

Geographical Ecology of *Tropidurus hispidus* (Squamata: Tropiduridae) and *Cnemidophorus ocellifer* (Squamata: Teiidae) in a Neotropical Region: A Comparison among Atlantic Forest, Caatinga, and Coastal Populations

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ABSTRACT.—Both phylogenetic and environmental forces can drive ecological variation across the geographic distribution of squamates. We compared microhabitat use, temperature, diet, and reproductive data among three *Tropidurus hispidus* and *Cnemidophorus ocellifer* populations (Caatinga; Atlantic Forest; and Restinga coastal environments) and tested whether these characteristics varied along that distribution. *Tropidurus hispidus* was found primarily on human-made structures or tree trunks, and *C. ocellifer* was more often found on open ground or associated with vegetation. Substrate temperature was the most influential factor on body temperature, and no difference in body temperatures was observed among populations. Overall, diet composition was similar among populations; however, some differences were observed for main prey categories for *C. ocellifer*. Mean clutch size (*T. hispidus* = 6 eggs; *C. ocellifer* = 2 eggs) did not significantly differ among populations. *Tropidurus hispidus* seems to avoid reproducing during the dry season, exhibiting seasonal reproduction in the Caatinga and continuous reproduction in the Restinga and Atlantic Forest. *Cnemidophorus ocellifer* exhibited seasonal reproduction in the Tabuleiro region of the Atlantic Forest and continuous reproduction in the other two environments. Microhabitat use, diet, and reproductive cycle varied among populations of each species, whereas body temperature and clutch size remained unaltered, showing the importance of both ecological and historical factors along their geographic range.

RESUMO.—Ao longo de sua distribuição geográfica, os Squamata podem apresentar variações ecológicas causadas pelas diferentes pressões de cada ambiente. Comparamos o uso de microhabitat, temperatura, dieta, dados reprodutivos de três populações de *Tropidurus hispidus* e *Cnemidophorus ocellifer* da Caatinga, Restinga e Mata Atlântica. *Tropidurus hispidus* foi mais encontrado em edificações e troncos de árvores, enquanto *C. ocellifer* foi mais encontrado em solos abertos ou associados a algum tipo de vegetação. A temperatura do substrato foi a que mais influenciou a temperatura corpórea dos lagartos e não houve diferença nas temperaturas corpóreas entre populações. Em geral, a dieta foi similar entre populações de cada espécie, exceto por algumas das principais presas consumidas por *C. ocellifer*. A média do tamanho da ninhada (*T. hispidus* = 6; *C. ocellifer* = 2) não variou significativamente entre populações. *Tropidurus hispidus* parece evitar reproduzir-se em épocas secas, exibindo reprodução sazonal na Caatinga, mas contínua na Restinga e Floresta Atlântica. *Cnemidophorus ocellifer* apresentou reprodução sazonal na região de Tabuleiro (Floresta Atlântica) e contínua nos demais ambientes. Em suma, uso de microhabitat, dieta, e ciclo reprodutivo variaram entre as populações de cada espécie, enquanto temperatura corpórea e tamanho da ninhada permaneceram inalteradas, mostrando a importância tanto de fatores ecológicos quanto históricos ao longo da distribuição geográfica dessas espécies.

Geographical variation in ecological characteristics may result in two main patterns. The ecological hypothesis says that when subjected to different environmental pressures, populations may respond by evolving different characteristics or strategies more adapted to the environmental conditions experienced (MacArthur, 1984; Mesquita and Colli, 2003a). The historical or phylogenetic hypothesis says, however, that such characteristics or strategies may remain unchanged and independent of environmental variation. In such cases, geographical variation may be limited by genetic constraints, reflecting a consequence of ancestral patterns (Brooks, 1991; Vitt and Pianka, 2005; Losos, 2008). These patterns can be identified through geographical ecology studies in which many traits can be compared among populations from contrasting environments (MacArthur, 1984), such as tropical and dry forests.

Ecological aspects such as life-history traits, diet, microhabitat use, and thermoregulation may be influenced by climate or physical aspects of the environment. For example, seasonality

and climate may directly influence clutch size and reproductive cycle (Vitt and Colli, 1994; Mesquita and Colli, 2003a, 2010). Seasonal effects are more evident in temperate regions where reproduction is deeply affected by a cold–warm seasonality than in tropical regions, where reproduction is mostly affected by a wet–dry seasonality (Mesquita and Colli, 2010; Mesquita et al., 2016). In tropical regions in Brazil, some populations reproduce continuously with several clutches per reproductive season where precipitation is evenly distributed throughout the year (e.g., Amazon Forest) or is unpredictable (e.g., Caatinga), whereas in regions with marked seasonality, reproductive cycles are reduced to one or a few clutches per reproductive season (e.g., Cerrado and Amazonian savannas) (see Vitt, 1982; Vitt and Goldberg, 1983; Wiederhecker et al., 2002; Mesquita and Colli, 2003a, 2010).

Tropidurus and *Cnemidophorus* are widely distributed genera across South America. More specifically, *Tropidurus hispidus* (Spix, 1825) occurs across Brazil from the south of Minas Gerais State to the northeast Brazilian coast and the northern Amazonian rock outcrops, as well as in Venezuela (Rodrigues, 1987; Vitt et al., 1996). *Cnemidophorus ocellifer* (Spix, 1825) is widely distributed throughout Brazil, except in the Amazon (Peters, 1970; Vanzolini et al., 1980; Oliveira et al., 2015). The diversity of environments in which these species occur makes them perfect models to study ecological plasticity and geo-

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graphical variation. They are both heliothermic species, occurring in open areas, such as forest borders, rock outcrops, and human altered areas, along their geographic range (Bergallo and Rocha, 1993; Teixeira-Filho et al., 2010). They also have distinct foraging strategies with *T. hispidus* a typical sit-and-wait forager and *C. ocellifer* an active forager (Vitt, 1991, 1995), which may lead to some ecological divergences in diet and activity patterns (Huey and Pianka, 1981).

Geographical variation has been documented in both *Tropidurus* and *Cnemidophorus* species. Vitt et al. (1996) showed that an Amazonian *T. hispidus* population inhabiting an isolated rock outcrop showed greater sexual size dimorphism than other populations from open savannas, possibly attributable to stronger sexual selection promoted by higher population density. The authors also observed lower diversity of prey consumed and higher body temperature in the rock outcrop population compared to the open savanna populations, caused probably by limited basking sites and prey availability in a more structurally homogeneous habitat (Vitt et al., 1996). *Cnemidophorus ocellifer* shows different reproductive cycles in populations from environments with different seasonality patterns. In the Cerrado, where a strong dry-wet seasonality exists, *C. ocellifer* reproduced during the dry season, whereas in the Caatinga, it reproduced yearlong, possibly attributable to the unpredictability of rains (Mesquita and Colli, 2003a).

