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Geographical Variation in the Ecology of Populations of Some Brazilian Species of *Cnemidophorus* (Squamata, Teiidae)

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We investigated geographical variation in ecological parameters among populations of *Cnemidophorus cryptus*, *Cnemidophorus gramivagus*, *Cnemidophorus lemniscatus*, *Cnemidophorus ocellifer*, and *Cnemidophorus parecis*, from three Brazilian biomes (Cerrado, Caatinga, and Amazonian Savannas). Lizards used mainly the open ground, with a high similarity in microhabitat use among populations. Differences in microhabitat use probably resulted from the availability of microhabitats and not from microhabitat preferences. Body temperatures were high and little influenced by environmental temperatures, there being no differences among populations. There were significant differences in diet among populations, with *C. ocellifer* from Caatinga and Cerrado consuming large quantities of termites, whereas Amazonian Savanna species used primarily ants and insect larvae. The data on reproductive seasonality indicated cyclical reproduction in seasonal biomes and continuous reproduction in unpredictable climate regions. We found significant differences in mean clutch size among populations, independent of body size, with *C. lemniscatus* having the smallest clutch size (1.50) and *C. ocellifer* from Cerrado the largest (2.10). There were fewer differences in clutch size among species from Amazonian Savannas, than between populations of *C. ocellifer* from Caatinga and Cerrado. Apparently, populations under seasonal climates concentrate their reproductive effort during the short reproductive season, producing larger clutches, whereas those under more stable or unpredictable climates reproduce continuously, yielding smaller clutches, corroborating the hypothesis that environmental conditions exert an important influence upon life-history parameters. There were significant differences in body shape among populations, but most of the variation was related to sex. We also observed significant differences in body size among populations, seemingly unrelated to differences in community structure, but the highly conservative morphology of *Cnemidophorus* species suggests the presence of historical constraints.

TWO major patterns have been identified in studies of geographic variation in life-history parameters among squamates. On one hand, species may exhibit the same attributes independently of variations in environmental parameters. For example, lizards of the large Neotropical genus *Anolis* exhibit an unusual reproductive characteristic, all species laying clutches of a single egg. This is compensated for by frequent ovipositions (e.g., Andrews and Rand, 1974; Roff, 1992), a pattern that is likely genetically constrained. Conversely, differences in environmental conditions among sites can lead to differences in life-history patterns among taxa resulting from ecotypical adaptations. For example, the Neotropical lizard *Ameiva ameiva* reproduces seasonally in areas where climate is highly seasonal (Cerrado and Amazonian Savannas) but continuously where precipitation is abundant throughout the year (Amazon Forest) or where climate is unpredictable (Caatinga, Vitt, 1982; Colli, 1991; Vitt and Colli, 1994). The influence of environmental conditions upon life-history parameters of squamates has usually been assessed through geographical variation studies (e.g., Tinkle and Dunhan, 1986; Vitt, 1992; Vitt et al., 1998).

The genus *Cnemidophorus* is distributed from the northern United States to central Argentina (Wright, 1993), comprising approximately 50 species (Cole and Dessauer, 1993; Wright, 1993; Rocha et al., 2000). Eight species of *Cnemidophorus* are presently known to occur in Brazil: the bisexuals *Cnemidophorus lemniscatus* and *Cnemidophorus gramivagus* and the unisexual *Cnemidophorus cryptus*, in Amazonia (Ávila-Pires, 1995); the bisexual *Cnemidophorus lacertoides*, in the southern region (Peters and Orejas-Miranda, 1986); the unisexual *Cnemidophorus nativo*, in the state of Espírito Santo (Rocha et al., 1997); the bisexuals *Cnemidophorus littoralis*, in the state of Rio de Janeiro (Rocha et al., 2000), *Cnemidophorus vacariensis*, in the state of Rio Grande do Sul (Feltrin and Lema, 2000), *Cnemidophorus ocellifer*, in the entire territory, except Amazonia (Vanzolini et al., 1980; Peters and Orejas-Miranda, 1986; Colli, 1998), and *Cnemidophorus parecis*

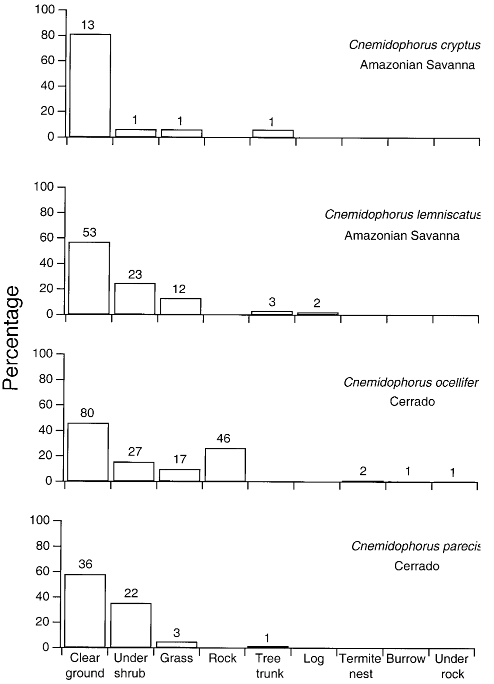

Fig. 1. Collecting localities of *Cnemidophorus* from Brazil. 1, Brasília (30); 2, Pirenópolis (90); 3, Cristalina (25); 4, Caldas Novas (6); 5, Alto Paraíso (28); 6, Minaçu (144); 7, Mineiros (4); 8, Barra do Garças (60); 9, Chapada dos Guimarães (35); 10, Vilhena (103); 11, São Domingos-GO (10); 12, Mateiros (33); 13, Palmas (43); 14, Sebastião Laranjeiras (4); 15, Cocos (3); 16, Coribe (19); 17, Correntina (16); 18, Irecê (32); 19, Salvador (3); 20, Paulo Afonso (3); 21, Exu (33); 22, Humaitá (62); 23, Boa Vista (40); 24, Alter do Chão (53); 25, Macapá (62); and 26, Tartarugalzinho (17). Sample size in parentheses. Adapted from "Mapa de Vegetação do Brasil" by Instituto Brasileiro de Geografia e Estatística (IBGE).

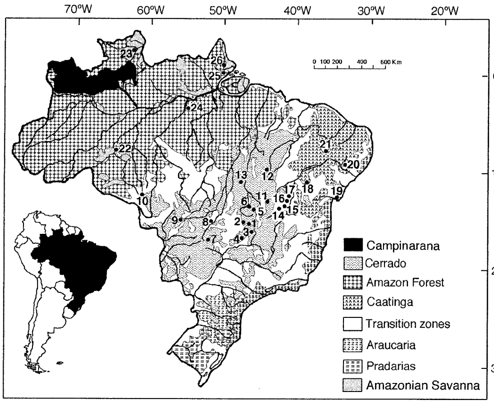

Fig. 2. Frequency distribution of individuals according to microhabitat categories, for four species of *Cnemidophorus* from Brazil. Sample sizes are indicated at the top of the bars.

in southern Rondônia (Vanzolini, 1986; Vitt and Caldwell, 1993; Colli et al., 2003).

