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Abstract.—We compared reproduction, diet, and body size of *Polychrus acutirostris* (Squamata: Polychrotidae) from the Cerrado and Caatinga biomes in Brazil. Because these two biomes have widely different climates, we predicted that lizards in Caatinga would produce smaller clutches in response to rainfall unpredictability. We also expected reproductive timing to differ between biomes, with lizards occurring in the Cerrado producing a single clutch in association with the predictable rains of October–November. Contrary to expectations, clutches had fewer (although larger) eggs in Cerrado. Reproductive period was remarkably similar (peak of female reproductive activity in November), but female reproduction started 1 month earlier in Cerrado. Diet composition was also similar, with the exception of spiders, that exhibited a high index of relative importance in Cerrado but were nearly absent in Caatinga lizard diets. Lizards from both biomes ingested a large proportion of plant material, as well as soft-bodied arboreal arthropods, such as orthopterans, and mostly slow-moving, large arboreal insects. Rainfall predictability in the Cerrado therefore did not influence *Polychrus* reproduction or diet in the same manner as in other lizard species. The large number of small eggs in the Caatinga suggests that the competitive environment for offspring is either unpredictable or that mortality is high but random. Rain forest *Polychrus* lizards produce few large eggs, suggesting that the competitive environment for offspring is predictably intense and mortality is non-random. Cerrado *Polychrus* lizards seem intermediate between Caatinga and rain forest *Polychrus* lizards, producing fewer and larger eggs than their conspecifics in the Caatinga but relatively more and smaller eggs than rain forest *Polychrus* species.

The low variability of reproductive traits in some lizard taxa reveals the influence of phylogenetic history (Ballinger, 1983; Dunham and Miles, 1985). For example, lizards in the genus *Anolis*, all gekkonids, and all gymnophthalmids deposit clutches of a single egg or two eggs (Pianka and Vitt, 2003). Conversely, traits that vary throughout a species' geographic distribution implicate other factors as influencing life-history traits (e.g., environmental variables and morphological constraints; Charnov et al., 2007). In temperate regions, altitude is associated with the evolution of viviparity in *Lacerta vivipara*, whereas temperature is the key factor determining timing of reproduction (Heulin et al., 1997). Likewise, viviparity has evolved at least four times in the genus *Sceloporus* (Méndez-de la Cruz et al., 1998). In tropical regions, in contrast, rainfall seasonality and predictability have been considered the most important factors shaping a species' reproductive biology (Fitch, 1985).

Life-history parameters, such as age at sexual maturity, survivorship, and growth and reproductive rates are fundamental to understanding a species' ecology (Stearns, 1992), and comparisons of conspecific populations living in disparate environments can help detect local adaptations and natural selection forces responsible for life-history variation in different environments (Niewiarowski and Dunham, 1994). For example, wide-ranging lizard species generally exhibit thermal clines in body size, with populations in warmer environments usually smaller than those in cold environments (Atkinson, 1994). Despite slower growth rates, populations in cold climates reach relatively larger body sizes by prolonging growth and delaying reproduction (Atkinson, 1994; but see Angilletta et al., 2004; Sears and Angilletta, 2004). Moreover, because digestive efficiency in lizards depends on environmental temperature (Chen et al., 2003; Zhang and Ji, 2004), warmer climates and reduced rainfall can provide better thermal conditions for promoting fast growth, improving foraging and digestive efficiencies, and allowing species to reach sexual maturity earlier and at smaller sizes. Reproductive cycles also may vary between seasonal and nonseasonal climates for species inhabiting both (Fitch, 1982). In seasonal environments, reproduction should be concentrated in favorable periods and clutches should be larger and composed of smaller eggs than in nonseasonal environments because predictability would allow species to increase clutch sizes by reducing offspring size without compromising hatchling viability (Fitch, 1982).

