



The autecology of *Anolis brasiliensis* (Squamata, Dactyloidae) in a Neotropical Savanna

Daniel O. Mesquita¹, Gabriel C. Costa², Adriano S. Figueredo³, Frederico G.R. França⁴, Adrian A. Garda², Ana H. Bello Soares³, Leonora Tavares-Bastos⁵, Mariana M. Vasconcellos⁶, Gustavo H. C. Vieira¹, Laurie J. Vitt⁷, Fernanda P. Werneck⁸, Helga C. Wiederhecker³, & Guarino R. Colli³

¹Departamento de Sistemática e Ecologia, CCEN, Universidade Federal da Paraíba. João Pessoa, Paraíba, Brazil

²Departamento de Botânica, Ecologia e Zoologia, Universidade Federal do Rio Grande do Norte, Campus Universitário-Lagoa Nova, Natal, RN, Brazil

³Departamento de Zoologia, Universidade de Brasília, 70910-900, Brasília, DF, Brazil

⁴Departamento de Engenharia e Meio Ambiente, CCAE, Universidade Federal da Paraíba, Rio Tinto, PB, Brazil

⁵Universidade Federal de Alagoas, Instituto de Ciências Biológicas e da Saúde, Setor de Histologia e Embriologia, Maceió, AL, Brazil

⁶Section of Integrative Biology, University of Texas at Austin, 1 University Station, C0990, Austin, TX, USA, 78712

⁷Sam Noble Museum, 2401 Chautauqua Avenue, Norman, OK, USA, 73072

⁸Programa de Coleções e Acervos Científicos, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Aleixo, Manaus, AM, Brazil

Anole lizards represent one of the best studied radiations of terrestrial vertebrates. Herein we examine the autecology of *Anolis brasiliensis* from the Cerrado of central Brazil, based on a large amount of data collected across much of its geographic range. Species Distribution Modelling (SDM) techniques revealed that *A. brasiliensis* likely has a wider distribution than currently verified. For ecological comparisons, we tested whether i) body temperature is influenced by microhabitat, ii) sexes differ in diet, iii) sexes differ in morphology, and iv) climatic variables influence reproduction. Lizards were collected primarily in seasonally dry forests and gallery forests. Body temperature is strongly associated with air temperature at 5 cm above the substrate. The most important diet items were Araneae, Orthoptera and Formicidae, and high diet niche overlap exists between sexes. Females are significantly larger in body size than males. Males, however, have larger heads than females. Due to allochronic ovulation, *A. brasiliensis* largely have clutches with single eggs. Females often contain an oviductal egg and an enlarged vitellogenic follicle, suggesting the production of multiple clutches largely in the rainy season from October to January. Recruitment occurred mostly from January to April. *Anolis brasiliensis* is ecologically more similar to other anoles than to sympatric lizards in other major clades. These results reiterate the impact of evolutionary history on ecological and life history traits of squamate reptiles.

Key words: Activity, body temperatures, Cerrado, clutch size, diet, reproduction, sexual dimorphism

INTRODUCTION

Anole lizards represent one of the most diverse and best-studied radiations of terrestrial vertebrates (Losos, 2009; Nicholson et al., 2012; Uetz et al., 2014). Their distribution extends from the southeastern United States, Mexico, Central America and Antilles, to approximately 20° S in South America (Ávila-Pires, 1995). Most anoles are predominantly arboreal, with specialised foot morphology for scansorial locomotion, streamlined bodies, and long tails. They range from 30 mm snout-vent length (SVL, *A. ophiolepis*) to more than 190 mm SVL (*A. equestris*, Butler et al., 2000; Nicholson et al., 2012). Most anoles are sexually dimorphic in size (with males larger than females), diurnal, sit-and-wait

foragers, and feed on arthropods (Pough et al., 2004; Vitt & Caldwell, 2014). All anoles have allochronic ovulation producing a single egg at a time (Smith et al., 1973), although it is common to find one egg in each oviduct at different stages of shell development. Nearly continual egg production is common (Roff, 1992, 2002).

Until recently, the Brazilian Amazon was thought to contain 10 species of anoles (*A. auratus*, *A. bombiceps*, *A. chrysolepis*, *A. fuscoauratus*, *A. ortonii*, *A. philopunctatus*, *A. phyllorhinus*, *A. punctatus*, *A. trachyderma* and *A. transversalis*) and the Cerrado two species (*A. chrysolepis* and *A. meridionalis*, Vanzolini & Williams, 1970; Ávila-Pires, 1995). However, a recent revision of *A. chrysolepis* recognised all four subspecies as full species: *A. scyphus*, distributed throughout Amazonian Colombia,

Correspondence: Daniel O. Mesquita (danmesq@dse.ufpb.br)

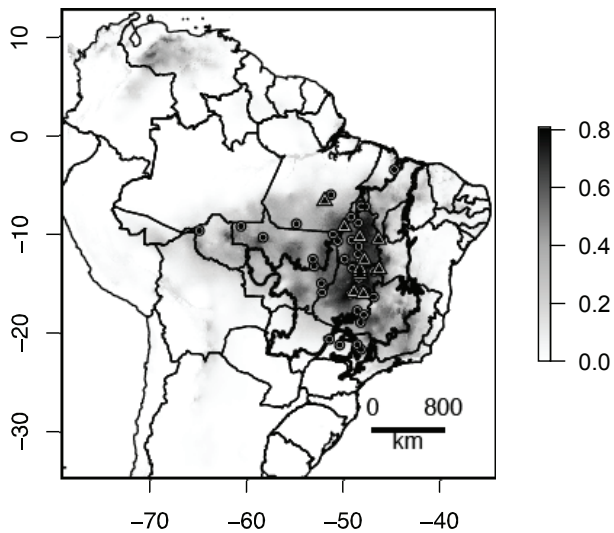


Fig. 1. Species distribution model of *Anolis brasiliensis*. Grey gradient indicates environmental suitability for the species; areas with higher values are climatically more favourable. Circles represent distribution records from specimens deposited in scientific collections and the literature. Triangles represent sites sampled in this study.

Ecuador, Peru and Brazil; *A. planiceps*, distributed throughout Venezuela, Trinidad, Guyana and northern Brazil; *A. brasiliensis*, distributed throughout open areas in Brazil; *A. chrysolepis*, distributed in forested habitats throughout Southern Guyana, Suriname, French Guiana and northern Brazil; and *A. tandai*, distributed in the Amazon rainforest south of the Amazon River and west of the Tapajós River in Brazil and Peru (D'Angiolella et al., 2011).

Considering the vast continental distribution of the group, our knowledge about the ecology of the *A. chrysolepis* complex is largely based on studies conducted at single sites. This compromises our understanding of life-history response to differing environments and geography. *Anolis tandai* is a leaf litter specialist, feeding mainly on grasshoppers, crickets, spiders and insect larvae, and showing pronounced sexual dimorphism in mass and limb length (Vitt et al., 2001a). A comparative study on *A. planiceps* and *A. scypheus* in the Amazon forests of Ecuador and Brazil, respectively, showed that *A. scypheus* attains higher body temperatures than *A. planiceps*, that both species are sexually dimorphic, and that their diets are similar (Vitt & Zani, 1996). *Anolis brasiliensis*, living in a transitional area between Cerrado and Amazonia, was found mostly on tree trunks and on the leaf litter in gallery forest, and its diet consisted mostly of spiders, crickets/grasshoppers, ants and beetles (Vitt et al., 2008b). Males were larger and heavier than females, but had relatively shorter hind limbs (Vitt et al., 2008b). Considering that *A. brasiliensis* has a large geographic distribution in the Cerrado, much remains to be learned about its ecology.

Most tropical savannahs in South America are disappearing at an extraordinary rate due to extensive cattle breeding, mining, agriculture and other human activities (Alho & Martins, 1995; Machado et al., 2004;

Klink & Machado, 2005). Surprisingly, many of these areas are vanishing even before scientists have the opportunity to perform simple biodiversity inventories (Wilson, 1992; Rodrigues, 2005). Paradoxically, the lack of studies could easily lead the government to designate these areas to development programs rather than protected areas. Herein we examine the autecology of *A. brasiliensis* from the Cerrado of central Brazil, based on a large amount of data collected across much of its geographic range. We test four hypotheses: i) body temperature is influenced by microhabitat, ii) diet differs between sexes, iii) morphology differs between sexes, and iv) climatic variables influence reproduction.

