in an Amazonian lizard community.

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Introduction

When compared to temperate regions, relatively few studies on assemblages of lizards were made in the Neotropics, especially the Amazon Basin. As commented by Duellman (1987), lizards are difficult to observe in tropical rain forests because of the density of vegetation and the abundance of leaf litter. Many species are active only in deep shade or are secretive in their habits. Furthermore, some lizards inhabit the canopy, whereas others live underground.

Although primarily systematic, most studies in the last decades have provided baseline data on lizard assemblages for some regions of the Amazon Basin (see a partial review on Amazonian herpetofaunas in Duellman, 1989). In his classical papers, Beebe (1944a and b, 1945) reports a lot of naturalistic data on the lizards of Kartabo (Guyana) and Caripito (Venezuela). The herpetofauna of Santa Cecilia, Ecuador, was extensively studied by Duellman (1978). In Peru, Dixon and Soini (1975) studied the lizards and amphisbaenians of Iquitos region and Duellman (1987) characterized a lizard assemblage in the Cuzco Amazonico region. Lescure and Gasc (1986) studied the herpetofaunas of two localities in northeastern Peru, one in southeastern Colombia, and another in French Guyana. In Bolivia, Fugler (1986) characterized the herpetofauna of the Beni river region. In Brazil, the lizards of Belém were studied by Crump (1971) and Rand and Humphrey (1968), and the reptiles of Carajás region were surveyed by Cunha et al. (1985) and Nascimento et al. (1987). Some other studies on the herpetofauna of broader areas have also provided baseline data on the ecology of Amazonian lizards (e.g., Hoogmoed, 1973; Vanzolini, 1972, 1986).

In the present study I tried to characterize qualitatively the lizard assemblage of Balbina, a site in central Amazon Basin. I compare the patterns observed to other studies in Amazonia and briefly review the hypothesis that try to explain how the members of Amazonian lizard assemblages coexist.

Methods

The study was conducted in the region of Balbina Hydroelectric Station, Uatumã river, some 60 km east of Presidente Figueiredo (approx. 2°09' S, 59°58' W; alt. 50 m), Amazonas State, Brazil (Fig. 1). The region is covered by dense tropical rainforests, predominantly "terra firme" and swamp forests (DNPM, 1976). "Terra firme" and swamp forests of Manaus region (some 100 km south of Balbina) are described by Guillaumet (1987). Except for the hydroeletric area, the region was disturbed only by fishermen and rosewood lumberers. Part of the region is now flooded by the hydroelectric station dam. In the Manaus region, total annual rainfall is about 2100 mm; a marked wet season (165-300 mm/month) occur from November to May, and a drier season (<65 mm/month) from July to September (Leopoldo et al., 1987). Temperatures at Manaus range from 18 to 37°C throughout the year (DNPM, 1976).

Specimens analysed here are from three sources: (1) I collected most specimens at undisturbed forests at Caititu creek, some 30 km north of the station; (2) some were collected by other persons at different stations along the Uatumã river; and (3) a few are from the wildlife rescue made during the flooding of the dam. A total of 140 specimens of 20 species of lizards were collected in Balbina. Only one species, *Iguana iguana*, was only observed and not collected.

I made collections and observations at Caititu creek during three field trips: two during the rainy season (28 November to 6 December, 1986, 16 to 30 April, 1987), and the last in the dry season (25 July to 3 August, 1987). I recorded, when possible, habitat, microhabitat, height above ground, time of the day, and activity for each lizard collected.

I measured (snout-vent length, SVL, and tail length, TL) each lizard in laboratory to the nearest 0.1 mm and recorded if its tail was regenerated. I examined the stomachs of all lizards from Balbina under a dissecting microscope and recorded prey items to order or class level. To compare the importance of each food item in the diet I estimated the size of each prey item found by multiplying maximum length by maximum width (Magnusson et al., 1985).

The purpose of the work at Balbina was to inventory the lizard fauna in the region and to gather basic biological and ecological data on this fauna. Consequently, I tried to collect at least a small series of each species found, but different capture efforts made the data useless for density estimates. Preserved specimens were deposited in the herpetological collection at the Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus.

Results

Twenty one species of lizards (four families) were found in Balbina (Table 1). This number is probably close to the actual composition of the local fauna since most lizard surveys in other localities in the Amazon Basin yielded 20 to 30 species (see Discussion).