The Cerrado is one of the major biomes in Brazil, being characterized climatically by strong wet–dry seasonality. It is a savanna-like landscape type that, along with the Chaco (to the southwest) and Caatinga (to the northeast), forms a South American diagonal belt of open formations (Ab'Saber, 1977). Comparisons among lizards living across these superficially similar yet ecologically and biogeographically different ecosystems are beginning to reveal life-history variation probably related to differences in rainfall amount and predictability (Colli, 1991; Colli et al., 2003; Mesquita and Colli, 2003). Climate in the Cerrado is highly seasonal, with a marked and predictable rainy season from October to March (Dias, 1992). In contrast, the Caatinga receives higher solar radiation; lower cloud coverage; higher mean annual temperature; lower relative humidity; and, most importantly, lower precipitation (on average, 300–800 mm compared with 1,100–1,600 in the Cerrado). This precipitation also is irregularly distributed and

FIG. 1. *Polychrus acutirostris* from Cerrado near the city of Brasília, Brazil.
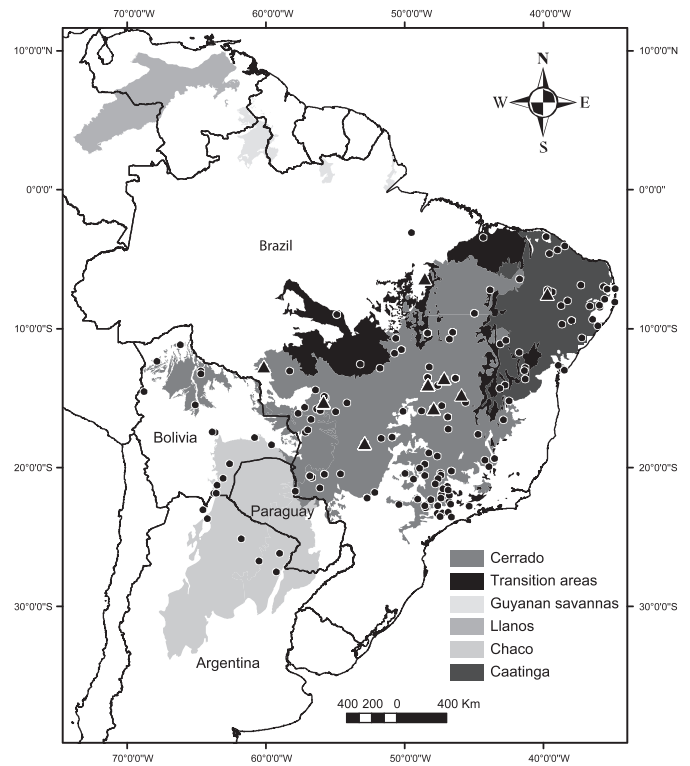

FIG. 2. Geographical distribution of *Polychrus acutirostris*. Circles represent all known localities based on museum collections (Coleção Herpetológica da Universidade de Brasília [CHUNB] and Museu de Zoologia da Universidade de São Paulo [MZUSP]) and literature. Triangles represent the sampled localities.

limited to a short period of the year, with 50–70% of the rainfall occurring in three consecutive months, usually from February to March (Reis, 1976; Prado, 2003).

Because of this climatic unpredictability, we expect breeding by lizards in Caatinga to be more scattered throughout the year. This would reduce the probability of losing all reproductive effort due to stochastic environmental effects, a trend already observed in other lizards occurring in both areas (Colli, 1991; Colli et al., 2003). Conversely, breeding in Cerrado should be concentrated in the more favorable rainy season (Colli, 1991; Van Sluys, 1993; Wiederhecker et al., 2002). In addition, clutches in Caatinga also should be smaller and composed of larger eggs (Fitch, 1982; Colli, 1991; Colli et al., 2003). Similarly, if climate or vegetation type imposes limits on prey availability, seasonal variations in diet should be more evident in Cerrado populations. Finally, Caatinga populations (subject to slightly warmer climates) should have smaller adult body sizes and reach sexual maturity earlier and at smaller sizes than their Cerrado counterparts living under a relatively cooler, seasonal climate.

Polychrus acutirostris (Spix 1825) (Squamata: Polychrotidae) is widespread along the South American diagonal belt of open formations that goes from Argentina and Bolivia to northeastern Brazil, encompassing the Chaco, Cerrado, and Caatinga biomes (Figs. 1 and 2). We compare Cerrado and Caatinga populations of *P. acutirostris* to test the effects of different environments on diet and reproduction of a wide-ranging lizard species. Specifically, we test whether 1) clutches are larger and composed of smaller eggs; 2) reproductive season is shorter; 3) diets differ among biomes, and 4) reproductive adults are larger in Cerrado.

