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Ecology of the Gecko *Gymnodactylus geckoides amarali* in a Neotropical Savanna

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ABSTRACT.—We describe the ecology of the gecko *Gymnodactylus geckoides amarali* in the Cerrado of central Brazil and using published data, compare it with the conspecific *Gymnodactylus geckoides geckoides* from the Caatinga of northeastern Brazil. *Gymnodactylus geckoides amarali* is rupicolous, living primarily in rock crevices in "campos rupestres" (rocky fields), which are highly patchy in Cerrado. Field body temperatures were low and associated with environmental temperatures, suggesting thermoconformity. Termites were the most important food item, and consumption was greatest during the dry season. We suggest that access to termites is facilitated by the shallow soils used by *G. g. amarali* and by its well-developed chemosensory apparatus. Reproduction was concentrated in the dry season, a pattern known for very few Cerrado squamates, possibly because of the higher availability of termites during that period. Clutch size was significantly correlated with female size, a pattern unknown in any other gecko, and there was no association between egg size and female size. *Gymnodactylus geckoides amarali* produced larger clutches of smaller eggs relative to *G. g. geckoides*, presumably because of the high climatic unpredictability of the Caatinga. We detected a significant sexual dimorphism in both body size and shape: females were larger and had smaller heads than males. We suggest that large female size is likely a plesiomorphic character of gekkonids and that large head size in males results from sexual selection theory.

Covering an area of approximately 2,000,000 km^2, the Cerrado is the second largest Brazilian biome (Oliveira and Marquis, 2002). This Neotropical savanna is currently one of the most threatened biomes of South America because of the expansion of agriculture. Among the approximately 50 lizard species that inhabit the Cerrado, five are members of the Gekkonidae: the gek-

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konines *Gymnodactylus geckoides*, *Hemidactylus mabouia*, and *Phyllopezus pollicaris*, and the sphaerodactylines *Coleodactylus brachystoma* and *Coleodactylus meridionalis* (Colli et al., 2002). With the exception of *H. mabouia*, an introduced species that is abundant in anthropical areas (Vanzolini, 1968, 1978), Cerrado geckos are inconspicuous and relatively uncommon in scientific collections. For example, Vitt (1991) noted a lack of gekkonids at Alto Araguaia in Brazil, attributing this result to the absence of appropriate microhabitats. If, as put by Doughty and Shine (1995), natural history studies on geckos are rare, detailed works on the ecology of Cerrado gekkonids are simply nonexistent. The few ecological studies on Brazilian geckos were carried out in Amazonia (e.g., Ramos, 1981; Nunes, 1984; Ávila-Pires, 1995; Vitt and Zani, 1997; Vitt et al., 1997, 2000), Caatinga (Vitt, 1986, 1995), and Restinga (Araujo, 1991; Zamprogno and Teixeira, 1998).

Lizards have contributed significantly to ecological theory, including population and community ecology, foraging and life-history theory, and the growing field of comparative biology (Huey et al., 1983; Vitt and Pianka, 1994; Pianka and Vitt, 2003). However, most studies were performed either in the temperate zone or on tropical anoles. The generality of such theoretical advances to the diverse tropical lizard fauna remains to be determined. For example, both historic (phylogenetic) and present-day (ecological) factors influence lizard life histories (e.g., Dunham et al., 1988). Therefore, synapomorphies of lineages restricted to the Neotropical region and underrepresented in life-history studies, such as Gymnophthalmidae, Hoplocercidae, Leiosauridae, and Sphaerodactylini, might affect life-history theory. In addition, tropical regions are characterized by unique ecogeographic features and conditions that may influence lizard ecologies in ways that challenge the generality of life-history models. Most studies on tropical lizards come from relatively aseasonal forested biomes, whereas those from strongly seasonal, open vegetation biomes are still poorly known (Colli et al., 2002).

Gymnodactylus geckoides contains two recognized subspecies: *G. g. geckoides* from the Caatinga and *G. g. amarali* from the Cerrado (Vanzolini, 1953, 1968). The only detailed works on the ecology of the genus were carried out on *G. g. geckoides* in the Caatinga (Vitt, 1986, 1995). Herein we present new data on the ecology of *G. g. amarali* from the Cerrado of central Brazil. We report on habitat use, thermal biology, sexual dimorphism, diet, and reproduction and make comparisons with published accounts on *G. g. geckoides* from the Caatinga and other Neotropical geckos, when appropriate. Because the Cerrado and Caatinga biomes differ considerably in several features, such as climate predictability (Nimer, 1989), we attempt to identify effects of environmental conditions upon the ecology of *G. geckoides*, by comparing two very closely related taxa from different regions.

MATERIALS AND METHODS

Study Sites and Specimens.—We collected specimens at three localities in central Brazil: Alto Paraíso de Goiás (14°07′S, 47°3′W; *N* = 19), Minaçu (13°49′S, 48°20′W; *N* = 288), and Pirenópolis (15°51′S, 48°57′W; *N* = 60), all in the state of Goiás. All specimens were deposited at the "Coleção Herpetológica da Universidade de Brasília" (CHUNB). Climate is strongly predictable and seasonal, with a wet season from October to April receiving almost all of the 1500–2000 mm of annual precipitation, and a dry season from May to September (Nimer, 1989). Annual temperatures average 20–22°C, and minimum and maximum daily temperatures drop noticeably during the dry months (Nimer, 1989). The phytophysiognomy varies from extensive grasslands with few trees to grasslands with dense stands of stunted trees, forming a nearly closed canopy in some areas. Trees are tortuous, with thick bark, xeromorphic leaves, and deep root systems, apparently adapted to natural sporadic fires and soils that are poor in nutrients and rich in aluminum. See Oliveira and Marquis (2002) for a review on the Cerrado.

