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The Ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a Neotropical Savanna

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ABSTRACT.—**We studied the ecology of the lizard *Cnemidophorus ocellifer* Spix 1825 in the central Brazilian Cerrado. *Cnemidophorus ocellifer* was active on open ground, in sandy soils and rocky fields, during the hottest hours of the day. Mean body temperatures (37.5°C) were high, relative to sympatric lizard species, and more associated with substrate temperatures than with air temperatures. The thermal ecology of *C. ocellifer* seems to be tightly associated with an active mode of foraging. Termites were the most important prey, and there was no significant association between head dimensions and prey dimensions. *Cnemidophorus ocellifer* showed strong sexual dimorphism in body size and shape, with males having larger bodies and head dimensions, and females having longer and thicker bodies. Clutch size averaged 2.1 and was positively correlated with female SVL. Females were reproductively active during the dry season (May to September) and recruitment occurred from July to November. Males were reproductively active throughout the year, peaking from March to August, coinciding with the period of female reproduction. The reproductive cycle in *C. ocellifer* may be determined by the greater availability of direct sunlight and its physiological effects upon breeding activities, such as courtship and mating, during the dry season.**

Covering approximately 2,000,000 km^2 or 25% of Brazil, the Cerrado is the largest open-vegetation biome in South America (Oliveira and Marquis, 2002). Marked by a pronounced wet-dry seasonality, the Cerrado harbors a diverse herpetofauna with several endemic species (Colli et al., 2002). However, the Cerrado has being undergoing habitat alteration at an accelerated pace (Alho and Martins, 1995). Unfortunately, detailed studies on the ecology of the Cerrado herpetofauna are few (see Vitt, 1991a; Colli, 2002).

Herein, we provide a detailed account of the ecology of *Cnemidophorus ocellifer* Spix 1825 from the central Brazilian Cerrado. The *C. ocellifer* species complex is distributed throughout Brazil, except in Amazonia (Vanzolini et al., 1980; Peters and Orejas-Miranda, 1986). Recently, several populations of the *C. ocellifer* complex have been described as new species (Rocha et al., 1997; Feltrin and Lema, 2000; Rocha et al., 2000; Colli et al., 2003). We specifically address the following questions: What is the nature of the variation in morphometric variables within the species? What are the patterns of habitat and microhabitat use? What are the most important prey items? Is there a reproductive cycle and what are the forces governing it? In addition, we make detailed comparisons between *C. ocellifer* and other lizard species from the Cerrado.

MATERIALS AND METHODS

Study Sites.—Collecting sites are indicated in Figure 1 and listed in Appendix 1. The Cerrado receives annually 1500–2000 mm of precipitation, which is highly predictable and strongly seasonal, restricted to the period from October to April. Annual temperatures average 20–22°C (Nimer, 1977). Long-term climatic data from Brasília, Distrito Federal, in the core region of the Cerrado, are summarized in Figure 2. The Cerrado vegetation includes forests, where arboreal species predominate; savannas, with trees and scrubs dispersed in a herbaceous stratum; and fields, with herbaceous species and some shrubs. For a recent review on the biome see Oliveira and Marquis (2002).

About 20% of the specimens were collected by third parties during the flooding of the Serra da Mesa hydroelectric dam at Minaçu, Goiás State. We captured lizards by hand or using a shotgun. At the time of capture, we took body, substrate, and air temperatures (at 5 cm from substrate and at chest height) to the nearest 0.2°C, with Miller and Weber® cloacal thermometers. 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: burrow, bush, fallen log, grass, clear ground on sandy soil, rock, termite nest, tree trunk, and under rock. We classified lizard activities as stationary, moving, and running. In the lab, we humanely killed live individuals with an injection of Tiopental®, measured, and fixed them with

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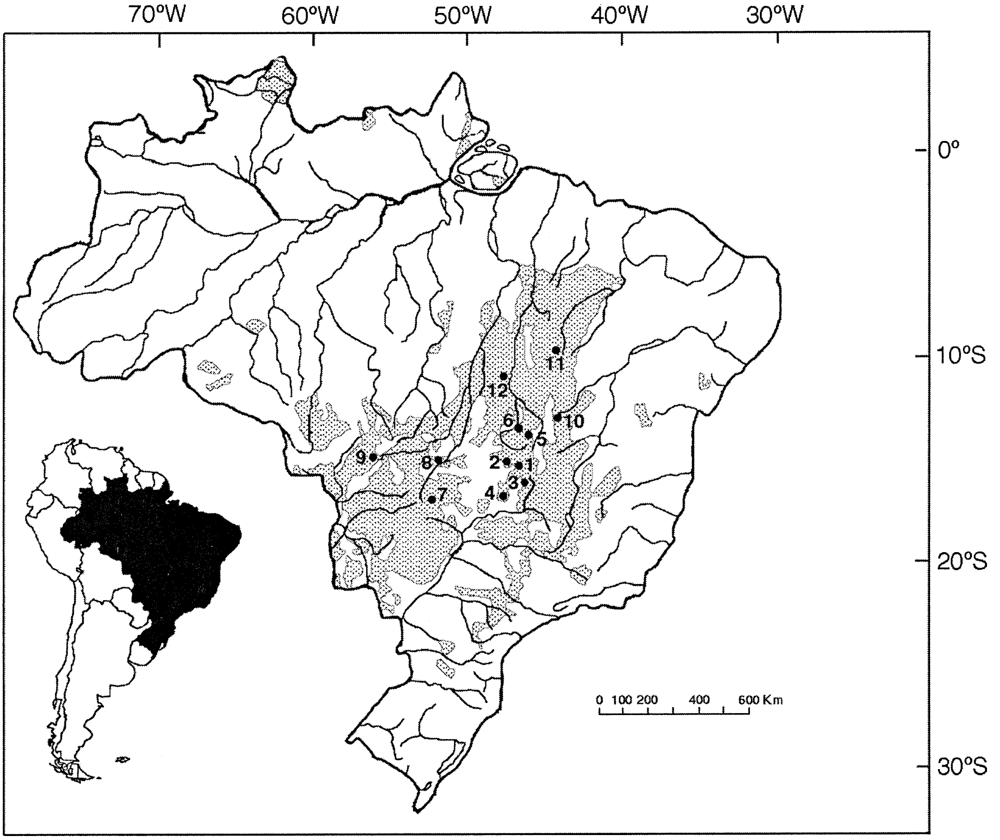