We describe and compare microhabitat use, activity when first sighted and after approach, body temperature, diet, clutch size, and reproductive cycle in three *T. hispidus* and *C. ocellifer* populations (six populations total) from different environments. We tested the hypothesis that each of these parameters will manifest differently in each locality, possibly attributable to different environmental conditions (ecological hypothesis). More specifically, we predict that 1) the proportion of microhabitat use, 2) activity levels (when first sighted and after approach of researcher), 3) body temperature (after controlling for environmental temperatures), 4) diet composition (represented by stomach contents), and 5) reproductive cycle are significantly different among populations. Even though we do not expect all variables to differ among populations, the hypotheses are proposed to identify which ecological characteristics are variable. We make no statistical comparisons between species.

MATERIALS AND METHODS

Study Sites.—We collected individuals of *T. hispidus* and *C. ocellifer* from November 2010 to February 2012, except for the Atlantic Forest population of *C. ocellifer*, which we collected from October 2008 to January 2011. Lizards were collected monthly with rubber bands, air guns, or by hand. They were sacrificed with Tiopental® and fixed in 10% formalin. We collected the lizards from the Caatinga environment in Cabaceiras municipality, Paraíba State (7°29'00.9"S, 36°20'22.2"W; Fig. 1). The region is a semiarid climate with hot summers and low rainfall, ranging from 250–800 mm/yr, concentrated from March to June (Eidt, 1969; Maia, 2004). Rainfall can be unpredictable, and droughts can sometimes last for 3 or 4 yr. Average rainfall for the 10 yr before this study in Cabaceiras is 590 mm/yr (SUDENE, 2013) and monthly average temperatures ranging from 21.2–24.9°C. The vegetation consists of shrubs, small trees, cacti, and bromeliads and can vary from open areas to forests or shrub woods (Andrade-Lima, 1981).

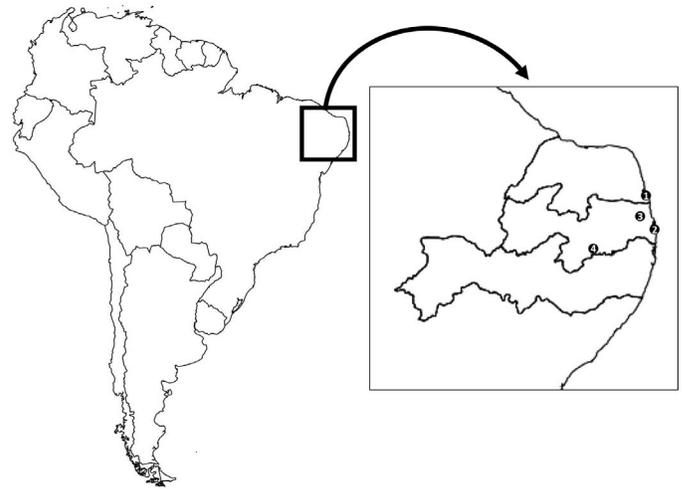


FIG. 1. Collection sites for *Cnemidophorus ocellifer* and *Tropidurus hispidus* from this study. Numbers refer to each field site: 1 = restinga of Barra do Cunhaú, Canguaretama municipality; 2 = Atlantic Forest where *T. hispidus* were collected, João Pessoa municipality; 3 = Atlantic Forest where *C. ocellifer* were collected, Mamanguape municipality; 4 = Caatinga, Cabaceiras municipality.

For the Atlantic Forest environment, we collected *T. hispidus* at the edge of forest fragments on the campus of the Universidade Federal da Paraíba (7°08'19.6"S, 34°50'47.4"W), João Pessoa Municipality, Paraíba State (monthly average temperature range: 23.5–26.3°C). Overall, the Atlantic Forest has an elevated and relatively constant temperature. Rainfall occurs almost year-round but is concentrated from March to August, with a short dry season from October to December (IBGE, 1985; Veloso et al., 1991). We collected *C. ocellifer* in an open area within the Atlantic Forest domain, known locally as a "Tabuleiro," in the Reserva Biológica Guaribas, Mamanguape municipality (06°40'40" and 06°44'59"S; 41°12'47" and 41°07'11"W), Paraíba State. The Tabuleiros are typically drier than the surrounding forest, with smaller trees and less dense vegetation, similar to a savanna, attributable to the shallow and rocky soils. The monthly average temperatures of this locality range from 23.9–27.2°C.

Restingas are usually included within the Atlantic Forest environment; however, Restingas present a set of unique environmental characteristics, such as specific phytophysiology, high temperature and salinity, intense solar exposure, sandy and dry soils, and intense rainfall through the year, particularly from January to August (Ormond, 1960; Franco et al., 1984; Henriques et al., 1984). In this environment, we collected both species at the beach of Barra do Cunhaú (6°18'25.1"S, 35°01'59.5"W), Canguaretama municipality, Rio Grande do Norte State (monthly average temperature range: 24.0–27.3°C). The vegetation consists mostly of bushes and grasses among widely spaced coconut trees.

Microhabitat, Activity, and Temperature.—At the moment of capture, we recorded the following temperatures: lizard body (cloacal); substrate; and air at breast height and at 5 cm above ground with a DeltaTAK® (Pleasanton, CA) thermometer. We performed a multiple regression with body temperature as a dependent variable and all the others as independent to determine which predictor had the biggest influence on body temperature. To compare body temperature among populations, we performed ANCOVAs with the most significant environmental temperature as covariable (Tabachnick and Fidell, 2007).

We also recorded microhabitat use and behavior (moving or stationary) at first sight and after researcher approach. We considered the following nine microhabitat categories: burrow; shrubs; among grass; exposed on open ground; under leaf litter; inside rock crevices or under rocks/logs; over rocks/logs (including human made); and tree trunks and walls (we called "walls" any human made vertical structure: walls; fences; light poles; or other objects). We used a Chi-square test to search for differences in microhabitat use among populations. We attributed a "zero" value to stationary lizards and "one" to moving lizards, both when first sighted and after the approach of the researcher. We considered the average of these values as an "activity index". The index ranges from 0 to 1, with 1 representing an active population. Because the data do not present a normal distribution, we tested for differences among population's median values of activity with Kruskal-Wallis followed by a Mann-Whitney post-hoc ranks comparison.