Several studies have been conducted on geographical variation in the ecology of some species of *Cnemidophorus*. In Colorado and Texas, two populations of *Cnemidophorus tigris* show marked variation in their reproductive strategies: the Colorado population has a larger body, produces a single but larger clutch, and breeds during a short warm season, whereas the Texas population produces two smaller clutches, associated with a longer activity period (McCoy and Hoddenbach, 1966). The northern populations of *C. tigris* emerge from hibernation later than southern populations because of the longer winters (Pianka, 1970). These studies suggest that life-history patterns of *Cnemidophorus* are influenced by regional variations in environmental conditions. Conversely, differences in microhabitat use, body size, and diet were observed among four populations of *Cnemidophorus* in the Brazilian Amazon, but no clear association could be established with ecological differences in habitats or resources among localities (Vitt et al., 1997).

The objective of this work is to compare data on the morphometry, microhabitat, reproductive biology, body temperature, and diet of six populations, belonging to five species of the genus *Cnemidophorus*, from three Brazilian open-vegetation biomes (Cerrado, Caatinga, and Amazonian Savannas). In addition, we test the hypothesis that variations in life-history patterns are associated with differences in environmental conditions.

Materials and Methods

Study sites.—The Cerrado covers about 1,500,000 km^2, about 18% of Brazil (Ferri, 1977). The region is characterized by the Aw climate (Köppen classification), annually receiving 1500–2000 mm of highly predictable and strongly seasonal precipitation, from October to April. Monthly temperatures average 20–22 C (Nimer, 1977a). The Cerrado biome includes forests, where arboreal species predominate; savannas, with trees and shrubs dispersed in a herbaceous stratum; and grasslands, with herbaceous species and some shrubs. Tree trunks are tortuous, with thick corky barks and hard, coriaceous leaves (Ribeiro and Walter, 1998).

The Caatinga covers about 850,000 km^2, about 10% of Brazil (Andrade-Lima, 1981). The dry tropical Bs climate (Köppen classification) is characterized by hot summers and precipitation rarely exceeding 1000 mm (Eidt, 1968; Ribeiro and Walter, 1998). Rains are highly unpredictable, and pronounced droughts can last several months or even years. Average monthly temperature is between 22 and 26 C (Nimer, 1977b). The vegetation consists of small tortuous shrubs, spiny trees, cactus, and bromeliads, varying from grasslands with few trees to small forest patches (Andrade-Lima, 1981).

Amazonian Savannas occur like scattered islands inside the Amazon Forest and cover about 150,000 km^2, or 2% of Brazil (Pires, 1973). The climate (Aw) is highly seasonal and annual precipitation averages 1700 mm (Eidt, 1968). The vegetation is dominated by species typical of the Cerrado, but diversity is lower (Eiten, 1978).

All specimens examined are deposited in the ''Coleção Herpetológica da Universidade de Brasília'' (CHUNB). Collecting sites are indicated in Figure 1 and listed in Appendix 1.

Microhabitat, activity, and temperatures.—We captured lizards by hand or using a shotgun. In the lab, we humanely killed live lizards with an injection of Tiopental® and fixed them with 10% formalin. At the time of capture, we took cloacal, substrate, and air temperatures to the nearest 0.2 C, with a Miller and Weber® cloacal thermometer. We also recorded microhabitat, activity when individuals were first sighted and after the approach by the investigator, hour, and date of capture. We used the following microhabitat categories: burrows, bushes, fallen logs, grass, open ground, rocks, termite nests, tree trunks, and under rocks. We classified lizard activities as stationary, moving, and running. To compute an activity index, we assigned a value of zero to the ''stationary'' category, and one to the ''moving'' and ''running'' categories, averaging the values of ''activity when first sighted'' and ''activity after approached'' for each individual. Therefore, the mean activity index for each species could range from zero to one. Microhabitat data were not available for *C. ocellifer* from Caatinga and *C. gramivagus.* To assess the contribution of environmental temperatures in the determination of lizard cloacal temperature, we used a stepwise regression (Tabachnick and Fidell, 1996) and to compare cloacal temperatures among species we used an ANCOVA with environmental temperatures as covariates (Tabachnick and Fidell, 1996). *Cnemidophorus ocellifer* from Caatinga and *C. gramivagus* were excluded from analyses because environmental temperatures for these species were not available.

Diet.—We analyzed stomach contents under a stereoscopic microscope, identifying prey items to level of order. We recorded the length and width (0.01 mm) of intact items with Mitutoyo® electronic calipers, and estimated prey volume (V) as an ellipsoid:

$$V = \frac{4}{3}\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right),$$

where w is prey width and l is prey length. We calculated the numeric and volumetric percentages of each prey category for individual lizards and for pooled stomachs. From these percentages, we computed niche breadths (B) for each individual and for pooled stomachs, using the inverse of Simpson's diversity index (Simpson, 1949):

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2},$$

where p is the numeric or volumetric proportion of prey category i and n is the number of categories. We also calculated the percentage of occurrence of each prey category (number of stomachs containing prey category i, divided by the total number of stomachs). We excluded from the volumetric analyses prey items that were too fragmented to allow a reliable estimation of their volumes. To determine the relative contribution of each prey category, we calculated the importance index for individuals and pooled stomachs using the following equation:

$$I = \frac{F\% + N\% + V\%}{3},$$

where $F\%$ is the percentage of occurrence, $N\%$ is the numeric percentage, and $V\%$ is the volumetric percentage.

To test for differences in diet composition among populations, we used a MANOVA with the importance index of prey categories as dependent variables. In this analysis, we only used prey categories with an importance index larger than 5%, considering the remaining categories as unimportant. Prior to analyses, we subjected the importance index to the arcsine transformation, to satisfy the assumption of normality (Zar, 1998).

We calculated the similarity in diet composition using the equation (Pianka, 1973):

$$\phi_{ij} = \frac{\sum_{i=1}^{n} p_{ij}p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}},$$

where p represents the proportion of prey category i, n is the number of categories, and j and

k represent the species being compared. $\O_{ij}$ varies from zero (no similarity) to one (complete similarity). To assess the similarity in prey use among species, we used the importance index calculated from pooled stomachs. We performed a cluster analysis on the diet similarity matrix, using the centroid method (Pielou, 1984).

Morphometry.—Using a Mitutoyo® electronic caliper, we recorded morphometric variables to the nearest 0.01 mm: snout–vent length (SVL), body width (at its broadest point); body height (at its highest point), head width (at its broadest point), head height (at its highest point), head length (from the tip of the snout to the commissure of the mouth), leg length, forelimb length, and tail length (from the cloaca to the tip of the tail). To maximize the availability of data, we estimated intact tail length of lizards with broken or regenerated tails using a regression equation relating tail length to SVL, calculated from lizards with intact tails, separately for populations and sexes. All regressions were highly significant ($P < 0.0001$), with coefficients of determination greater than 0.68. We log-transformed (base 10) all morphometric variables prior to analyses to meet the requirements of normality (Zar, 1998). To partition the total morphometric variation between size and shape, we defined body size as an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986). We calculated 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 postmultiplying the n by p matrix of log-transformed data, where n is the number of observations, by the p by 1 isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used Burnaby's method (Burnaby, 1966), by postmultiplying the n by p matrix of the log-transformed data by a p by p symmetric matrix, L, defined as:

$$L = I_p - (V^T V)^{-1} V^T,$$

where I_p is a p by p identity matrix, V is the isometric size eigenvector defined above, and V^T is the transpose of matrix V (Rohlf and Bookstein, 1987). Hereafter we refer to the resulting size-adjusted variables as shape variables. To test the null hypothesis of no difference between sexes and populations, we conducted separate analyses on body size (ANOVA) and shape variables (MANOVA).