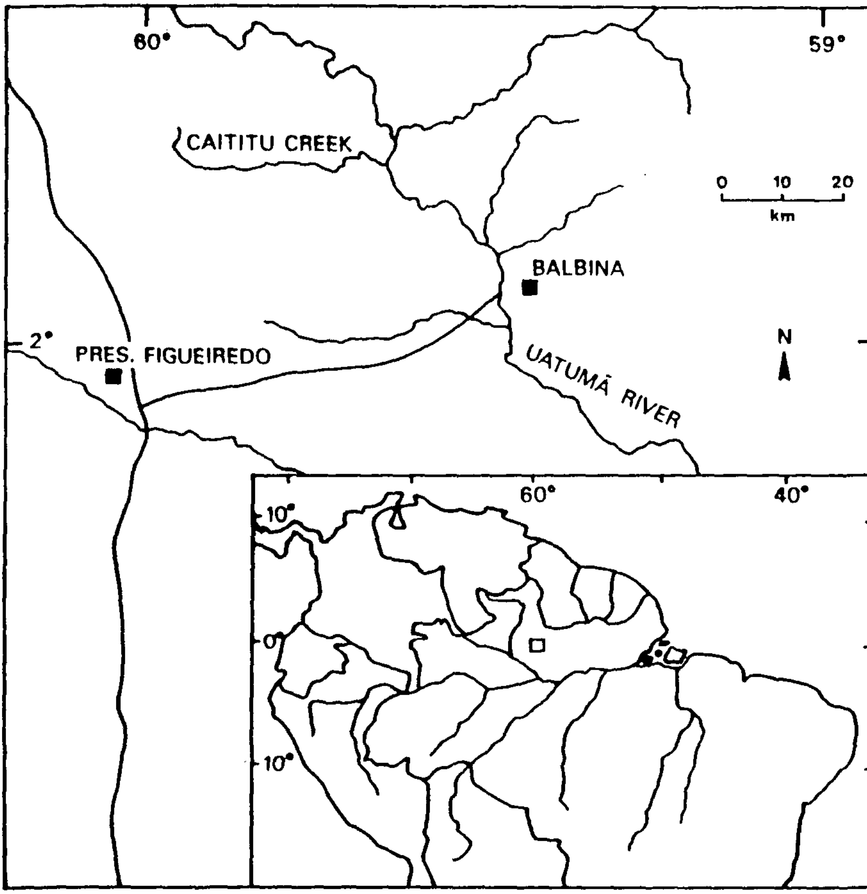

Fig. 1. Location of Balbina region, Amazonas State, Brazil.

Measurements of SVL and TL for all species, except *I. iguana,* are shown in Table 1. Most species (85%) have maximum SVL below 100 mm, and six of them below 50 mm. Four species are widespread in South America, 11 in Amazonia, one is restricted to eastern South America, four are restricted to eastern Amazonia, and one to Central Amazonia (Table 2) (for a recent review on the distribution of Amazonian lizards, see Vanzolini, 1988).

Except by the nocturnal gekkonid *Thecadactylus rapicaudus,* all the lizards found in Balbina are diurnal (Table 2, but see Hoogmoed and Ávila-Pires, 1989). Most of them enter activity soon after sunrise and retreat before sunset. Heliophilic species *(Mabuya bistriata, Ameiva ameiva, Kentropyx calcarata, Tupinambis nigropunctatus, Neusticurus bicarinatus, Tretioscincus agilis,* and *Iguana iguana)* are less active or not active at all in cloudy days. I observed no marked seasonal difference in activity.

Habitats and microhabitats utilized by each species found in Balbina are shown in Table 2. As shown in Table 2, except for *A. ameiva* and *T. nigropunctatus* that

Table 1. Measurements and numbers of intact and regenerated tails of the lizards from Balbina. All measurements are in millimeters. Total number of specimens collected are in parenthesis after species names. SVL = snout-vent length; TL = tail length; $\bar{x}$ = mean; SD = standard deviation. Tails broken and lost during collecting are not included.