Diet.—We identified stomach contents to the lowest taxonomic level possible (usually order) using a stereomicroscope. We took maximum length and width measurements of intact prey with digital calipers, and used the spheroid formula to estimate the volume of each intact prey:

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

Here, " w " is prey width and " l " prey length. We also measured the numeric and volumetric proportion of each prey category and the diversity index of these proportions for each lizard specimen and for pooled stomach contents. The diversity index was calculated through the inverted Simpson diversity index (Simpson, 1949):

$$S = \frac{1}{\sum_{i=1}^n P_i^2},$$

Here, " P " is the proportion (numeric or volumetric) of the prey type " i ", and " n " is the number of prey categories. To determine the relative importance of each identified prey category, we averaged numeric and volumetric percentages for pooled and individual stomach contents. We measured the similarity of prey consumption among populations with Pianka's symmetric niche overlap index (Pianka, 1973):

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

Here, " P " is the proportion (importance index) of the prey type " i ", " n " is the number of prey categories, and " j " and " k " are the populations being compared. The overlap index can vary from 0 (no similarity) to 100% (identical diet composition).

Reproductive Biology.—We sexed the lizards by direct observation of the gonads. We considered males with enlarged testicles and convoluted epididymis and females with eggs in oviducts or vitellogenic follicles in the ovaries as reproductively active. We considered the simultaneous presence of vitellogenic follicles and eggs as evidence of sequential production of more than one clutch per reproductive season. We used the smallest (SVL) reproductively active lizard to define the size of maturity; smaller individuals were considered juveniles. We used the proportion of reproductively active adult lizards each month to determine the reproductive cycle of the population. We also observed the occurrence of juveniles in each month to confirm this pattern. To compare clutch size among populations, we used an ANCOVA with SVL as a covariate.

TABLE 1. Number of lizards moving and stationary when first sighted and after the researcher approached and activity index (see text) from *Tropidurus hispidus* and *Cnemidophorus ocellifer* from Caatinga, Restinga, and Atlantic Forest environments. *Activity of *T. hispidus* from Atlantic Forest was significantly different from Restinga and Caatinga (see text).

	<i>Tropidurus hispidus</i>			<i>Cnemidophorus ocellifer</i>		
	Caatinga	Restinga	Forest	Caatinga	Restinga	Forest
N	124	141	134	122	103	111
First sighted						
Still	108	129	124	29	34	39
Moving	16	12	10	93	69	72
Activity index	0.13	0.09	0.07	0.76	0.67	0.65
After approach						
Still	35	53	84	15	9	8
Moving	89	88	50	107	94	103
Activity index	0.72	0.62	0.37*	0.88	0.91	0.93

Kruskal-Wallis and Chi-square analyses were performed in R v3.2.0 (R Core Team, 2015), regressions, and ANCOVAs were performed on SPSS v22 (IBM, Armonk, NY) and diet niche overlap were performed with Ecosim v7.72 (<http://garyentsminger.com/ecosim/index.htm>). Descriptive statistics are reported as means \pm SD.

RESULTS

We collected a total of 963 lizards: 413 *T. hispidus* (128 from Caatinga, 149 from Restinga, and 136 from Atlantic Forest populations); and 550 *C. ocellifer* (130 from Caatinga, 142 from Restinga, and 278 from Atlantic Forest populations). All lizards in this study (except for *C. ocellifer* from Atlantic Forest) were collected during the same year and field trips were done in the same months to each population site (total of three trips per month). Unlike previous studies that collected data for each species or population across different years (Vitt et al., 1997; Mesquita and Colli, 2003a), the populations in this study were subject to the same broad scale meteorological conditions, reducing variation caused by temporal effects of particular environmental conditions over different years.

Microhabitat, Activity, and Temperature.—The most frequent microhabitat used varied somewhat among populations of each species (Fig. 2), but the three most commonly used microhabitats were the same in all populations within each species. *Tropidurus hispidus* was mostly found on tree trunks, walls, and open ground. *Cnemidophorus ocellifer* was mostly found inside bushes, among grasses, or on open ground. Our results showed significant variation in microhabitat use among populations for both species (*T. hispidus*: $\chi^2 = 91.2973$, $df = 16$, $P < 0.0001$; *C. ocellifer*: $\chi^2 = 93.6146$, $df = 10$, $P < 0.0001$).

In all three populations, most of the *T. hispidus* were stationary when first sighted and the *C. ocellifer* were moving (Table 1). No significant difference in initial activity was found among populations (Kruskal-Wallis: *T. hispidus*: $H = 2.47$, $df = 2$, $P = 0.29$; *C. ocellifer*: $H = 4.03$, $df = 2$, $P = 0.13$). In contrast, activity after approach was significantly reduced in the *T. hispidus* from the Atlantic Forest population, which had an activity index of 0.37, (Kruskal-Wallis: $H = 33.81$, $df = 2$, $P < 0.0001$) compared to the other environments (Forest vs. Caatinga, $U = 5445.00$, $df = 2$, $P < 0.0001$; Forest vs. Restinga, $U = 7076$, $df = 1$, $P = 0.0009$). No significant difference was observed among any of the *C. ocellifer* populations (Kruskal-Wallis: $H = 1.85$, $df = 2$, $P = 0.40$).