Reproduction.—We sexed each individual by dissection and direct examination of the gonads, considering females as reproductively active by the presence of vitellogenic follicles or oviductal eggs. We regarded the simultaneous presence of enlarged vitellogenic follicles and either oviductal eggs or corpora lutea as evidence for the sequential production of more than one clutch of eggs during the year. In addition, we considered males as reproductively active by the presence of enlarged testes and convoluted epididymides. When possible, we analyzed for each population the monthly distribution of mature individuals of each sex to determine the timing of reproduction. We estimated size at maturity for females based on the smallest individual containing vitellogenic follicles or oviductal eggs and, for males, based on the smallest individual bearing enlarged testes and convoluted epididymides. To compare clutch size among populations, we used an ANCOVA with SVL as the covariate. When data were available, we also made comparisons of the breeding period among populations.

Statistical analyses.—We carried out statistical analyses using SYSTAT 5.2.1 for Macintosh and SAS 6.12 for Macintosh (Cary, NC), with a significance level of 5% to reject null hypotheses. Throughout the text, means appear ± 1 SD.

RESULTS

Microhabitat, activity, and body temperatures.—For all species, the most frequently used microhabitat categories were "clear ground," followed by "under shrubs," with the exception of *C. ocellifer* from the Cerrado, where "rocks" was the second most used microhabitat category (Fig. 2). However, there was no significant difference in microhabitat use among populations ($\chi^2 = 38.83$; $P = 0.48$).

Overall, lizards were moving when first sighted, but there were significant differences among populations (Kruskall-Wallis $H = 172.51$; $P < 0.001$). Most noticeably, a large fraction of the individuals of *Cnemidophorus parecis* were stationary at first sighting (Table 1). Populations also differed significantly in the "activity after approached" (Kruskall-Wallis $H = 172.51$; $P < 0.001$), with Amazonian Savanna species (*C. cryptus* and *C. lemniscatus*) running when approached and Cerrado species (*C. ocellifer* and *C. parecis*) remaining stationary (Table 1). In most comparisons, Amazonian Savanna species had a significantly higher activity index, relative to species from Cerrado (Table 1). There was no significant correlation between mean activity

Table 1. Activity and Temperatures of *Cnemidophorus* from Brazil.

	Amazonian Savanna			Cerrado	
	C. cryptus (n = 80)	*C. gramivagus* (n = 42)	*C. lemniscatus* (n = 92)	*C. ocellifer* (n = 174)	*C. parecis* (n = 54)
When first sighted[1]					
Moving	88 (14)	—	87 (80)	71 (123)	47 (29)
Stationary	12 (2)	—	13 (12)	25 (44)	47 (29)
Running	—	—	—	4 (7)	6 (4)
After approached[1]					
Moving	6 (1)	—	36 (34)	17 (29)	22 (14)
Stationary	25 (4)	—	8 (7)	61 (107)	40 (25)
Running	69 (11)	—	56 (52)	22 (38)	38 (24)
Activity index[2]	0.77 ± 0.10^{bc}	—	0.88 ± 0.08^{c}	0.57 ± 0.09^{a}	0.57 ± 0.09^{ab}
Cloacal temperature (C)[3]	39.40 ± 1.95 (34.60–44.40)	37.65 ± 2.29 (30.40–40.00)	38.48 ± 1.86 (33.20–44.40)	37.52 ± 2.35 (28.00–41.60)	38.24 ± 2.21 (31.00–42.00)
Substrate temperature (C)	37.42 ± 3.43	—	37.21 ± 3.84	32.25 ± 3.78	34.79 ± 3.05
Air temperature at 5 cm (C)	34.66 ± 2.35	—	34.57 ± 2.09	30.73 ± 2.99	32.85 ± 2.09
Air temperature (C)	32.27 ± 3.59	—	31.60 ± 1.22	29.39 ± 2.72	30.85 ± 3.50

[1] Numbers indicate percentage, with sample size in parentheses.

[2] Different letters indicate groups of means that differed statistically (Tukey test, $P < 0.05$).

[3] Values in parentheses indicate minimum and maximum.

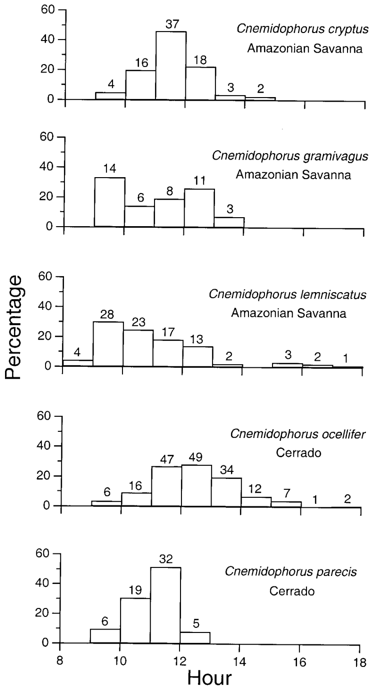

Fig. 3. Frequency distribution of individuals collected according to hour of the day, for five species of *Cnemidophorus* from Brazil. Sample sizes are indicated at the top of the bars.

index and mean cloacal temperature (Spearman's $r = 0.80$, $n = 4$, $P = 0.20$).

The mean cloacal temperature of all species was relatively high (Table 1). In most species, cloacal temperatures were more influenced by substrate temperature than air temperatures (*Cnemidophorus cryptus*: partial $r = 0.566$, $P < 0.001$; *C. lemniscatus*: partial $r = 0.619$, $P < 0.001$; *C. ocellifer* from Cerrado: partial $r = 0.363$, $P < 0.001$), whereas in *C. parecis* the cloacal temperature was more influenced by air temperature (partial $r = 0.508$, $P < 0.001$). There were no significant differences in cloacal temperatures among populations, independent of the effects of environment temperatures (ANCOVA $F_{3,387} = 2.55$; $P = 0.056$). As noted previously, *C. ocellifer* from Caatinga and *C. gramivagus* were excluded from analysis for lack of temperature data. Lizards were found mainly during the hottest hours of the day (Fig. 3).

Diet.—The Cerrado and Caatinga populations ate mainly termites, whereas Amazonian Savanna populations ate chiefly orthopterans, insect larvae, ants, spiders, and beetles (Table 2). Overall, Amazonian Savanna populations presented a broader diet than Cerrado and Caatinga populations (Table 2). The Cerrado and Caatinga populations of *C. ocellifer* were the most similar in diet composition, forming a cluster followed by *C. lemniscatus*, *C. cryptus*, and *C. gramivagus* (Fig. 4). There were significant differences among populations in diet composition (MANOVA, Wilks' Lambda = 0.694; $P < 0.001$), and a stepwise discriminant analysis indicated that hymenopterans, orthopteras, hemipterans/homopterans, ants, insect larvae, beetles, termites, neuropterans, and spiders were the prey categories that best discriminated the populations of *Cnemidophorus.* Overall, these are the most important prey in the diet of all populations combined, but the discriminatory power of diet composition was low: only 49.54% of the individuals were correctly classified, based on cross-validation (SAS/STAT user's guide, rele. 6.03, SAS Institute, Inc., Cary, NC, 1988). These results indicate a high similarity in diet composition of all populations. There was no significant correlation between population means of prey volume and body size ($r = 0.37$; $P = 0.47$) nor between maximum prey volume and maximum body size ($r = 0.66$; $P = 0.16$), indicating that differences in diet composition among populations were not produced by differences in body size.