MATERIAL AND METHODS

Sampling.—Data on Cerrado lizards were obtained from specimens deposited at Coleção Herpetológica da Universidade de Brasília (CHUNB), and data for Caatinga were derived from Vitt and Lacher (1981). We measured the snout–vent length (SVL) of all Cerrado lizards with a ruler to the nearest 1 mm. Data on reproduction, diet, and body size from Caatinga were obtained from the same specimens used by Vitt and Lacher (1981). We analyzed stomach contents and reproductive data from 289 lizards from eight Cerrado localities and 105 from one Caatinga locality (Exu, Pernambuco state, Brazil; Fig. 2).

Clutch Size and Reproduction.—We examined females and considered the presence of vitellogenic follicles or oviductal eggs as evidence of reproductive activity. Simultaneous presence of vitellogenic follicles and oviductal eggs or corpora lutea was considered evidence of multiple clutches during the year. We counted and measured length and width (0.01 mm) of each vitellogenic follicle, egg, or both with Mitutoyo™ electronic calipers. Males were considered reproductively active if bearing enlarged testes and convoluted epididymides. We measured length and width (0.01 mm) of the largest testis with Mitutoyo electronic calipers. Egg and testis volume were estimated as an ellipsoid (see formula in Diet Composition). Reproductive condition of females and males was assessed to determine timing of reproduction.

To account for the influence of SVL upon gonadal attributes (testis volume for males; clutch size, and mean egg volume for females), we conducted analysis of covariance (ANCOVA) tests (SVL as covariate), when applicable, on monthly samples of testis volume, clutch size, and mean egg volume. To meet the assumptions of normality all variables were $\log_{10}$ or $\sqrt{x+0.5}$ transformed before analyses (Zar, 1999). We conducted Tukey's

post-hoc tests to assess monthly differences for mean testis, egg, and clutch size. Size at reproductive maturity was estimated based on 1) the smallest female containing vitellogenic follicles or oviductal eggs and 2) the smallest male bearing both enlarged testis and convoluted epididymides. Due to seasonal variations in the amount and distribution of precipitation, some error in the evaluation of reproductive cycle could have been introduced when individuals collected in different years were pooled in different classes. Average annual variation in precipitation is <15% in the Cerrado (Nimer, 1977), suggesting little error in monthly assignments due to rainfall variation among years. Data from Caatinga were collected during 1 year and are thus not affected by annual variations in precipitation.

Diet Composition.—Stomachs were removed from preserved specimens and examined under a stereomicroscope to identify prey items to broad taxonomic categories (usually order). Prey items that were too fragmented to allow a reliable estimate of their volumes were excluded. We recorded 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 numeric and volumetric percentages of each prey category for individual lizards and for pooled stomachs. We computed niche breadths from numerical percentages using Shannon diversity index (Shannon, 1948):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i,$$

where p_i is the proportion of the diet represented by prey i and ln is the natural logarithm. Because niche breadth can be influenced by sample size, we used the Species Diversity module in EcoSim (Gotelli and Entsminger, 2004) to compare Cerrado vs. Caatinga. To determine the relative contribution of each prey category, we calculated an index of relative importance for individuals and pooled stomachs by using the average of percentage of prey occurrence ($F\%$), numeric percentage ($N\%$), and volumetric percentage ($V\%$), according to the following equation (Pinkas, 1971):

$$IRI = F\% \times (N\% + V\%).$$

We then calculated overlap in diet composition between populations by using the equation (Pianka, 1973):

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

where p represents the volumetric proportion of prey category i, n is the number of categories, and j and k represent the species being compared. $\varnothing_{ij}$ varies from 0 (no similarity) to 1 (complete similarity).

To account for differences in sampling efforts in the comparison of prey categories between Cerrado and Caatinga populations, we calculated rarefaction curves with individual stomachs as sampling units for Cerrado and Caatinga and used these curves for comparisons (Gotelli and Entsminger, 2004). We compared indices of relative importance between biomes using a Wilcoxon test.