	SVL		tail intact	TL	
Species	$\bar{x}$±SD	range	(regenerated)	$\bar{x}$±SD	range
Coleodactylus amazonicus (11)	20.2±1.2	17.4-21.5	6(1)	16.2±1.4	14.6-18.2
Gonatodes humeralis (18)	34.2±2.4	28.8-37.3	6(9)	41.3±3.7	39.6-47.3
Theacadactylus rapicaudus (2)	61.2 and 82.3		0(2)	-----	
Anolis chrysolepis (17)	49.3±17.7	28.4-75.2	15(1)	108.1±48.1	49.0-161.7
Anolis fuscoauratus (8)	43.3±1.0	42.1-45.1	8(0)	80.6±2.1	77.1-83.0
Anolis philopunctatus (3)	65.5±8.5	59.8-75.3	2(0)	154.3 and 190.2	
Plica umbra (1)	87.5		1(0)	184.8	
Uracentron azureum (1)	71.8		1(0)	38.7	
Uranoscodon superciliosa (8)	109.0±41.7	43.0-142.3	6(2)	214.9±100.1	92.4-303.0
Mabuya bistriata (6)	87.4±7.6	73.1-95.0	2(2)	124.1 and 131.7	
Alopoglossus carinicaudatus (3)	43.1±6.3	37.9-50.1	2(2)	69.8 and 88.7	
Ameiva ameiva (14)	115.8±38.6	49.1-170.5	9(4)	251.0±104.1	102.2-391.2
Arthrosaura reticulata (12)	42.3±9.8	24.5-54.3	10(1)	73.6±21.4	38.9-100.7
Bachia cophias (1)	32.6		1(0)	36.5	
Kentropyx calcarata (18)	66.9±22.2	31.9-95.0	13(2)	140.8±52.8	71.9-192.3
Leposoma guianense (5)	28.7±3.8	22.4-32.6	3(1)	56.8±4.3	52.0-60.3
Leposoma percarinatum (3)	32.3±1.7	30.4-33.8	2(0)	59.8 and 62.9	
Neusticurus bicarinatus (2)	49.9 and 63.4		2(0)	101.7 and 128.4	
Tretioscincus agilis (3)	41.5±5.2	35.9-46.1	1(1)	53.0	
Typinambis nigropunctatus (4)	251.6±41.2	190.5-279.7	2(2)	398.0 and 590.6	

Table 2. Types of distribution, habitats occupied, and microhabitat utilization by the lizards of Balbina. Distributions from Gallagher *et al.* (1986), Hoogmoed (1973), Vanzolini (1988), and Rodrigues (1988). CA = Central Amazonia; ESA = Eastern South America; EA = Eastern Amazonia; WA = Widespread in Amazonia; WSA = Widespread in South America. CL = clearing; FC = forest creek; FE = forest edge; GF = gallery forest; O = open; SW = swamp; TFF = terra firme forest.

	Type of Distribution	Habitat	Microhabitat	Height (cm) above ground
Coleodactylus amazonicus	WA	TFF	Shade, leaf litter	0
Gonatodes humeralis	WA	TFF	Shade, trunk, trunk base	0-100
Theacadactylus rapicaudus	WA	TFF	Night, trunk	>150
Anolis chrysolepis	WA	TFF	Shade, trunk, bush, leaf litter	0-50
Anolis fuscoauratus	WSA	TFF	Shade, trunk base, bush, leaf litter	0-20
Anolis philopunctatus	CA	TFF	Shade, trunk, bush	20-200
Iguana iguana	WSA	GF	Sun, canopy	>500
Plica umbra	WA	TFF	Shade, trunk	100-200
Uracentron azureum	EA	TFF	Sun (?), canopy	?
Uranoscodon superciliosa	WA	FC, SW	Shade, trunk, bush, vine	30-150
Mabuya bistriata	WA	CL, FE	Sun, log, leaf litter	0-50
Alopoglossus carinicaudatus	WA	TFF	Shade, leaf litter	0
Ameiva ameiva	WSA	CL, FE, O	Sun, leaf litter, open ground	0
Arthrosaura reticulata	WA	TFF	Shade, leaf litter	0
Bachia cophias	EA	TFF	Shade, under log	0
Kentropyx calcarata	ESA	CL, FE	Sun, bush, log, leaf litter	0-75
Leposoma guianense	EA	TFF	Shade, leaf litter	0
Leposoma percarinatum	WA	TFF	Shade, leaf litter	0
Neusticurus bicarinatus	WA	FC, SW	Sun, leaf litter	0
Tretioscincus agilis	EA	CL, FE	Sun, trunk, bush, log, leaf litter	0-100
Tupinambis nigropunctatus	WSA	FE, CL, O	Sun, leaf litter, open ground	0

are found both in open and forested areas, all species are exclusive forest dwellers. The heliophilic *M. bistriata, A. ameiva, K. calcarata, T. agilis,* and *T. nigropunctatus* inhabit clearings and forest edges. *Iguana iguana, Uranoscodon superciliosa,* and *N. bicarinatus* are good swimmers associated with water. Species cited as terra firme forest dwellers are also found on creek margins and gallery forests, but are not necessarily associated to these habitats like the latter three species.