MATERIALS AND METHODS

Species distribution modelling

To determine the potential distribution of *A. brasiliensis*, we used Species Distribution Modelling (SDM) techniques (for a review of methods see Elith et al., 2006) as implemented in MaxEnt (Elith et al., 2006; Elith & Leathwick, 2009). The algorithm in MaxEnt fits a probability distribution for species occurrence to the set of pixels across the region of interest (for a detailed explanation on how the maximum entropy principle applies to SDM see Elith et al., 2011). We performed 10 replications using a cross-validation procedure where we divided our dataset using 75% of data for model calibration and retained 25% of the data to evaluate the models. We report the mean and standard deviation of AUC test values across the 10 runs. We used MaxEnt default parameters (Phillips & Dudik, 2008) in the R package *dismo* (Hijmans et al., 2013). The output model is projected in geographical space and the result can be interpreted as a map of environmental suitability for the species where areas with higher values are climatically more favourable.

We obtained 45 locality records from museum collections and the literature (Costa et al., 2007; Nogueira et al., 2011). We used bioclimatic environmental variables from the Worldclim project (Hijmans et al., 2005), downloaded at a 30" (1 km²) spatial resolution (available on-line at: <http://www.worldclim.org/>). Layers were cropped to span from latitude 1247' N to 3446' S and longitude 7831' W to 35 W, representing a larger spatial range than the Cerrado region. To avoid over-fitting of models and use of redundant climatic variables, we identified highly correlated variables ($r > 0.9$) and excluded those considered less relevant (see Rissler & Apodaca, 2007). We used a total of 10 abiotic environmental variables: Bio 3–isothermality, Bio 4–temperature seasonality, Bio 7–temperature annual range, Bio 10–mean temperature of warmest quarter, Bio 11–mean temperature of coldest quarter, Bio 14–precipitation of driest month, Bio 15–precipitation seasonality, Bio 16–precipitation of wettest quarter, Bio 17–precipitation of driest quarter, and altitude.

Microhabitat, activity and temperatures

During several biodiversity inventories conducted from 1986 to 2005, we collected *A. brasiliensis* specimens

across 15 localities distributed throughout the Cerrado. We captured lizards by hand, rubber bands or using a shotgun and dust shot cartridges. When specimens were captured alive, they were killed in the same day with a lethal injection of Tiopental®, preserved with 10% formalin and stored in 70% alcohol. Because the present study is part of a larger project involving other studies, alternative techniques (such as stomach flushing for diet analysis) were not possible. All collected specimens are housed in the Coleção Herpetológica da Universidade de Brasília (CHUNB). At time of capture, we recorded body, substrate and air temperatures (at 5 cm from substrate and at chest height) to the nearest 0.2 degree Celsius with Miller & Weber® cloacal thermometers. We also recorded microhabitat and activity when individuals were first sighted and after approached by the investigator. Data recorded included hour, date of capture, and lizard exposure to sun (in sun, shade or filtered sun). We used the following microhabitat categories: burrow, bush, fallen log, grass, clear ground on sandy soil, rock, termite nest, tree trunk and under rock. When lizards were perched, we estimated height above ground (± 5 cm). We classified lizard activities as stationary, moving or running. To assess the contribution of environmental temperatures to lizard cloacal temperatures, we used a stepwise multiple regression (Tabachnick & Fidell, 1996).

Diet

We obtained diet information from dissected stomachs of 229 preserved lizards from 16 localities. Prey items were carefully separated and identified to broad taxonomic levels (order or family). Prey items with preserved body dimensions were measured (length and width) to produce an estimate of the volume of consumed items. We calculated the volume of individual prey items using the following ellipsoid volume formula where V is volume, w is prey width and l is prey length:

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

For each prey category, we calculated its frequency, numeric and volumetric percentage and calculated an importance index based on individual stomachs, IIS ($(N\% + V\%)/2$) and on pooled stomachs, IPS ($(F\% + N\% + V\%)/3$).

To investigate diet overlap between males and females, we calculated numeric and volumetric niche overlap indices (Pianka, 1973) using the following formula in the R package *spaa* (Zhang, 2013)

$$O_{FM} = O_{MF} = \frac{\sum p_{Mi} p_{Fi}}{\sqrt{(p_{Mi}^2)(p_{Fi}^2)}},$$

where p_{Mi} is the proportion of prey category i for males and p_{Fi} the proportion for females. We calculated volumetric and numeric niche breadth for individual and pooled stomachs using the inverse of the Simpson's diversity index (Simpson, 1949)

$$D = \frac{1}{\sum p_i^2},$$

where p_i represents the proportion of prey category i .

We assessed intersexual differences in diet niche breadth considering both individual and pooled stomachs. For individual stomachs, we performed an ANCOVA with niche breadth as the dependent variable, sex as the class variable, and size (SVL) as covariate. This controlled for the effects of the positive association between SVL and niche breadth for individual stomachs. For pooled stomachs, we compared the overall niche breadth with a rarefaction analysis to control for the influence of the number of individuals sampled in each sex. We calculated the diversity index for 1000 random sub-samples of size 100 for each sex and tested the mean differences with a t -test.

Morphometry and Sexual Dimorphism

From each individual, we took the following measurements to the nearest 0.01 mm with digital calipers: snout-vent length (SVL), body width (at widest point in mid-body), body height (at highest point in mid-body), head width (at the widest point), head height (at highest point), head length (from tip of snout to anterior margin of ear opening) and tail length (from cloaca to tip of tail). Some measurements could not be assessed for all specimens analysed (e.g., animals with broken tails). A variety of methods can be used to estimate missing observations (Tabachnick & Fidell, 1996; Quinn & Keough, 2002). Multiple imputation is regarded as the most robust approach (Rubin, 1996; Van Buuren et al., 2006, Penone et al., in press), and we used chained equations using the R package *mice* (Van Buuren et al., 2006; Van Buuren & Groothuis-Oudshoorn, 2011). We log-transformed (base 10) all morphometric variables after multiple imputation, and screened the data for multivariate outliers with the R package *mvoutlier* (Filzmoser & Gschwandtner, 2014). Eleven females (2.9 % of all females) and 30 males (8.5 %) were considered as outliers using a maximum threshold for adaptive outlier detection of 0.001, and were dropped from further analyses.

To partition the total morphometric variation between size and shape variation, we defined body size as an isometric size variable (Rohlf & Bookstein, 1987, following Somers, 1986): we calculated an isometric eigenvector, defined *a priori* with values equal to $p^{-0.5}$, where p is the number of variables (Jolicœur, 1963), and obtained scores from this eigenvector, hereafter called body size, by post multiplying the $n \times p$ matrix of \log_{10} transformed data, where n is the number of observations, by the $p \times 1$ isometric eigenvector. To remove the effects of body size from the \log_{10} -transformed variables we used Burnaby's method (Burnaby, 1966). We post-multiplied the $n \times p$ matrix of the \log_{10} transformed data by a $p \times p$ symmetric matrix, L , defined as:

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

where I_p is a $p \times p$ identity matrix, V is the isometric size eigenvector defined above, and V^T is the transpose of matrix V (Rohlf & Bookstein, 1987). Hereafter we refer to the resulting size-adjusted variables as shape variables. To assess difference between sexes, we conducted an analysis of variance on body size (ANOVA) and a

logistic regression on the shape variables. To assess the statistical significance of the full model based on shape variables, we compared it against a constant-only (null) model using a chi-square test of the scaled deviance (Chambers & Hastie, 1992; Faraway, 2006). We assessed the importance of each variable by model selection via single term addition (Chambers & Hastie, 1992): (i) the full model was tested against a constant-only model; (ii) the significant term with the lowest AIC value was added to the null model; (iii) step 2 was repeated; (iv) any non-significant terms were dropped from the model; (v) steps 3 and 4 were repeated until no significant terms could be added or no non-significant terms could be dropped from the model. After the model selection analysis, we assessed the misclassification error of the reduced model using 100 bootstrap replications of a linear discriminant analysis with the R package *ipred* (Peters & Hothorn, 2013). We further assessed variable importance using model averaging, retaining only models with $DAIC_c < 4$ (Crawley, 2007). Model averaging analysis was conducted in the R package *MuMIn* (Burnham & Anderson, 2002).