Habitat, Microhabitat, and Temperatures.—Approximately two-thirds (*N* = 220) of the specimens were collected by third parties during the flooding of the Serra da Mesa hydroelectric dam at Minaçu, from November 1996 to August 1997. We hand collected the remaining one-third (*N* = 147) of specimens, recording habitat and microhabitat at the capture site. We used the following microhabitat categories: rock crevice, termite nest, rock, and ground. All individuals were collected during the day. Immediately after capture, we took cloacal, air, and substrate temperature of 28 individuals using a Miller and Weber™ cloacal thermometer. In the lab, geckos were killed by injection with Tiopental®, measured, and fixed with 10% formalin.

Sexual Dimorphism.—From each individual, we recorded the following morphometric variables: snout–vent length (SVL), body width (at broadest point), body height (at highest point), head width (at broadest point), head height (at highest point), head length (from tip of snout to anterior margin of ear opening), and tail length (from cloaca to tip of tail). We took all measurements with Mitutoyo® electronic calipers, to the nearest 0.01 mm. Since the majority of the individuals had broken tails, we excluded tail length from the analyses. We also log-transformed (base 10) all morphometric variables prior to analyses. 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), and obtained scores from this eigenvector, hereafter called body size, by postmultiplying the $n \times p$ matrix of $\log_{10}$ transformed data, where n is the number of observations, by the $p \times 1$ isometric eigenvector. To remove the effects of body size from the $\log_{10}$-transformed variables we used Burnaby's method (Burnaby, 1966): we postmultiplied the $n \times p$ matrix of the $\log_{10}$-transformed data by a $p \times p$ symmetric matrix, L, defined as:

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

where I_p is a $p \times p$ 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).

Diet Composition.—We removed stomachs by dissection and examined their contents under a stereomicroscope. We identified prey items usually to the ordinal level, recorded the length and width (±0.01 mm) of intact items with a micrometric ocular, 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 = prey width and l = prey length. We calculated numeric and volumetric percentages of each prey category for each lizard, to obtain mean values per stomach. We also obtained numeric and volumetric percentages from 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 i stands for prey category, n for number of categories, and p for the numeric or volumetric proportion of prey category i. We also calculated percentage of occurrence of each prey category (number of stomachs containing prey category i, divided by total number of stomachs). We excluded from analyses of volumetric representation prey items that were too fragmented to allow a reliable estimation of their volumes.

To investigate the relationship between prey dimensions and head dimensions, we conducted a canonical correlation analysis between two sets of variables: maximum prey length and maximum prey width versus lizard head width, height, and length. Canonical correlation analysis finds a linear function from each set of variables, termed the first canonical variables, maximizing the correlation between them. Next, successive pairs of canonical variables are calculated, such that the correlation between two canonical variables of each pair is also maximized and each successive pair is uncorrelated with all the preceding canonical variables (Tabachnick and Fidell, 2001). The first canonical correlation is at least as large as the multiple correlations between any variable and the opposite set of variables. To determine how well prey dimensions can be predicted from the canonical variables of head dimensions, we also performed a canonical redundancy analysis.

Reproduction.—We determined the sex of each individual by dissection and direct examination of the gonads. We considered females as reproductively active by the presence of vitellogenic follicles or oviductal eggs and males as reproductively active by the presence of enlarged testes and convoluted epididymides. For reproductively active females, we counted and measured width and length (to the nearest 0.01 mm) of vitellogenic follicles and oviductal eggs. We considered presence of enlarged vitellogenic follicles and either oviductal eggs or corpora lutea as evidence of sequential production of more than one clutch of eggs. Further, 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.

We analyzed monthly distributions of adults according to reproductive condition to determine timing of reproduction. By pooling individuals collected during different years, we recognize that some error was introduced in estimating reproductive cycle, presumably caused by annual variations in amount and distribution of precipitation. However, we assumed that this error was small, because (1) average annual deviations in precipitation from the normal are less than 15% in the Cerrado (Nimer, 1989) and (2) about two-thirds of the individuals were collected in a single year.

Statistical Analyses.—We carried out statistical analyses using SYSTAT 5.2.1 (SYSTAT, Inc., Cary, North Carolina, 1992) and SAS 6.12 (SAS Institute, Inc., Cary, North Carolina, 1988), both for Macintosh, and used a significance level of 5% to reject null hypotheses. Data are expressed as means ± 1 SD.

RESULTS

Habitat, Microhabitat, and Temperatures.—In the localities sampled, *G. g. amarali* was found exclusively in rocky habitats ("campos rupestres"). In these areas, soils were often less than 1 m deep over a solid bedrock (lithosols), and the vegetation was low and sparse (Fig. 1, top). Twenty-eight (89%) individuals collected were in rock crevices, whereas remaining individuals were on rocks (7%) or on the ground (4%). All individuals were motionless at first sight; 68% remained still after approached whereas the remaining individuals fled into rock crevices. When cornered, *G. g. amarali* often exhibited a display in which the tail, usually bearing transverse white bands, was lifted and held still (Fig. 1, bottom). We also made unquantified observations of individuals active in late afternoon on rock piles.