Body Size Comparisons.—We used a two-way analysis of variance to assess the effects of region (Caatinga vs. Cerrado) and sex on adult lizard SVL. The SVL was log-transformed
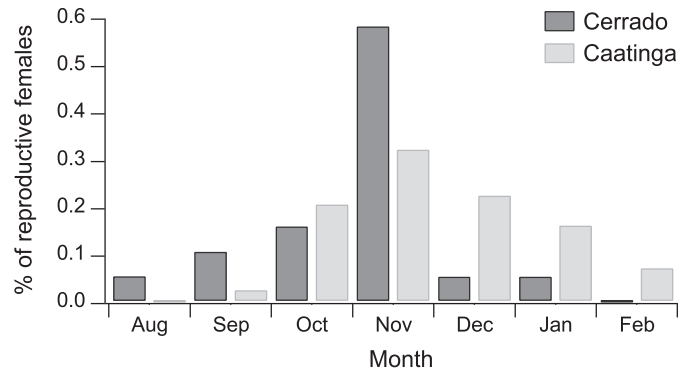

Fig. 3. Comparative monthly distribution of reproductive *Polychrus acutirostris* females from Cerrado and Caatinga.

before analysis to meet the assumptions of normality for parametric tests. Because some specimens were damaged or inadequately preserved, SVL was available for 174 lizards from the Cerrado and 105 lizards from the Caatinga.

RESULTS

Clutch Size and Reproduction.—We obtained reproductive data from 182 Cerrado females and 80 Caatinga females, of which 11.7% and 55%, respectively, carried vitellogenic follicles or eggs and were considered reproductive. Female breeding activity lasted 6 months in both biomes, with a 1-month delay in Caatinga (September vs. August; Fig. 3). No female contained both vitellogenic follicles and eggs; therefore, there was no evidence of multiple clutches. Reproductive activity of *P. acutirostris* peaks in November in both biomes, but the Caatinga peak was less distinctive. Despite such similarities, the monthly distribution of reproductive females differed significantly between biomes ($F_{1,61} = 6.05$, $P < 0.05$).

Clutch size based on number of vitellogenic follicles or eggs did not differ significantly within biomes, independently of SVL (ANCOVA: Caatinga: $F_{1,41} = 1.75$, $P = 0.19$; Cerrado: $F_{1,16} = 2.51$, $P = 0.13$). Thus, we pooled both clutch size estimates. Clutch size differed significantly between biomes ($F_{1,61} = 48.04$, $P < 0.001$), being larger in Caatinga (adjusted mean, 17.82 ± 6.55; range, 7–31) than in Cerrado (adjusted mean, 11.21 ± 3.31; range, 6–19). Mean egg volume differed between biomes, regardless of SVL (ANCOVA: $F_{1,25} = 53.51$, $P < 0.001$), being larger in Cerrado (919.51 ± 161.95 mm^3) than in Caatinga (563.02 ± 63.89 mm^3).

We analyzed 61 males from animals captured in Cerrado and 36 in Caatinga. Testicular data were derived from January to March and from October to November in Cerrado and from January to February, in April, and from September to December in Caatinga. There was no monthly variation in mean testis volume among Cerrado lizards (ANCOVA: $F_{4,56} = 0.29$, $P = 0.88$). In Caatinga, mean testis weight was significantly greater in April than in January, February, and December (ANCOVA: $F_{6,29} = 17.80$, $P < 0.001$). Male *P. acutirostris* in Caatinga attain sexual maturity at 75-mm SVL, and all males analyzed from Cerrado had SVL >75 mm. In Cerrado, the smallest reproductive male was 88-mm SVL.

Diet Composition.—We identified 20 prey categories in *P. acutirostris* from the Cerrado. Based on rarefaction curves, we found on average 14.16 categories for the Cerrado, with 95% confidence levels of 12–15, suggesting limited or no differences compared with the 13 prey categories reported for the Caatinga population. However, when comparing niche breadth using an index that relies on richness and equitability (H'), Caatinga lizards exhibited a larger niche breadth. The most frequent items in the Cerrado were spiders, grasshoppers, beetles, and

TABLE 1. Diet composition of *Polychrus acutirostris* from Cerrado and Caatinga. F = frequency; N = number; V = volume; IRI = index of relative importance.