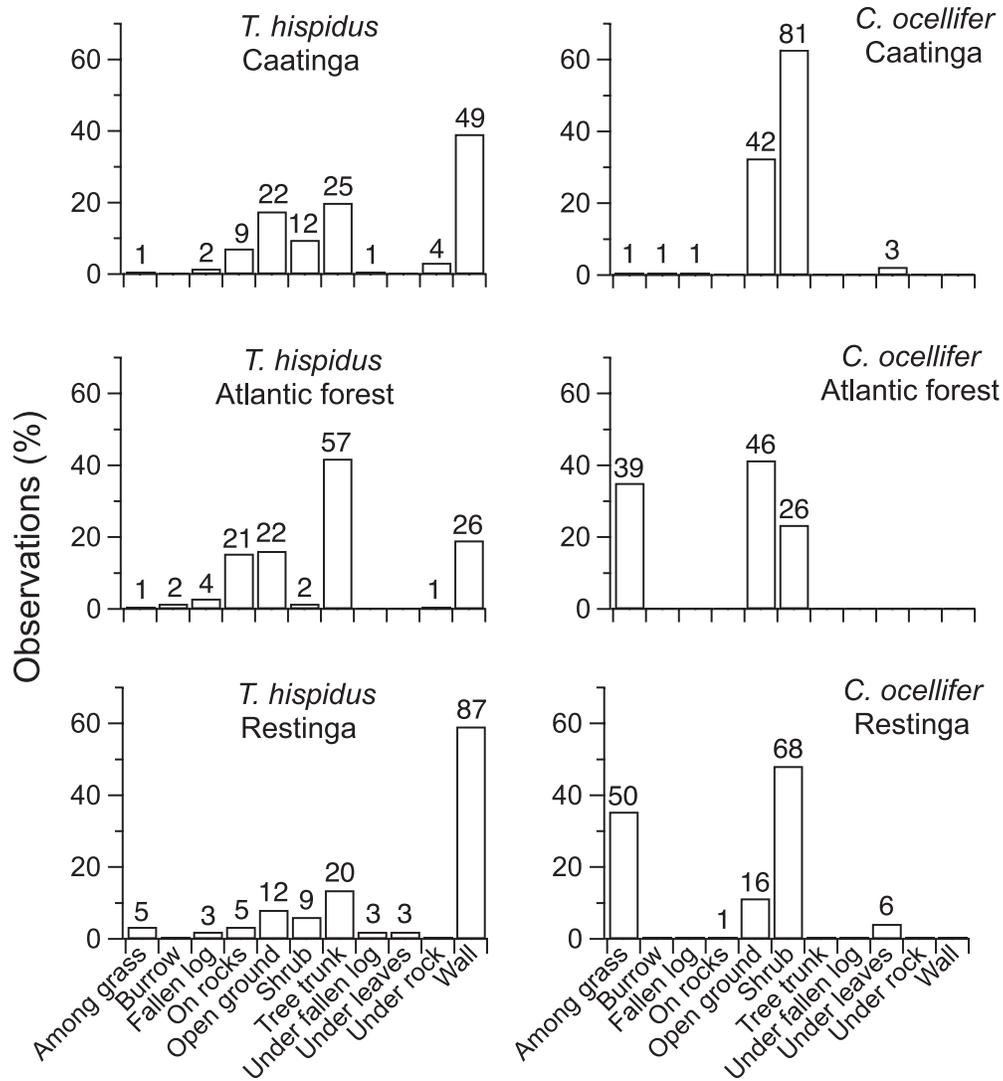


FIG. 2. Microhabitat use percentages of *Cnemidophorus ocellifer* and *Tropidurus hispidus* lizards from Caatinga, Restinga, and Atlantic Forest populations. Numbers represent sample sizes.

Substrate temperature was the most significant variable to influence lizard body temperature in all populations of both species, except for the *T. hispidus* population from the Restinga environment, which had similar *P*-values for both substrate and air temperatures (Table 2). There was no significant difference in

average body temperatures among populations, considering substrate temperature as a covariate (ANCOVA: *T. hispidus*: $F_{2,314} = 0.71, P = 0.49$; *C. ocellifer*: $F_{2,309} = 2.95; P = 0.05$).

Diet.—The most important prey categories for *T. hispidus* were ants, plant material, and beetles in the Restinga and Atlantic

TABLE 2. Lizard body (T_B), substrate (T_S), air 5 cm above the substrate (T_5), and air temperatures at chest height (T_A) measured during *Tropidurus hispidus* and *Cnemidophorus ocellifer* captures in Caatinga, Restinga, and Atlantic Forest environments (means \pm SD). *P*-values for each environmental temperature used as independent variable (T_B as dependent variable) and with R^2 for the multiple regression models.

	<i>Tropidurus hispidus</i>			<i>Cnemidophorus ocellifer</i>		
	Caatinga	Restinga	Forest	Caatinga	Restinga	Forest
T_B	34.23 \pm 2.67	34.85 \pm 2.75	34.18 \pm 2.62	37.95 \pm 2.60	38.08 \pm 2.27	37.76 \pm 2.70
T_S	31.98 \pm 3.47	33.59 \pm 3.92	32.22 \pm 2.86	35.27 \pm 4.29	37.82 \pm 4.66	36.58 \pm 5.92
T_5	30.55 \pm 3.02	30.96 \pm 2.69	30.26 \pm 2.00	32.50 \pm 2.91	32.76 \pm 1.81	34.84 \pm 4.39
T_A	30.37 \pm 2.59	30.42 \pm 2.21	29.56 \pm 1.21	31.38 \pm 2.36	31.18 \pm 1.67	33.16 \pm 2.32
Multiple regressions						
T_S	0.014	< 0.001	< 0.001	0.006	< 0.001	0.005
T_5	0.539	0.011	0.416	0.416	0.179	0.341
T_A	0.376	< 0.001	0.959	0.233	0.353	0.005
R^2 (model)	0.33	0.72	0.47	0.31	0.50	0.30
<i>N</i>	104	105	113	118	86	111

TABLE 3. Diet composition (means of both the numeric and volumetric percentages of each prey category), numeric (N), and volumetric (V) trophic niche breadths (Simpson diversity indexes) from pooled stomachs (PS) and averaged stomachs (AS) of *Tropidurus hispidus* and *Cnemidophorus ocellifer* from Caatinga, Restinga, and Atlantic Forest populations. * represents the most important items.

	<i>Tropidurus hispidus</i>						<i>Cnemidophorus ocellifer</i>					
	Restinga		Caatinga		Forest		Restinga		Caatinga		Forest	
	PS	AS	PS	AS	PS	AS	PS	AS	PS	AS	PS	AS
Acari	0.00	0.00	1.51	1.64	0.80	0.80	0.00	0.00	2.92	2.61	0.00	0.00
Annelida	0.00	0.00	0.00	0.00	0.40	0.34	0.00	0.00	0.00	0.00	0.00	0.00
Araneae	10.47	11.18	9.99	10.63	11.82	12.69	25.65*	28.60*	12.94	13.75	14.30	14.76*
Blattodea	0.22	0.21	0.35	0.48	1.81	1.59	2.76	1.25	2.64	2.21	3.99	5.04
Chilopoda	1.01	0.93	0.54	0.54	4.28	3.71	0.42	0.34	0.00	0.00	0.48	0.82
Coleoptera	26.47*	27.00*	29.11	30.95	17.82*	18.23	17.32*	18.01*	17.01*	18.75*	11.14	11.26
Diplopoda	0.00	0.00	1.77	1.74	0.53	0.54	0.00	0.00	0.62	0.61	0.18	0.16
Diptera	1.82	1.86	2.74	2.81	1.17	1.16	1.41	1.47	0.00	0.00	0.54	0.66
Gastropoda	2.91	3.14	2.08	2.48	2.37	2.74	3.13	2.80	5.47	6.49	0.00	2.80
Hemiptera	17.96	20.58	10.59	12.52	17.38*	16.25	13.63	14.28	4.52	5.89	4.95	5.56
Hymenoptera												
Apoidea	9.51	9.93	16.32	16.96	17.62*	18.23*	2.20	2.15	0.63	1.33	2.70	3.82
Formicidae	53.91*	50.67*	43.06*	44.47*	61.00*	60.63*	18.85*	16.67*	2.90	3.29	7.92	8.51
Isopoda	2.16	2.41	1.10	1.11	1.24	1.44	0.60	0.59	0.31	0.32	0.00	0.00
Isoptera	8.96	7.01	4.90	3.45	9.63	8.51	10.01	9.73	31.54*	17.77*	17.78*	9.47
Lizard	1.34	0.57	0.00	0.00	0.48	0.53	0.00	0.00	0.00	0.00	0.00	0.00
Larvae (insect)	19.81	18.20	36.77*	36.81*	16.83	18.39*	45.97*	42.69*	54.34*	56.99*	20.59*	19.86*
Lepidoptera	2.74	2.41	2.22	2.17	1.91	1.96	2.30	2.24	4.86	3.83	0.82	0.74
Mantodea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.55	0.56	1.32	1.33
Odonata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	1.06
Orthoptera	5.57	5.59	7.49	8.87	8.78	8.38	9.03	7.80	10.28	13.83	33.11*	34.87*
Squamate egg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.55	0.45
Feather	0.00	0.00	0.65	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pseudoscorpionida	0.00	0.00	0.27	0.27	1.70	1.79	0.00	0.00	0.66	0.67	0.00	0.00
Pupa	0.00	0.00	0.00	0.00	0.32	0.29	0.00	0.00	0.00	0.00	1.04	0.73
Scorpionida	0.00	0.00	0.65	0.60	0.41	0.40	0.00	0.00	0.00	0.00	4.74	2.29
Dermaptera	2.94	3.05	0.00	0.00	1.39	1.42	3.80	3.84	0.00	0.00	0.00	0.00
Plant matter	31.80*	30.57*	35.18*	27.81*	28.84*	27.99*	3.08	3.39	0.63	0.37	7.96	4.88
Breadth (N)	2.24	3.48	4.33	4.66	2.18	2.60	5.28	5.99	2.44	3.93	5.18	7.46
Breadth (V)	4.69	7.05	3.56	5.86	5.57	5.94	4.10	5.83	2.58	3.63	5.12	8.83
Breadth (V+N)/2	3.47	5.27	3.94	5.26	3.87	4.27	4.69	5.91	2.51	3.78	5.15	8.15
Richness	17		20		23		16		17		19	
Evenness	0.204		0.197		0.168		0.293		0.148		0.271	