Morphometry.—The SVL of the smallest individual was similar across populations, except for *C. gramivagus* where the smallest female was much larger than in other populations (Table 3). The largest individuals were found in *C. parecis*, with the SVL of the largest individual being similar in the remaining populations (Table 3). A two-way ANOVA on body size of adults revealed significant effects of population ($F_{5,615} = 41.04$; $P < 0.001$), sex ($F_{1,615} = 7.43$; $P = 0.007$), and the interaction of the two factors ($F_{4,615} = 17.23$; $P < 0.001$). Tukey multiple comparisons tests indicated that *C. parecis* (mean = 4.14 ± 0.16, $n = 55$) was significantly larger than *C. gramivagus* (mean = 4.01 ± 0.11, $n = 30$), *C. lemniscatus* (mean = 3.97 ± 0.14, $n = 74$), *C. ocellifer* from Cerrado (mean = 3.92 ± 0.15, $n = 324$), and *C. cryptus* (mean = 3.91 ± 0.08, $n = 54$); *C. ocellifer* from Caatinga (mean = 4.09 ± 0.17, $n = 98$) was significantly larger than *C. lemniscatus*, *C. ocellifer* from Cerrado, and *C. cryptus*; *C. gramivagus* was significantly larger than *C. ocellifer* from Cerrado and *C. cryptus.* Furthermore, males (mean = 4.01 ± 0.11, $n = 30$) were significantly larger than females of bisexual species (mean = 3.92 ± 0.14, $n = 226$) and parthenogenetic females of *C. cryptus* (mean = 3.91 ± 0.08, $n = 54$).

There were significant differences among populations in shape variables for males (Wilk's

TABLE 2. IMPORTANCE INDEX OF PREY CATEGORIES IN THE DIET OF *Cnemidophorus* FROM BRAZIL.

	Amazonian Savanna				Caatinga				Cerrado			
	C. cryptus		*C. gramivagus*		*C. lemniscatus*		*C. ocellifer*		*C. ocellifer*		*C. parecis*	
Prey categories	IIS	IPS	IIS	IPS	IIS	IPS	IIS	IPS	IIS	IPS	IIS	IPS
Annelida	—	—	—	—	—	—	—	—	—	—	0.87	0.60
Aranae	21.53	21.49	20.65	19.14	18.17	15.69	9.62	7.77	17.08	14.01	19.78	16.97
Blattaria	—	—	—	—	—	—	1.16	0.73	2.04	2.20	4.46	3.70
Chilopoda	—	—	—	—	—	—	—	—	0.74	1.09	—	—
Coleoptera	12.25	11.82	16.83	15.37	23.22	22.25	5.96	5.38	7.33	6.92	16.56	15.25
Crustacea Isopoda	—	—	—	—	—	—	0.37	0.29	0.73	0.44	—	—
Diplopoda	—	—	—	—	—	—	—	—	—	—	2.38	1.90
Diptera	—	—	6.01	6.13	5.06	4.96	2.67	2.43	3.07	2.45	0.42	0.35
Formicidae	8.92	7.51	33.19	51.14	10.65	9.84	—	—	5.50	4.81	24.94	21.99
Gastropoda	—	—	—	—	—	—	0.31	0.29	—	—	—	—
Orthoptera	31.28	32.25	16.76	16.41	18.48	24.02	13.01	12.84	18.48	17.09	9.31	5.54
Hemiptera/Homoptera	7.22	6.47	23.38	21.55	10.23	9.49	6.28	4.97	9.41	8.84	7.50	2.16
Other Hymenoptera	15.57	15.16	28.87	29.16	2.35	2.34	—	—	1.47	1.36	—	—
Isoptera	14.07	21.67	—	—	18.79	32.36	47.84	62.95	46.12	60.03	43.95	60.86
Insect larva	30.21	33.28	7.49	7.64	24.50	27.87	34.07	28.41	15.37	13.44	9.44	9.51
Lepidoptera	2.57	3.48	—	—	—	—	—	—	0.31	0.28	—	—
Mantodea	—	—	—	—	—	—	0.72	0.67	1.97	1.92	—	—
Plant material	1.77	1.85	—	—	—	—	1.85	1.48	1.32	0.89	3.07	3.24
Neuroptera	—	—	—	—	—	—	0.87	0.65	6.67	5.67	7.06	4.98
Odonata	—	—	—	—	—	—	—	—	0.57	0.41	0.36	0.36
Insect egg	8.86	10.32	—	—	—	—	0.86	1.05	1.10	0.38	—	—
Phasmidae	—	—	—	—	1.14	1.35	—	1.02	—	—	—	—
Pseudoescopriones	—	—	—	—	1.26	0.87	—	—	0.18	0.18	0.87	0.36
Scorpiones	—	—	—	—	—	—	—	—	0.33	0.28	6.88	4.63
Solifuga	—	—	—	—	—	—	—	—	0.89	0.68	2.79	1.54
Num. niche breadths	2.94 ± 2.06	5.27	2.29 ± 1.01	4.44	2.25 ± 1.27	3.43	1.57 ± 0.72	1.40	1.75 ± 0.97	4.09	2.38 ± 2.42	1.54
Vol. niche breadths	1.43 ± 0.66	5.22	1.47 ± 0.54	2.6	1.29 ± 0.46	4.17	1.42 ± 1.10	2.79	1.57 ± 0.80	1.51	1.50 ± 0.63	4.22

Note: IIS—importance index for individual stomachs, IPS—importance index for pooled stomachs.

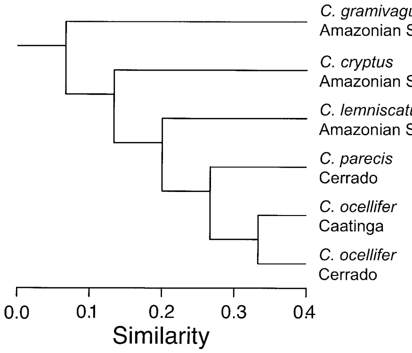

Fig. 4. Cluster analysis calculated with the diet similarity index of six *Cnemidophorus* populations from Brazil.

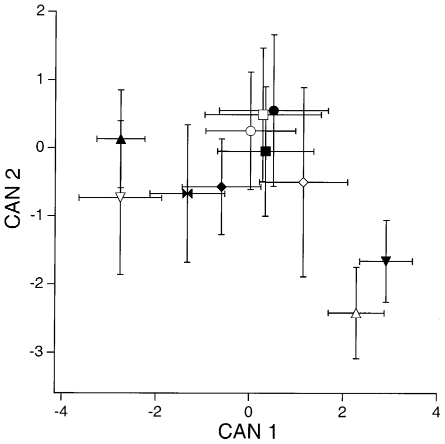

Fig. 5. Scores of first two canonical discriminant functions derived from size-adjusted morphometric variables of six populations of *Cnemidophorus* from Brazil. Horizontal and vertical lines represent one standard deviation, above and below the mean canonical score. *Cnemidophorus cryptus*: butterfly, *Cnemidophorus gramivagus*: triangles, *Cnemidophorus lemniscatus*: diamonds, *Cnemidophorus ocellifer* from Caatinga: squares, *C. ocellifer* from Cerrado: circles, *Cnemidophorus parecis*: inverted triangles. Empty symbols indicate males and filled symbols indicate females.

