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Life in the grasses: The autecology of the whiptail lizard *Ameivula ocellifera* from a savanna enclave in the Atlantic Forest of northeastern Brazil

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Abstract. Understanding a species' natural history is fundamental for identifying patterns and enabling ecological and evolutionary comparisons. We investigated the autecology of the heliophilous, actively foraging whiptail lizard *Ameivula ocellifera* in a Neotropical savanna enclave in within the Atlantic Forest of northeastern Brazil. Lizards were active during the hottest hours of the day and were primarily associated with grassy areas on sandy soil. Body temperatures were relatively high (mean: 37.8°C) and positively correlated with both substrate and air temperatures, consistent with observations in other populations of the species. *Ameivula ocellifera* fed mainly on orthopterans, spiders, and insect larvae, similar to other teiid lizards. Sexual dimorphism was evident, with males being larger and having taller heads, while females had longer bodies, a trait typically linked to reproductive investment. Clutch size averaged 1.89 eggs (n = 1–4), but no correlation was found between clutch size and female snout–vent length. Reproductive males were observed year-round, whereas reproductive females were only found during the dry season, suggesting that females regulate the reproductive cycle. Reproduction occurred primarily during the dry season and followed a bimodal pattern, with recruitment also bimodal and concentrated at the onset of the wet season. These reproductive and recruitment patterns may be shaped by the environmental characteristics of Tabuleiro savannas. While our findings support the notion of niche conservatism in several ecological aspects of *A. ocellifera,* they also highlight how local environmental factors can significantly influence the ecology—particularly diet and reproduction—of some populations.

Keywords. Diet; Microhabitat; Natural history; Reproduction; Sexual dimorphism; Teiidae.

INTRODUCTION

The use of lizards as models for ecological studies is common because lizards are often abundant, relatively easy to collect, and exhibit a wide diversity of ecological strategies such as different locomotor, foraging, and reproductive styles (Bennett, 1983; Vitt and Pianka, 1994; Pianka and Vitt, 2003). These studies have led to several ecological theories, in multiple topics, such as population and community ecology, comparative biology, and life history (Huey and Pianka, 1981; Garland and Losos, 1994; Mesquita et al., 2006b). As with any organism, lizard ecology is affected by several factors, which could be derived from two origins: historical (phylogenetic origin, a genetic heritage that affects ecological patterns) and ecological (recent origin, directly related to the physical environment or to contemporary ecological interactions); e.g., predation and/or competition (Vitt et al., 2003; Vitt and Pianka, 2005).

Historical factors can play a significant role on feeding habits and behaviour of some lizard families (Vitt and Pianka, 2005). For example, among Teiid lizards, the genus *Ameivula* Harvey et al., 2012, has a wide distribution but a relatively low variation in their feeding habits (most populations show high proportion of termites in the stomachs), characterizing a strong phylogenetic conservatism (Vitt, 1991a; Mesquita and Colli, 2003a). Meanwhile, the influence of ecological and environmental factors can be observed in many reproductive characteristics of several tropical lizard species (Mesquita and Colli, 2010). In regions where rainfall occurs regularly through the year or is unpredictable, some lizard species reproduce continuously throughout the year, with multiple clutches of few eggs (Vitt, 1983; Mesquita and Colli, 2003a, 2010). On the other hand, in regions marked by seasonal climate, lizards tend to present a seasonal reproduction period, laying one or few clutches with more eggs (Vitt, 1992; Mesquita and Colli, 2003a, 2010).

The ecological aspects of *Ameivula ocellifera* (Spix, 1825) are quite similar along its distribution (e.g., Cerrado, Caatinga and Restinga), with few exceptions. *Ameivula ocellifera* shows heliophylic behaviour, and is usually active during the hottest hours of the day (Mesquita and Colli, 2003a; Menezes and Rocha, 2011; Menezes et al., 2011). It preys primarily on termites, but also ingests a considerable number of spiders, insect larvae, and orthopterans (Mesquita and Colli, 2003a; Santana et al., 2010; Menezes et al., 2011). Caatinga's populations reproduces

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continuously throughout the year, presenting several clutches of few eggs (Vitt, 1983; Zanchi-Silva et al., 2014) while Cerrado's populations reproduce seasonally, presenting a single larger clutch (Mesquita and Colli, 2003a). Furthermore, some studies point whiptail lizards as very important genera among life history studies (Mesquita and Colli, 2010), as these lizards seems to present a high phylogenetic inertia on their reproductive characteristics, a peculiar pattern for tropical lizards (Mesquita and Colli, 2010). Sexual dimorphism is found in most populations with females presenting larger bodies than males (probably due to increased fecundity) and males presenting larger heads (advantageous during mating and male-to-male competition; Anderson and Vitt, 1990).

In this study we focus on ecological aspects of an Atlantic Forest savanna (Tabuleiro) population of *Ameivula ocellifera*. We gathered thermal ecology, diet, reproductive, and morphological data and tested for correlations between environmental temperatures and lizard body temperatures; seasonal differences in diet composition; ontogenetic changes in diet; sexual dimorphism; and correlation between the body and clutch size. To our knowledge, this is the first *A. ocellifera* autecology study in a Tabuleiro environment.