FIG. 1. Map with collecting localities of *Cnemidophorus ocellifer* in the Brazilian Cerrado. Shaded area indicates open vegetation, including Cerrado and Amazonian Savanna. 1, Brasília (30 individuals); 2, Pirenópolis (90); 3, Cristalina (25); 4, Caldas Novas (6); 5, Alto Paraíso (28); 6, Minaçu (144); 7, Mineiros (4); 8, Barra do Garças (60); 9, Chapada dos Guimarães (35); 10, São Domingos (10); 11, Mateiros (33); and 12, Palmas (43). Adapted from "Mapa de Vegetação do Brasil," Instituto Brasileiro de Geografia e Estatística.

10% formalin. We deposited all specimens at the Coleção Herpetológica da Universidade de Brasília (CHUNB). To assess the contribution of environmental temperatures to lizard cloacal temperatures, we used a stepwise multiple regression (Tabachnick and Fidell, 2001).

Diet Composition.—We analyzed stomach contents under a stereoscope, identifying prey items to order. We recorded the length and width (0.01 mm) of intact prey with 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. Data from individual stomachs highlight what an average individual of *C. ocellifer* ingests, whereas data from pooled stomachs reveal what the population as a whole is preying upon, highlighting its potential impacts on the food web. From numeric and volumetric percentages of prey, we computed niche breadths (*B*) for each lizard and also for pooled stomachs, using Simpson's diversity index (Simpson, 1949). In addition, we calculated the percentage of occurrence of each prey category (number of stomachs containing the prey category, 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 an 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

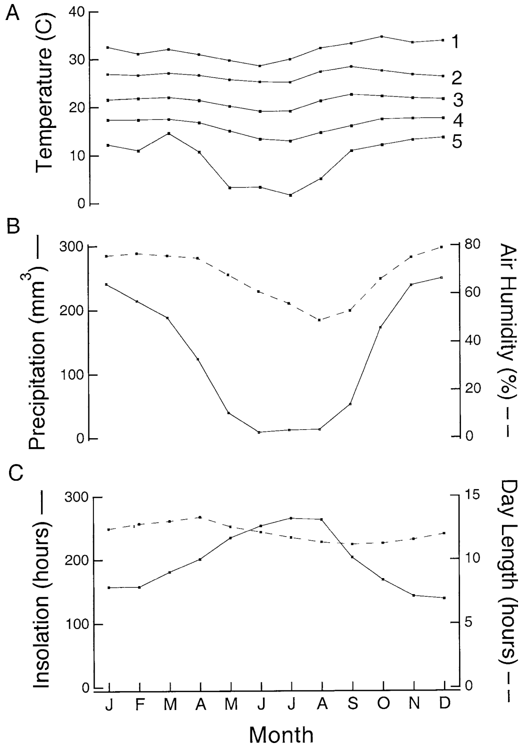

FIG. 2. Montly values of climatic variables (Instituto Nacional de Metereologia) and day length (Observatório Nacional) in Brasília, Distrito Federal between 1961 and 1990. (A) Maximum absolute (1), average maximum (2), average (3), average minimum (4), and minimum absolute temperature (5); (B) total precipitation and relative air humidity; and (C) insolation.

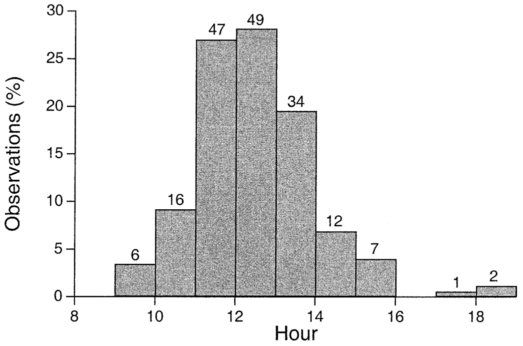

FIG. 3. Frequency distribution of individuals of *Cnemidophorus ocellifer* from Cerrado according to time of capture. Numbers on top of bars indicate sample sizes.

volumetric percentage. To investigate the relationship between prey and head dimensions, we used a canonical correlation analysis with two sets of variables: maximum prey length and width versus lizard head width, height, and length.