In relation to microhabitat (Fig. 2), seven species are exclusively terrestrial, five are exclusively arboreal, five explore both vertical and horizontal spaces, two are arboreal/semiaquatic, one is terrestrial/semi-aquatic, and one is fossorial. The gekkonid *Coleodactylus amazonicus* and the teiids *Alopoglossus carinicaudatus, Arthrosaura reticulata, Leposoma guianense,* and *L. percarinatum* were found amidst leaf litter in shaded areas, whereas the teiids *Ameiva ameiva* and *Tupinambis nigropunctatus* were found in sunny areas of the leaf litter. The latter species were also observed on open ground. The gekkonids *Gonatodes humeralis* and *Thecadactylus rapicaudus,* and the iguanids *Anolis philopunctatus* and *Plica umbra* were found on trunks, whereas the iguanid *Iguana iguana* was observed in tree canopies, always near or inside water; the iguanid *Uracentron azureum* lives also in the canopy of high trees (Hoogmoed, 1973). *Uranoscodon superciliosa* was found always on the vegetation of creek margins and occasionally jumped into the water when disturbed, and the teiid *Neusticurus bicarinatus* was found in the leaf litter also at creek margins. The iguanids *Anolis chrysolepis* and *A. fuscoauratus,* the scincid *Mabuya bistriata* and the teiids *Kentropyx calcarata* and *Tretioscincus agilis* were found both in leaf litter and on the vegetation, the latter three always in sunny areas. *Bachia cophias* with greatly reduced limbs is fossorial and was found under a fallen log.

The stomach contents of 10 species for which three or more stomachs had identifiable items are listed in Table 3. The stomach contents found in the ten remaining species are the following (number of stomachs with identifiable items in parenthesis): *T. rapicaudus* (2), one scorpion, one cricket, and one cockroach: *P. umbra* (1), five ants; *A. carinicaudatus* (1), one spider and one bug; *B. cophias* (1), five dipterous larvae; *L. guianense* (2), one fly, one ant, and one homopteran; *L. percarinatum* (1), one Collembola and one diplopod; *N. bicarinatus* (2), 14 flies and four spiders; *T. agilis* (1), one grasshopper; *T. nigropunctatus* (2), two spiders, one caterpillar, one bone, fruit remains, leaves, flower buds, pieces of bark, and one flea.

Although my samples are small, data in Table 3 and from literature (references in Introduction) suggest that nearly all lizard species found in Balbina are arthropod generalists, eventually consuming other prey types. Exceptions are the antspecialist *P. umbra* (see also Hoogmoed, 1973) and the generalist *T. nigropunctatus; Iguana iguana* adults are herbivorous and *U. azureum* seems to eat mainly ants (see Hoogmoed, 1973).

Table 4 summarizes the resource utilization by the lizards found in Balbina; similarities and differences in resource utilization can be easily visualized (see also Fig. 2). Three guilds are obvious: (1) the six first species have SVLs smaller than 60 mm, eat arthropods of similar size, and live in shaded areas of the leaf litter of terra firme forests; (2) the five following species have a wide range of SVLs (but greatly overlapping), eat arthropods of a wide and similar size range,