Forest populations and ants, insect larvae, and plant material in Caatinga (Table 3). For *C. ocellifer*, insect larvae, spiders, ants, and beetles were most consumed in the Restinga population, insect larvae, termites, and beetles in the Caatinga population and grasshoppers, insect larvae, and termites in the Atlantic Forest population. All three *T. hispidus* populations had similar diet niche breadths. *Cnemidophorus ocellifer* from Caatinga had the lowest diet niche breadth, whereas Atlantic Forest and Restinga populations had similar indices (Table 3).

Among the *T. hispidus* populations, the highest similarity (overlap index) was observed between the Restinga and

Atlantic Forest populations (96%), followed by Restinga and Caatinga (89%), and Atlantic Forest and Caatinga (76%). *Cnemidophorus ocellifer* showed less similarity among its populations, with the highest similarity index between Restinga and Caatinga (82%), followed by Atlantic Forest and Caatinga (70%), and Atlantic Forest and Restinga (66%).

Reproduction.—Body size at age of maturity was similar among all populations, except for *C. ocellifer* females from Atlantic Forest, which reached maturity at a smaller size than females in populations from Caatinga and Restinga (Table 4). We found no significant difference in clutch size among populations

TABLE 4. Life-history parameters of *Tropidurus hispidus* and *Cnemidophorus ocellifer* lizards from Caatinga, Restinga, and Atlantic Forest populations. Size at maturity is the size of the smallest reproductively active lizard.

	<i>Tropidurus hispidus</i>						<i>Cnemidophorus ocellifer</i>					
	Caatinga		Restinga		Forest		Caatinga		Restinga		Forest	
	M	F	M	F	M	F	M	F	M	F	M	F
Smallest lizard (mm)	41	49	30	40	28	35	37	39	31	32	28	28
Largest lizard (mm)	143	95	110	91	109	89	79	73	73	70	67	73
Size at maturity (mm)	72	71	78	69	74	64	49	54	48	52	45	44
Clutch size												
Mean ± SD	7.56 ± 3.50		6.59 ± 1.51		5.86 ± 1.66		2.03 ± 0.52		1.5 ± 0.61		1.91 ± 0.74	
Range	2–16		4–11		1–10		1–3		1–3		2–4	
Sample size	16		37		51		34		20		35	