Reproduction.—We determined the sex of lizards by dissection and direct examination of the gonads. We considered females as reproductively active by the presence of vitellogenic follicles or oviductal eggs, regarding 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. We considered males as reproductively active by the presence of enlarged testes and convoluted epididymides. We analyzed the monthly distribution of mature individuals of each sex to determine the timing of reproduction. In addition, we estimated testis volume using the ellipsoid formula (above). To remove the influence of SVL upon testis volume, we used residuals of the SVL versus testis volume regression and analyzed the monthly distribution of adjusted means of adult individuals. 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. By pooling individuals collected during different years, we recognize that some error was introduced in the estimate of the reproductive cycle, presumably caused by annual variations in the amount and distribution of precipitation. However, we assumed that this error was small, because average annual deviations in precipitation from the normal are less than 15% in the Cerrado (Nimer, 1977).

Sexual Dimorphism.—For each individual, we measured: snout–vent length (SVL); body width (at its broadest point) and height (at its highest point); head width (at its broadest point), height (at its highest point), and length (from the tip of the snout to the commissure of the mouth); and tail length (from the cloaca to the tip of the tail). We took all measurements with electronic calipers to the nearest 0.01 mm. To maximize the availability of data, we estimated tail length of lizards with broken or regenerated tails using a regression analysis relating tail length to SVL on data from lizards with intact tails. We conducted separate analyses for different populations and sexes. 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 variation, 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

TABLE 1. Diet composition of *Cnemidophorus ocellifer* from Cerrado (N = 202). [a]Number of stomachs containing prey item; [b]IIS—importance index based on individual stomachs; [c]IPS—importance index based on pooled stomachs.

	Occurrence		Stomach means				Pooled stomachs				Importance	
Prey items	f[a]	f%	*N*	%*N*	Vol. (mm^2)	%Vol.	*N*	%*N*	Vol. (mm^2)	%Vol.	IIS[b]	IPS[c]
Aranae	68	33.67	0.45 ± 0.75	9.34 ± 21.08	7.95 ± 32.56	8.24 ± 22.31	90	3.25	1605.33	5.12	17.08	14.01
Blattaria	8	3.96	0.04 ± 0.20	1.28 ± 9.25	3.65 ± 41.28	0.87 ± 8.30	8	0.29	736.84	2.35	2.04	2.20
Chilopoda	3	1.49	0.02 ± 0.17	0.11 ± 1.20	2.53 ± 31.08	0.61 ± 6.53	4	0.14	510.41	1.63	0.74	1.09
Coleoptera	35	17.33	0.19 ± 0.44	3.12 ± 9.09	3.13 ± 30.89	1.52 ± 7.65	39	1.41	633.34	2.02	7.32	6.92
Diplopoda	2	0.99	0.01 ± 0.10	0.06 ± 0.59	–	–	2	0.07	–	–	–	–
Diptera	13	6.45	0.09 ± 0.44	1.57 ± 8.89	0.37 ± 2.86	1.17 ± 9.18	18	0.65	75.68	0.24	3.06	2.45
Hemiptera	17	8.42	0.10 ± 0.36	1.84 ± 9.17	6.41 ± 40.86	2.98 ± 13.58	21	0.76	1294.03	4.13	4.41	4.44
Homoptera	20	9.91	0.11 ± 0.36	1.88 ± 7.47	3.86 ± 18.62	3.19 ± 13.01	23	0.83	779.38	2.49	4.99	4.41
Hymenoptera												
Formicidae	23	11.41	0.29 ± 1.64	3.40 ± 13.06	1.43 ± 10.42	1.68 ± 9.60	58	2.09	288.61	0.92	5.50	4.81
Other	6	2.98	0.03 ± 0.21	1.03 ± 8.27	1.33 ± 13.91	0.39 ± 3.43	7	0.25	269.76	0.86	1.47	1.36
Insect eggs	2	0.99	0.01 ± 0.16	0.99 ± 9.93	0.07 ± 0.74	1.32 ± 11.47	3	0.11	13.93	0.04	1.10	0.38
Insect larvae	48	23.77	0.33 ± 0.71	6.57 ± 16.46	21.94 ± 58.16	15.76 ± 29.79	67	2.42	4431.22	14.14	15.37	13.44
Isopoda	2	1.00	0.01 ± 0.16	0.51 ± 7.04	0.32 ± 3.43	0.69 ± 8.14	3	0.11	64.95	0.21	0.73	0.44
Isoptera	110	54.46	11.15 ± 19.97	43.36 ± 43.16	68.81 ± 126.18	40.53 ± 42.49	2252	81.27	13899.35	44.35	46.12	60.03
Lepidoptera	1	0.50	0.01 ± 0.07	0.25 ± 3.52	0.46 ± 6.58	0.18 ± 2.19	1	0.04	93.51	0.29	0.31	0.28
Mantodea	8	3.96	0.04 ± 0.20	0.81 ± 7.50	2.33 ± 30.50	1.12 ± 9.55	8	0.29	471.54	1.50	1.96	1.92
Neuroptera	24	11.90	0.22 ± 0.86	3.49 ± 13.07	5.41 ± 27.09	4.61 ± 16.36	45	1.62	1092.23	3.48	6.67	5.67
Non-identified	30	14.85	0.15 ± 0.36	9.18 ± 27.40	–	–	30	1.08	–	–	–	–
Odonata	2	0.99	0.01 ± 0.10	0.16 ± 1.85	0.27 ± 3.63	0.55 ± 4.74	2	0.07	53.92	0.17	0.57	0.41
Orthoptera												
Grillidae	4	1.98	0.02 ± 0.14	0.25 ± 2.05	1.99 ± 20.15	0.61 ± 5.33	4	0.14	402.45	1.28	0.95	1.13
Other	63	31.19	0.36 ± 0.58	8.79 ± 21.37	21.78 ± 64.34	12.63 ± 27.02	73	2.63	4399.67	14.04	17.54	15.95
Plant material	5	2.48	0.02 ± 0.16	1.46 ± 10.72	0.03 ± 0.38	0.01 ± 0.07	5	0.18	5.38	0.02	1.32	0.89
Phasmida	1	0.50	0.01 ± 0.07	0.03 ± 0.39	–	–	1	0.04	–	–	–	–
Pseudoescorpiones	1	0.50	0.01 ± 0.07	0.02 ± 0.25	0.01 ± 0.12	0.01 ± 0.09	1	0.04	1.70	0.01	0.18	0.18
Scorpiones	1	0.50	0.01 ± 0.07	0.05 ± 0.78	0.46 ± 6.57	0.43 ± 5.30	1	0.04	93.36	0.29	0.33	0.28
Solifuga	3	1.49	0.02 ± 0.17	0.28 ± 2.66	0.61 ± 5.42	0.89 ± 8.43	4	0.14	123.75	0.39	0.89	0.67
Vertebrates	1	0.50	0.01 ± 0.07	0.02 ± 0.35	–	–	1	0.04	–	–	–	–