Reproduction

We determined the sex of each specimen by direct observation of gonads. In females, reproductive activity was described by observation of the presence and number of vitellogenic follicles, oviductal eggs and corpora lutea. We measured the width and length of oviductal eggs with Mitutoyo electronic calipers (0.1 mm). Egg volume was estimated using the ellipsoid formula:

$$V = \frac{\pi w^2 l}{6},$$

where V is egg volume, w is egg width, and l is egg height. The minimum size for sexual maturity was determined by the SVL of the smallest reproductive female. We considered the simultaneous presence of oviductal eggs, vitellogenic follicles, or corpora lutea as an indication of more than one clutch per reproductive season.

Reproductive activity of males was described by measuring the width and length of testes with Mitutoyo electronic calipers (0.1 mm), and testis volume (TV) was estimated using the ellipsoid formula described above. Testes and epididymides were removed by dissection and fixed in Bouin's fixative. Next, samples were dehydrated in ascending alcohol concentrations, and embedded in paraffin. For histological analysis, four longitudinal sections were obtained from each individual and stained with hematoxylin-eosin. From each section ten measurements of seminiferous tubule diameter and germinative epithelium height were obtained using a staged micrometer. The mean seminiferous tubule diameter (STD) and mean germinative epithelium height (GEH) were calculated from each measurement. We categorised testes according to spermatogenesis activity following Vieira et al. (2001). Five stages of spermatogenic activity were recognised: stage I, seminiferous tubules without lumen, containing some cells at different stages of differentiation, such as spermatocytes, spermatids and spermatozoa; stage II, opened lumen of the seminiferous

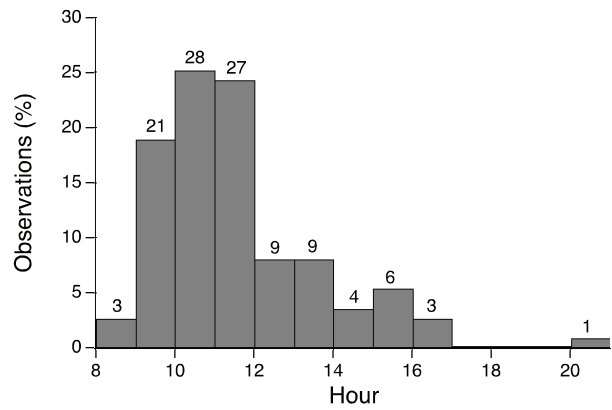


Fig. 2. Frequency distribution of individuals of *Anolis brasiliensis* from Cerrado according to time of capture. Numbers on top of bars indicate sample sizes.

tubules and presence of spermatocytes in their margins; stage III, presence of spermatids in the luminal margin; stage IV, presence of spermatozoa in the lumen; stage V, lack of connection between the seminiferous tubule epithelium and spermatocytes, spermatids and spermatozoa, as well as cellular debris obstructing the lumen of tubules (Vieira et al., 2001). Minimum size for sexual maturity was determined by the SVL of the smallest male with spermatozoa in the testes.

RESULTS

Species distribution modelling

We obtained 45 unique localities for *A. brasiliensis* spread across the species' distribution (Fig. 1). The MaxEnt model had good accuracy ($AUC_{test} = \bar{x}=0.945$, $SD=0.008$), revealing higher climatic suitability throughout the Cerrado distribution (Fig. 1). The most important variables were precipitation of the driest month (43.3% of training gain) and precipitation of the wettest quarter (35.9% of training gain). The response curves for these two variables show that higher suitability for *A. brasiliensis* occurs in areas where precipitation of the driest month is low (<100 mm) and precipitation of the wettest quarter is intermediate (>750mm). These results mainly reflect that this species is endemic to the Cerrado, a highly seasonal environment with well-marked dry and rainy seasons.

Microhabitat, activity, and temperatures

All individuals were found in seasonally dry forests and gallery forests and adjacent habitats. Of the 111 individuals of *A. brasiliensis* for which we collected microhabitat data, 46.9% were perched in trunks, 38.7% in leaf litter, 4.5% in logs, 3.6% under logs, 1.8% in shrubs, 1.8% in roots, 0.9% in rocks, 0.9% in burrows and 0.9% in vines. Of the 47 individuals for which we obtained activity data, 78.7% were stationary when first sighted; after approached, 59.6% remained still, 28% ran, 8.5% ran to lower perches and only 4.3% walked. We found active lizards from 0800 to 1600 hours, with a peak between 0900 and 1100 (Fig. 2). Approximately 49.1% of the individuals were in shade, 35.5% were under filtered light and 15.5% were exposed to direct sunlight. Of the 63 individuals for which data on perch height were

Table 1. Diet composition of *Anolis brasiliensis* from Cerrado ($n=229$). n =prey number; v =prey volume; SD=standard deviation; f =number of stomachs containing prey item; iis - importance index based on individual stomachs; ips - importance index based on pooled stomachs.

Category	Pooled stomachs							Individual stomachs				
	F	f %	n	$n\%$	v	$v\%$	ips	$n\pm SD$	$n\%\pm SD$	$v\pm SD$	$v\%\pm SD$	iis
Araneae	88	24.24	141	24.44	10564.96	28.24	25.64	0.616 \pm 1.05	25.36 \pm 37.05	46.14 \pm 123.55	26.07 \pm 38.75	25.72
Araneae egg sac	1	0.28	2	0.35	461.4	1.23	0.62	0.009 \pm 0.13	0.22 \pm 3.30	2.01 \pm 30.49	0.16 \pm 2.39	0.19
Blattaria	26	7.16	27	4.68	3270.17	8.74	6.86	0.118 \pm 0.34	7.34 \pm 22.90	14.28 \pm 53.82	7.80 \pm 24.33	7.57
Chilopoda	5	1.38	5	0.87	589.18	1.57	1.27	0.022 \pm 0.15	0.62 \pm 4.65	2.57 \pm 27.01	0.98 \pm 8.50	0.8
Coleoptera	26	7.16	35	6.07	996.36	2.66	5.3	0.153 \pm 0.49	6.01 \pm 18.95	4.35 \pm 17.41	5.45 \pm 18.98	5.73
Collembola	1	0.28	1	0.17	13.29	0.04	0.16	0.004 \pm 0.07	0.15 \pm 2.20	0.06 \pm 0.88	0.13 \pm 1.98	0.14
Diplopoda	6	1.65	6	1.04	208.16	0.56	1.08	0.026 \pm 0.16	0.86 \pm 5.96	0.91 \pm 8.09	0.69 \pm 6.52	0.77
Diptera	2	0.55	6	1.04	45.86	0.12	0.57	0.026 \pm 0.34	0.41 \pm 5.54	0.20 \pm 2.23	0.11 \pm 1.20	0.26
Formicidae	44	12.12	97	16.81	2391.8	6.39	11.77	0.424 \pm 1.66	11.08 \pm 26.54	10.44 \pm 44.48	8.88 \pm 25.09	9.98
Gastropoda	8	2.2	8	1.39	458.99	1.23	1.61	0.035 \pm 0.18	1.91 \pm 11.33	2.00 \pm 18.58	1.61 \pm 10.98	1.76
Gryllidae	31	8.54	32	5.55	6905.14	18.46	10.85	0.140 \pm 0.36	8.84 \pm 25.10	30.15 \pm 113.29	10.63 \pm 28.88	9.73
Hemiptera	13	3.58	14	2.43	575.33	1.54	2.52	0.061 \pm 0.26	4.51 \pm 19.47	2.51 \pm 12.46	4.23 \pm 19.12	4.37
Homoptera	9	2.48	9	1.56	197.31	0.53	1.52	0.039 \pm 0.19	2.66 \pm 14.45	0.86 \pm 4.57	2.45 \pm 14.23	2.55
Hymenoptera	6	1.65	6	1.04	466.04	1.25	1.31	0.026 \pm 0.16	1.16 \pm 8.41	2.04 \pm 16.19	0.97 \pm 8.06	1.07
Isopoda	3	0.83	3	0.52	111.26	0.3	0.55	0.013 \pm 0.11	0.39 \pm 3.78	0.49 \pm 6.64	0.44 \pm 6.44	0.42
Isoptera	17	4.68	97	16.81	672.2	1.8	7.76	0.424 \pm 1.88	5.96 \pm 22.52	2.94 \pm 12.89	5.44 \pm 21.41	5.7
Insect larvae	18	4.96	25	4.33	2953.7	7.89	5.73	0.109 \pm 0.42	4.94 \pm 19.20	12.90 \pm 61.45	5.51 \pm 20.93	5.22
Mantodea	1	0.28	1	0.17	24.52	0.07	0.17	0.004 \pm 0.07	0.11 \pm 1.65	0.11 \pm 1.62	0.04 \pm 0.56	0.07
Plant material	4	1.1	6	1.04	139.8	0.37	0.84	0.026 \pm 0.23	1.05 \pm 9.49	0.61 \pm 5.56	0.92 \pm 9.34	0.99
Myrmelionidae larvae	3	0.83	3	0.52	83.77	0.22	0.52	0.013 \pm 0.11	0.26 \pm 2.31	0.37 \pm 3.45	0.25 \pm 2.86	0.25
Odonata	1	0.28	1	0.17	27.64	0.07	0.17	0.004 \pm 0.07	0.44 \pm 6.61	0.12 \pm 1.83	0.44 \pm 6.61	0.44
Opiliones	2	0.55	2	0.35	13.43	0.04	0.31	0.009 \pm 0.09	0.27 \pm 3.40	0.06 \pm 0.78	0.11 \pm 1.34	0.19
Orthoptera	44	12.12	46	7.97	5740.38	15.34	11.81	0.201 \pm 0.42	14.63 \pm 33.10	25.07 \pm 67.14	15.99 \pm 34.43	15.31
Insect egg	1	0.28	1	0.17	8.93	0.02	0.16	0.004 \pm 0.07	0.15 \pm 2.20	0.04 \pm 0.59	0.03 \pm 0.43	0.09
Phasmida	1	0.28	1	0.17	46.9	0.13	0.19	0.004 \pm 0.07	0.11 \pm 1.65	0.20 \pm 3.10	0.07 \pm 1.08	0.09
Scorpionida	2	0.55	2	0.35	449.04	1.2	0.7	0.009 \pm 0.09	0.58 \pm 6.96	1.96 \pm 21.17	0.59 \pm 7.00	0.59
Total			577									