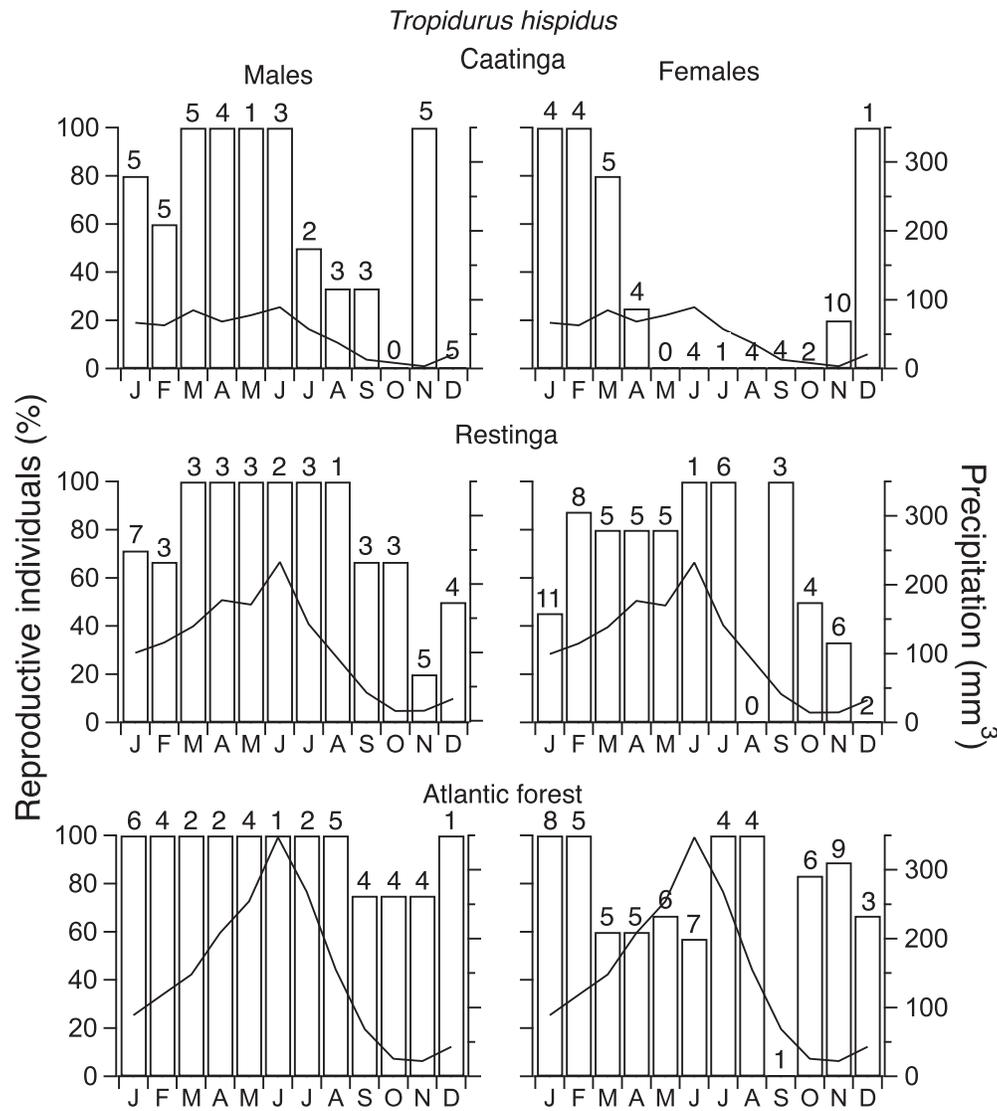


FIG. 3. Annual reproductive cycle of *Tropidurus hispidus* lizards from Caatinga, Restinga, and Atlantic Forest populations. Bars represent percentages of reproductively active adult females and males, with the numbers above bars representing the total number of adult lizards. Line represents annual variation of monthly pluviometric averages.

(ANCOVA: *T. hispidus*: $F_{2,100} = 2.638$, $P = 0.076$; *C. ocellifer*: $F_{2,85} = 3.318$, $P = 0.041$). Clutch size range was also similar among *T. hispidus* populations, except for a single female from Caatinga with 16 vitellogenic follicles.

Tropidurus hispidus from Caatinga reproduced seasonally, with reproductively active females observed only at the beginning of the rainy season, between November and April (Fig. 3) and the smallest lizards (juveniles) starting to appear in April (Fig. 4). In the Restinga and Atlantic Forest populations, we found reproductively active females during the entire year, but a peak was observed in the rainy season in the Restinga (March to September); the proportion of active females was constant along the year in the Atlantic Forest (Fig. 3).

Cnemidophorus ocellifer reproduced seasonally only in the Atlantic Forest (Fig. 5), with reproductively active females occurring during the dry season and juveniles appearing in the beginning of the wet season (Fig. 4). The Caatinga and Restinga populations reproduced constantly throughout the year. Juveniles of *C. ocellifer* from Caatinga and Restinga occurred throughout the year, with no specific period of absence. Despite

the low number of adult individuals in some months, recruitment graphs confirm the observed reproductive cycles (Fig. 4). Multiple clutches occurred during the reproductive cycle of four *T. hispidus* from the Restinga and one from the Atlantic Forest, and four *C. ocellifer* females from the Caatinga; this was indicated by the simultaneous presence of vitellogenic follicles and eggs.

DISCUSSION

Microhabitat, Activity, and Temperature.—Overall microhabitat use varied among populations of each species; however, some similarity in the main categories was observed among the three populations of both species. The two microhabitat categories most explored (representing at least 59% when grouped together) by *T. hispidus* were “tree trunks” and “walls.” These categories are both vertical and/or rigid substrates, as observed in other populations in different environments (Vitt, 1993; Vitt and de Carvalho, 1995; Van Sluys et al., 2004). As for *C. ocellifer*, the three most used categories were “open ground,” “shrubs,” and “among

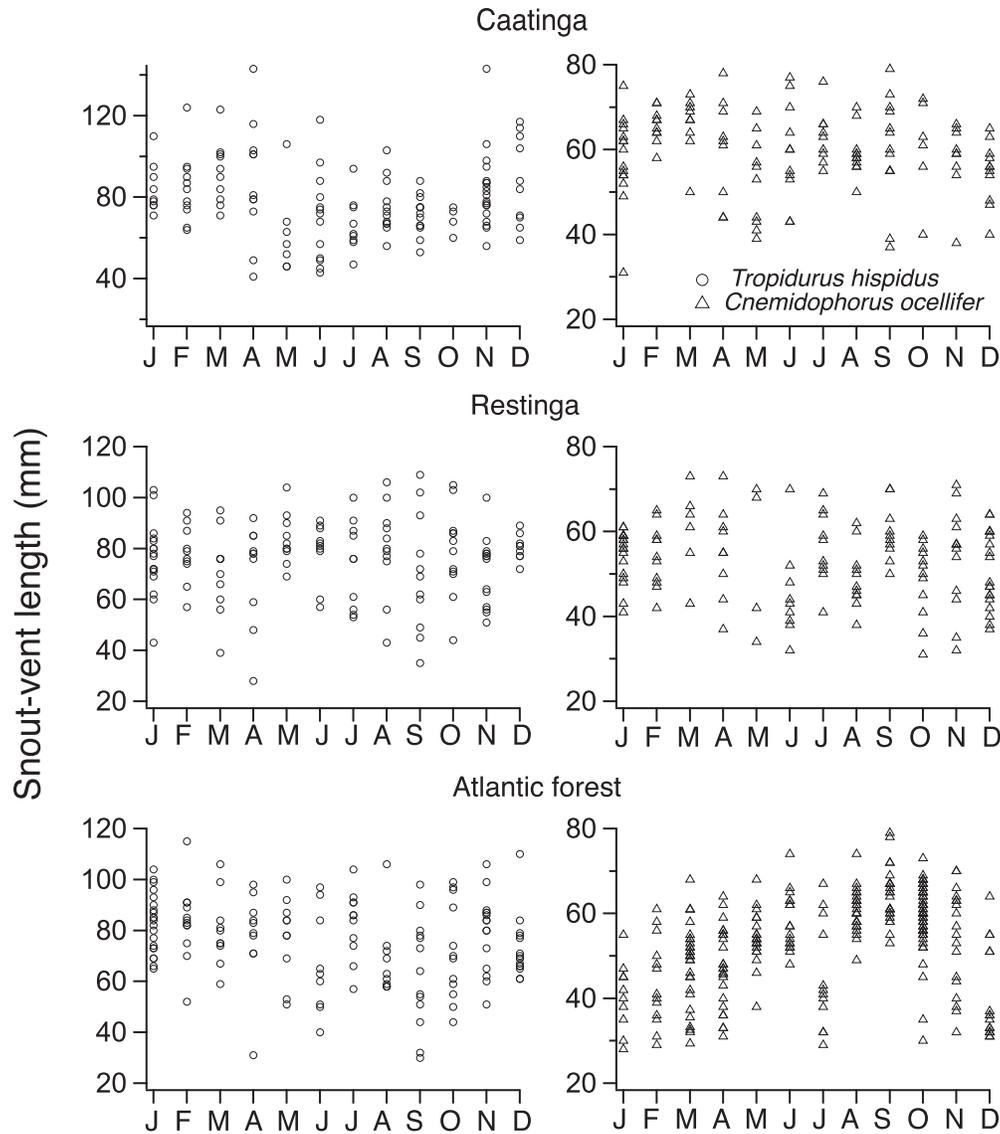


FIG. 4. Monthly distribution of *Tropicurus hispidus* and *Cnemidophorus ocellifer* individuals from Caatinga, Restinga, and Atlantic Forest lizard populations, according to snout-vent length (mm).