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): we postmultiplied the n by p matrix of the log-transformed data by a p by p symmetric matrix, L, defined as:

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

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, we conducted separate analyses of variance on body size (ANOVA) and the shape variables (MANOVA).

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

RESULTS

Microhabitat, Activity, and Temperatures.—Of 174 individuals of *C. ocellifer*, 46% were active in clear ground on sandy soils, 26.4% in rupicolous habitats, 15.5% under shrubs, 9.8% among grasses, and 2.3% inside termite nests, burrows, or under rocks. Approximately 71% of the individuals were moving when first sighted; after approached, 61% stopped, 22% ran, and only 17% remained moving. We found active lizards throughout the day, from 0900–1900 h, but primarily during the hottest hours of the day, from 1100–1400 h (Fig. 3). Approximately 53% of individuals were exposed to direct sunlight, 34% were under filtered light, and 2% were in the shadow.

Body temperatures averaged 37.52 ± 2.35°C (N = 174, range = 28.00–41.60°C), substrate temperatures averaged 32.25 ± 3.78°C (range = 24.00–43.00°C), air temperatures at 5 cm from the substrate averaged 30.73 ± 29°C (range = 23.20–39.60°C), and air temperatures at chest height averaged 29.39 ± 2.72°C (range = 23.00–38.00°C). A stepwise multiple regression analysis indicated that body temperature is more strongly associated with substrate temperature ($r = 0.132$; $F = 9.84$; $P < 0.001$).

Diet Composition.—Approximately 33% (67) of the stomachs were empty. We identified 27 prey categories, the most frequent of which were termites, spiders, grasshoppers, and insect larvae (Table 1). Based on the mean number of prey items per stomach, the diet consisted mainly of termites. Volumetrically, the average stomach contained primarily termites, insect larvae, and grasshoppers. The mean diversity index, obtained from numeric percentages of prey, was 1.75 ± 0.97. When using volumetric percentages of prey, the mean diversity index was 1.57 ± 0.80.

The results based on data from pooled stomachs were similar (Table 1). Numerically, the diet consisted almost exclusively of termites and, volumetrically, of termites, insect larvae, and grasshoppers. The diversity index calculated from numeric percentages of prey was 1.51, whereas using volumetric percentages it was 4.09.

With the exception of termites, the importance indices of prey categories calculated from individual stomachs and from pooled stomachs were very similar. This suggests that, in most cases, there was little interindividual variation in the average diet composition of *C. ocellifer*, but some individuals ate disproportionally more termites than others. This is underscored by the high standard deviations of the numeric and volumetric percentages of termites obtained from individual stomachs (Table 1).

The correlations between prey and head measurements were low, the smallest being 0.124, between head width and maximum prey length, and the largest being 0.198, between head length and maximum prey width. The first canonical variable for the head measurements was a contrast between head width and the other variables, whereas the second was a contrast between head length and head height. The first canonical variable for prey measurements had more emphasis on maximum prey width. The first canonical variable was 0.274, but the hypothesis that all canonical correlations are zero was not rejected ($P = 0.202$); hence, body dimensions and prey dimensions were not obviously associated.