Lambda = 0.76, $P < 0.001$) and females (Wilk's Lambda = 0.62, $P < 0.001$). A canonical discriminant analysis maximizing the separation among populations indicated that lizards with high values in the first canonical variable (64% of the total shape variation) have elongate bodies and short tails, whereas lizards with high values in the second canonical variable (19%) have longer but shallower heads (Table 4). By far, most of the variation in shape is based on sex, rather than population (Fig. 5). *Cnemidophorus parecis* and *C. gramivagus* displayed the most pronounced sexual dimorphism, followed by *C. lemniscatus* and *C. ocellifer*. Interestingly, females of *C. parecis* were more similar to males of *C. gramivagus* and vice versa. *Cnemidophorus cryptus* displayed an intermediate shape between females of *C. gramivagus* and *C. lemniscatus*.

Reproduction.—The smallest SVL at reproduction was very similar across lizard populations, with the exception of females of *Cnemidophorus parecis* and males of *C. ocellifer* from Cerrado (Table 3). Populations differed significantly in clutch size, independently of differences in SVL (ANCOVA $F_{5,103} = 9.36$, $P < 0.001$), with *C. lemniscatus* showing the smallest and *C. ocellifer* of Cerrado the largest clutch size (Table 3). The range of clutch size was similar among populations, with *C. ocellifer* from the Cerrado having the largest range while *C. lemniscatus* and *C. parecis* had the smallest range (Table 3).

TABLE 3. LIFE-HISTORY PARAMETERS OF *Cnemidophorus* FROM BRAZIL.

	Amazonian Savanna			Caatinga				Cerrado			
	C. cryptus	*C. gramivagus*		*C. lemniscatus*		*C. ocellifer*		*C. ocellifer*		*C. parecis*	
Parameters	f	m	f	m	f	m	f	m	f	m	f
Smallest lizard SVL (mm)	31	32	44	35	37	32	33	30	31	36	39
Largest lizard SVL (mm)	65	69	76	74	61	87	74	74	72	90	89
Sexual maturity SVL (mm)	50	56	56	51	49	52	52	40	51	57	72
Clutch size											
Raw means	1.56 ± 0.63	1.67 ± 1.15		1.50 ± 0.52		1.83 ± 0.51		2.10 ± 0.74		1.64 ± 0.51	
SVL-adjusted means	1.59	1.54		1.87		1.60		2.15		0.69	
Range	1–3	1–3		1–2		1–3		1–4		1–2	
Sample size	16	3		16		23		41		11	
Means comparisons[1]	bcd	abcd		bcd		c		d		a	

[1] Different letters indicate means significantly different at the 5% level through Tukey multiple comparisons tests. SVL = snout–vent length, m = males, f = females.

In *C. ocellifer* from Cerrado, reproduction is concentrated mainly in the dry season (May to September), whereas *C. ocellifer* from Caatinga seems to reproduce throughout the year (Table 5). In the other populations, samples are restricted to fewer months, making it difficult to infer the reproductive cycle (Table 5). In *C. cryptus*, the simultaneous occurrence of eggs/vitellogenic follicles and vitellogenic follicles/corpora lutea indicates the production of multiple clutches during the reproductive season.

DISCUSSION

Microhabitat, activity, and temperatures.—Overall, populations of *Cnemidophorus* used similar microhabitats, regardless of the biome from which they came. The minor differences observed among populations probably resulted from among-region differences in microhabitat availability, but not from contrasting microhabitat preferences. For instance, lizards in Amazonian Savannas were most often encountered on ‘‘clear ground,'' but no lizards were found in ‘‘rocks.'' However, rock outcrops are uncommon in Amazonian Savannas. Conversely, rock outcrops are frequent in Cerrado and *C. ocellifer* is often seen using this microhabitat. Our results underscore the view that these lizards are ground-dwellers, with a strong preference for open microhabitats (Magnusson et al., 1986; Vitt, 1991b; Vitt et al., 1997).

Lizards in the genus *Cnemidophorus* are heliothermic, being active during the hottest hours of day (except in deserts) and having high body temperatures when compared to sympatric species (Bergallo and Rocha, 1993; Teixeira-Filho et al., 1995; Vitt, 1995). Several studies indicate that the intensity of environmental temperatures may influence activity levels of lizards (e.g., Magnusson et al., 1985; Haigen and Fengxiang, 1995). The higher levels of activity we observed in Amazonian Savanna *Cnemidophorus* relative to Cerrado is probably a consequence of higher environmental temperatures encountered in Amazonian Savannas (Wilks' Lambda = 0.652; $P < 0.0001$).

Considering that lizard body temperatures are often correlated with environmental temperatures (Schall, 1977; Colli, 1991; Vitt, 1991a), we expected that in areas with high environmental temperatures, lizards would show higher cloacal temperatures. For instance, *Ameiva ameiva* from Caatinga have higher body temperatures than lizards from Amazon Forest, Amazonian Savanna, or Cerrado (Sartorius et al., 1999). However, we found no significant difference among populations. ‘‘Sit-and-wait'' lizards are less vagile and more associated with restricted portions of the environment, often showing a good association between cloacal temperatures and environmental temperatures (Rocha and Bergallo, 1990; Bergallo and Rocha, 1993). However, lizards in the genus *Cnemidophorus*, being active foragers, are highly mobile, resulting in a poor fit between cloacal temperatures and environmental temperatures (Schall, 1977; Teixeira-Filho et al., 1995). Our results are in agreement with a study with five sympatric species of *Cnemidophorus*, where cloacal temperatures did not vary with site, season, and sex, suggesting that thermal tolerance, independent of external influences, is a conservative trait of the genus (Schall, 1977).

TABLE 4. CANONICAL DISCRIMINANT ANALYSIS OF SIZE-ADJUSTED MORPHOMETRIC VARIABLES OF *Cnemidophorus* FROM BRAZIL ($n = 650$).

Variable	Canonical discriminant function	
	CAN1	CAN2
SVL	1.27	−0.05
TL	−0.38	0.56
BW	0.70	0.93
BH	0.52	0.24
HW	0.70	0.48
HH	0.75	−0.12
HL	0.59	1.12
FL	0.49	−0.06
LL	0.12	0.09

Note: SVL = snout–vent length, TL = tail length, BH = body height, BW = body width, HL = head length, HH = head height, HW = head width, FL = forelimb length, and LL = leg length.