MATERIALS AND METHODS

Study site

The study was conducted on Reserva Biológica Guaribas, a federal conservation area managed by the Instituto "Chico Mendes" de Conservação da Biodiversidade. The reserve is located in the Atlantic Rain Forest domain, presenting ombrofilous semi-deciduous forest vegetation in Mamanguape and Rio Tinto municipalities, Paraíba, Northeast Brazil. The climate of this region is hot and humid according to the Köppen Classification, with an annual average temperature of approximately 24–26°C (Nimer, 1989). The area receives approximately 1,750–2,000 mm of rainfall per year, with rains starting in February and reaching their highest levels in April–July (Barbosa et al., 2011.). The dry season lasts two or three months, from October–December. To illustrate the wet and dry season, we used monthly precipitation values for the area ranging from 2006 to 2011 (Fig. 1). The study was conducted in a savanna vegetation enclave inside the Atlantic Forest, commonly known as Tabuleiro. The Tabuleiros from Northeast Brazil are savanna formations, presenting an herbaceous layer, sparse trees and shrubs with suberous and wry trunks (Oliveira-Filho and Carvalho, 1993).

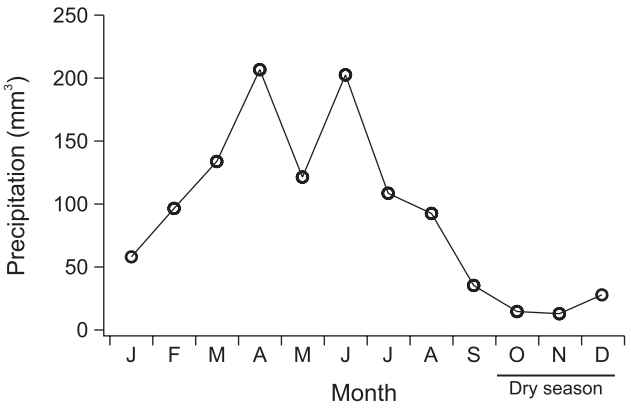

Figure 1. Average monthly distribution of precipitation of the last five years from collecting period (2006-2011) at Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil. Provided by PROCLIMA (SUDENE, 2013).

Data collecting, microhabitat, thermal biology and activity

A total of 278 *Ameivula ocellifera* were collected using pitfall traps with drift fences or actively captured haphazardly from October 2008 to January 2011. The capture ratio in the pitfall traps related to those captured by haphazard searches was 3:2. We placed 25 grids of traps on a 2 km trail. Each grid (separated by at least 50 m) consisted of four 60-L buckets countersunk to soil level, arranged in a Y shape, with a central bucket and three marginal ones (Cechin and Martins, 2000). Between the central bucket and the periferal ones, four galvanized sheets 5 m long were installed as drift fences. These traps were checked daily during each expedition. The 25 grids remained open for 336 d, resulting in a sampling effort of 8,400 grid-days.

Haphazard searches were performed monthly by two researchers during 3-d expeditions, total ca. 720 h of sampling effort (20 h/d). These searches where conducted during morning and afternoon, between 8:00 and 18:00. Animals were captured by hand or using rubber bands. At the time of capture, body (cloacal), substrate and air temperature (5 cm from substrate and at collector's chest height) were recorded to 0.1°C with DeltaTrak® thermometers. We noted microhabitat use and movement behavior (stationary, moving or running) of every individual when they were first sighted and after approach by researchers. The microhabitat categories were: burrow, clear ground on sandy soil, under shrub, shrub trunk, under tree, tree trunk, under rock, rock, and grass. Sunlight exposure was also recorded for each animal as: direct sunlight, filtered light (when the lizard was under partial shade, such as under sparse canopy leaves), and shadow. The living animals were killed with a lethal injection of 2% lidocaine hydrochloride. Lizards were then measured and fixed in 4% formalin and conserved in 70% ethylic alcohol. Individuals were housed at Coleção Herpetológica da Universidade Federal da Paraíba.

Diet

We analyzed diet by direct observation of stomach contents under a stereomicroscope after lizard dissection. Prey items were identified to the lowest taxonomic level possible (usually order), except ants, which were

identified as Formicidae, and other prey were categorized into artificial categories (e.g., insect larvae, pupae, reptile egg, etc). We used pooled stomach-content information (sum of each prey category in all stomach) to described diet composition.

For each category, we calculated the absolute and relative occurrence values, and numeric and volumetric percentage values. To calculate volume, we measured the width and length of each intact prey with a Mitutoyo® electronic caliper to the nearest 0.01 mm and applied the ellipsoid volume formula:

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

where *l* is prey length and *w* is prey width. Using the numeric and volumetric percentages of each category, we calculated the niche breadth (*B*) for each lizard using the inverse Simpson's index (Simpson, 1949):

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

finally, we used an importance index (*I*) to determine the relative contribution of each prey category for both individual stomach means and pooled stomach data, using the formula:

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

where *F*% is the relative occurrence, *N*% is the numeric percentage and *V*% is the volumetric percentage.

To test the hypothesis of ontogenetic variation on diet by the relation between lizard's head dimensions and prey dimensions, we conducted a canonical correlation with two groups of variables: maximum prey length and maximum prey width (per stomach) versus head length, width, and height (see below).

Sexual dimorphism

Before preservation process, we measured the following characters for each individual using Mitutoyo® digital calipers (0.01 mm accuacy): snout–vent length (SVL), body width at broadest point (BW), body height at highest point (BH), head width at broadest point (HW), head height at highest point (HH), head length from tip of snout to anterior margin of ear opening (HL), and tail length from cloaca to tip of the tail (TL).

Reproduction

We determined the sex and the reproductive stage of each lizard by the direct observation of gonads with a stereomicroscope. Lizards with enlarged testis and convoluted epididymis or with vitellogenic follicles, corpora lutea and/or oviductal eggs were considered reproductive. To calculate egg volume, we used the ellipsoid formula used in our diet analysis described above. Clutch size was determined by the total number of eggs and/or vitellogenic follicles. The simultaneous presence of vitellogenic follicles and corpora lutea or oviductal eggs were indications that more than one clutch per year was present. Recruitment was determined by the highest range values from SVL, considering a monthly distribution. We also estimated the size at sexual maturity based on the smaller reproductive male and female. The reproductive season was determined by calculating the monthly proportion of reproductively active individuals.