Sexual Dimorphism.—The smallest individual examined was a male measuring 30 mm SVL, whereas the largest was a male (74 mm SVL). The smallest female measured 31 mm SVL and the largest measured 72 mm SVL. There was a significant difference between the sexes in body size (ANOVA $F_{1,321} = 14.624$; $P < 0.001$), with males larger than females (Table 2). In addition, there was a significant difference between the sexes in shape variables (MANOVA Wilk's Lambda = 0.599, $P < 0.001$). To determine which of the shape variables contributed most to sexual dimorphism, we performed a stepwise discriminant analysis (Tabachnick and Fidell, 2001). Six shape variables were selected as the most powerful discriminators of the two sexes, correctly classifying 74% of the individuals (Table 3). Head height was the first variable to be selected, correctly classifying 67.2% of the individuals, being followed by SVL, head length, head width,

TABLE 2. Summary statistics of morphometric characters of *Cnemidophorus ocellifer* from Cerrado. Values indicate mean ± SD. Size-adjusted values (see text) are in parentheses. Values are in millimeters.

Character	Males (N = 191)	Females (N = 131)
Body size	3.944 ± 0.157	3.881 ± 0.125
Snout–vent length	59.283 ± 6.587 (0.454 ± 0.018)	59.413 ± 5.226 (0.476 ± 0.020)
Tail length	130.00 ± 17.900 (0.796 ± 0.030)	126.332 ± 11.851 (0.806 ± 0.034)
Body width	12.251 ± 1.876 (−0.232 ± 0.040)	12.452 ± 2.125 (−0.205 ± 0.049)
Body height	8.934 ± 1.383 (−0.368 ± 0.039)	8.489 ± 1.438 (−0.371 ± 0.048)
Head width	9.479 ± 1.438 (−0.343 ± 0.023)	8.624 ± 3.015 (−0.368 ± 0.053)
Head height	7.747 ± 1.179 (−0.431 ± 0.025)	6.874 ± 0.877 (−0.460 ± 0.032)
Head length	14.596 ± 1.858 (−0.154 ± 0.016)	13.498 ± 1.335 (−0.166 ± 0.023)
Forelimb length	20.694 ± 2.368 (−0.002 ± 0.023)	20.048 ± 2.532 (0.005 ± 0.036)
Hind-limb length	39.501 ± 4.064 (0.280 ± 0.025)	37.818 ± 3.829 (0.282 ± 0.038)

body width, and forelimb length. To determine whether important variables were excluded from the analysis because of intercorrelation with head height, we excluded head height and repeated the analysis. Snout–vent length was then selected first, correctly classifying 66.7% of the individuals, being followed by six other variables. We repeated the analysis once more after the exclusion of SVL. This time, head length was selected first. These results indicate that head shape and body elongation are the most important differences between the sexes, with females having more elongated bodies, whereas males have larger heads (Table 3).

Reproduction.—The smallest reproductive female measured 51 mm SVL, whereas the smallest reproductive male measured 40 mm SVL (Fig. 4). Clutch size averaged 2.25 ± 0.46 (range = 2–3, N = 8), based on egg counts, and 2.03 ± 0.73 (range = 1–3, N = 33), based on vitellogenic follicle counts. There was no significant difference between the two estimates, independent of SVL (ANCOVA $F_{1,38}$ = 0.59, P = 0.45). Clutch size based on the combined data averaged 2.07 ± 0.69 (range = 1–3, N = 41). There was a positive and significant correlation between clutch size and female SVL (Fig. 5).

Mean egg length was 14.50 ± 1.51 mm, mean egg width was 7.93 ± 0.91 mm, and mean egg volume was 487.44 ± 139.01 mm^3. There was no correlation between egg volume and female SVL (r = 0.06, P = 0.86). We recorded no gravid female containing simultaneously enlarged vitellogenic follicles and either oviductal eggs or corpora lutea. Hence, if multiple clutches are produced during the breeding season, they are relatively separated in time.

Reproduction occurred primarily during the dry season, from May to September, with reproductive activity decreasing from October to November (Fig. 6). In October, there were no reproductive individuals, but sample size was very small (N = 1). Reproductive males occurred throughout the year, but reproduction was apparently concentrated during the dry season as well (Fig. 6). Indeed, adjusted testis volume was higher from March to August, coinciding with the dry season (Fig. 7). However, the difference in adjusted testis volume between dry and wet months was only marginally significant (ANCOVA $F_{1,123}$ = 3.77, P = 0.055). Recruitment took place mainly from July to November (Fig. 8).

DISCUSSION

Habitat, Microhabitat, and Temperatures.—*Cnemidophorus ocellifer* is a conspicuous element of lizard assemblages from open habitats in the Cerrado landscape, being especially common in sandy and rupicolous areas. An association with sandy soils seems to be a plesiomorphic trait of the genus, since congeneric species from other biomes, such as Restinga, Caatinga, and Amazonian Savanna, use similar microhabitats (Vitt, 1983; Magnusson et al., 1986; Teixeira-Filho et al., 1995; Vitt et al., 1997). In Cerrado, *C. ocellifer* is active primarily during the hottest hours of the day. Other sympatric heliophilic lizards, such as

TABLE 3. Stepwise discriminant analysis of shape variables of *Cnemidophorus ocellifer* from Cerrado. Error-rate indicates posterior probability error-rate estimates based on cross-validation.