| | Cerrado (n = 229) | | | | | | | Caatinga (n = 105) | | | | | | |
| | Occurrence | | Pooled stomachs | | | | | Occurrence | | Pooled stomachs | | | | |
Prey item	F	F%	N	N%	V (mm³)	V%	IRI	F	F%	N	N%	V (mm³)	V%	IRI
Araneae	129	56.33	395	19.87	2,900.21	12.21	1,807.07			6	2.01	1,490.00	3.08	33.90
Araneae (egg sac)	4	1.75	4	0.20	333.78	1.40	2.80	7	6.66	—	—	—	—	—
Blattaria	6	2.62	8	0.40	394.51	1.66	5.40	—	—	—	—	—	—	—
Cicadellidae	31	13.54	51	2.57	948.06	3.99	88.82	—	—	—	—	—	—	—
Coleoptera	76	33.19	140	7.04	813.82	3.42	347.17	35	33.34	26	8.72	1,840.00	3.80	417.42
Diplopoda	—	—	—	—	—	—	—	1	0.95	1	0.34	350.00	0.72	1.01
Diptera	3	1.31	861	43.31	14.93	0.06	56.81	2	1.90	2	0.67	70.00	0.14	1.54
Gastropoda	1	0.44	2	0.10	122.08	0.51	0.27	—	—	—	—	—	—	—
Hemiptera	6	2.62	7	0.35	25.15	0.11	1.21	12	11.42	16	5.37	1,530.00	3.16	97.41
Homoptera	16	6.99	23	1.16	104.22	0.44	11.18	16	15.23	34	11.41	1,670.00	3.45	226.32
Hymenoptera	11	4.80	18	0.91	478.88	2.02	14.06	15	14.28	29	9.73	2,860.00	5.90	223.20
Insecta (nonidentified)	11	4.80	19	0.96	2,974.41	12.52	64.70	—	—	—	—	—	—	—
Isoptera	1	0.44	6	0.30	3.04	0.01	0.14	1	0.95	30	10.07	500.00	1.03	10.55
Lepidoptera (adults)	—	—	—	—	—	—	—	10	9.53	18	6.04	770.00	1.59	72.71
Lepidoptera (larvae)	5	2.18	6	0.30	738.72	3.11	7.43	9	8.57	17	5.70	2,150.00	4.44	86.90
Mantodea	9	3.93	13	0.65	825.77	3.48	16.23	—	—	—	—	—	—	—
Neuroptera	1	0.44	1	0.05	—	—	—	—	—	—	—	—	—	—
Odonata	34	14.85	57	2.87	574.03	2.42	78.56	4	3.81	3	1.01	900.00	1.86	10.93
Orthoptera	89	38.86	124	6.24	9,004.06	37.89	1,714.89	79	75.24	75	25.17	22,120.00	45.66	5,329.25
Phasmatodea	3	1.31	3	0.15	236.87	1.00	1.51	—	—	—	—	—	—	—
Plant material	58	25.33	250	12.58	3269.66	13.76	667.19	51	48.57	41	13.76	10,630.00	21.94	1,733.95
Squamata (skin)	4	1.75	—	—	—	—	—	4	3.81	—	—	1,560.00	3.22	—
Total			1,988		23,762.21					298		48,440.00		
Niche breadth (H′)		1.782			(1.640–1.868)[a]				2.206					

[a] Confidence interval calculated by rarefaction.

plant material (Table 1). Based on the mean number of prey items, the diet consisted mainly of flies, spiders, and plant material. Volumetrically, the diet consisted mainly of grasshoppers, plant material, unidentified insects, and spiders (Table 1). Diets of *P. acutirostris* in Cerrado and Caatinga were similar for the most common categories, such as grasshoppers, plant material, and beetles, despite pronounced differences in spiders; spiders were almost absent in the diet of Caatinga lizards (Fig. 4). The importance value index indicated that the more important prey items were spiders, beetles, grasshoppers, and plant material (Table 1). The similarity index among populations was significantly high (observed = 0.92, mean simulated = 0.54, P < 0.001). Despite the overall similarity, significant differences existed among these biomes in importance indices (Wilcoxon's test, Z = –3.408, P = 0.001).