Statistical analysis

To estimate the effect of environmental temperatures on lizard body temperature we performed a multiple stepwise regression with best model selection using R project software (R Core Team, 2012). To assess seasonal specialization in diet, we used a multinomial species classification method (CLAM) that classifies prey categories into generalist, if present in the stomach throughout the year, or specialist, if present primarily in a specific season (Chazdon et al., 2011), based on occurrence values for each category in wet and dry season. This classification method is a modification of the CLAM method, which was designed to compare species composition and abundance between two different areas, assessing which species are generalists, specialists, or too rare to classify (Chazdon et al., 2011). We treated each season as an area and each prey category as a species. We chose for a more conservative analysis, setting a super-majority K threshold (K = 0.0667) and P level = 0.005 (Chazdon et al., 2011). To determine the wet and dry season, we used monthly precipitation values for the area ranging from 2006 to 2011 (Fig. 1).

For sexual dimorphism analysis, we first checked all the morphological data for univariate outliers. For each morphometric variable, we estimated a probability that an observation did not match with distribution pattern of the dataset, considering a significance level of $P < 0.0001$ (conservative approach). We also checked for multivariate outliers for each sex, using the R Project 2.15 command *mvoutier.CoDa* from package *mvoutlier,* as described by Menezes et al. (2011). To partition total morphometric variation between size and shape variation we defined body size as an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986). We calculated an isometric eigenvector defined *a priori* with values equal to $p^{-0.5}$, where *p* is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size, by postmultiplying the *n* by *p* matrix of log-transformed data, where *n* is the number of observations, by the *p* by *1* isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used Burnaby's

method (Burnaby, 1966): we postmultiplied the *n* by *p* matrix of the log-transformed data by a *p* by *p* symmetric matrix, *L*, defined as:

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

where I_p is a *p* by *p* identity matrix, *V* is the isometric size eigenvector defined above, and V^T is the transpose of matrix *V* (Rohlf and Bookstein, 1987). Hereafter we refer to the resulting size variables as shape variables. To test the null hypothesis of no morphological difference between males and females (sexual dimorphism hypothesis), we conducted a separate analysis of variance on body size (ANOVA), and we created an empty model based on logistic regressions and included the significant shape variables with the lowest Akaike Information Criteria (AIC) values to create the best model that explains the variation between shape variables among sexes.

To evaluate the correlation between female SVL and clutch size, we conducted a linear regression. We conducted all statistical analysis using the R project Version 2.15 (R Core Team, 2012), except for the Classification method, which was conducted on CLAM program (Chao and Lin, 2011). We used a 5% significance threshold for the tested hypothesis. Mean values are in $\bar{x}$ ± SD.

RESULTS

Microhabitat, activity, and thermal ecology

Most animals were moving when first sighted (*n* = 69, 62.16%) and ran after the approach of investigator (57.66%). Lizards were mostly found on open ground (41.44%) or among grasses (35.14%, Table 1), and looked for shelter mostly under shrubs (54.05%, Table 1). Almost all individuals were exposed to direct sunlight (*n* = 63, 56.76%) or under filtered light (35.14%) and only a few were under shade (8.11%, Table 1). *Ameivula ocellifera* is more active during the hottest hours of the day (10:00–13:00; *n* = 60; 54.05%), but can also be found during early hours of the morning and at dusk (Fig. 2). Body temperature averaged 37.8 ± 2.7°C, mean substrate temperature 36.6 ± 5.9°C, mean air temperature 5 cm from the substrate 34.8 ± 4.4°C, and air temperature at chest height 33.2 ± 2.3°C. Linear multiple regression indicated that body temperature was significantly positively associated (r^2 = 0.2989, $F_{3–107}$ = 15.20, P < 0.0001) with substrate temperature (t = 2.896; P = 0.00458) and with air temperature at chest height (t = 2.894; P = 0.00461).

Table 1. Movement behavior and microhabitat use of *Ameivula ocellifera* (*n* = 111) from Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil).

Ecological trait	When first sighted		After approach	
	Number	Percent	Number	Percent
Activity				
Moving	69	62.16	39	35.14
Running	3	2.70	64	57.66
Standing	39	35.14	8	7.20
Microhabitat				
Among grasses	39	35.14	38	34.23
Ground burrow	-	-	1	0.90
Open ground	46	41.44	12	10.81
Under shrub	26	23.42	60	54.05
Sunlight exposure				
Direct sunlight	63	56.76	-	-
Filtered light	39	35.14	-	-
Shade	9	8.11	-	-

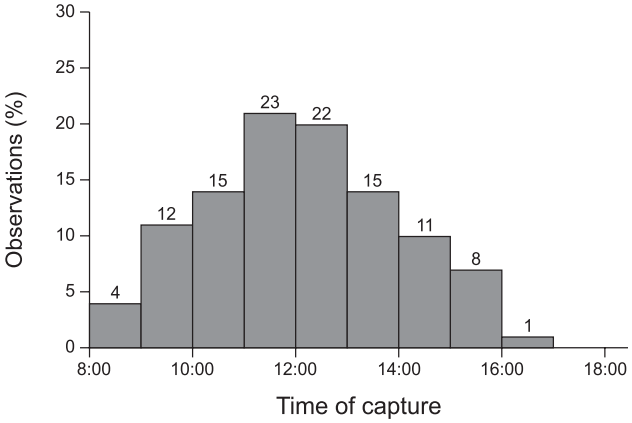

Figure 2. Frequency distribution of individuals *Ameivula ocellifera* from Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil) according to time of time of capture. Numbers above bars indicate sample size.