Step	Variable entered	R^2	Wilk's Lambda	$P<$	Error-rate
1	Adjusted head height	0.164	0.836	0.0001	0.33
2	Adjusted snout–vent length	0.061	0.785	0.0001	0.30
3	Adjusted head length	0.046	0.748	0.0001	0.28
4	Adjusted head width	0.026	0.729	0.0010	0.27
5	Adjusted body width	0.016	0.717	0.0101	0.26
6	Adjusted forelimb length	0.009	0.710	0.0500	0.26

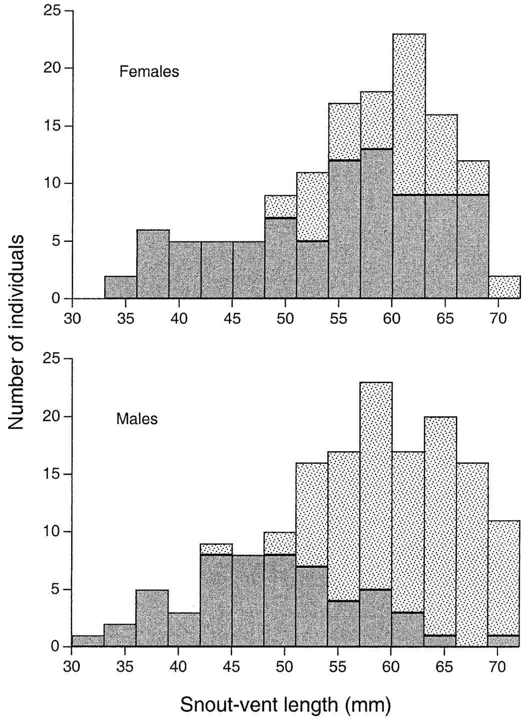

FIG. 4. Frequency distribution of male and female individuals of *Cnemidophorus ocellifer* from Cerrado according to snout–vent length and reproductive condition. Gray bars represent nonreproductive and stippled bars represent reproductive individuals.

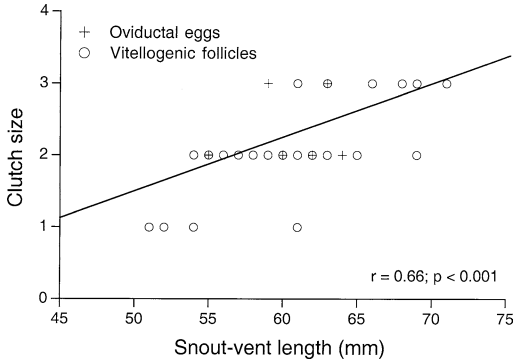

FIG. 5. Relationship between clutch size and snout–vent length in *Cnemidophorus ocellifer* from Cerrado.

Ameiva ameiva Linnaeus 1758 (Vitt and Colli, 1994), *Mabuya frenata* (Cope 1862) (Vrcibradic and Rocha, 1998), and *Tropidurus itambere* Rodrigues 1987 (Van Sluys, 1992), have a more extended daily period of activity. Presumably, this difference is associated with the higher body temperatures of *C. ocellifer* relative to these other species (with the exception of *A. ameiva*). High body temperatures are characteristic of many teiid genera, being often associated with an active mode of foraging (Huey and Pianka, 1981; Vitt et al., 1993; Vitt and Colli, 1994). Indeed, a number of studies reveal that muscle performance and sprint speed are positively correlated with body temperature (e.g., Swoap et al., 1993; Jayne and Daggy, 2000; Van Damme and Vanhooydonck, 2001). Despite being significant, the correlation between body and substrate temperatures in *C. ocellifer* was low. It is likely that the high mobility characteristic of lizards in the genus *Cnemidophorus* (Magnusson et al., 1985; Anderson, 1993) results in a poor fit between body temperatures and environmental temperatures (e.g., Schall, 1977; Teixeira-Filho et al., 1995).

Diet Composition.—In agreement with an earlier study (Vitt, 1991a), we found that termites are the most important prey for *C. ocellifer* in the Cerrado. Termites are a prominent and diverse group in this biome. The density of termitaria may reach 323 nests per hectare, and each nest may contain up to 17 termite species (Redford, 1984; Gontijo and Domingos, 1991). Given the diversity and abundance of Cerrado termites and that active foraging predators can easily find sedentary, spatially unpredictable but clumped prey (Huey and Pianka, 1981; Pianka, 1986), it is easily understood how individuals of *C. ocellifer* can include a large number and volume of termites in their diet. With the exception of *Gymnodactylus geckoides amarali* Barbour, 1925 and *Mabuya frenata*, all Cerrado lizards studied to date ingest smaller amounts of termites than *C. ocellifer* (Van Sluys, 1993a; Vitt and Colli, 1994; Colli and Zamboni, 1999; Mesquita et al., 2000; Vieira et al., 2000). *Gymnodactylus geckoides* has a diet consisting almost exclusively of termites (unpubl. data), whereas *Mabuya frenata* eats a similar amount of termites relative to *C. ocellifer* (Vrcibradic and Rocha, 1998). The low dietary diversity indices and the lack of association between prey and head dimensions in *C. ocellifer* seemingly results from the high importance of termites in the diet.