Body Size Comparisons.—There were significant size differences between sexes and biomes, but no interactions among these factors (sex: $F_{1,279}$ = 96.53, P < 0.0001; region: $F_{1,279}$ = 49.08, P < 0.0001; sex vs. region: $F_{1,279}$ = 0.001, P = 0.98). Females are larger than males in the Caatinga and Cerrado, whereas both sexes are smaller in the Cerrado. Females averaged 120.04 ± 20.26 mm (n = 79) in the Caatinga and 107.33 ± 11.23 mm (n = 93) in the Cerrado, whereas males averaged 102.23 ± 13.81 mm (n = 47) in the Caatinga and 89.61 ± 11.14 mm (n = 62) in the Cerrado.

DISCUSSION

Clutch Size and Reproduction.—Oviposition in *P. acutirostris* occurs at the onset of the rainy season in Caatinga, Chaco, and Cerrado (Vitt and Lacher, 1981; Luedemann et al., 1997; Alvarez et al., 2005). The reproductive season starts slightly later in the Caatinga, but so does the rainy season. Like Vitt and Lacher (1981), we found no evidence for multiple clutches in *P. acutirostris*. Because of high environmental unpredictability of rainfall in Caatinga (Reis, 1976), the deposition of more than one clutch of smaller eggs scattered throughout the rainy season was expected, as reported for other lizards (Fitch, 1982; Colli, 1991; Colli et al., 2003) because of indirect influences on hatchling survival. Moisture during the rainy season can produce adequate microhabitat conditions for egg deposition and embryo development in lizards (Andrews and Sexton, 1981). *Polychrus* lizards produce only a single clutch, but unlike anoles (the most diverse group of polychrotid lizards), the clutch consists of many eggs and comprises a large mass relative to body mass. In effect, all eggs are in one basket. Timing of egg deposition is tied to seasonal rainfall that produces conditions necessary for egg development. Comparisons among lizard species living in Caatinga and Cerrado environments in Brazil have shown that certain species, such as *Ameiva ameiva* (Colli, 1991), *Cnemidophorus* spp. (Mesquita and Colli, 2003), and *Gymnodactylus amarali* (Colli et al., 2003), reproduce continuously and, in some cases (*A. ameiva* and *G. amarali*), produce smaller clutches in the more unpredictable Caatinga. *Polychrus* lizards lack both continuous reproduction and smaller clutches, which could indicate that environmental unpredictability is not strong enough to counterbalance other, possibly intrinsic constraints in the oviposition period in Caatinga populations. Still, the delay observed in the presence of females with oviductal eggs in Caatinga is probably a response to delayed rain in this region.

The average clutch size for *P. acutirostris* is large compared with congenerics such as *P. marmoratus* (average, 8.7; range, 8–10; Rand, 1982), *P. gutturosus* (one gavid female containing nine eggs; Taylor, 1956), and *P. femoralis* (note on one female with 12 eggs; Gorman et al., 1969). Variation in clutch and egg sizes among lizard species has been correlated with female SVL and age at maturity (Fitch, 1970; Tinkle et al., 1970), environmental factors such as rainfall in tropical species (Fitch, 1970, 1982), resource availability (Ballinger, 1977; Ballinger and Ballinger, 1979; Warne and Charnov, 2008), foraging modes and predator escape behavior (Vitt and Congdon, 1978; Vitt, 1981), and
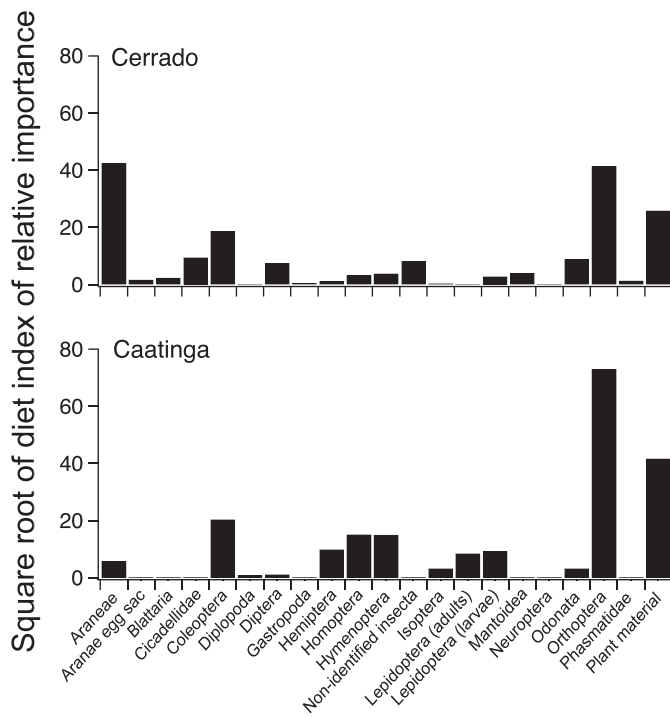
FIG. 4. Comparative diet composition of *Polychrus acutirostris* from Cerrado and Caatinga.