Diet

Sixteen percent (37) of stomachs were empty. Among the 21 observed prey categories, orthopterans, insect larvae, and spiders/hemipterans were most frequent. Individual stomach means indicated that orthopterans, insect larvae, and isopterans were numerically more common, while orthopterans, insect larvae, and spiders were volumetrically more abundant (Table 2). Isopterans, orthopterans, and insect larvae were numerically most common, while orthopterans, insect larvae, and plant material—mostly cactus fruits of the genus *Melocactus* Link and Otto, 1827—were the most volumetrically common categories (Table 2). Considering importance indexes, orthopterans and insect larvae were the two consecutive most important prey categories.

According to the CLAM analysis, most prey categories (11) were consumed by lizards year round: Araneae, Blattaria, Coleoptera, Hemiptera, Formicidae and other Hymenoptera, insect larvae, Isoptera, Orthoptera, plant material, and Scorpionida. In contrast, the following 9 prey categories were too rare to classify: Chilopoda, Diplopoda, Diptera, insect egg, insect pupae, Lepidoptera, Mantodea, Odonata, and reptile egg. The importance index for the two seasons indicates that orthopterans, insect larvae, and spiders were the most important prey categories for *Ameivula ocellifera* in Tabuleiro (Table 3). The numeric and volumetric niche breadth for both wet and dry seasons were also similar, being 1.97 ± 1.07 (numeric) and 1.12 ± 0.84 (volumetric) in the wet season and 1.86 ± 1.00 and 1.33 ± 0.55, respectively, in the dry season.

Table 2. Diet composition of *Ameivula ocellifera* (*n* = 233) from Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil). f^a = number of stomachs containing the following prey category. Importance index based on stomach means (IPS). Raw values are described in cubic millimeters (mm^3). Italic numbers refer to the three highest values for each column.

Categories	Occurrence		Pooled stomachs				Importance
	f^a	f%	N	N%	Vol.	Vol.%	IPS
Aranae	*63*	*27.04*	93	8.39	1310.32	7.05	14.16
Blattaria	18	7.73	18	1.62	466.35	2.51	3.95
Chilopoda	2	0.86	2	0.18	74.16	0.40	0.48
Coleoptera	49	21.03	84	7.57	829.02	4.46	11.02
Diplopoda	1	0.43	1	0.09	2.81	0.02	0.18
Diptera	3	1.29	3	0.27	11.42	0.06	0.54
Hemiptera	24	10.30	33	2.98	268.11	1.44	4.91
Hymenoptera							
Formicidae	37	15.88	79	7.12	97.49	0.52	7.84
Other	15	6.44	17	1.53	14.37	0.08	2.68
Insect egg	1	0.43	2	0.18	3.00	0.02	0.21
Insect larvae	*72*	*30.90*	*133*	*11.99*	*3365.14*	*18.11*	*20.33*
Insect pupae	3	1.29	3	0.27	283.22	1.52	1.03
Isoptera	34	14.59	*398*	*25.89*	306.69	1.65	*17.38*
Lepidoptera	4	1.72	4	0.36	65.27	0.35	0.81
Mantodea	7	3.00	7	0.63	57.37	0.31	1.31
Odonata	4	1.72	4	0.36	131.05	0.71	0.93
Orthoptera	*116*	*49.79*	*151*	*13.62*	*6452.89*	*34.73*	*32.71*
Plant material	16	6.87	25	2.25	*2672.47*	*14.38*	7.83
Reptile egg	1	0.43	1	0.09	753.20	4.05	1.52
Scorpionida	16	6.87	18	1.62	1030.48	5.55	4.68
Unidentified	33	14.16	33	2.98	386.22	2.08	6.41

Table 3. Diet composition based on pooled stomachs of *Ameivula ocellifera* (*n* = 109) from Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil) according with season the wet season (February–July). f^a, number of stomachs containing the following prey category; IPS^d, importance index based on dry season data; IPS^w, importance index based on wet season data; IPS^d, raw values described in cubic millimeters (mm^3). Italics indicate the three highest values for each column.

Categories	Dry season			Wet season			Importance	
	f^a%	N%	Vol.%	f^a%	N%	Vol.%	IPS^d	IPS^w
Aranae	*26.61*	9.27	*8.53*	*27.42*	7.64	4.60	*15.07*	12.95
Blattaria	6.42	2.17	3.50	8.87	1.16	0.86	4.85	2.81
Chilopoda	-	0.39	0.64	1.61	-	-	0.88	-
Coleoptera	22.02	9.47	5.69	20.16	5.98	2.42	11.77	10.14
Diplopoda	0.92	-	-	-	0.17	0.04	-	0.38
Diptera	1.83	0.20	-	0.81	0.33	0.16	0.34	0.77
Hemiptera	17.43	1.18	0.27	4.03	4.49	3.40	1.83	8.44
Hymenoptera								
Formicidae	16.51	8.68	0.52	15.32	5.81	0.53	8.17	7.62
Other	4.59	2.37	0.08	8.06	-0.83	-0.08	3.50	-1.83
Isoptera	17.43	*26.23*	0.80	12.10	*44.02*	3.06	13.04	*21.50*
Insect egg	0.92	-	-	-	0.33	0.04	-	0.43
Insect larvae	*34.86*	*14.00*	*22.31*	*27.42*	*10.30*	*11.14*	*21.24*	*18.77*
Insect pupae	0.92	0.39	1.78	1.61	0.17	1.09	1.26	0.73
Lepidoptera	2.75	0.20	0.04	0.81	0.50	0.86	0.35	1.37
Mantodea	3.67	0.59	0.47	2.42	0.66	0.04	1.16	1.46
Not identified	13.76	3.55	0.78	14.52	2.49	4.23	6.28	6.83
Odonata	1.83	0.39	0.16	1.61	0.33	1.61	0.72	1.26
Orthoptera	*51.38*	*15.98*	*34.21*	*48.39*	*11.63*	*35.60*	*32.86*	*32.87*
Plant material	8.26	2.17	5.58	5.65	2.33	*29.01*	4.47	13.20
Reptile egg	-	0.20	6.49	0.81	-	-	2.50	-
Scorpionida	4.59	2.56	8.14	8.87	0.83	1.23	6.52	2.22