Interestingly, we detected a significant difference in diet composition between the average lizard and the whole sample, which resulted from a pronounced interindividual variation in the dietary importance of termites. A variety of factors could account for this result, including differences in the dietary importance of termites based on sex, ontogeny, season, and geography. However, the importance index of termites was similar in the sexes (males: 53.00 ± 27.64; females: 57.56 ± 25.56; $F_{1,100} = 0.77$, $P = 0.38$); there was no significant correlation between the importance index of termites and SVL ($r = -0.05$, $N = 103$, $P = 0.64$), and despite a significant seasonal variation in the abundance of termites in Cerrado

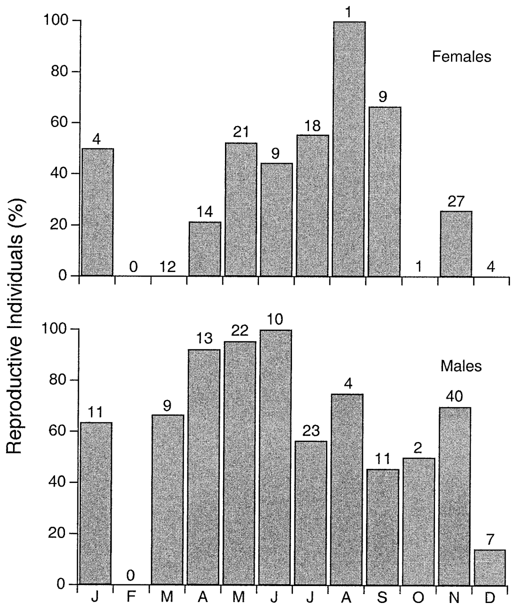

FIG. 6. Monthly distribution of male and female individuals of *Cnemidophorus ocellifer* from Cerrado according to reproductive condition. Numbers on top of bars indicate sample sizes.

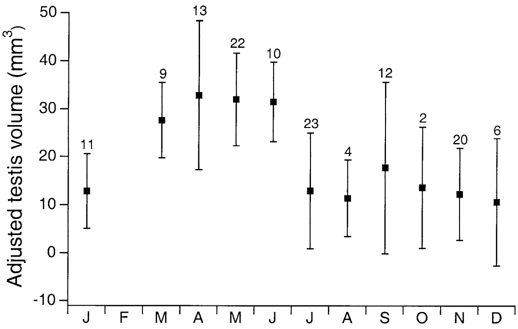

FIG. 7. Adjusted monthly means and standard deviations of testicle volume in *Cnemidophorus ocellifer* from Cerrado. Adjusted means indicate values independent of the effects of snout–vent length.

(Pinheiro et al., 2002), there was no seasonal variation in the dietary importance of termites in *C. ocellifer* (dry season: IIS = 79.09 ± 37.30; wet season: IIS = 70.59 ± 31.20; $F_{1,9} = 0.06$, $P = 0.81$). Nevertheless, there was significant variation in the importance index of termites among localities ($F_{7,127} = 4.40$, $P < 0.001$): lizards from Alto Paraíso had significantly higher importance indices relative to those from Minaçu, Pirenópolis, and São Domingos, whereas lizards from Cristalina had significantly higher importance indices relative to those from São Domingos (Tukey test, $P < 0.05$). Therefore, the interindividual variation in the dietary importance of termites we observed may be attributed to geographic variation in the availability of termites.

Sexual Dimorphism.—We detected significant sexual dimorphism in body size and shape in *C. ocellifer.* Even though reaching sexual maturity at a smaller body size, males attained larger overall body size and had larger heads than females. In addition, females had relatively longer bodies. Similar trends have been recorded in other congeneric species, such as *Cnemidophorus gramivagus, Cnemidophorus lemniscatus, Cnemidophorus parecis* (Mesquita and Colli, 2003), *Cnemidophorus murinus* (Dearing and Schall, 1994), and a population of *C. ocellifer* from Caatinga (Vitt, 1983). The sexual dimorphism in body size and head shape is also widespread in other teiid genera, including *Ameiva* (e.g., Vitt and Colli, 1994; Censky, 1995), *Aspidoscelis* (Anderson and Vitt, 1990; Vitt et al., 1993; Ramirez-Bautista et al., 2000), *Kentropyx* (Vitt, 1991b; Vitt and Carvalho, 1992; Vitt et al., 1995), *Teius* (Cruz et al., 1999), and *Tupinambis* (Fitzgerald et al., 1993; Herrera and Robinson, 2000). This strongly suggests that the sexual dimorphism in body size and head shape is plesiomorphic among teiids, even though it may be maintained by present-day selective forces. Sexual selection is the most popular among these selective agents (Noble and Bradley, 1933; Stamps, 1983; Anderson and Vitt, 1990). According to this hypothesis, males with large heads will have enhanced reproductive success by winning intrasexual aggressive encounters to access mating. Despite its popularity, only a few studies provide critical evidence in favor of the sexual selection hypothesis among teiids (Anderson and Vitt, 1990; Censky, 1995, 1996; Lewis et al., 2000).

Reproduction.—Clutch size is small in *C. ocellifer,* as in most congeneric species (e.g., Schall, 1983; Vitt and Breitenbach, 1993). This is likely a reflection of the small body size and the foraging mode of the species. For instance, there is an overall trend of increasing clutch size with increasing body size both among and within lizard species (Fitch, 1970; Tinkle et al., 1970; Dunham et al., 1988). In addition, teiids and other scleroglossan squamates are characterized by a reduced clutch size when compared with iguanians, as a result of their active mode of foraging, streamlined morphology, and predator escape tactic, which usually involves a reliance on wariness and running speed (Vitt and Price, 1982).