phylogenetic constraints (Andrews and Rand, 1974; Vitt and Price, 1982; Dunham et al., 1988). These intrinsic, environmental, and phylogenetic factors also play important roles in intraspecific variation on clutch size and mass (Pianka, 1970; Fitch, 1985; Colli et al., 2003). Seasonality, for example, can be a fundamental factor influencing the reduction or halt of reproductive activity in lizards because of related adverse conditions such as extremely wet, dry, or cool environments (Vitt and Breitenbach, 1993; Castro-Franco et al., 2011).

Polychrus acutirostris is the only species of the genus occurring in dry habitats (Caatinga, Chaco, and Cerrado) and, as expected (Rand, 1982; Vitt and Colli, 1994), it has clutches of more and relatively smaller eggs than its tropical rain forest congenerics (Vitt and Lacher, 1981). Contrary to expectations for seasonal vs. nonseasonal climates (Fitch, 1982), however, Cerrado populations had smaller clutches of larger eggs than Caatinga populations. The expected pattern, where rainfall unpredictability in Caatinga would account for smaller clutches but larger eggs, and seasonality in Cerrado would make reproductive period shorter, was not observed. This difference may reflect lineage specific constraints, intrinsic weakness of the initial hypothesis, or both. In fact, several previously accepted generalizations on lizard reproductive patterns are being revised with the accumulation of more data. Lizards from the genus *Kentropyx*, for example, do not produce larger clutches of smaller eggs in Cerrado compared to Amazonian species (Werneck et al., 2009). *Ameiva ameiva* from Cerrado and Caatinga sites have larger eggs than populations in Amazon forest sites (Vitt and Colli, 1994), contrary to patterns observed for some Brazilian iguanid lizards (Rand, 1982). Teiids (*A. ameiva* and *Cnemidophorus ocellifer*) in Caatinga can breed continuously, with some annual variation due to wet and dry seasonality, but tropidurid lizards (*Tropidurus semitaeniatus* and *Tropidurus hispidus*) breed over an extended period during the dry season or only at the beginning of the rainy season, as does *P. acutirostris* (Vitt and Lacher, 1981; Pianka and Vitt, 2003). This clear phylogenetic effect is widespread in squamate communities, and its detailed documentation has been fundamental to show that proximal

environmental factors are not necessarily the predominant forces shaping reproduction or major ecological traits in squamate assemblages (Vitt, 1992; Cadle and Greene, 1993).

Polychrus acutirostris is a sit-and-wait predator (Vitt and Lacher, 1981), with one reproductive event per year; thus, it relies more on energy accumulated in previous seasons for each reproductive event. Compared with teiids and geckos, *P. acutirostris* can be classified as a capital breeder (Drent and Daan, 1980; Niewiarowski and Dunham, 1994). Active foragers such as teiids have a high degree of resource intake and convert this energy directly to reproduction (income breeding), thereby allowing multiple clutches per year, as observed for species studied across biomes (*A. ameiva* and *C. ocellifer*; Colli, 1991; Mesquita and Colli, 2003). *Polychrus acutirostris* produces a single clutch per year in both biomes, probably because of the large relative clutch mass. Because this single clutch pattern is observable in both biomes, the differences in clutch size we report are probably attributable to the size differences in reproductive lizards (Caatinga lizards larger than Cerrado lizards) that we also report among regions. The large number of small eggs in the Caatinga suggests that the competitive environment for offspring is either unpredictable or that mortality is high but random (Vitt and Congdon, 1978). Rain forest *Polychrus* lizards produce few large eggs, suggesting that the competitive environment for offspring is predictably intense and mortality is nonrandom. Cerrado *Polychrus* lizards seem intermediate between Caatinga and rain forest *Polychrus* lizards, producing fewer and larger eggs than its conspecific in the Caatinga but relatively more and smaller eggs than rain forest *Polychrus* species.