Body temperatures averaged 30.2 ± 2.6°C (N = 28, range = 26.2–34.0°C); substrate temperatures averaged 26.8 ± 2.5°C (range = 24.0–34.0°C); air temperatures at 5 cm from the substrate averaged 26.5 ± 2.1°C (range = 23.0–32.0°C); and shaded air temperatures averaged 25.7 ± 2.2°C (range = 22.2–29.6°C). A stepwise multiple regression analysis indicated that body temperature was most strongly associated with air temperature at 5 cm from the substrate (model selected: body temperature = 0.8 × air temperature + 8.9; r = 0.65; $P < 0.001$). The Caatinga *G. g. geckoides* (Vitt, 1995) exhibits a significantly higher body temperature than *G. g. amarali* (33.5 ± 0.5, $N = 10$, $t_{36} = 6.3$, $P < 0.001$).

Sexual Dimorphism.—The smallest individual examined was a female measuring 20.04 mm SVL, whereas the largest individual was a female measuring 54.70 mm SVL. The largest male measured 52.48 mm SVL. Sexes differed significantly in body size (ANOVA $F_{1,368} = 4.72$, P = 0.03), with females larger than males (Table 1). In addition, there was a significant difference between the sexes in shape variables (MANOVA Wilk's Lambda = 0.93, $P < 0.001$). To determine which of the shape variables contributed most to sexual dimorphism, we performed a stepwise discriminant analysis using the stepwise method of variable selection and Wilk's Lambda as the indicator of discriminatory power (SAS Institute, Inc., Cary, North Carolina, 1988). Three shape variables were selected as the most powerful discriminators of the two sexes (Table 2). Adjusted head width was the first to be selected, correctly classifying 59.7% of the individuals. The discriminant function based on both adjusted head width and adjusted body width classified 63.2% of the lizards correctly. The addition of adjusted SVL to the model did not improve its classification power (Table 2). Analyses indicate that adjusted head width and adjusted body width were the most powerful discriminators of the sexes, with males having larger heads, whereas females were stockier (Fig. 2, Table 1).

Diet Composition.—A relatively small proportion (17.6%) of individuals examined had empty stomachs. We recorded 24 prey categories, by far the most frequent of which was termites (40%), followed by nonidentified arthropods (20.8%), and ants (18%) (Table 3). Based on the mean number of prey items per stomach, the diet consisted mainly of termites (39%), nonidentified arthropods (19.3%), and ants (14.5%), whereas termites (68%) and ants (12.9%) dominated volumetrically (Table 3). The mean diversity indexes, calculated for numeric and volumetric percentages of prey, were 1.39 ± 0.62 (N = 204) and 1.04 ± 0.16 (N = 40), respectively.

Results based on data from pooled stomachs were similar to results on a per stomach basis. Numerically, the diet consisted mainly of termites (59%) and ants (17%), while termites (81%) dominated volumetrically (Table 3). The diversity index calculated from numeric percentages of prey was 2.61, whereas using volumetric percentages of prey it was 1.50. Overall, dietary diversity was low and the diet consisted largely of termites, followed by ants. Importance of termites (mean percentage of termite number in the diet plus mean percentage of termite volume in the diet, divided by two) in the diet was higher in the dry season than in the rainy season (dry season: mean = 33.23 ± 30.41; rainy season: = mean = 12.13 ± 22.39; ANOVA of arcsine-transformed data: $F_{1,221} = 25.98$, $P < 0.0001$).

Correlations between prey and head measurements were low. The lowest correlation was 0.16, between prey width and head width. The largest correlation was 0.33, between prey length and head length. The first canonical variable for head measurements was a contrast between head height and head length, with more emphasis on head length, whereas the second was a contrast between head width and head height. The first canonical variable for the prey measurements was a contrast between maximum prey width and maximum prey length, with more emphasis on the latter, whereas the second canonical variable put more emphasis on the former. The first canonical correlation was 0.44, but the hypothesis that all canonical correlations were zero was not rejected (P = 0.21); thus, no firm association between body dimensions and prey dimensions could be established. Indeed, the canonical redundancy analysis indicated that neither of the two canonical variables for head measurements were good predictors of prey measurements, with only 10% of the variance in the latter being explained by the former.