Diet.—Most studies to date indicate that lizards in the genus *Cnemidophorus* feed primarily on termites (e.g., Vitt et al., 1993; Bergallo and Rocha, 1994; Eifler and Eifler, 1998). Some species of *Cnemidophorus*, however, may depend heavily on other prey categories, such as insect larva, orthopterans, ants, and beetles (Vitt, 1991b; Paulissen and Walker, 1996; Vitt et al., 1997). Still, there are species that consume large quantities of plant material, such as *C. lemniscatus* (Mijares-Urrutia et al., 1997; Vitt et al., 1997) and even fully herbivorous species, such as *C. murinus* (Dearing, 1993; Schall, 1996). Considering such broad range in dietary composition, the differences we observed among populations might result from differences in dietary preferences. Other factors, however, may prevail, such as food availability (that we did not address in this study) and seasonality. For instance, *C. ocellifer* from Caatinga and Cerrado were collected throughout the year, but in different years, and

TABLE 5. PERCENTAGE OF REPRODUCTIVE INDIVIDUALS OF *Cnemidophorus* DURING THE YEAR.

Month	Amazonian Savanna			Caatinga				Cerrado			
	C. cryptus	*C. gramivagus*		*C. lemniscatus*		*C. ocellifer*		*C. ocellifer*		*C. parecis*	
	f	m	f	m	f	m	f	m	f	m	f
January	—	—	—	—	—	—	100 (1)	64 (7)	50 (2)	—	—
February	—	—	—	—	—	—	—	—	—	—	—
March	—	—	—	—	—	—	—	67 (6)	0 (0)	—	—
April	—	—	—	—	—	100 (1)	—	92 (12)	21 (3)	—	—
May	—	—	—	—	—	100 (8)	83 (5)	95 (21)	52 (11)	—	—
June	—	—	—	—	—	100 (3)	—	100 (10)	44 (4)	—	—
July	—	—	—	—	—	—	—	57 (13)	56 (10)	—	—
August	—	—	—	59 (14)	75 (9)	92 (65)	45 (15)	75 (3)	100 (1)	100 (2)	—
September	50 (20)	—	—	97 (30)	100 (8)	—	—	45 (5)	67 (6)	71 (10)	30 (3)
October	20 (1)	36 (4)	5 (1)	—	—	83 (5)	25 (1)	50 (1)	0 (0)	—	—
November	—	—	67 (2)	—	—	—	100 (1)	70 (28)	26 (7)	100 (24)	35 (8)
December	—	—	—	—	—	100 (1)	—	14 (1)	0 (0)	—	—

Note: Number of reproductive individuals in parentheses.

the Amazonian Savanna species (*C. cryptus*, *C. gramivagus*, and *C. lemniscatus*) were collected during the dry season in different years. *Cnemidophorus lemniscatus* ingested small amounts of plant material, whereas other investigators recorded large quantities of plant material in the diet of this species (Mijares-Urrutia et al., 1997). This may indicate that diet for this species varies seasonally. In addition, another study conducted during the wet season in Roraima, Brazil concluded that the diet of *C. lemniscatus* consisted mainly of fruits from *Byrsonima* (Malpighiaceae; Vitt and Carvalho, 1995; Vitt et al., 1997). Species of *Byrsonima* in Amazonian Savannas produce fruits primarily during wet season (Miranda, 1991), making it unlikely that lizards will use these fruits during the dry season. Because of the possible influence of seasonality, it is difficult to determine whether the dietary differences among populations are caused by variations in food preferences or in prey availability. The correlation between prey size and body size was not significant, indicating that dietary differences among populations do not reflect differences in body size.

Reproduction and morphometry.—South American populations of *Cnemidophorus* display a variety of reproductive patterns. In Amazonian Savannas, *C. lemniscatus* breeds seasonally, with egg deposition occurring during the wet season and recruitment occurring at the peak of the dry season (Magnusson, 1987). *Cnemidophorus ocellifer* breeds throughout the year in Caatinga (Vitt, 1983) but mainly during the dry season in the Cerrado (this work). Reproductive parameters are often related to environmental factors that limit reproduction (Tinkle et al., 1970; Dunham et al., 1988; Vitt, 1990). For instance, in temperate regions reproduction is associated with cold-warm seasonality, whereas in tropical regions it is dictated by wet-dry seasonality. For example, *Gymnodactylus geckoides* in Caatinga breeds continuously and produces a fixed clutch of one large egg (Vitt, 1986), whereas the Cerrado population breeds seasonally during dry season (unpubl. data). Our results corroborate the view that reproduction is cyclical in seasonal biomes (Amazonian Savannas and Cerrado) and continuous in regions with unpredictable climates (Caatinga; Colli, 1991; Vitt and Colli, 1994).

We observed fewer differences in clutch size within biomes, even when different species are considered (e.g., *C. cryptus*, *C. gramivagus*, and *C. lemniscatus*), than among biomes, when considering the same species (e.g., *C. ocellifer* from Caatinga and Cerrado). Nevertheless, there were no differences in clutch size between Amazonian Savanna and Caatinga populations. Because we found evidence of multiple clutches in *C. cryptus* from the savannas of Amapá, the high levels of precipitation in Amazonian Savannas (Eidt, 1968) may induce prolonged reproductive seasons and smaller clutches relative to Cerrado populations. Environmental predictability is probably the main determinant of clutch size differences among populations of *Cnemidophorus.* Seemingly, populations under seasonal climates (e.g., Cerrado) concentrate their reproductive effort during the short reproductive season, producing larger clutches, whereas those under stable or unpredictable climates (e.g., Caatinga) reproduce continually, yielding smaller clutches. Other studies also indicate that the length of the reproductive season is inversely correlated with clutch size (Vitt, 1982; Colli, 1991; Vitt and Colli, 1994).

In addition to the length of the reproductive season, clutch size can also be influenced by microhabitat preferences (Dunham et al., 1988; Roff, 1992; Stearns, 1992). The use of rock crevices as shelter to avoid predators has strong influences in the morphology of *Tropidurus semitaeniatus,* resulting in a reduced clutch size (Vitt, 1981). However, there is no evidence that differences in body size among populations of *Cnemidophorus* result from differential microhabitat use, because in all populations the microhabitat used most often was the ground in open areas. Clutch size is also intimately related to female body size, with larger females generally producing larger clutches (Dunham et al., 1988; Roff, 1992). In a study with four populations of *Cnemidophorus* from Amazonian Savannas populations, however, no significant association between body and clutch size was found, in spite of significant differences in body size (Vitt et al., 1997). We observed differences in clutch size among populations independently of differences in body size, a result that underscores the strong influence local environmental conditions might exert upon life-history parameters.

Lizards of the genus *Cnemidophorus* are a conspicuous element in practically all lizard communities in Brazilian open biomes. Along with other species of Teiidae and Gymnophthalmidae, they form the active foraging guild in these communities, characterized by highly similar body shapes but different body sizes, presumably an evolutionary consequence of intraguild interactions (Vitt, 1995; Vitt and Zani, 1996; Vitt et al., 2000). We observed significant differences in body size among populations, seemingly unrelated to differences in community structure. For example, the two populations with the largest body size, *C. parecis* and *C. ocellifer* from Caatinga, coexist with four and three active foraging species, respectively (Vitt and Caldwell, 1993; Vitt, 1995; GRC, unpubl. data), whereas the two populations with the smallest body size, *C. ocellifer* from Cerrado and *C. cryptus,* coexist with 5–10 and two active foraging species, respectively (Colli et al., 2002; GRC, unpubl. data). Therefore, it is possible that body size differences result from historical factors and also from other local influences not associated with community structure. The highly conservative morphology of *Cnemidophorus* species throughout the huge geographic distribution of the genus suggests the prevalence of historical constraints.