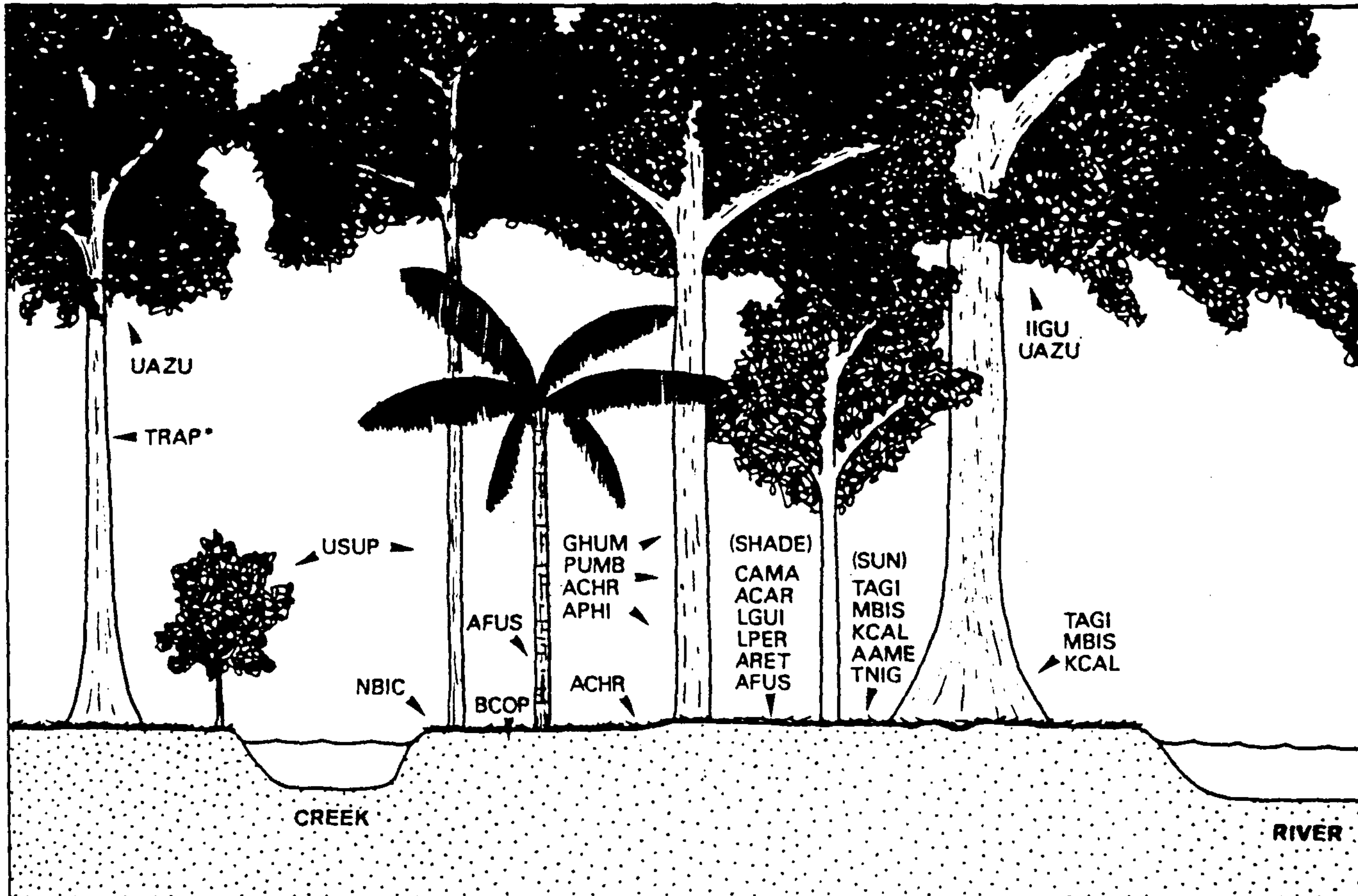

Fig. 2. Schematic profile of a forest showing microhabitats where the 21 lizard species from Balbina were found. In species abbrevations the first letter corresponds to the first letter of the genus and the following three are the first three letters of the species (see species names in Table 2). The asterisk indicates that the species is nocturnal. Note that some species were found in more than one microhabitat and that three guilds are evident at the center of the figure (six terrestrial species in shaded areas, five terrestrials in sunny areas, and four arboreals; see text and Table 4).