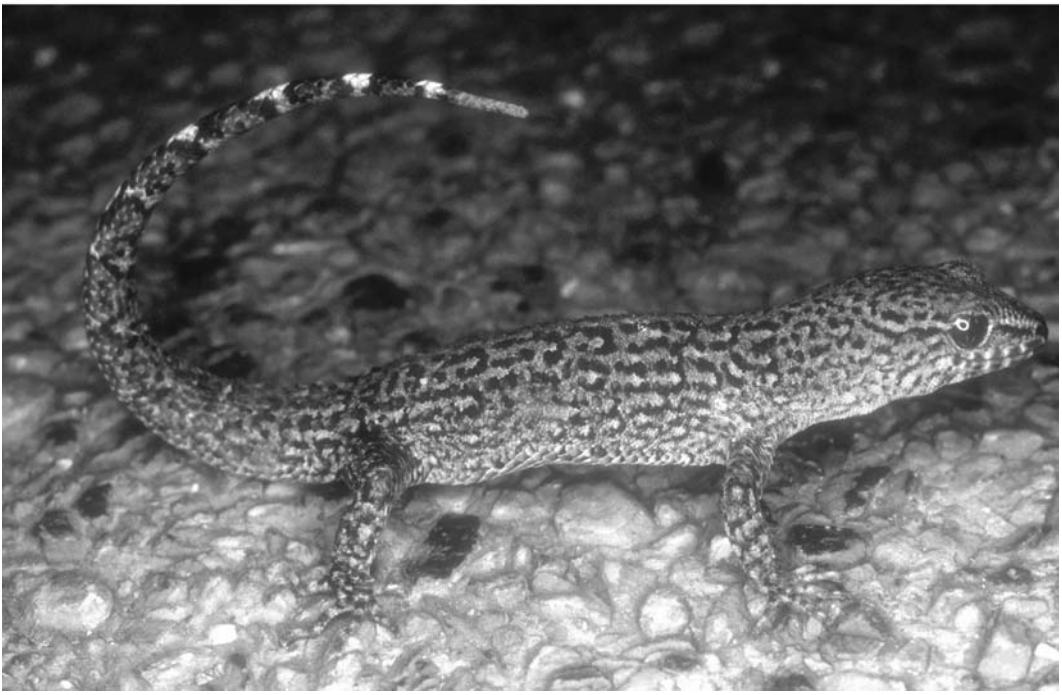

FIG. 1. (Top) Typical habitat of *Gymnodactylus geckoides amarali*. Locality shown is Pirenópolis, Goiás state, Brazil. (Bottom) Adult individual of *G. g. amarali* showing defensive tail display.

TABLE 1. Mean and standard deviation of morphometric characters of *Gymnodactylus geckoides amarali*. Size-adjusted values (see text) are in parentheses. Body size is a linear function with equal contributions of each measurement (see text). All measurements in millimeters.

Character	Males (N = 200)	Females (N =170)
Body size	2.90 ± 0.22	2.95 ± 0.24
Snout–vent length	38.60 ± 6.79 (0.56 ± 0.02)	40.50 ± 7.13 (0.56 ± 0.02)
Body width	10.20 ± 2.25 (−0.03 ± 0.04)	11.03 ± 2.55 (−0.01 ± 0.05)
Body height	6.05 ± 1.33 (−0.25 ± 0.04)	6.50 ± 1.55 (−0.24 ± 0.05)
Head width	7.85 ± 1.31 (−0.14 ± 0.02)	8.04 ± 1.35 (−0.15 ± 0.02)
Head height	4.93 ± 0.85 (−0.34 ± 0.03)	5.09 ± 0.88 (−0.34 ± 0.03)
Head length	9.23 ± 1.37 (−0.06 ± 0.02)	9.50 ± 1.33 (−0.07 ± 0.02)
Forelimb length	12.30 ± 2.09 (0.06 ± 0.03)	12.75 ± 2.15 (0.06 ± 0.03)
Hind-limb length	17.31 ± 2.96 (0.21 ± 0.03)	18.00 ± 3.05 (0.21 ± 0.03)

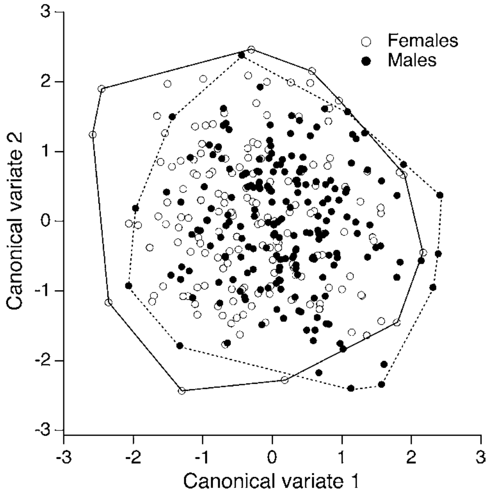

FIG. 2. Canonical discriminant scores for males and females of *Gymnodactylus geckoides amarali* using size-adjusted values of snout–vent length, head width and body width. The first canonical variate was a contrast between head width (+) versus body width and snout–vent length (–), with males averaging 0.24 and females averaging −0.28. The second canonical variate was largely influenced by snout–vent length, with both sexes averaging 0.

Reproduction.—The smallest reproductive female measured 38.57 mm SVL, whereas the smallest reproductive male measured 28.94 mm SVL (Fig. 3). Clutch size, based on presence of eggs or vitellogenic follicles, averaged 1.65 ± 0.48 (range = 1–2, N = 32). When females had two follicles (N = 6) or two oviductal eggs (N = 13), both follicles or eggs were at the same stage of development. Females with a clutch size of two were significantly larger than those with a clutch size of one (mean = 45.54 ± 2.83 vs. mean = 41.60 ± 1.89, respectively; $F_{1,31}$ = 18.45, $P <$ 0.001). Mean egg length was 8.77 ± 0.64 mm, mean egg width was 5.72 ± 0.47 mm, and mean egg volume was 151.92 ± 30.15 mm^3 (based on 22 oviductal eggs). Apparently, oviductal eggs are elongated, becoming more spherical after deposition. Egg volume was not correlated with female SVL (r = 0.25, N = 22, P = 0.26) and there was no difference in mean egg volume between clutches of one egg (mean = 157.91 ± 38.41 mm^3, N = 4) and clutches of two eggs (mean = 150.59 ± 29.19 mm^3, N = 18, t_{21} = −0.36, P = 0.74). We incubated a clutch of two eggs in the lab (in moist vermiculite at ambient temperature); upon hatching, lizards measured 21.50 and 23.24 mm SVL, and both weighed 0.2 g. No gravid female simultaneously contained enlarged vitellogenic follicles and either oviductal eggs or corpora lutea. Hence, if multiple clutches were produced during the breeding season, they were relatively well spaced in time or corpora lutea degenerated rapidly in time.