available, 39 were above ground and perches averaged 0.31 ± 0.40 m (range=0.10–1.80 m).

Body temperatures averaged $31.62\pm 2.52^\circ\text{C}$ ($n=102$, range=26.50–36.60 $^\circ\text{C}$), substrate temperatures averaged $30.99\pm 3.07^\circ\text{C}$ ($n=107$, range=25.80–42.00 $^\circ\text{C}$), air temperature at 5 cm above the substrate averaged $30.90\pm 3.10^\circ\text{C}$ ($n=45$, range=24.20–38.00 $^\circ\text{C}$), and air temperatures at chest height averaged $30.76\pm 2.76^\circ\text{C}$ ($n=106$, range=23.80–37.60 $^\circ\text{C}$). A stepwise multiple regression analysis showed that body temperature is more strongly associated with air temperature at 5 cm from the substrate ($r=0.83$; $F_{2,42}=27.32$; $p<0.001$) than with the other environmental temperatures recorded.

Diet

We compiled data on 578 food items identified in 26 different categories. The diet was mainly composed of invertebrates (insects, spiders and molluscs) and occasionally plant material (Table 1). The most important item was Araneae, representing approximately one

quarter of the diet considering number, volume, frequency, or the relative importance of prey categories (Table 1). Orthoptera and Formicidae were always among the four most important categories. Considering pooled stomachs, Isoptera and Blattaria were most important numerically and volumetrically, respectively (Table 1). Prey importance indices for both individual and pooled stomachs indicated that more than 60% of the diet consists of only four prey categories.

Overall, diet niche overlap was high between males and females for both frequency (0.76) and volume (0.951), indicating that males and females eat similar items. The intersexual comparison of niche breadth using individual stomachs and controlling for SVL showed a significant difference in prey number (ANCOVA $F_{2,209}=6.203$, $p<0.005$; males= 1.407 ± 0.531 , females= 1.595 ± 0.892), and no difference for volume (ANCOVA $F_{2,209}=2.113$, $p<0.1235$; males= 1.296 ± 0.447 , females= 1.367 ± 0.610). Both mean prey volume and maximum prey volume were moderately related to SVL (mean volume: $r=0.171$, $p=0.0117$; max

Table 2. Summary of morphometric variables of *Anolis brasiliensis* according to sex. Values represent mean±standard deviation of isometric body size and shape (size-free) variables. Raw values (in mm) are in parentheses.

Variables	Females (n=372)	Males (n=325)
Body size	4.06±0.08	4.04±0.11
Snout-vent length	0.43±0.02 (60.83±3.73)	0.44±0.02 (60.78±5.36)
Tail length	0.78±0.02 (138.15±10.84)	0.82±0.02 (146.38±14.69)
Body width	-0.25±0.05 (12.78±1.86)	-0.33±0.05 (10.28±1.56)
Body height	-0.37±0.04 (9.84±1.37)	-0.40±0.05 (9.00±1.49)
Head width	-0.37±0.02 (9.78±0.68)	-0.36±0.02 (9.81±0.77)
Head height	-0.45±0.03 (8.08±0.75)	-0.45±0.03 (7.98±0.69)
Head length	-0.19±0.02 (14.78±0.89)	-0.18±0.01 (14.70±1.19)
Forelimb length	0.09±0.02 (27.69±1.79)	0.11±0.02 (28.66±2.44)
Hindlimb length	0.33±0.02 (48.30±3.13)	0.35±0.02 (49.75±3.81)

volume: $r=0.209$, $p=0.002$). Minimum prey volume was not associated with SVL ($r=0.099$, $p=0.144$).

Considering pooled stomachs, males had a wider volumetric niche breadth ($t=39.96$, $df=1960,7$, $p<0.001$). Females had a slightly wider numeric niche ($t=4.44$, $df=1993,82$, $p<0.001$, males= 6.27 ± 0.98 , females= 6.46 ± 0.93).

Morphometry and sexual dimorphism

Morphometric variables are summarised in Table 2. Females have a larger body size than males ($F_{1,695}=17.87$, $p<0.001$). A significant intersexual difference exists on the shape variables taken simultaneously ($\chi^2=490.31$, $p<0.001$). The model selection analysis indicated that body width, tail length, head length, head height and SVL are the most powerful discriminators between sexes (Table 3). The linear discriminant function using the five selected variables had a misclassification error of 0.14 based on 100 bootstrap replications. The model averaging analysis retained 24 models with $DAIC_c<4$; averaged coefficients were significant only for head length and tail length, which were also the variables with highest relative importance (Table 3). Females have shorter heads and tails relative to males (Table 2).

Reproduction

Males of *A. brasiliensis* varied from 30 to 75 mm ($n=396$). The smallest male bearing spermatozoa had a SVL of 46 mm. Five stages of spermatogenic activity were recognised. Mitotic activity of the germinative epithelium is pronounced in stage II and even more pronounced in stage III (Table 4). In stage IV, testes contained spermatozoa

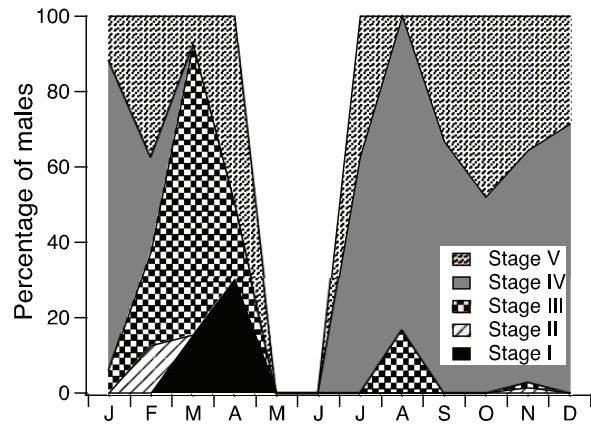


Fig. 3. Spermatogenesis activity in male *Anolis brasiliensis* from Cerrado.

in the lumen, and mitotic activity reached its maximum level, coupled with maximal values of testes parameters (Table 4). Epididymides in stages I, II and III contained no sperm and had reduced lumina, and lower epithelium with cuboid cells. In stage IV, the lumen of the epididymis was completely filled with spermatozoa, while in stage V the lumen had spermatozoa and/or an amorphous material (sometimes with a few spermatozoa). Stages I to III occurred only in the period between January and August (Fig. 3). Stages IV and V occurred in some males almost year-round, from June to January, with peaks from November to January (Fig. 3).