Cnemidophorus ocellifer breeds seasonally in the Cerrado, with an activity peak from May to September, during the dry season. In addition, recruitment occurs from July to November, at the end of the dry season. Earlier studies on lizard reproduction indicate that most tropical species tend to breed continuously and that, when there exists a breeding season, it is limited to the time of maximal rainfall (Fitch, 1970, 1982). Recent studies, however, revealed an astonishingly high diversity of reproductive strategies among tropical lizard species, even within a given assemblage (e.g., Vitt, 1986, 1992). In the Cerrado, for example, despite the strong wet-dry seasonality and high climatic predictability, some lizard species reproduce in the wet season, such as *Tropidurus torquatus* (Wiederhecker et al., 2002), *T. itambere* (Van Sluys, 1993b), and *A. ameiva* (Colli, 1991), whereas others breed during the dry season, like *Amphisbaena alba* (Colli and Zamboni, 1999) and *Gymnodactylus geckoides amarali* (unpubl. data).

Seasonal cycles in the abundance of arthropods have long been known in tropical regions (e.g., Janzen and Schoener, 1968; Stamps and Tanaka, 1981; Levings and Windsor, 1982; Smythe, 1982). As a consequence, food shortage became a popular explanation for seasonal reproduction in tropical lizards. Nevertheless, in the vast majority of studies, food shortage has not been demonstrated but only assumed based on the seasonal lowering in arthropod abundance. In the Cerrado, there are significant variations in arthropod abundance during the dry season (Pinheiro et al., 2002). However, lizards build up large lipid reserves during the dry season in the Cerrado, suggesting abundant food supplies at this time of the year (Colli et al., 1997). Further, termites, the most important item in the diet of *C. ocellifer*, are more abundant in the first half of the wet season (Pinheiro et al., 2002), but there is no seasonal variation in the dietary importance of termites in this species (see above). Therefore, there is no evidence that seasonal variations in food supply influence the reproductive cycle of *C. ocellifer* in the Cerrado.

Desiccation can substantially lower egg survival, therefore limiting reproduction to the wet season (Andrews and Wright, 1994; Overall, 1994). However, *C. ocellifer* breeds during the dry season, and recruitment takes place from late dry season to early wet season. Therefore, microenvironmental conditions for egg development apparently are not limiting in the Cerrado or, alternatively, individuals bury their eggs in suitable portions of the environment.

Monthly means of air temperatures in Cerrado are fairly constant, fluctuating around 20°C (Nimer, 1989). Even though day length is shorter during the dry season, total insolation is higher when compared with the rainy season (Fig. 2). Prolonged periods of rains that last all day long are relatively common during the rainy season. Considering that lizards in the genus *Cnemidophorus* are characterized by relatively high values of mean activity body temperature (e.g., Schall, 1977; Magnusson, 1993), it is possible that the reduced availability of direct sunlight during the rainy season limits activities such as courtship and mating. Extended periods of sunny days may be necessary for *C. ocellifer* to maintain reproductive activities. Nevertheless, *A. ameiva*, a syntopic teiid that is also heliotherm and has high activity temperatures, breeds during the rainy season in the Cerrado (Colli, 1991).

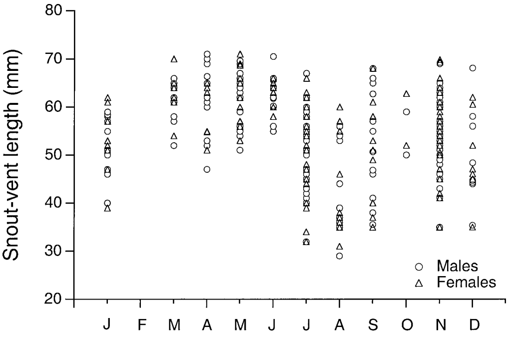

FIG. 8. Monthly distribution of individuals of *Cnemidophorus ocellifer* from Cerrado, according to snout–vent length.

At present, it is unclear what are the main determinants of the reproductive cycle of *C. ocellifer* in Cerrado. Populations of *Cnemidophorus* display a variety of reproductive patterns. In Amazonian Savanna, *C. lemniscatus* breeds seasonally, with egg deposition occurring during the wet season and recruitment occurring at the peak of the dry season (Magnusson, 1987), whereas *C. ocellifer* breeds year-round in Caatinga (Vitt, 1983) and seasonally in Cerrado. Hence, it is clear that variations in environmental parameters do influence the reproductive cycle in the species (Mesquita and Colli, 2003). We advance that, in Cerrado, breeding in the dry season may be related to greater availability of direct sunlight and its physiological effects upon reproductive activities such as courtship and mating. Nevertheless, much additional work is necessary to corroborate this hypothesis.

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APPENDIX I

Specimens Examined

Cnemidophorus ocellifer. DISTRITO FEDERAL: Brasília (15°47′S, 47°55′W), June 1987, April to 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 to June 1992, October to November 1992, November to December 1996, January, July to August 1997, September to December 1998; March, May to 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 to 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 to December 1999; Mateiros (10°11′S, 46°40′W), November 1999.