Reproductive males occurred throughout the year, but mating was concentrated during the dry season, from May to September (Fig. 4). In November, at the onset of the rainy season, three adult males examined were all reproductive. Reproductive condition was significantly associated with season in males (χ^2_1 = 10.34, P = 0.001), indicating higher frequency of reproductive males during the dry season than in the wet season. Likewise, a larger proportion of reproductive females were observed during the dry season (Fig. 4), with a significant association between reproductive condition and season

TABLE 2. Stepwise discriminant analysis of shape variables of *Gymnodactylus geckoides amarali*. 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 width	0.044	0.956	<0.001	0.403
2	Adjusted body width	0.013	0.944	<0.001	0.368
3	Adjusted snout–vent length	0.008	0.936	<0.001	0.370

TABLE 3. Diet composition of *Gymnodactylus geckoides amarali* from the Cerrado of central Brazil. *F* is the number of stomachs containing each prey category, *N* is the number of prey in each category, and *V* is the volume (mm^3) of prey in each category.

	Occurrence		Stomach means				Pooled stomachs			
Prey items	*F*	*F*%	*N*	*N*%	*V*	*V*%	*N*	*N*%	*V*	*V*%
Araneae	22	8.30	0.083 ± 0.276	5.60 ± 19.76	0.05 ± 0.71	2.70 ± 16.44	22	2.59	11.13	0.61
Arthropoda	55	20.75	0.219 ± 0.441	19.30 ± 35.87	—	—	58	6.83	—	—
Blattaria	7	2.64	0.026 ± 0.161	1.32 ± 8.66	0.13 ± 1.45	3.79 ± 17.54	7	0.82	32.82	1.78
Chilopoda	1	0.38	0.004 ± 0.061	0.49 ± 7.00	—	—	1	0.12	—	—
Coleoptera	11	4.15	0.042 ± 0.200	2.31 ± 12.23	0.02 ± 0.17	5.26 ± 22.63	11	1.30	3.86	0.21
Diplopoda	1	0.38	0.004 ± 0.061	0.10 ± 1.40	0.04 ± 0.59	2.50 ± 15.81	1	0.12	9.56	0.52
Diptera	4	1.51	0.015 ± 0.122	1.39 ± 10.70	0.01 ± 0.09	0.23 ± 1.45	4	0.47	1.37	0.07
Formicidae	48	18.11	0.558 ± 2.264	14.46 ± 30.31	0.19 ± 1.95	12.86 ± 33.85	148	17.43	41.97	2.28
Hemiptera	3	1.13	0.011 ± 0.106	0.99 ± 9.88	0.06 ± 0.99	0.17 ± 1.05	3	0.35	16.04	0.87
Homoptera	7	2.64	0.026 ± 0.161	1.44 ± 10.41	0.16 ± 1.99	2.80 ± 16.04	7	0.82	41.02	2.23
Hymenoptera	6	2.27	0.026 ± 0.183	1.72 ± 10.52	0.02 ± 0.27	2.62 ± 15.81	7	0.82	4.81	0.26
Insect eggs	2	0.76	0.158 ± 2.402	0.76 ± 7.86	0.02 ± 0.23	5.00 ± 22.07	42	4.95	3.99	0.22
Insect pupae	1	0.38	0.004 ± 0.061	0.08 ± 1.17	0.18 ± 2.86	2.50 ± 15.81	1	0.12	46.61	2.53
Isoptera	106	40.03	1.879 ± 5.432	38.92 ± 42.75	8.38 ± 31.01	68.05 ± 46.52	498	58.66	1499.05	81.46
Lepidoptera	2	0.75	0.008 ± 0.087	0.98 ± 9.88	—	—	2	0.24	—	—
Mantodea	1	0.38	0.004 ± 0.061	0.16 ± 2.33	—	—	1	0.12	—	—
Odonata	1	0.38	0.004 ± 0.061	0.49 ± 7.00	—	—	1	0.12	—	—
Orthoptera	16	6.04	0.064 ± 0.260	4.11 ± 16.96	0.13 ± 1.62	3.99 ± 17.74	17	2.00	32.65	1.77
Plant material	4	1.51	0.015 ± 0.122	0.73 ± 7.34	0.01 ± 0.10	2.56 ± 16.01	4	0.47	1.66	0.09
Plecoptera	1	0.38	0.004 ± 0.061	0.49 ± 7.00	0.33 ± 5.38	2.50 ± 15.81	1	0.12	87.60	4.76
Lizard skin	10	3.77	0.038 ± 0.191	3.06 ± 15.49	—	—	10	1.18	—	—
Lizard tail	1	0.38	0.004 ± 0.061	0.49 ± 7.00	—	—	1	0.12	—	—
Scorpiones	1	0.38	0.004 ± 0.061	0.10 ± 1.40	—	—	1	0.12	—	—
Thysanura	1	0.38	0.004 ± 0.061	0.49 ± 7.00	0.02 ± 0.38	2.50 ± 15.81	1	0.12	6.16	0.34