Females of *Anolis brasiliensis* had an SVL between 26 mm and 70 mm ($n=417$). The smallest reproductive female had a SVL of 49.4 mm. Although mean egg production based on oviductal eggs was 1.74 ($n=228$), the number of eggs deposited at one time (clutch size) is one, because each egg was at a different stage of shell development. Potential egg production based on vitellogenic follicles was 5.14 ($n=264$), and on corpora lutea was 1.97 ($n=221$). Estimates of egg production based on oviductal eggs and vitellogenic follicles were not statistically different (ANOVA $F_{490,1}=0.831$, $p=0.363$). Egg production based on combined oviductal eggs and vitellogenic follicles varied from 1 to 8 ($=1.44\pm0.57$, $n=303$) and was correlated with female SVL ($F_{1,299}=23.65$, $p<0.001$). Based on a paired t -test, we found significant differences of egg volume

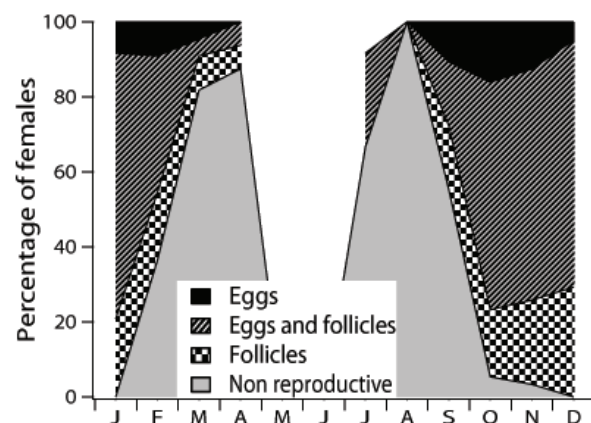


Fig. 4. Reproductive condition of female *Anolis brasiliensis* from Cerrado.

Table 3. Model selection and model averaging of shape variables as predictors of sex in *Anolis brasiliensis*. Best model is the shortest model based on manual selection of variables and the Akaike Information Criterion (AIC). Values represent coefficients of variables in different models. Asterisks indicate significant model-averaged coefficients ($p < 0.05$). svl: snout-vent length, tl: tail length, bw: body width, bh: body height, hw: head width, hh: head-height, hl: head length, fl: forelimb length, hll: hindlimb length.

	Intercept	svl	tl	bw	bh	hw	hh	hl	fl	hll	AIC	χ^2	p
Full model	-42.06	-21.75	40.30	-31.36	-13.74	21.11	1.63	-64.24	10.25	NA	490.77	490.31	<0.001
Best model	-46.228	-25.24	33.72	-37.94	-18.77	—	—	-62.72	—	—	489.18	8.74	0.003
Model-averaged coefficients	-43.25	-18.05	42.87*	-28.89	-10.99	20.41	5.32	-60.24*	11.29	3.96			
Relative variable importance	1.00	0.83	0.97	0.89	0.86	0.74	0.59	0.97	0.55	0.50			

within lizards with more than one oviductal egg ($t=8.57$, $df=106$, $p < 0.001$, volume of largest egg= 539.71 ± 139.31 , volume smallest egg= 432.25 ± 120.48), indicating that these lizards deposit a single egg sequentially. The presence of oviductal eggs and vitellogenic follicles was more evident in the rainy season, mainly from October to January (Fig. 4). Mean egg volume was 480.84 ± 103.20 mm³, and was positively correlated with female SVL ($F_{1,224}=3.94$, $p=0.048$). Recruitment occurred mostly from January to April, but a few newborns were present in November (Fig. 5).

DISCUSSION

Species distribution modelling

Anolis brasiliensis has a large distribution within the Cerrado biome in central Brazil, with additional areas of suitability within the Caatinga biome in northeastern

Table 4. Descriptive testis parameters according with spermatogenic activity stages. n=sample size, DST=diameter of seminiferous tubule, GEH=germinative epithelium height and V=testis volume (mm³).

Stages	n	Parameters	Average	Min	Max
I	5	DST	1.31	0.43	2.31
		GEH	-	-	-
		V	9.73	0.42	22.99
II	2	DST	1.54	0.67	2.41
		GEH	0.66	0.13	1.20
		V	7.70	6.76	8.63
III	17	DST	1.54	0.91	2.76
		GEH	0.42	0.16	1.16
		V	10.66	1.66	29.70
IV	95	DST	2.60	1.34	3.72
		GEH	0.86	0.43	1.36
		V	29.01	0.39	55.33
V	56	DST	2.44	1.08	3.57
		GEH	0.20	0.06	1.21
		V	25.33	1.73	45.48

Brazil, and northern savannahs in Venezuela and Colombia. The species is associated with areas with strong precipitation seasonality. At a finer scale, it is associated with rather forested areas compared to the grasslands and savannahs otherwise typical of the Cerrado (e.g., Vitt et al., 2008a). Habitat structural changes within the Cerrado can be determined by soil type, terrain declivity, nutrient and water availability, and fire dynamics (Oliveira & Marquis, 2002). The thermal ecology of *A. brasiliensis* (previously discussed in Vitt et al., 2008a) could partly explain its distribution within the Cerrado.

Microhabitat, activity and temperatures

Anolis brasiliensis were collected only at, or next to, forested sites on trees and leaf litter. These anoles typically rely on crypsis, and are most commonly observed prior to the hottest hours of the day in shaded areas. Concerning activity and microhabitat use, *A. brasiliensis* is therefore similar to other species in the *A. chrysolepis* species group, as well as more distantly related Amazonian anoles such as *A. trachyderma* and *A. fuscoauratus* (Vitt et al., 2002; 2008b). However, *A. brasiliensis* is more active early in the morning, contrasting with the patterns reported for *A. nitens*, *A. tandai* and *A. scyphus* (Vitt & Zani, 1996; Vitt et al., 2001a). Anoles in the Amazon rainforest do not experience extreme daily or seasonal temperature fluctuations as do anoles in Cerrado, where they are exposed to a prolonged dry season (Vitt et al.,

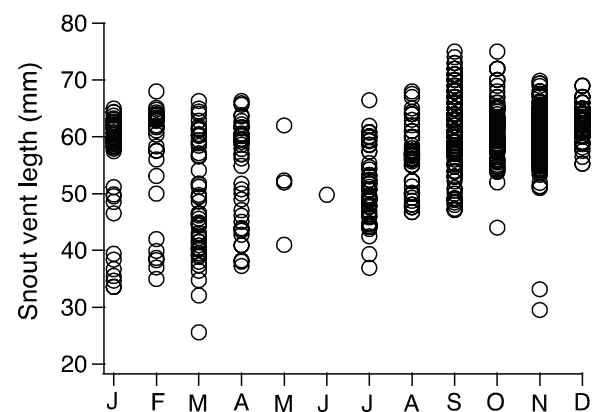


Fig. 5. Snout-vent-length of *Anolis brasiliensis* from Cerrado.

2008b). Nevertheless, it appears to retain physiological traits of other species within the *A. chrysolepis* group.