Table 3. Percent size (maximum length multiplied by maximum width) of stomach contents of ten lizard species from Balbina for which three or more stomachs had identifiable items (see text for the stomach contents of the other species). Number of specimens analysed are below species abreviation. CA = *C. amazonicus;* GH = *G. humeralis;* AC = *A. chrysolepis;* AF = *A. fuscoauratus;* AP = *A. punctatus;* US = *U. superciliosa;* MB = *M. bistriata;* AA = *A. ameiva;* AR = *A. reticulata;* KC = *K. calcarata.*

	CA 6	GH 9	AC 11	AF 4	AP 3	US 6	MB 3	AA 10	AR 5	KC 13
ARACHNIDA										
Araneida	12	–	26	6	–	5	2	1	24	15
Opilionida	–	–	–	–	–	–	–	<1	–	–
Pedipalpida	–	–	–	–	–	–	–	16	–	–
Pseudoscorpionida	–	1	–	–	–	–	–	–	–	–
Ricinulei	–	–	–	–	–	–	3	–	–	–
Scorpionida	–	–	–	–	–	–	6	7	–	–
CHILOPODA	–	–	–	–	–	11	–	4	–	–
CRUSTACEA										
Gastropoda	7	–	–	–	–	–	–	–	–	–
Isopoda	–	–	9	–	–	–	–	–	–	–
INSECTA										
Diptera										
adult	9	5	–	–	–	–	–	–	–	<1
larvae	–	3	–	–	–	–	–	1	–	–
Coleoptera										
adult	–	7	2	–	–	8	–	2	–	–
larvae	7	15	–	–	–	–	–	–	–	<1
Collembola	7	–	–	–	–	–	–	–	–	–
Hemiptera	–	<1	6	–	–	8	–	3	–	–
Homoptera	–	–	–	18	15	10	–	–	–	–
Hymenoptera										
ants	–	–	4	–	3	4	–	28	–	–
others	–	<1	2	–	–	–	–	2	–	1
Isoptera	23	55	–	–	–	13	–	–	–	–
Lepidoptera										
larvae	35	–	3	20	13	8	17	1	2	–
pupae	–	–	–	–	–	8	–	–	–	–
Odonata										
nimph	–	–	–	–	–	1	–	–	–	–
Orthoptera										
grasshoppers	–	–	–	–	51	–	35	–	–	11
crickets	–	4	29	18	18	–	–	18	–	65
cockroaches	–	6	–	37	–	15	37	14	73	8
OLIGOCHAETA	–	1	18	–	–	–	–	–	–	–
HIRUDINEA	–	–	–	–	–	7	–	–	–	–
Fruit	–	–	–	–	–	–	–	–	–	1

Table 4. A summary of body size and recource utilization of the lizards of Balbina. The three first groups separated by spaces have species with similar requirements and are considered guilds. In the abbreviations of species names the first letter corresponds to the first letter of the genus and the following three are the first three letters of the species names in table 2). G = arthropod generalist; S = specialist; O = omnivorous; H = herbivorous; SU = sun; SH = shade; TF = terra firme forest; CL = clearing; CR = forest creek; SW = swamp; ED = forest edge; OP = open; GF = gallery forest; LL = leaf litter; UG = underground. Measurements in the SVL and Prey size columns are in millimiters and heights in the Microhabitat column are in meters.

	SVL range			Prey size				prey type				sun/ shade		Habitat							Micro-habitat			
SPP	20-60	60-100	>100	0-<20	20-<60	60-<140	>140	G	S	O	H	SU	SH	TF	CL	CR	SW	ED	OP	GF	LL	<1	<5	UG
Cama	---			----				-					--	--							--			
Acar	---			----				-					--	--							--			
Lgui	---			----				-					--	--							--			
Lper	---			----				-					--	--							--			
Aret	---			----	----	----		-					--	--							--			
Afus	---			----	----			-					--	--							--	--		
Tagi	---				?			-				--			--			--			--	--		
Mbis	---	---		----	----	----	----	-				--			--			--			--	--		
Kcal	---	---		----	----	----	----	-				--			--			--			--	--		
Aame	---	---	---	----	----	----	----	-				--			--			--	--		--			
Tnig		---	---			----	----			-		--			--			--	--		--			
Ghum	---			----	----			-					--	--								--		
Pumb	---	---			----				-				--	--								--		
Achr	---	---		----	----	----		-					--	--							--	--		
Aphi	---	---		----	----	----	----	-					--	--								--	--	
Usup	---	---	---	----	----	----	----	-					--			--	--					--	--	
Nbic	---	---		----	----			-				--				--	--				--			
Uazu	---	---			?				?			?		--									c	
Bcop	---			----				-					--	--										--
Iigu		---	---		l						-	--								--			c	
Trap	---	---					----	-				n		--									--	