grass" (representing at least 95% when grouped together) as reported elsewhere (Mesquita and Colli, 2003a,b; Dias and Rocha, 2004; Teixeira-Filho et al., 2010). These results suggest that both species have the capacity to explore and inhabit different substrates and microenvironments but tend to use the same categories more frequently. The capacity to explore different microhabitats suggests that ecology can play an important role on the geographical variation of these traits. To clarify that, further studies considering microhabitat availability are needed to test whether these patterns are caused by preference or simply random choice.

As expected, *C. ocellifer* showed a much higher activity index than did *T. hispidus*, both when first sighted and after the researcher approached (Table 1). This could be a consequence of the different foraging and predator escape strategies, a reflection of phylogenetic history, or both (Huey and Pianka, 1981; Perry, 1999; Cooper et al., 2005). Comparisons among populations showed activity to be a well-established trait in these lizards, however; thus, maybe these two species are constrained in the range of activity level they can adopt. Further studies should

test whether this consistency is related to optimal foraging intensities and escape strategies used by each species. The only exception for this pattern was observed in the *T. hispidus* population from the Atlantic Forest, which showed a much lower activity index after the researcher approached. This population is located on the campus of the Universidade Federal da Paraíba, where more frequent contact with people could lead to habituation and reduced escape attempts and flight initiation distance (Burger and Gochfeld, 1990; Labra and Leonard, 1999). Combined, these results suggest that undisturbed activity is mostly explained by historical factors (possibly attributable to an optimal foraging intensity for each species), whereas escape strategies can be adjusted to different conditions experienced by each population (e.g., predation intensity).

Body temperature is mostly influenced by substrate temperature compared to other measured environmental temperatures; however, substrate temperature does not explain most of the variation in body temperature (R^2 -values ranged from 0.30 to 0.50, except for *T. hispidus* from Restinga, for which $R^2 = 0.72$),

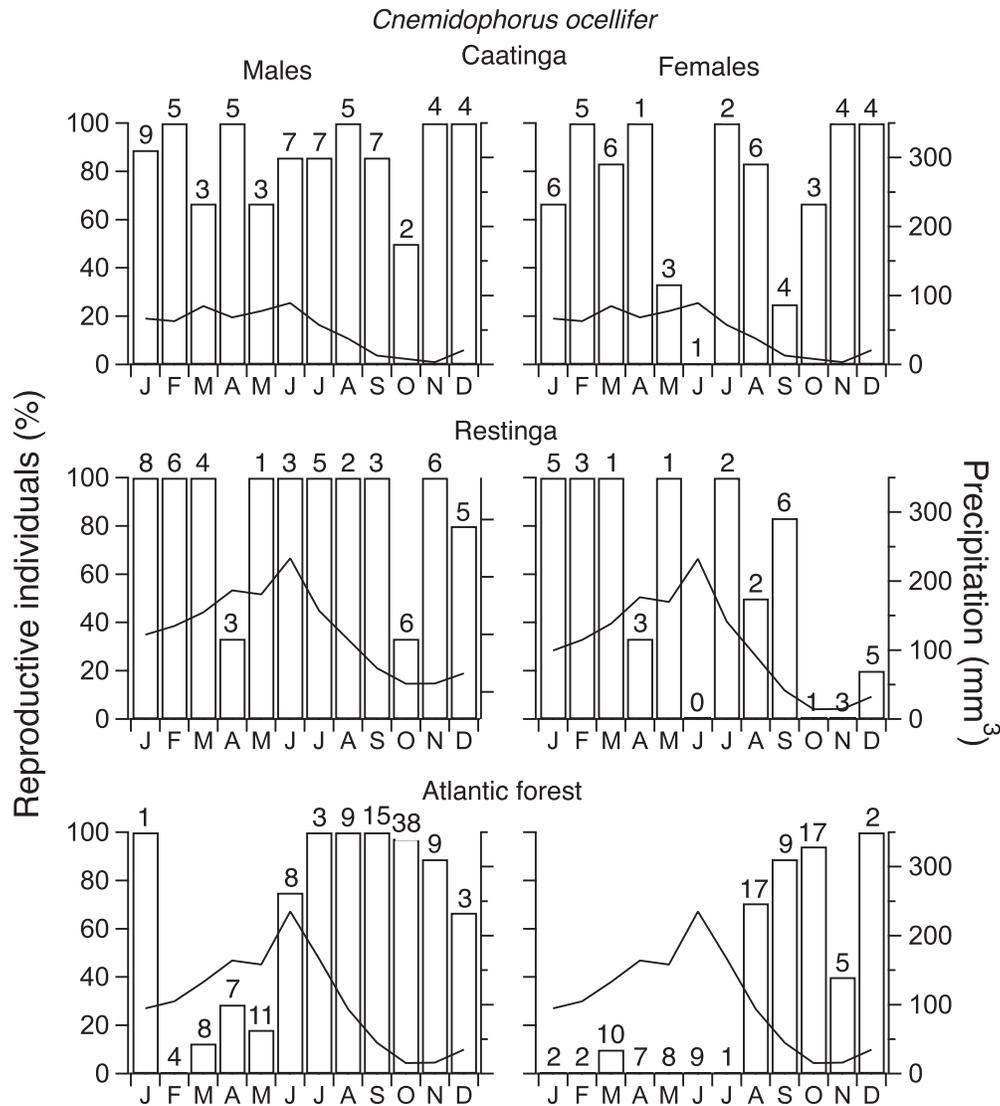


FIG. 5. Annual reproductive cycle of *Cnemidophorus ocellifer* lizards from Caatinga, Restinga, and Atlantic Forest populations. Bars represent percentages of reproductively active adult females and males, with the numbers above bars representing the total number of adult lizards. Line represents annual variation of monthly pluviometric averages.

suggesting that other factors are affecting the body temperature of these lizards. Because both *T. hispidus* and *C. ocellifer* are heliothermic, they may gain heat directly from direct solar radiation and not just by conduction from the substrate or convection from the air surrounding the lizard (Adolph, 1990; Bauwens et al., 1996). Also, lizards can experience very different substrate temperatures along their path caused by different shading conditions or from variation in substrate heating capacity (e.g., grasses compared to rocks). Consequently, the more active the lizard, the more difficult it is to draw a correlation between body and substrate temperature (Bogert, 1949). This could also explain why *C. ocellifer* (more active) showed lower R^2 -values in all populations compared to *T. hispidus* (less active).