Diet.—The majority of dietary studies on polychrotid lizards have been conducted on a single but very specious genus, *Anolis*, in North, Central, and South America. Diets of Brazilian anoles have been studied in Amazon savannas (Vitt and Carvalho, 1995), Amazon Rainforest (Vitt et al., 2001, 2003), and Cerrado (Vitt et al., 2008). Most *Anolis* species are generalists, but some seem to systematically avoid ants in Amazon Forest sites studied (Vitt et al., 2001). Lizards in the *Anolis chrysolepis* (=*A. nitens*) complex rely on a small set of prey types and show low variation across the species' geographic range (Vitt et al., 2001). Vitt et al. (2008) observed that Amazonian anoles rely mostly on a similar set of prey categories, suggesting that some degree of niche conservatism may exist in the diets of *Anolis* lizards. The *Anolis* genus, which contains nearly 400 species, represents one of the major radiations within iguanian lizards (Poe, 2004). Because *Polychrus* is one of the putative sister taxa to anoles, a comprehensive understanding of the ecology of *Polychrus* might help clarify possible ecological factors related to the radiation of anoline lizards as well as to infer the existence of niche conservatism or dietary shifts related to the origin of this large lizard radiation.

Slow-moving, large arboreal insects dominate the diet of *Polychrus* lizards in Caatinga and Cerrado, with plant material comprising a significant proportion of items eaten. Diets of *P. acutirostris* in the Caatinga and Cerrado are superficially similar, but importance indices and niche breadths were significantly different among populations in these biomes. The variation that we have observed in *Polychrus* lizards is minimal, although significant. Despite this overall similarity, *Polychrus* lizards in the Caatinga population showed larger niche breadth. This is consistent with recent work showing that less diverse assemblages tend to present higher niche breadth due to ecological release (Costa et al., 2008).

Spiders were almost absent in the diet of Caatinga lizards and probably account for the difference observed. Spiders can impact lizards directly (as food or as predators) or indirectly (as competitors or in providing microhabitats). Many lizards are known to eat spiders and some large spiders are known to eat small lizards. For example, one spider constructs burrows

that seem to serve as shelter for lizards (Fellows et al., 2009). Trophic interactions are known between spiders and lizards as well. For example, variation in spider densities mediated by rainfall directly affects lizard density on islands in the Bahamas (Spiller and Schoener, 2008).

One possible explanation for differences in diets between *P. acutirostris* in Cerrado and Caatinga may simply be that spider populations are relatively low on an annual basis in the semiarid Caatinga compared with those in Cerrado. The much longer and more predictable wet season in Cerrado may result in an increase in spider populations resulting from higher insect populations. Dietary shifts in lizards that are capable of eating a wide variety of organisms (e.g., arthropods, fruits, and flowers) can be difficult to interpret in the absence of quality data on prey availability. Nevertheless, differences in seasonality between the Caatinga and Cerrado may account for differences in diets between *Polychrus* populations inhabiting these biomes.

Resource availability has been invoked as one of the most important drivers of reproductive investment affecting clutch and offspring size trade-offs (Jordan and Snell, 2002; Olsson et al., 2002). However, it has been difficult to clearly establish this link (Warne and Charnov, 2008). Diets of other well-studied lizards that occur in both Caatinga and Cerrado do not vary much across biomes (Colli, 1991; Vitt and Colli, 1994; Colli et al., 2003; Mesquita and Colli, 2003). Despite this overall similarity, rainfall amount and predictability may not affect lizard prey type or availability. Rather, the total amount of food available over extended periods may be the best variable to link food with reproduction. These data are unavailable for *Polychrus* lizards, but studies on *Anolis* lizards have demonstrated a link between food availability and reproductive response (Andrews, 1991).

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