l = leaves; n = nocturnal; c = canopy

and live in sunny areas of the leaf litter in clearings and forest edges; and finally, (3) the following four species have an also wide range of SVLs, eat arthropods of similar sizes, and are found in trunks in shaded areas of terra firme forests. However, it is worth noting that some species can be included in more than one guild depending on the resource considered (e.g., *A. fuscoauratus*, here included in the first guild, is also found in trunks at low heights and so could be included in the third guild; *Anolis chrysolepis* and *A. punctatus*, included in the third guild feed on leaf litter arthropods by jumping from tree trunks or shrubs to the leaf litter, pers. obs., and so, at least for feeding habitat and prey size and type, could be included in the first guild). The remaining species cannot be assigned to any guild because they differ in the utilization of key-resources (e.g., *I. iguana* is herbivore and lives in canopy; *T. rapicaudus* is nocturnal; *B. cophias* is fossorial).

Discussion

The lizard fauna found in the rainforest of Balbina is nearly as rich as those found in most localities studied in the Amazon Basin (20 forest species found at Carajás, Brazil, by Cunha et al., 1985, and Nascimento et al., 1987; 21 at Belém, Brazil, by Rand and Humphrey, 1968; 37 at Iquitos region, Peru, by Dixon and Soini, 1975; 30 at Santa Cecilia, Ecuador, and 21 at Cuzco Amazonico, Peru, by Duellman, 1978, and Duellman, 1987, respectively; 11 at Beni River region, Bolivia, by Fugler, 1986; 16 at Kuiru, Colombia, 26 at Colonia and 20 at Yubineto, Peru, and 23 at Trois-Sauts, French Guyana, by Lescure and Gasc, 1986; 24 at several localities in Rondônia, Brazil, by Vanzolini, 1986). Duellman (1978) suggested that the rich herpetofauna of Santa Cecilia may be related to large amount of rainfall (4000 mm), climatic equability, and historical biogeography of the region (see also Duellman, 1989). Similarly, differences in species composition and the consequent differences in resource utilization in diverse Amazonian localities largely depend on the history of each particular assemblage (Duellman, 1989).

The results on resource utilization presented here are very similar to those found in other localities in the Amazon Basin (references above; Duellman, 1989), probably because of the similarity in faunal compositions (both in genera and species) and structural habitats of these localities. However, Hoogmoed and Ávila-Pires (1989) found *C. amazonicus*, *A. reticulata*, and *L. guianense* also active during nights with a nearly full moon.

Studies of resource utilization in natural communities have documented differences among ecologically similar species that were generally been inferred to reduce competition facilitating stable coexistence (Dunham, 1983). For lizards, the great majority of these studies were made in deserts (reviews in Pianka, 1973, 1986) and on assemblages of *Anolis* species in the West Indies (see Roughgarden, 1983, and references therein).

Lizard assemblages in the Amazon Basin are rich and structurally complex (references above; this study). Several factors, such as physiological and morphological constraints, predation, and competition may be responsible for the patterns of resource utilization found in herpetofaunal assemblages (Toft, 1985). In Amazonia, the extensive overlaps observed within guilds (review in Duellman, 1989), the apparent abundance of resources, and the low density of most lizards (see Duellman, 1987; Vanzolini, 1988:325) lead some authors to suggest that competition is weak or inexists in Amazonian lizard assemblages (Duellman, 1978; Rand and Humphrey, 1968). Duellman (1978) suggested that the probable absence of interspecific competition at Santa Cecilia could be the result of not only resource abundance, but also structural heterogeneity and climatic equability of the environment, and differential resource utilization by its members.

What, then, control lizard populations in Amazonia? Duellman (1978) reasonably concluded that aperiodic environmental fluctuations (e.g., severe drought, excessive rainfall) and predation are the primary factors controlling the populations in the Santa Cecilia herpetofauna. In fact, in Amazonia, lizards are preyed upon by diverse predators such as fishes (Goulding, 1980), other lizards (Duellman, 1978; pers. obs.), snakes (Duellman, 1978; Cunha and Nascimento, 1978), birds (Hilty and Brown, 1986), and mammals (Snowdon and Soini, 1988), and some of them are specialized lizard predators (see, e.g., Cunha and Nascimento, 1978; Duellman, 1978; Hilty and Brown, 1986). However, there is no published study demonstrating the role of predation and/or competition in an Amazonian lizard assemblage. Future long term studies on lizard assemblages in Amazonia will be very useful to our understanding of the structure and dynamics of these rich, complex and poorly known assemblages.

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