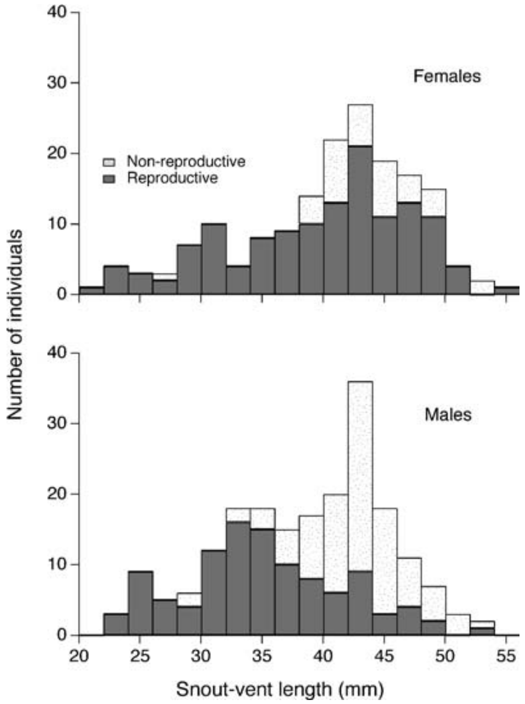

FIG. 3. Frequency distribution of male (bottom) and female (top) *Gymnodactylus geckoides amarali* according to snout–vent length and reproductive condition.

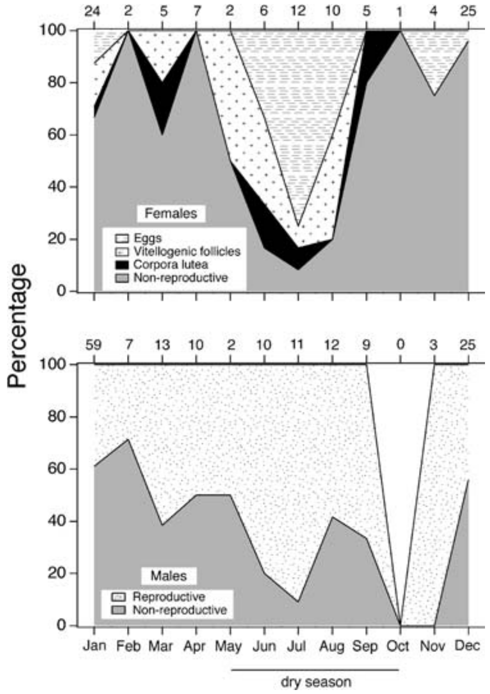

FIG. 4. Monthly distribution of male (bottom) and female (top) *Gymnodactylus geckoides amarali* according to reproductive condition. Sample sizes are indicated on top of bars.

($\chi^2_1 = 39.80$, $P < 0.001$). Therefore, although reproductive individuals can be found throughout the year, reproductive activity is seasonal, being concentrated during the dry season. In contrast to *G. g. amarali*, *G. g. geckoides* in the Caatinga breeds continuously and lays smaller clutches of larger eggs, even though adult females are similarly sized (Table 4).

DISCUSSION

Habitat, Microhabitat, and Temperatures.—*Gymnodactylus geckoides amarali* is rupicolous, as has been previously reported for *G. g. geckoides* (Vitt, 1995) and *G. guttulatus* (Vanzolini, 1982). Conversely, the congeneric *G. darwinii* lives in forests and "restingas" (Araujo, 1991; Freire, 1998). Based on a lizard assemblage from Alto Araguaia, Brazil, Vitt (1991) stated that the Cerrado is depauperate in terms of gekkonid species, relative to other Brazilian biomes. However, this conclusion likely stems from the lack of rock outcrops in Alto Araguaia. Geckos are often more diverse in rocky habitats (Bauer, 1993) and these habitats have a patchy distribution in the Cerrado (e.g., Giullietti and Pirani, 1988; Harley, 1988). Biological reserves in the Cerrado that exclude rocky areas may fail to preserve a significant portion of the lizard fauna.

The low body temperatures of *G. g. amarali* seem to be characteristic of gekkonids (e.g., Pianka, 1986; Dial and Grismer, 1992; Werner et al., 1996). The significant association between

TABLE 4. Reproductive characteristics of *Gymnodactylus geckoides* from the Cerrado and Caatinga of Brazil.

Species	Clutch size	Egg length (mm)	Egg width (mm)	Adult female SVL (mm)
G. g. geckoides[a]	1.00 ± 0.00	9.33 ± 0.83	6.05 ± 0.75	42.80 ± 1.94
(Caatinga)	(*N* = 47)	(*N* = 47)	(*N* = 47)	(*N* = 104)
G. g. amarali	1.65 ± 0.48	8.77 ± 0.64	5.72 ± 0.47	43.77 ± 4.43
(Cerrado)	(*N* = 32)	(*N* = 22)	(*N* = 22)	(*N* = 38)
t	7.66	3.07	2.43	1.30
P	<0.001	0.003	0.018	0.201

[a] Data from Vitt (1986).

body temperature and environmental temperatures suggests that this species is a thermoconformer. However, since body temperatures were higher than substrate temperatures, lizards gained additional heat and were not thermoconformers in the strict sense. The higher body temperature of *G. g. geckoides* in Caatinga likely results from higher environmental temperatures in that biome (Vitt, 1995). Our observations on activity are rare, but they suggest that *G. g. amarali* is predominantly a nocturnal species or most activity occurs under rocks (dark places) and that crypsis is used to evade predators. Some anecdotal information indicates that these lizards may be active during the day (L. J. Vitt, pers. comm.).