Table 4. Descriptive statistics of body size and morphometric variables (mm) for males and females of *Ameivula ocellifera* from Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil). Size-adjusted values based on Burnaby's method are in italics. See Material and Methods for details.

Character	Females (*n* = 80)	Males (*n* = 108)
Body size	3.76 ± 0.16	3.87 ± 0.17
Snout–vent length	56.20 ± 6.10	59.42 ± 7.06
	0.49 ± 0.03	*0.48 ± 0.02*
Tail length	116.20 ± 12.59	123.05 ± 14.86
	0.81 ± 0.03	*0.80 ± 0.03*
Body width	9.10 ± 2.09	9.85 ± 1.94
	-0.31 ± 0.07	*-0.30 ± 0.06*
Body height	7.24 ± 1.66	7.84 ± 1.57
	-0.40 ± 0.07	*-0.40 ± 0.05*
Head width	7.78 ± 0.95	8.68 ± 1.42
	-0.36 ± 0.03	*-0.36 ± 0.03*
Head height	6.59 ± 0.89	7.58 ± 1.13
	-0.44 ± 0.03	*-0.41 ± 0.03*
Head length	14.47 ± 2.27	15.64 ± 2.54
	-0.10 ± 0.05	*-0.10 ± 0.05*
Forelimb length	18.45 ± 2.39	20.20 ± 2.90
	0.01 ± 0.04	*0.01 ± 0.04*
Hind-limb length	35.35 ± 4.48	38.34 ± 4.72
	0.29 ± 0.03	*0.29 ± 0.03*

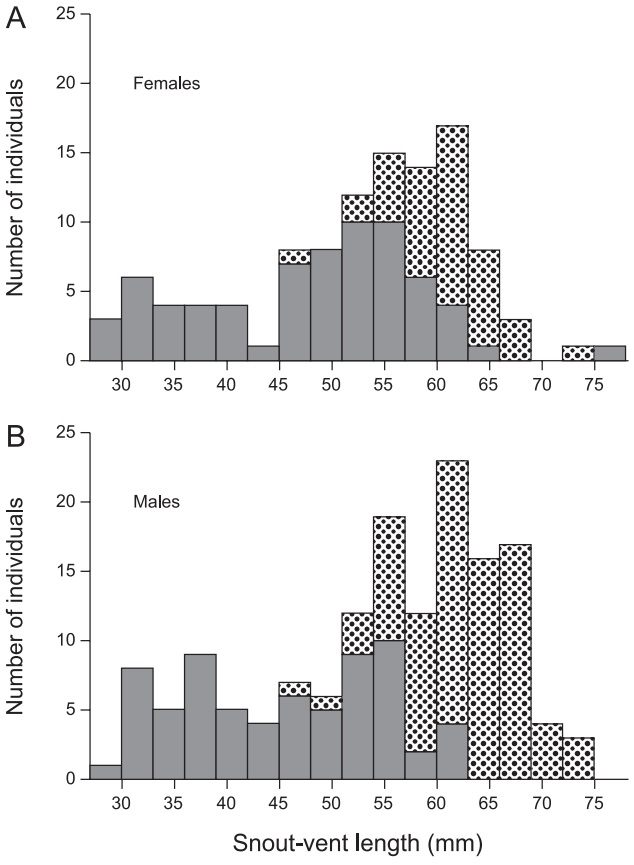

Figure 3. Snout–vent length of reproductive (stippled) and non-reproductive (solid) *Ameivula ocellifera* from Reserva Biológica Guaribas (Mamanguape, Paraíba, Brazil). **(A)** Females, **(B)** males.

Sexual dimorphism

The smallest individual was a male (25 mm SVL), and the largest was also a male (74 mm SVL). The smallest female measured 28 mm SVL and the largest 67 mm SVL. Based on body size variable, males were significantly larger than females (ANOVA $F_{1,186}$ = 20.52, P < 0.0001; Table 4). The logistic regression indicated that males had taller heads, whereas females had longer bodies (n = 188, Model = sex ~ HH + SVL, AIC = 234.56, P < 0.0001).

Reproduction

The smallest reproductive male measured 45 mm SVL, and the smallest reproductive female measured 44 mm SVL, suggesting that both sexes reach maturity at the same age/size (Fig. 3). Clutch size averaged 1.89 ± 0.75 (mode = 2, range 1–4, n = 35) and is not related to SVL (n = 25, r < 0.001; P = 1.00). Mean egg length, width, and volume were respectively 14.44 ± 1.58 mm, 7.48 ± 1.10 mm³, and 288.97 ± 17.67 mm³ (n = 9).