Body temperatures of active *Anolis brasiliensis* were similar to Amazon rainforest anoles including *A. tandai* (27.7°C, Vitt et al., 2001a), *A. nitens*, *A. scypheus* (27.9°C, Vitt & Zani, 1996), *A. punctatus* and *A. transversalis* (29.2°C and 27.6°C, Vitt et al., 2003c), and *A. fuscoauratus* (28.7°C, Vitt et al., 2003b). However, body temperatures of active *A. brasiliensis* were considerably lower than those of sympatric species such as *Ameiva ameiva* (37.0–39.4°C, Vitt & Colli, 1994), *Cnemidophorus ocellifer* (37.5°C, Mesquita & Colli, 2003a, b), *Kentropyx calcarata* (37.6°C, Vitt, 1991b; Vitt et al., 1997a), *Tropidurus oreadicus* (33.48°C, Faria & Araujo, 2004), *Micrablepharus maximiliani* (34.6°C, Vieira et al., 2000), but similar to *Copeoglossum nigropunctatum* (32.9°C, Vitt & Blackburn, 1991; Vitt et al., 1997a) and *Gymnodactylus amarali* inside termite nests during daytime (31.3°C, Colli et al., 2003; Vitt et al., 2007). Forest thermoconformers (e.g., *Sphaerodactylus*) are usually active at relatively low temperatures, and are considered intolerant to extreme temperatures (Huey, 1974; Huey & Slatkin, 1976; Huey et al., 2009). Although low body temperatures in anoles may reflect phylogenetic conservatism, they are influenced by environmental temperatures. For example, *A. auratus* in Amazonian savannahs operates at higher body temperatures (e.g., 33.9°C, Vitt & Carvalho, 1995). Considering that body temperatures of *A. brasiliensis* and closely related forest species are similar, a combination of habitat choice (forested areas) and behaviour (activity period) likely allows *A. brasiliensis* to live in the thermally more extreme Cerrado.

Diet

Dietary differences among closely related species, populations, and seasons are common, and have been shown for many lizard species (Dunham, 1983; Pianka, 1986; Vitt, 1991c; Vitt et al., 2003b; Losos, 2009). Spiders, grasshoppers, ants and termites are common items in the stomachs of a previously studied population of *A. brasiliensis* (Vitt et al., 2008a), as well as other Neotropical anoles (Vitt et al., 2003b, c). This is not unexpected, because anoles are generalists and share a similar morphology and foraging behaviour. Similarity in diets among anole species likely represents niche conservatism nested in the species' evolutionary history. These prey types are not only common among anoles (Vitt et al., 2001b; Vitt & Zan, 2005; Vitt et al., 2008a), but among other Amazonian insectivorous sit-and wait iguanians (Huey & Pianka, 1981; Cooper et al., 2001). Dietary differences are often expressed in relative proportions rather than prey types, with the exception of species that specialise on ants (Pianka & Pianka, 1970; Pianka & Parker, 1975; Vitt, 1991a; Vitt et al., 1997b). In Amazonian anoles, species from the same forest strata can differ in prey type or in prey size (Vitt et al., 2002; 2003b, c).

Differences in niche breadth between sexes were detected, even when the effect of body size was taken into account, but could not be associated with head dimensions considering that prey types overlapped between sexes. Intersexual differences in diet appear a

consequence of the interaction of low specialisation in diet and social behaviour, which could promote differences in microhabitat use and foraging (Perry, 1996; Butler et al., 2000; 2007; Butler, 2007).

Sexual Dimorphism

Female *A. brasiliensis* are larger but have shorter heads and tails than males, similar to *A. chrysolepis* and *A. trachyderma* from Amazonia (Vitt & Zani, 1996; Vitt et al., 2002). Sexual size and shape dimorphism is widespread in *Anolis* (Losos, 2009), and can result from differences in mating systems, diets and habitat use (Losos et al., 2002). Caribbean anoles exhibit sexual differences in microhabitat use (perch height and diameter, Butler et al., 2000; Butler & Losos, 2002), which might also be the case for *A. brasiliensis*. Sexual differences in head shape have been correlated with dietary performance, with males ingesting harder and more robust prey (Herrel et al., 2003; 2006), as well as sexual selection (Vitt & Zani, 1996; Butler & Losos, 2002). Because we observed high diet niche overlap between sexes in *A. brasiliensis*, the observed head size differences may be a sexually selected trait important for male-male combat or interactions with females. Tail length in *Anolis* is related to locomotion (especially in arboreal habitats, Gillis et al., 2009) and differences in tail length may result from shifts in microhabitats between sexes (Losos, 1990a, b). This reinforces the demand for detailed information about microhabitat use in *A. brasiliensis* to address whether sexual dimorphism and diet differences are explained by habitat use or social interactions.

Reproduction

Reproduction in *A. brasiliensis* is extended and markedly seasonal. Males begin reproductive activity before females. Early initiation of reproduction by males has a low cost because spermatozoa production is energetically inexpensive (Marshall & Hook, 1960). When females are not in breeding condition, the frequency of reproductive males decreases, suggesting a benefit of synchronisation of extended male reproductive activity with female reproduction (Vieira et al., 2001; Wiederhecker et al., 2002). Reproduction of several other tropical lizard species is markedly seasonal (Barbault, 1976; Rocha, 1992; Van Sluys, 1993; Colli, 1991; Wiederhecker et al., 2002; Mesquita & Colli, 2003b), with low food availability and egg desiccation during the dry season as likely reasons (Janzen & Schoener, 1968; Andrews et al., 1982; Andrews & Wright, 1994). However, the critical level of arthropod abundance has never been established, and a study of 13 tropical lizard species showed that fat accumulation occurs mainly in the dry season, suggesting that reproductive seasonality is not constrained by food (Colli et al., 1997). Egg survival can also be a critical factor for lizard recruitment (Overall, 1994), and poor hydric conditions can reduce embryo size, thereby restricting the breeding season (Packard et al., 1982; Packard & Packard, 1988). The predominance of incubating eggs during the rainy season observed in *A. brasiliensis* suggest that environmental conditions for egg development can influence the seasonal reproductive pattern.

During the peak of reproductive activity in females (October to January), only stages IV (full reproduction) and V (beginning of degeneration) were observed in males. This suggests that variation in the germinative epithelium activity is small and cell division is restored shortly after arrest (degeneration). Thus, although spermatozoa are present in males practically year-round, during the female breeding season there is a marked increase in germinative epithelium cell division. This pattern has also been observed in *A. opalinus* (Jenssen & Nunez, 1994) and *Tropidurus torquatus* (Vieira et al., 2001).

Clutch size in *A. brasiliensis* is one egg, which is small compared to other Cerrado lizards which lay between 2 and 16 eggs (Colli, 1991; 2003b; Colli & Zamboni, 1999; Mesquita & Colli, 2003a, Wiederhecker et al., 2002). However, *A. brasiliensis* and other anoles can produce clutches of a single egg in rapid succession, such that seasonal egg production may not be different from other Cerrado lizard species that produce multiple egg clutches (e.g., Vieira et al., 2000). Even though anoles produce only a single egg at a time, they have been much more successful in terms of diversification than most other lizards. Seasonal egg production and oviductal egg volume in *A. brasiliensis* was correlated with female SVL. The former is common in species that do not have a fixed clutch size (Tinkle et al., 1970; Dunham & Miles, 1985; Dunham et al., 1988), and the latter has previously been suggested for anoles (Andrews & Rand, 1974). We also show that the total complement of oviductal eggs and vitellogenic follicles (an indicator of seasonal reproductive potential) increases with female size. Breeding by *A. brasiliensis* took place in the rainy season and likely reflects the effect of the hydric environment on egg development. The Cerrado dry season experiences long periods of high temperatures and little rainfall. Microhabitats for egg development of *A. brasiliensis* are poorly known, and nothing is known about the physiological response of their eggs to desiccation. However, studies on other lizard species have demonstrated that substrate water potential affects hatchling size and condition (Muth, 1980; Tracy, 1980; Packard & Packard, 1988; Packard, 1991; Lin & Ji, 1998), and wet (but not dry) mass of hatchlings (Ji & Brana, 1999).

In this study, we have shown that the widespread Cerrado anole, *A. brasiliensis*, is ecologically very similar to other species in the *A. chrysolepis* species group as well as more distantly related anoles, some of which live in tropical lowland rainforests such as the Amazon. These observations of conserved life-history traits reiterate the importance of evolutionary history for squamate reptiles (Vitt et al., 2003a; Vitt & Pianka, 2005).