Sexual Dimorphism.—Our results revealed significant sexual dimorphism in body size and shape in *G. g. amarali*: females are larger, stockier, and have significantly smaller heads than males. In most geckos studied to date, females are larger than males (e.g., Fitch, 1981; Vitt, 1986; Doughty and Shine, 1995), but reasons for this sexual size dimorphism are unclear. Selection should favor large size in females if this is associated with increased clutch or offspring size, whereas large male size is usually driven by sexual selection (Trivers, 1976; Cooper and Vitt, 1989; Anderson and Vitt, 1990). When clutch size is fixed, pelvic girdles are often tightly associated with egg diameter, and if selection favors large offspring, females will tend to be larger (Doughty, 1996; but see Vitt, 1986). Hence, large female size in geckos should be favored by increased offspring size, independent of males. In *G. g. amarali*, however, it is clutch size that varies with female size. Two explanations seem plausible in this situation. First, females of *G. g. amarali* are larger than males because of increased reproductive success associated with the production of larger clutches. Second, large female size (in relation to male size) is the ancestral condition of *Gymnodactylus* or a larger subset of Gekkonidae including that genus and is present in *G. g. amarali* because of phylogenetic inertia. Given that *G. g. geckoides* females from the Caatinga are larger than males and there is no correlation between reproductive output and female size (Vitt, 1986), the second hypothesis is more parsimonious.

In *G. g. amarali*, males have larger heads than females, independent of body size. This kind of sexual dimorphism in squamate reptiles has been attributed to two main causes: intraspecific niche divergence and sexual selection. The first explains intersexual differences as a mechanism to reduce competition for food resources (e.g., Schoener, 1967; Perry, 1996), whereas the latter invokes intrasexual competition among males for access to females (e.g., Trivers, 1976; Vitt and Cooper, 1985). Our results do not support the intraspecific niche divergence hypothesis, since we observed no association between head dimensions and prey dimensions and no trophic differences between the sexes. In addition, this hypothesis assumes that food is a limiting resource, and apparently this is not true for lizards in the Cerrado (Colli et al., 1997). The sexual selection hypothesis predicts that males with large heads will have increased reproductive success by winning intrasexual aggressive encounters for access to mates. However, detailed information on these aspects is currently lacking for *G. g. amarali*. Vitt (1986) indicated that *G. g. geckoides* is territorial, without presenting quantitative data, but found no sexual dimorphism in head shape. It is conceivable that, because of the shorter breeding season of *G. g. amarali* in the Cerrado, the potential for males to monopolize multiple females increases, in contrast to *G. g. geckoides* in the Caatinga, where continuous reproduction would render the efforts to monopolize females energetically impractical (Emlem and Oring, 1977). Hence, sexual selection for larger head size in males would be stronger in the Cerrado. Clearly, additional comparative work, including other species of *Gymnodactylus*, is necessary to determine the potential role of sexual selection in producing sexual size dimorphism.

Diet Composition.—The diet of *G. g. amarali* in the Cerrado consists largely of termites. Based on pooled stomachs, termites comprised a remarkable 81% of the prey volume and 59% of the prey number. Simply taking the average values for individual geckos, termites comprised approximately 39% of the prey number and 68% of the prey volume of *G. g. amarali*. These figures are far greater than those described for any other Cerrado lizard or amphisbaenian studied to date (Vitt and Colli, 1994; Colli et al., 1998; Colli and Zamboni, 1999), resembling some Australian geckos which are termite specialists, such as *Diplodactylus conspicillatus*, *Diplodactylus pulcher*, and *Rhynchoedura ornata* (Pianka, 1986). The disproportional representation of termites in the diet is clearly reflected in the reduced values of dietary diversity. For instance, the syntopic teiid *Ameiva ameiva* has a diet that is approximately five times as diverse as the diet of *G. g. amarali* (Vitt and Colli, 1994). The diversity of prey used by *G. g. amarali* is comparable to that reported for a syntopic and highly fossorial squamate, *Amphisbaena alba* (Colli and Zamboni, 1999). In addition, the large numbers of termites and ants in the diet seem to be responsible for the lack of correlation between prey size and lizard head measurements.

Termites are a diverse and prominent group in the Cerrado. The termitaria of some species, such as the mound building termite *Cornitermes* *cumulans*, can reach impressive densities and it has been suggested it may act as a keystone species (Redford, 1984). Termitaria densities range from 336–776/ha (Redford, 1984; Gontijo and Domingos, 1991), and local diversity can be as high as 46 termite species per 0.25 ha (Mathews, 1977; Gontijo and Domingos, 1991). Given diversity and abundance of Cerrado termites, it is not surprising that *G. g. amarali* might include large numbers and volumes of termites in their diet. Less clear, however, is why termites are a much less important dietary item among syntopic, actively foraging species, such as *Ameiva ameiva* (Vitt and Colli, 1994) and *Cnemidophorus ocellifer* (Mesquita and Colli, 2003). Termites are regarded as a food item typical of actively foraging lizards (Huey and Pianka, 1981), and like most gekkonids (Cooper, 1994), *G. geckoides* is best classified as a sit-and-wait or ambush forager (Vitt, 1995).