The reproductive period (based on direct observation enlarged testes, and vitellogenic follicles) was mainly confined to the dry season (August–December) with its peak in September (Figs. 1 and 5). Only one reproductive female was found at the beginning of the wet season (Fig. 4). Reproductive males were present all year round, whereas reproductive females were found from August to December (Fig. 4). However, the percentage of

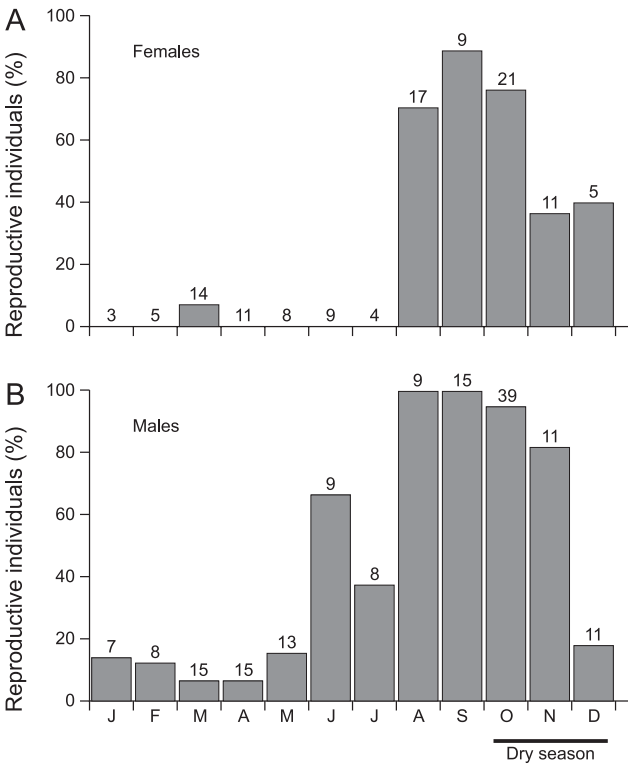

Figure 4. Monthly distribution of the percentage of reproductive *Ameivula ocellifera* from Reserva Biológica Guaribas (Mamanguape, Paraíba state, Brazil). **(A)** Females, **(B)** males. Numbers above bars indicate sample sizes.

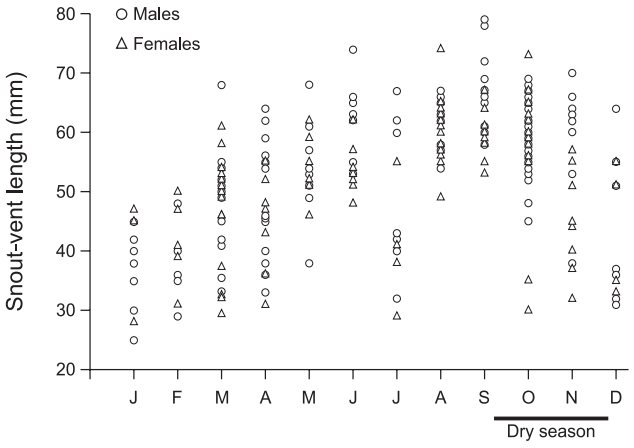

Figure 5. Monthly distribution of snout–vent length of *Ameivula ocellifera* from Reserva Biológica Guaribas (Mamanguape, Paraíba state, Brazil).

reproductively active males was more prominent in the dry season too (Fig. 4), indicating a tendency of seasonal reproduction. Only one female had vitellogenic follicles and corpora lutea simultaneously, indicating that *Ameivula ocellifera* from Tabuleiro usually lay one clutch per year, but some individuals can occasionally produce more than one clutch in the same reproductive period. It is also possible that *A. ocellifera* produces more than one clutch per year but our sample size of gravid females was not sufficient to detect this reproductive pattern. Recruitment took place mainly in the end of the dry season, when most hatchlings were found (small SVL individuals). However, a new recruitment season seems to take place during the end of the wet season, reinforcing the idea of more than one clutch per year (Fig. 5).

DISCUSSION

Microhabitat, activity, and thermal ecology

Ameivula ocellifera from Tabuleiro is associated with open areas with grasses and shrubs and direct sunlight, similar to many whiptail lizards from other regions, such as *Am. nativo* (Rocha et al., 1997) (Rocha, 1997; Peloso et al., 2008), *Aspidoscelis tigris* (Baird and Girard, 1852) (*As. deppii* [Wiegmann, 1834]; Pianka, 1970; Vitt et al., 1993), *Cnemidophorus lemniscatus* (Linnaeus, 1758) (Mesquita and Colli, 2003a; Montgomery et al., 2007), *C. vanzoi* (Baskin and Williams, 1966; Dickinson et al., 2001), *Glaucomastix abaetensis* (Dias et al., 2002) (Dias and Rocha, 2007), and *Am. ocellifera* populations from many other biomes, such as Cerrado (Mesquita and Colli, 2003a, b), Caatinga (Vitt, 1995), and Restinga (Dias and Rocha, 2007). The similarity in microhabitat use suggests that these patterns may have historical origins, as they seems to be commonly observed on “cnemidophorine” lizards.