ACKNOWLEDGEMENTS

All data were collected following ethical guidelines provided by the American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL), the Society for the Study of Amphibians and Reptiles (SSAR) and Conselho Brasileiro de Biologia (CBO). GCC and AAG thank CNPq - Conselho Nacional de Desenvolvimento Científico e Tecnológico and FAPERN - Fundação de Apoio à Pesquisa do Rio Grande do Norte for financial support

(Grants # 563352/2010-8 and 552031/2011-9). GCC and GRC also thank CNPq for their productivity research grants (302776/2012-5). DOM thanks CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for financial support and University of Texas and Eric Pianka for help in finalising this manuscript. GRC thanks CAPES, CNPq and FAPDF - Fundação de Apoio à Pesquisa do Distrito Federal for financial support. LJV thanks the National Science Foundation for support under Grant No. 0415430. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. Personal funds of LJV and Janalee P. Caldwell supported one field vehicle. Portions of this research were conducted under IACUC Assurance Number A3240-01, University of Oklahoma.

REFERENCES

- Alho, C.J.R. & Martins, E.S. (1995). *De Grão em Grão, o Cerrado Perde Espaço*. Brasília: WWF-Fundo Mundial para a Natureza.
- Andrews, R. & Rand, A.S. (1974). Reproductive effort in anoline lizards. *Ecology* 55, 1317–1327.
- Andrews, R.M. & Wright, S.J. (1994). Long-term population fluctuations of a tropical lizard: a test of causality. In *Lizard Ecology: Historical and Experimental Perspectives*, 267–285. Vitt, L.J. and Pianka, E.R. (Eds). Princeton, New Jersey: Princeton University Press.
- Andrews, R.M., Rand, A.S. & Guerrero, S. (1982). Seasonal and spatial variation in the annual cycle of a tropical lizard. In *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*, 441–454. Rhodin, A.G. and Miyata, K. (Eds). Washington, D.C.: Smithsonian Institution Press.
- Ávila-Pires, T.C.S. (1995). Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandlungen, Leiden* 299, 1–706.
- Barbault, R. (1976). Population-dynamics and reproductive patterns of three African skinks. *Copeia* 1976, 483–490.
- Burnaby, T.P. (1966). Growth-invariant discriminant functions and generalized distances. *Biometrics* 22, 96–110.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, New York, USA: Springer-Verlag.
- Butler, M.A. (2007). Vive le difference! Sexual dimorphism and adaptive patterns in lizards of the genus *Anolis*. *Integrative and Comparative Biology* 47, 272–284.
- Butler, M.A. & Losos, J.B. (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecological Monographs* 72, 541–559.
- Butler, M.A., Schoener, T.W. & Losos, J.B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* Lizards. *Evolution* 54, 259–272.
- Butler, M.A., Sawyer, S.A. & Losos, J.B. (2007). Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature* 447, 202–205.
- Chambers, J.M. & Hastie, T.,J. (1992). *Statistical Models in S*. New York, NY: Chapman & Hall.
- Colli, G.R. (1991). Reproductive ecology of *Ameiva ameiva* (Sauria: Teiidae) in the cerrado of central Brazil. *Copeia*

- 1991, 1002–1012.
- Colli, G.R. & Zamboni, D.S. (1999). Ecology of the worm-lizard *Amphisbaena alba* in the cerrado of central Brazil. *Copeia* 1999, 733–742.
- Colli, G.R., Péres, A.K., Jr. & Zatz, M.G. (1997). Foraging mode and reproductive seasonality in tropical lizards. *Journal of Herpetology* 31, 490–499.
- Colli, G.R., Mesquita, D.O., Rodrigues, P.V.V. & Kitayama, K. (2003). The ecology of the gecko *Gymnodactylus geckoides amarali* in a Neotropical savanna. *Journal of Herpetology* 37, 694–706.
- Cooper, W.E., Jr., Vitt, L.J., Caldwell, J.P. & Fox, S.F. (2001). Foraging modes of some American lizards: Relationships among measurement variables and discreteness of modes. *Herpetologica* 57, 65–76.
- Costa, G.C., Nogueira, C.C., Machado, R.B. & Colli, G.R. (2007). Squamate richness in the Brazilian Cerrado and its environmental–climatic associations. *Diversity and Distributions* 13, 714–724.
- Crawley, M.J. (2007). *The R Book*. Chichester, England: John Wiley & Sons Ltd.
- D'Angiolella, A., Gamble, T., Avila-Pires, T., Colli, G., et al. (2011). *Anolis chrysolepis* Duméril and Bibron, 1837 (Squamata: Iguanidae), revisited: molecular phylogeny and taxonomy of the *Anolis chrysolepis* species group. *Bulletin of the Museum of Comparative Zoology* 160, 35–63.
- Dunham, A.E. (1983). Realized niche overlap, resource abundance, and interespecific competition In *Lizard Ecology: Studies of a Model Organism*, 261–280. Huey, R.B., Pianka, E.R. & Schoener, T.H. (Eds). Cambridge, Massachusetts: Harvard University Press.
- Dunham, A.E. & Miles, D.B. (1985). Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. *American Naturalist* 126, 231–257.
- Dunham, A.E., Miles, D.B. & Reznick, D.N. (1988). Life history patterns in squamate reptiles In *Biology of the Reptilia. Vol. 16, Ecology B. Defense and Life History*, 441–522. Gans, C. and Huey, R.B. (Eds). New York : Alan R. Liss, Inc.
- Elith, J. & Leathwick, J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics* 40, 677–697.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., et al. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17, 43–57.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Faraway, J.J. (2006). *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Boca Raton, FL: Chapman & Hall/CRC.
- Faria, R.G. & Araujo, A.F.B. (2004). Sinytopy of two *Tropidurus* species (Squamata: Tropiduridae) in a rocky Cerrado habitat in Central Brazil. *Brazilian Journal of Biology* 64, 775–786.
- Filzmoser, P. & Gschwandtner, M. (2014). mvoutlier: Multivariate outlier detection based on robust methods. R package version 2.0.5. Available from: <<http://CRAN.R-project.org/package=mvoutlier>>.
- Gillis, G.B., Bonvini, L.A. & Irschick, D.J. (2009). Losing stability: tail loss and jumping in the arboreal lizard *Anolis carolinensis*. *Journal of Experimental Biology* 212, 604–609.
- Herrel, A., Vanhooydonck, B. & Irschick, D.J. (2003). Ontogeny of head shape, bite performance and diet in the Jamaican lizard *Anolis lineatopus*. *Integrative and Comparative Biology* 43, 1077.
- Herrel, A., Joachim, R., Vanhooydonck, B. & Irschick, D.J. (2006). Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal Of The Linnean Society* 89, 443–454.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965–1978.
- Hijmans, R.J., Phillips, S., Leathwick, J. and Elith, J. (2013). Package 'dismo'. Available online at: <<http://cran.r-project.org/web/packages/dismo/index.html>>.
- Huey, R.B. (1974). Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184, 1001–1003.
- Huey, R.B. & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51, 363–384.
- Huey, R.B. & Pianka, E.R. (1981). Ecological consequences of foraging mode. *Ecology* 62, 991–999.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., et al. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B-Biological Sciences* 276, 1939–1948.
- Janzen, D.H. & Schoener, T.W. (1968). Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49, 96–110.
- Jenssen, T.A. & Nunez, S.C. (1994). Male and female reproductive-cycles of the Jamaican lizard, *Anolis opalinus*. *Copeia* 767–780.
- Ji, X. & Brana, F. (1999). The influence of thermal and hydric environments on embryonic use of energy and nutrients, and hatchling traits, in the wall lizards (*Podarcis muralis*). *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology* 124, 205–213.
- Jolicoeur, P. (1963). The multivariate generalization of the allometry equation. *Biometrics* 19, 497–499.
- Klink, C. & Machado, R.B. (2005). Conservation of the Brazilian Cerrado. *Conservation Biology* 19, 707–713.
- Lin, Z.H. & Ji, X. (1998). The effects of thermal and hydric environments on incubating eggs and hatchlings of the grass lizard, *Takydromus septentrionalis*. *Zoological Research* 19, 439–445.
- Losos, J.B. (1990a). Ecomorphology, performance capability, and scaling of west-Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* 60, 369–388.
- Losos, J.B. (1990b). The evolution of form and function: morphology and locomotor performance in West-Indian *Anolis* lizards. *Evolution* 44, 1189–1203.
- Losos, J.B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, CA: University of California Press.
- Losos, J.B., Butler, M.A. & Schoener, T.W. (2002). Sexual dimorphism in size and shape in relation to habitat use in Caribbean *Anolis* lizards In *Lizard Social Behavior*, Stanley F. Fox, and Troy A. Baird (Eds). Baltimore: Johns Hopkins University Press.