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LITERATURE CITED

ANDRADE-LIMA, D. 1981. The caatingas dominium. Rev. Bras. Bot. 4:149–163.

ANDREWS, R., AND S. A. RAND. 1974. Reproductive effort in anoline lizards. Ecology 55:1317–1327.

ÁVILA-PIRES, T. C. S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zool. Verh. 1995:3–706.

BERGALLO, H. G., AND C. F. D. ROCHA. 1993. Activity patterns and body temperatures of two sympatric lizards (*Tropidurus torquatus* and *Cnemidophorus ocellifer*) with different foraging tactics in southeastern Brazil. Amphib.-Reptilia 14:312–315.

———, AND ———. 1994. Spatial and trophic niche differentiation in two sympatric lizards (*Tropidurus torquatus* and *Cnemidophorus ocellifer*) with different foraging tactics. Aust. J. Ecol. 19:72–75.

BURNABY, T. P. 1966. Growth-invariant discriminant functions and generalized distances. Biometrics. 22:96–110.

COLE, C. J., AND H. C. DESSAUER. 1993. Unisexual and bisexual whiptail lizards of the *Cnemidophorus lemniscatus* complex (Squamata: Teiidae) of the Guiana region, South America, with descriptions of new species. Am. Mus. Novit.:1–30.

Colli, G. R. 1991. Reproductive ecology of *Ameiva ameiva* (Sauria: Teiidae) in the cerrado of central Brazil. Copeia 1991:1002–1012.

———. 1998. Guia dos lagartos do Distrito Federal, http://www.unb.br.ib.zoo.grcolli.index.html.

———, R. P. Bastos, and A. F. B. Araújo. 2002. The character and dynamics of the Cerrado herpetofauna, p. 223–241. *In:* The Cerrados of Brazil: ecology and natural history of a Neotropical savanna. P. S. Oliveira and R. J. Marquis (eds.). Columbia Univ. Press, New York.

———, G. C. Costa, A. A. Garda, K. A. Kopp, D. O. Mesquita, A. K. Péres Jr., P. H. Valdujo, G. H. C. Vieira, and H. C. Wiederhecker. 2003. A critically endangered new species of *Cnemidophorus* (Squamata, Teiidae) from a Cerrado enclave in southwestern Amazonia, Brazil. Herpetologica 59:76–88.

Dearing, M. D. 1993. An alimentary specialization for herbivory in the tropical whiptail lizard *Cnemidophorus murinus.* J. Herpetol. 27:111–114.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles, p. 441–522. *In:* Biology of the Reptilia. Vol. 16. Ecology B. Defense and life history. C. Gans and R. B. Huey (eds.). Alan R. Liss, Inc., New York.

Eidt, R. C. 1968. The climatology of South America, p. 54–81. *In:* Biogeography and ecology in South America. Vol. 1. E. J. Fitkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli (eds.). Dr. W. Junk N. V. Publishers, The Hague, Netherlands.

Eifler, D. A., and M. A. Eifler. 1998. Foraging behavior and spacing patterns of the lizard *Cnemidophorus uniparens.* J. Herpetol. 32:24–33.

Eiten, G. 1978. Delimitation of the Cerrado concept. Vegetatio 36:169–178.

Feltrin, A. C., and T. Lema. 2000. Uma nova espécie de *Cnemidophorus* (Waagler, 1830) do Estado do Rio Grande do Sul, Brasil (Sauria, Teiidae). Biociências 8:103–114.

Ferri, M. G. 1977. Ecologia dos Cerrados, p. 15–36. *In:* IV Simpósio Sobre o Cerrado. M. G. Ferri (ed.). Editora Itatiaia, Belo Horizonte, Italy.

Haigen, X., and Y. Fengxiang. 1995. Simulation model of activity of *Phrynocephalus przewalskii.* Ecol. Model. 77:197–204.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

Magnusson, W. E. 1987. Reproductive cycles of teiid lizards in Amazonian savanna. J. Herpetol. 21:307–316.

———, L. J. D. Paiva, R. M. D. Rocha, C. R. Franke, L. A. Kasper, and A. P. Lima. 1985. The correlates of foraging mode in a community of Brazilian lizards. Herpetologica 41:324–332.

———, C. R. Franke, and L. A. Kasper. 1986. Factors affecting densities of *Cnemidophorus lemniscatus.* Copeia 1986:804–807.

McCoy, C. J., and G. A. Hoddenbach. 1966. Geographic variation ovarian cycles and clutch size in *Cnemidophorus tigris* (Teiidae). Science:1671–1672.

Mijares-Urrutia, A., B. Colvee, and R. A. Arends. 1997. Sauria: *Cnemidophorus lemniscatus* (NCN). Herbivory. Herpetol. Rev. 28:88.

Miranda, I. S. 1991. Estrutura e Fenologia de uma Comunidade Arbórea da Savana Amazônica de Alter do Chão, Pará. Instituto Nacional de Pesquisas da Amazônia, Fundação Universidade do Amazonas, Manaus, AM, Brazil.

Nimer, E. 1977a. Clima, p. 35–58. *In:* Geografia do Brasil. Vol. 4. Região Centro-Oeste. F. I. B. d. G. e. Estatística (ed.). Diretoria de Divulgação, Centro Editorial, Centro de Servicos Gráficos, Rio de Janeiro, Brazil.

———. 1977b. Clima, p. 47–84. *In:* Geografia do Brasil. Vol. 2. Região Nordeste. F. I. B. d. G. e. Estatística (ed.). Diretoria de Divulgação, Centro Editorial, Centro de Servicos Gráficos, Rio de Janeiro, Brazil.

Paulissen, M. A., and J. M. Walker. 1996. Lacertilia: *Cnemidophorus sackii gigas* (giant spotted whiptail). Diet. Herpetol. Rev. 27:20.

Peters, J. A., and B. Orejas-Miranda. 1986. Catalogue of the Neotropical Squamata. Part II. Lizards and Amphisbaenians. Smithsonian Institution Press, Washington, DC.

Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703–720.

———. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4:53–74.

Pielou, E. C. 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley and Sons, New York.

Pires, J. M. 1973. Tipos de vegetação da Amazônia. Pub. Av. Mus. Par. Emílio Goeldi 20:179–202.

Ribeiro, J. F., and B. M. T. Walter. 1998. Fitofisionomias do bioma Cerrado, p. 89–166. *In:* Cerrado: Ambiente e Flora. S. M. Sano and S. P. Almeida (eds.). EMBRAPA-CPAC, Planaltina, DF, Mexico.

Rocha, C. F. D., and H. G. Bergallo. 1990. Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria: Iguanidae) in an area of amazonian Brazil. Ethol. Ecol. Evol. 2:263–268.

———, ———, and D. Peccinini-Seale. 1997. Evidence of an unisexual population of the Brazilian whiptail lizard genus *Cnemidophorus* (Teiidae), with description of a new species. Herpetologica 53:374–382.

———, A. F. B. Araújo, D. Vrcibradic, and E. M. M. Costa. 2000. New *Cnemidophorus* (Squamata; Teidae) from coastal Rio de Janeiro State, southeastern Brazil. Copeia 2000:501–509.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, London.

Rohlf, F. J., and F. L. Bookstein. 1987. A comment on shearing as a method for "size correction." Syst. Zool. 36:356–367.