The preferred diurnal microhabitats of *G. g. amarali* are spaces underneath rocks and rock crevices in large outcrops. They are moist, even during the dry season, and rich in organic matter in the form of dead leaves, branches, and roots, being intensively used by termites (pers. obs.). Because the soil is very shallow, termite galleries are built next to the surface (R. Constantino, pers. comm.). Geckos in general are highly chemosensory (Schwenk, 1993a,b); therefore *G. g. amarali* likely has no problem uncovering and eating large numbers of termites. *Gymnodactylus geckoides geckoides* from Caatinga uses similar microhabitats and consumes a remarkably similar volume of termites (82.7% for the pooled data; Vitt, 1995).

Reproduction.—Although reproductive individuals of *G. g. amarali* were found throughout the year, female reproduction was concentrated during the dry months (May to September). All of the Cerrado squamates studied to date have a well-defined reproductive cycle, such as *Ameiva ameiva* (Colli, 1991), *Amphisbaena alba* (Colli and Zamboni, 1999), *Tropidurus itambere* (Van Sluys, 1993), and *Tropidurus torquatus* (Wiederhecker et al., 2002). However, among these species, only *A. alba* reproduces primarily during the dry season. In strongly seasonal, Neotropical habitats, such as the Cerrado, reproduction is often tightly correlated with rainfall (Fitch, 1970, 1982; Licht and Gorman, 1970), presumably because of the influence of rainfall upon arthropod abundance (Levings and Windsor, 1982; Smythe, 1982) and/or microenvironments for egg deposition (Andrews and Sexton, 1981; Andrews and Wright, 1994; Overall, 1994). Foraging activity of termites increases during the dry season (Pinheiro et al., 2002) to support the production of alates that swarm at the onset of the rainy season. Some Cerrado animals that feed largely on termites, such as the Hoary Fox, *Lycalopex vetulus*, ingest termites more frequently during the dry season (Dalponte, 1997). Because the consumption of termites is higher during the dry season, individuals of *G. g. amarali* may concentrate breeding in the dry season because access to termites is maximized.

Contrary to its Cerrado relative, *G. g. geckoides* in the Caatinga breeds continuously and lays smaller clutches of larger eggs. A similar situation exists for *A. ameiva*: the Cerrado population breeds primarily during the rainy season and lays larger clutches of smaller eggs (Colli, 1991), whereas the Caatinga population breeds year-round and lays smaller clutches of larger eggs (Vitt, 1982). An analogous variation was reported between Mediterranean populations of *Lacerta lepida* (Mateo and Castanet, 1994). This pattern may reflect ecotypic adaptations produced by environmental differences between the two regions: Climate is predictable in the Cerrado, but unpredictable in the Caatinga (Colli, 1991). Our results are consistent with the notion that, in unpredictable environments, selection may favor an optimal clutch size that is smaller than what a female could produce, because of the effect of high mortality in "bad" years (Roff, 1992). Alternatively, selection favors larger clutches in the Cerrado because the reproductive season is shorter than in the Caatinga. However, if a clutch of two eggs is the ancestral condition for *Gymnodactylus*, then single egg clutches of *G. g. geckoides* are derived, thus favoring the hypothesis of reduced clutch size caused by climate unpredictability. In this case, the larger clutches of *G. g. geckoides* would simply be a product of phylogenetic conservatism (Harvey and Pagel, 1991). However, a phylogenetic analysis of the genus is necessary before adaptation can be inferred (Garland and Adolph, 1994). The smaller eggs of *G. g. amarali* in the Cerrado may simply reflect the trade-off between egg size and clutch size (e.g., Abell, 1999), given that there exists no significant difference in SVL of reproductive females between the two regions. More comparisons between the two biomes, involving taxa of different lineages and sizes, will help resolve how much environmental differences have influenced the evolution and shaped the character of the Cerrado and Caatinga faunas.

The correlation we observed between clutch size and female SVL is, to the best of our knowledge, the first to be reported for any gecko. Most gekkonids studied to date have a fixed clutch size of one or two eggs, and females are unable to increase clutch size by increasing body size (Fitch, 1970; Selcer, 1986; Vitt, 1986; Marquet et al., 1990; Vitt and Zani, 1997). Instead, in fixed clutch species, it is egg size that varies with female body size (e.g., Andrews and Rand, 1974;

Doughty, 1996). In *G. g. amarali* there was no correlation between egg size and female SVL and no difference in mean egg volume between clutches of one egg and clutches of two eggs. Why is there a correlation between clutch size and female SVL in *G. g amarali*? One possible explanation is that since clutch size cannot increase beyond two eggs with increasing body size, selection should favor early production of eggs, as long as egg size is large enough to produce viable offspring (Vitt, 1986; Doughty, 1996). Thus, with approximately 38 mm SVL, females are able to start producing eggs, but morphological constraints (Congdon and Gibbons, 1987; Shine, 1992) or selection against increased physical burden, such as reduced mobility and increased visibility to predators (Vitt and Congdon, 1978; Shine, 1980; Vitt and Price, 1982; Sinervo et al., 1989), may prevent the production of clutches of two eggs. With increasing body size, females start producing clutches of two eggs.

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