Lizards from open areas might have higher body temperatures compared to populations from mostly shaded areas as a consequence of higher availability of basking sites, or because they have higher preferred temperatures (Kiefer et al., 2005); however, this pattern was not observed in the populations studied here. Body temperature appears to be a conserved characteristic, being essentially identical in *T. hispidus* and *C.*

ocellifer, not only in the Caatinga, Restinga, and Atlantic Forest populations observed in this study but also for other populations from these and other environments (Hatano et al., 2001; Mesquita and Colli, 2003a; Dias and Rocha, 2004; Kiefer et al., 2005). The similar body temperatures observed in such different environmental conditions suggests that historical factors strongly influence this trait. Thermoregulatory behavior may be highly selected upon to maintain the observed body temperatures independent of the surrounding conditions, possibly to support important physiological needs (e.g., muscle or digestive performance) for each species. Further studies are needed to clarify the proximate and ultimate causes of the body temperature similarity.

Diet.—As expected, *T. hispidus* presented a diet composed mainly of ants (Vitt et al., 1996; Van Sluys et al., 2004); however, individuals of *T. hispidus* frequently also consume plant material (mainly leaves and flowers, but also fruits) as one of their main food sources (Van Sluys et al., 2004; Kolodiuk et al., 2010; Ribeiro and Freire, 2011). This could be interpreted as an adaptation to environments with high hydric stress (Silva and Araújo, 2008). That plant matter is one of the main categories in the Forest and

Restinga populations (where lizards should not be experiencing hydric stress) suggests, however, these lizards likely are not only consuming plants for a water source but also extracting nutritive benefits. Another remarkable characteristic of *T. hispidus* is that, even though only a few prey categories represent most of the diet, a wide taxonomic diversity can be found in the stomachs, ranging from arthropods, plant material, mollusks, and other small lizards. Individuals of *T. hispidus* have also been documented consuming fruits and frogs (Van Sluys et al., 2004; Ribeiro and Freire, 2011).

We observed termites as one of the main prey categories consumed by *C. ocellifer* in the Caatinga and Atlantic Forest localities, as usually reported in other studies (Mesquita and Colli, 2003a,b; Mesquita et al., 2006; Dias and Rocha, 2007) but not in the Restinga. The lack of termites in the Restinga suggests that *C. ocellifer* may rely on a broader dietary diversity than previously described (Vitt, 1995; Mesquita and Colli, 2003a; Menezes et al., 2011). This difference might simply reflect prey availability in each environment. For example, the Atlantic Forest population occurs in an area (REBIO Guaribas) with low termite density (Vasconcellos et al., 2008). This suggests that both historical and ecological factors can explain the patterns observed in diet composition for these two species. As with microhabitat use, some variation in diet can be observed among populations of both species suggesting some capacity to adapt to different environments. Because we did not evaluate prey availability, however, similarities in diet among populations might be related to a preference for some prey types that would suggest a stronger effect of historical factors.

Reproduction.—Environmental and historical factors seem to influence lizard life-history parameters (Dunham and Miles, 1985; Vitt, 1992; Mesquita and Colli, 2010). Clutch sizes in both *T. hispidus* and *C. ocellifer* were similar to what has been observed in other studies (Vitt, 1992; Mesquita and Colli, 2010). This finding suggests that clutch size may be constrained by phylogenetic conservatism (historical factors). However, both species also showed strong variation in reproductive cycle among populations, indicating the importance of ecological factors for both populations. *Tropidurus hispidus* showed a gradient in the reproductive cycle among populations: in the Caatinga, lizards avoided reproducing in the dry season, whereas in the Atlantic Forest and Restinga they reproduced continuously throughout the year, with a peak during the wet season on the Restinga (Fig. 3). Apparently, the unpredictability of the Caatinga environment does not affect this species. Vitt (1992) observed a seasonal reproductive cycle for *T. hispidus* in a different population from the Caatinga, although lizards reproduced during the dry season in that population.

However, *C. ocellifer* reproduced continuously at the Caatinga and Restinga environments but seasonally (during the rainy season) at the Atlantic Forest site. Apparently, this species reproduces as expected based on the seasonality of the environment (Vitt and Colli, 1994; Mesquita and Colli, 2003a). In the Caatinga, where the rains are more unpredictable than in the other environments, the lizards reproduced continuously throughout the year. The same (but less intense) pattern was observed in the Restinga, where the proximity to the sea increases relative humidity and might reduce the contrast between the dry and wet seasons. In the Tabuleiro (Atlantic Forest), where seasonality is present, the contrast between the dry and wet season possibly causes *C. ocellifer* to reproduce

seasonally during the dry period, similar to Cerrado populations (Mesquita and Colli, 2003a,b).

Despite the observed differences in the reproductive cycle of both species, there is no difference in clutch size among populations. This could suggest that clutch sizes supported by each species are at their maximum, meaning that even if seasonal populations can gather and store more energy for the reproductive cycle, they are not able to produce a bigger clutch. It also could mean that the species are not under energetic stress; thus, even the populations that reproduce throughout the whole year can produce their maximum clutch size. In addition, because there is no change in clutch size, egg size or clutch mass could be influenced by the differences in the reproductive cycle of each population (Vitt, 1982; Colli, 1991; Vitt and Colli, 1994; Ji and Braña, 2000). Unfortunately, we were not able to find enough females with developed eggs to test this; hence, further studies would be necessary.

The results obtained in this study show that both historical and ecological factors affect biological patterns along *T. hispidus* and *C. ocellifer* distributions. Some traits seem to be more susceptible to the environment, such as microhabitat use, activity after approach, diet, and reproductive cycle, whereas others seem to be more restricted, such as clutch size and body temperature. Interestingly, variation does not occur in the same way or with the same intensity in each species, reinforcing the importance of the ecological hypothesis of geographical variation and showing that each species interacts and reacts differently with its environment. Observing phenotypic differences among populations from different environments is the first step to understanding how these traits can be affected by the environment and the extent to which populations can respond to changing environments. If followed by observations of additional ecological traits (e.g., preferred nesting sites or predation intensity throughout the year), measures of performance or reproductive success (e.g., transgenerational studies observing the reproductive success of individuals breeding at different times of the year), and common garden experiments testing for phenotypic plasticity (e.g., whether females of *T. hispidus* from the Caatinga population would lay eggs throughout the year if moved to an Atlantic Forest environment), our knowledge of the adaptability of lizards to novel conditions would be greatly improved.

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