Sartorius, S. S., L. J. Vitt, and G. R. Colli. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforests by the teiid lizard *Ameiva ameiva.* Biol. Conserv. 90:91–101.

Schall, J. J. 1977. Thermal ecology of five sympatric species of *Cnemidophorus* (Sauria: Teiidae). Herpetologica 33:261–272.

———. 1996. Lacertilia: *Cnemidophorus murinus ruth-*

veni (Bonaire Island whiptail lizard). Seeds in diet. Herpetol. Rev. 27:142–143.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Somers, K. M. 1986. Multivariate allometry and removal of size with principal component analysis. Syst. Zool. 35:359–368.

Stearns, S. C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford.

Tabachnick, B. G., and L. S. Fidell. 1996. Using multivariate statistics. Harper Collins Publishers, Inc., New York.

Teixeira-Filho, P. F., C. F. D. Rocha, and S. C. Ribas. 1995. Aspects of thermal ecology and habitat use by *Cnemidophorus ocellifer* (Sauria: Teiidae) in the Restinga of Barra de Maricá, Rio de Janeiro, p. 155–165. *In:* Oecologia Brasiliensis. Vol. 1. Structure, function and management of Brazilian ecosystems; symposium on ecosystems structure, function and management, Rio de Janeiro, Brazil, May 27–29, 1992. F. D. A. Esteves (ed.). Institute of Biology, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil.

Tinkle, D. W., and A. E. Dunhan. 1986. Comparative life histories of two syntopic sceloporine lizards. Copeia 1986:1–18.

———, H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Vanzolini, P. E. 1986. Levantamento Herpetológico da Área do Estado de Rondônia sob a Influência da Rodovia BR 364. Conselho Nacional do Desenvolvimento Científico e Tecnológico, Assessoria Editorial, Brasília, Distrito Federal, Brasil.

———, A. M. M. Ramos-Costa, and L. J. Vitt. 1980. Répteis das Caatingas. Academia Brasileira de Ciências, Rio de Janeiro, Brasil.

Vitt, L. J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. Am. Nat. 117:506–514.

———. 1982. Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habitat. Can. J. Zool. 60:3113–3120.

———. 1983. Reproduction and sexual dimorphism in the tropical teiid lizard *Cnemidophorus ocellifer.* Copeia 1983:359–366.

———. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Ibid.* 1986:773–786.

———. 1990. The influence of foraging mode and phylogeny on seasonality of tropical lizard reproduction. Pap. Avul. Zool., S. Paulo 37:107–123.

———. 1991a. Ecology and life history of the wide-foraging lizard *Kentropyx calcarata* (Teiidae) in Amazonian Brazil. Can. J. Zool. 69:2791–2799.

———. 1991b. An introduction to the ecology of Cerrado lizards. J. Herpetol. 25:79–90.

———. 1992. Diversity of reproductive strategies among Brazilian lizards and snakes: the significance of lineage and adaptation, p. 135–149. *In:* Reproductive Biology of South American Vertebrates. W. C. Hamlett (ed.). Springer-Verlag, New York.

———. 1995. The ecology of tropical lizards in the Caatinga of northeast Brazil. Occ. Pap. Okla. Mus. Nat. Hist. 1:1–29.

———, and J. P. Caldwell. 1993. Ecological observations on Cerrado lizards in Rondônia Brazil. J. Herpetol. 27:46–52.

———, and C. M. Carvalho. 1995. Niche partitioning in a tropical wet season: lizards in the Lavrado area of northern Brazil. Copeia 1995:305–329.

———, and G. R. Colli. 1994. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Can. J. Zool. 72:1986–2008.

———, and P. A. Zani. 1996. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. *Ibid.* 74:1313–1335.

———, ———, J. P. Caldwell, and R. D. Durtsche. 1993. Ecology of the whiptail lizard *Cnemidophorus deppii* on a tropical beach. *Ibid.* 71:2391–2400.

———, ———, T. C. S. Avila-Pires, M. C. D. Araujo, and W. E. Magnusson. 1997. Ecology of whiptail lizards (*Cnemidophorus*) in the amazon region of Brazil. Copeia 1997:745–757.

———, ———, ———, and M. C. Esposito. 1998. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecpleopus* in the Amazon rainforest. Can. J. Zool. 76:1671–1680.

———, S. S. Sartorius, T. C. S. Ávila-Pires, M. C. Espósito, and D. B. Miles. 2000. Niche segregation among sympatric Amazonian teiid lizards. Oecologia 122:410–420.

Wright, J. W. 1993. Evolution of the lizards of the genus *Cnemidophorus*, p. 27–81. *In:* Biology of Whiptail Lizards (Genus *Cnemidophorus*). J. W. Wright and L. J. Vitt (eds.). Oklahoma Museum of Natural History, Norman.

Zar, J. H. 1998. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ.

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Appendix 1

Specimens Examined

Cnemidophorus cryptus (Amazonian Savanna). Amapá: Macapá (0°02′N, 51°03′W) and Tartarugalzinho (1°26′N, 1°04′W), September to October 1991.

Cnemidophorus gramivagus (Amazonian Savanna). Amazonas: Humaitá (7°31′S, 63°02′W), October–November 1991.

Cnemidophorus lemniscatus (Amazonian Savanna). Pará: Alter do Chão (39°12′S, 7°40′W), August 1992. Roraima: Boa Vista (2°49′N, 60°40′W), September 1992.

Cnemidophorus ocellifer (Caatinga). Bahia: Cocos

(14°10′S, 44°33′W), June 1992; Coribe (13°50′S, 44°28′W), May 1988; Correntina (13°20′S, 44°28′W), January 1993, October–December 1992; Irecê (11°18′S, 41°53′W), August 1991; Paulo Afonso (9°21′S, 38°14′W), July 1976; Salvador (12°59′S, 38°31′W), October 1991; Sebastião Laranjeiras (14°35′S, 45°3′W), April 1991. Pernambuco: Exu (7°31′S, 39°43′W), January 1993, 1994.

Cnemidophorus ocellifer (Cerrado). Distrito Federal: Brasília (15°47′S, 47°55′W), June 1987, April–May 1988, April 1989, December 1989, September 1990, August 1991, October 1993. Goiás: Alto Paraíso (14°05′S, 47°31′W), March 2000; Caldas Novas (17°45′S, 48°38′W) August, October 1999; Cristalina (16°45′S, 47°36′W), June 1997, May 1998, January, July, November 1999; Minaçu (13°49′S, 48°20′W), November 1986, May–June 1992, October–November 1992, November–December 1996, January, July–August 1997, September–December 1998; March, May–July 1999; Mineiros (17°34′S, 52°34′W), January 1991, May, July 1999; Pirenópolis (15°51′S, 48°57′W), January, June, December 1990, April, September 1991, May 1992, July, October 1999, April–May 2000; São Domingos (13°24′S, 46°19′W), May 1999. Mato Grosso: Barra do Garças (15°53′S, 52°15′W), no date; Chapada dos Guimarães (15°26′S, 55°45′W), June, September 1988. Tocantins: Palmas (26°50′S, 52°00′W), July, September, November–December 1999; Mateiros (10°11′S, 46°40′W), November 1999.

Cnemidophorus parecis (Cerrado). Rondônia: Vilhena (12°43′S, 60°07′W), August 1998, September–October 1999.