Ameivula ocellifera from Tabuleiro were more active during the hottest hours of the day, similar to other populations in different environments (Mesquita and Colli, 2003b; Dias and Rocha, 2004, 2007) and to teiid lizards such as *Ameiva ameiva* Linnaeus, 1758 from open vegetation biomes (Vitt and Colli, 1994; Blair, 2009). The high body temperatures associated with high environmental temperatures are probably associated with activity patterns similarly reported elsewhere (Menezes and Rocha, 2011). As active foragers, whiptail lizards are strongly associated with high temperature environments during foraging (Bergallo and Rocha, 1993). Furthermore, the high body temperature values observed in *A. ocellifera* from Tabuleiro are similar to other *A. ocellifera* populations from different environments (Vitt, 1995; Mesquita and Colli, 2003b; Dias and Rocha, 2004), suggesting that body temperature is also more related to historical factors than to local environment conditions (Schall, 1977; Mesquita and Colli, 2003a; Menezes and Rocha, 2011). However, we can only precisely assure this trend with experimental studies with thermal gradients on laboratory conditions (Sinervo et al., 2010). Finaly, a small influence of environment over *A. ocellifera* body temperature can be observed across populations (Menezes and Rocha, 2011), reinforcing the necessity of further research.

Diet

Ameivula lizards frequently feed on insects, mostly termites (Mesquita and Colli, 2003a; Menezes et al., 2006, 2008). *Ameivula ocellifera* from Tabuleiro did not include substantial numbers of termites in their feeding habits; however, orthopterans and insect larvae were observed in high number and frequency. Recently, some studies on an *A. ocellifera* population and the close relative *Glaucomastix abaetensis* from Brazilian Northeastern Restinga also presented a similar pattern (Dias and Rocha, 2007; Santana et al., 2010). Both species had a high occurrence of grasshoppers, crickets, and insect larvae in their diet. A plausible explanation for the low frequency of isopterans is the low density of terrestrial termites present at our study site (Vasconcellos et al., 2008). This explanation was also proposed for a study of a northeastern Restinga population of *A. ocellifera* (Santana et al., 2010).

Despite the presence of isopterans in the diet of *Ameivula ocellifera* from Tabuleiro, the importance indices of the secondary categories, such as spiders and insect larvae were congruent with many other *A. ocellifera* populations from other regions, such as the Cerrado and Caatinga biomes (Vitt, 1991a, 1995; Mesquita and Colli, 2003a, b). These prey categories were also important diet components of a significant number of whiptail species, such as *Ameivula mumbuca* (Colli et al., 2003) (Mesquita and Colli, 2003a; Mesquita et al., 2006a, b), *Cnemidophorus cryptus* Cole and Dessauer, 1993, *C. gramivagus* McCrystal and Dixon, 1987, *C. lemniscatus* (Magnusson and Silva, 1993; Mesquita and Colli, 2003a), *C. nativo* (Menezes et al., 2008), *Glaucomastix littoralis* (Rocha et al., 2000) (Teixeira-Filho et al., 2003), and other teiid species (Vitt, 1991b; Vitt and Colli, 1994; Vitt and Zani, 1996). This pattern could be a consequence of the active foraging mode, an important characteristic of the family (Schoener, 1971;

Pianka and Vitt, 2003). Most active-foraging lizards seem to use chemical discrimination to find their prey (Cooper et al., 2000), enabling them to find prey with low diurnal activity (like some orthopterans and spiders) and that occupy dark habitats, such as leaf litter, burrows, and fallen logs.

The absence of seasonal variation in diet composition and the low niche breadths could be related with the relatively high abundance of just a few prey categories consumed at Tabuleiro throughout the year (Barbosa et al., 2005). Another interesting result is the presence of considerable amounts of plant matter. Some whiptail lizard species from isolated areas also present plant matter in their feeding habits. *Cnemidophorus murinus* (Laurenti, 1768), is a strictly herbivorous species from Bonaire, West Indies (Dearing, 1993), and *C. lemniscatus,* from Cerrado isolated areas inside the Amazon Forest, can also ingest significant amounts of fruits in their diet (Vitt et al., 1997). Perhaps, herbivory in whiptail lizards (*Cnemidophorus* and *Ameivula*) is more likely to appear in isolated populations (but see Passos et al., 2013).

Sexual dimorphism

Overall males were larger than females, as observed in other *Ameivula* populations (Vitt, 1983; Santana et al., 2010) and Teiid genera, such as *Ameiva* (Vitt and Colli, 1994) and *Kentropyx* Spix, 1825 (Vitt et al., 2001). One possible explanation is that in these populations larger males may have been selected due to their success during intrasexual combat and mating behaviour while holding females for hemipenes insertion (Anderson and Vitt, 1990; Lewis et al., 2000). The size difference in sexual dimorphism can also be produced by selection of smaller females, caused by an energy trade-off between growth and reproduction due to energetic costs associated with egg production (Taylor and Denardo, 2005). However, this contrasts with studies of other populations of *A. ocellifera* (Mesquita and Colli, 2003b) and other whiptail lizard species, such as *Contomastix vacariensis* (Feltrim and Lema, 2000; Rezende-Pinto et al., 2009), which presented larger females. Usually, a relationship between female body size and clutch size results in increased fecundity in larger females (Fitch, 1970; Tinkle et al., 1970). The absence of this association in *A. ocellifera* at Tabuleiro may explain why females do not grow large and so are smaller than males.

Reproduction

On Tabuleiro, *Ameivulla ocellifera* population reproduces seasonally, mainly during dry season, with recruitment occurring mainly in the end of dry season and beginning of wet season. There is also a small recruitment peak in the middle of wet season (July). Primarily, classic life-history studies suggest that most of the Neotropical lizards tend to reproduce continuously through the year, laying several clutches (Fitch, 1970, 1982). However, Vitt (1992) indicated that Neotropical lizards in fact possess many different reproductive strategies. Some Neotropical lizards from environments with stable (e.g., Amazon Forest) or unpredictable (e.g., Caatinga) climatic variation throughout the year tend to lay several clutches of few eggs and reproduce continuously (Colli, 1991; Vitt and Colli, 1994; Mesquita and Colli, 2010). On the other hand, in Neotropical regions with pronounced seasonality (e.g., Cerrado), lizards tend to reproduce seasonally, laying a few or just one clutch, but with more eggs (or bigger eggs) per clutch (Vitt and Colli, 1994; Mesquita and Colli, 2010), which is clearly the condition of *A. ocellifera* from REBIO Guaribas Tabuleiros.

Initially, most studies considered environmental factors as the strongest influence on lizards life history (Tinkle et al., 1970). Later, some researchers began to consider historical influences on these patterns (Dunham and Miles, 1985; Dunham et al., 1988). A recent study with Neotropical lizards indicated that whiptail lizards show strong historical influence on reproduction strategies and patterns (Mesquita and Colli, 2010). Some *Ameivulla ocellifera* populations from Cerrado also reproduce seasonally, which is consistent with our results (Mesquita and Colli, 2003a, b). However, as we emphasized before, Tabuleiro savannas are strongly influenced by the Atlantic Forest, so we might expect a continuous reproduction pattern typical of rain forests, which is continuous (Colli, 1991; Vitt and Colli, 1994; Mesquita and Colli, 2010). In addition, we collected one female with simultaneously vitellogenic follicles and corpora lutea in December, and a reproductive female in March. These observations suggest that even though *A. ocellifera* from Tabuleiro breeds seasonally, it seems to be more extended than the Cerrado populations (Mesquita and Colli, 2003b) and producing more than one clutch per year. Simultaneous presence of oviductal eggs and vitellogenic follicles also occur in a Caatinga population continuous reproduction throughout the year (Sales and Freire, 2016). This may indicate some environmental influence on the reproductive characteristics of *A. ocellifera* from Tabuleiro. The reproductive condition of *A. ocellifera* from Tabuleiro (seasonal, but with some evidence of a continuous pattern) is corroborated by the aseasonal male reproduction (Fig. 4), although decreasing reproductive activity in the wet season and the second recruitment evidence in July (Fig. 5). Finaly, studies on similar environments are essential to unravel this pattern.

Even with these results, it is hard to assume that phylogeny plays a key role in the reproduction of *Ameivula ocellifera* from Tabuleiro. Although Tabuleiro savannas are wet and strongly associated with ombrofilous forest vegetation, they also present well-defined seasonality (dry and wet season), as occurs throughout the northeastern Atlantic Forest. Relative to Cerrado savannas, there are no significant differences in mean temperatures during the year. However, Cerrado minimum temperatures are considerably lower and more variable throughout the year than in Tabuleiro (Nimer, 1989). Temperature and photoperiod influence on testicular recrudescence was reported

for *Anolis carolinensis* Voigt, 1832 (Licht, 1966). It seems higher and constant temperatures hasten spermatogenesis. This phenomenon could promote a more continuous reproductive cycle in Tabuleiro compared to Cerrado. In addition, studies on *Am. ocellifera* from Caatinga suggest that this species reproduces continuously, laying several clutches through the year (Vitt, 1983; Mesquita and Colli, 2003a, b), an expected result considering previous life history studies (Colli, 1991; Vitt and Colli, 1994). The Caatinga biome is a semi-arid and unpredictable environment, so lizards should tend to breed continuously (Mesquita and Colli, 2010). As Tabuleiro savannas and Caatinga are geographically proximate, we also expect populations of *A. ocellifera* from the two areas to be similar due to recent shared ancestry recently for *A. ocellifera* on another Caatinga site and in coastal regions of northeastern Brazil (Zanchi-Silva et al., 2014; Oliveira et al., 2015). In both regions, *A. ocellifera* reproduces continuously, but with reproductive activity diminishing at the onset of the dry season.

The clutch size of *Ameivula ocellifera* from the Tabuleiro savanna was similar to that reported for other populations inhabiting savanna environments, although individuals from the Cerrado appear to have slightly smaller clutches (Mesquita and Colli, 2003a, b). However, it is important to emphasize that the reproductive cycle is not the sole factor influencing clutch size. Actively foraging lizards exhibit traits, such as body elongation, that could constrain the number of eggs per clutch (Vitt and Congdon, 1978; Vitt and Price, 1982). Our linear regression analysis found no relationship between clutch size and female SVL, even though a strong positive correlation between these variables is common (Dunham et al., 1988), even in other populations of *A. ocellifera* (Mesquita and Colli, 2003a, b). The number and size of eggs are often limited by the available space in the female's body cavity, with morphology playing a key role in determining clutch size (Shine and Schwarzkopf, 1992). As previously noted, energetic tradeoffs related to reproductive investment, combined with morphological adaptations associated with active foraging in *Ameivula,* may explain the absence of a relationship between female size and clutch size in this population (Vitt and Congdon, 1978; Vitt and Price, 1982).

Overall, *Ameivula ocellifera* from the Tabuleiro savannas displayed natural history traits consistent with other neotropical populations of the species, including heliophilous behavior, preference for open vegetation, sexual dimorphism, seasonal reproduction (during the dry season), and a diet primarily composed of grasshoppers and spiders. These characteristics align with the common ecological patterns observed in other neotropical teiid lizards, suggesting niche conservatism within the clade. However, unique aspects in the diet (notably, reduced amount of termites) and reproductive patterns (multiple clutches per year) in our studied population indicate that local environmental factors may significantly also shape the ecological traits of these whiptail lizards. Such findings highlight the adaptability of *A. ocellifera* and potentially other lizards in response to local ecological pressures, offering valuable insights into their niche flexibility and the factors that define their ecological roles. This understanding could be instrumental in predicting how these species might respond to environmental changes across different habitats.

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