- Machado, R.B., Ramos Neto, M.B., Pereira, P.G.P., Caldas, E.F., et al. (2004). Estimativas de perda de área do Cerrado brasileiro. Unpublished technical report. Conservation International, Brasília, DF.
- Marshall, A.J. & Hook, R. (1960). The breeding biology of equatorial vertebrates: reproduction of the lizard *Agama agama lionotus* Boulenger at Lat. 0°01'N. *Proceedings of the Zoological Society of London* 134, 197–205.
- Mesquita, D.O. & Colli, G.R. (2003a). Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). *Copeia* 2003, 285–298.
- Mesquita, D.O. & Colli, G.R. (2003b). The ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a Neotropical savanna. *Journal of Herpetology* 37, 498–509.
- Muth, A. (1980). Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. *Ecology* 61, 1335–1343.
- Nicholson, K.E., Crother, B.I., Guyer, C. & Savage, J.M. (2012). It is time for a new classification of anoles (Squamata: Dactyloidae). *Zootaxa* 3477, 1–108.
- Nogueira, C.C., Ribeiro, S., Costa, G.C. & Colli, G.R. (2011). Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography* 38, 1907–1922.
- Oliveira, P.S. & Marquis, R.J. (2002). *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York, NY: Columbia University Press.
- Overall, K.L. (1994). Lizard egg environments In *Lizard Ecology: Historical and Experimental Perspectives*, 51–72. Vitt, L.J. and Pianka, E.R. (Eds). Princeton, New Jersey: Princeton Univ. Press.
- Packard, G.C. (1991). Physiological and ecological importance of water to embryos of oviparous reptiles In *Egg Incubation, its Effect on Embryonic Development in Birds and Reptiles*, 213–228. Deeming, D.C. and Ferguson, M.W.J. (Eds). Cambridge: Cambridge University Press.
- Packard, G.C. & Packard, M.J. (1988). The physiological ecology of the reptilian eggs and embryos In *Biology of the Reptilia*, 523–606. Gans, C. and Huey, R.B. (Eds). New York: A.R. Liss, Inc.
- Packard, M.J., Packard, G.C. & Boardman, T.J. (1982). Structure of eggshells and water relations of reptilian eggs. *Herpetologica* 38, 136–155.
- Penone, C., Davidson, A.D., Shoemaker, K.T., Di Marco, M., et al. (2014). Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* 5, 961–970.
- Perry, G. (1996). The evolution of sexual dimorphism in the lizard *Anolis polylepsis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology* 74, 1238–1245.
- Peters, A. & Hothorn, T. (2013). ipred: Improved Predictors. R package. Available from: <<http://CRAN.R-project.org/package=ipred>>.
- Phillips, S.J. & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Pianka, E.R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* 4, 53–74.
- Pianka, E.R. (1986). *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure*. Princeton, New Jersey: Princeton Univ. Press.
- Pianka, E.R. & Pianka, H.D. (1970). Ecology of *Moloch horridus* (Lacertilia: Agamidae) in western Australia. *Copeia* 1970, 90–103.
- Pianka, E.R. & Parker, W.S. (1975). Ecology of horned lizards: review with special reference to *Phrynosoma platyrhinos*. *Copeia* 1975, 141–162.
- Pough, F.H., Andrews, R.M., Cadle, J.E., Crump, M.L., et al. (2004). *Herpetology*. Upper Saddle River, New Jersey: Prentice Hall.
- Quinn, G.P. & Keough, M.J. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge, UK: Cambridge University Press.
- Rissler, L.J. & Apodaca, J.J. (2007). Adding more ecology into species delimitation: Ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). *Systematic Biology* 56, 924–942.
- Rocha, C.F.D. (1992). Reproductive and fat body cycles of the tropical sand lizard (*Liolaemus lutzae*) of Southeastern Brazil. *Journal of Herpetology* 26, 17–23.
- Rodrigues, M.T. (2005). The conservation of the Brazilian reptiles: challenges for a megadiversity country. *Conservation Biology* 19, 659–664.
- Roff, D.A. (1992). *The Evolution of Life Histories: Theory and Analysis*. London: Chapman and Hall.
- Roff, D.A. (2002). *Life History Evolution*. Sunderland, MA, USA: Sinauer Associates, Inc.
- Rohlf, F.J. & Bookstein, F.L. (1987). A comment on shearing as a method for “size correction”. *Systematic Zoology* 36, 356–367.
- Rubin, D.B. (1996). Multiple imputation after 18+ years. *Journal of the American Statistical Association* 91, 473–489.
- Simpson, E.H. (1949). Measurement of diversity. *Nature* 163, 688.
- Smith, H.M., Sinelnik, G., Fawcett, J.D. & Jones, R.E. (1973). A survey of the chronology of ovulation in anoline lizard genera. *Transactions of the Kansas Academy of Science* 75, 107–120.
- Somers, K.M. (1986). Multivariate allometry and removal of size with principal component analysis. *Systematic Zoology* 35, 359–368.
- Tabachnick, B.G. & Fidell, L.S. (1996). *Using Multivariate Statistics*. New York, New York: HarperCollins Publishers Inc.
- Tinkle, D.W., Wilbur, H.M. & Tilley, S.G. (1970). Evolutionary strategies in lizard reproduction. *Evolution* 24, 55–74.
- Tracy, C.R. (1980). Water relations of parchment-shelled lizard (*Sceloporus undulatus*) eggs. *Copeia* 478–482.
- Uetz, P. & Hošek, J. (2014). The Reptile Database, Available from: <<http://www.reptile-database.org>>. Accessed: June 23, 2014.
- Van Buuren, S., Brand, J.P.L., Groothuis-Oudshoorn, C.G.M. & Rubin, D.B. (2006). Fully conditional specification in multivariate imputation. *Journal of Statistical Computation and Simulation* 76, 1049–1064.
- Van Buuren, S. & Groothuis-Oudshoorn, K. (2011). MICE: multivariate imputation by chained equations in R. *Journal of Statistical Software* 45, 1–67.
- Van Sluys, M. (1993). The reproductive cycle of *Tropidurus*

- itambergi* (Sauria: Tropicuridae) in Southeastern Brazil. *Journal of Herpetology* 27, 28–32.
- Vanzolini, P. & Williams, E. (1970). South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia* 19, 1–124.
- Vieira, G.H.C., Wiederhecker, H.C., Colli, G.R. & B ao, S.N. (2001). Spermiogenesis and testicular cycle of the lizard *Tropidurus torquatus* (Squamata, Tropicuridae) in the Cerrado of central Brazil. *Amphibia-Reptilia* 22, 217–233.
- Vieira, G.H.C., Mesquita, D.O., Peres Jr., A.K., Kitayama, K. & Colli, G.R. (2000). Natural History: *Micrablepharus atticolus*. *Herpetological Review* 31, 241–242.
- Vitt, L.J., Sartorius, S., Avila-Pires, T. & Esposito, E. (2001a). Life on the leaf litter: The ecology of *Anolis nitens tandai* in the Brazilian Amazon. *Copeia* 401–412.
- Vitt, L.J., Shepard, D., Vieira, G., Caldwell, J., et al. (2008a). Ecology of *Anolis nitens brasiliensis* in Cerrado woodlands of Cant ao. *Copeia* 144–153.
- Vitt, L.J. (1991a). Ecology and life history of the scansorial arboreal lizard *Plica plica* (Iguanidae) in Amazonian Brazil. *Canadian Journal of Zoology* 69, 504–511.
- Vitt, L.J. (1991b). Ecology and life history of the wide-foraging lizard *Kentropyx calcarata* (Teiidae) in Amazonian Brazil. *Canadian Journal of Zoology* 69, 2791–2799.
- Vitt, L.J. (1991c). Desert reptile communities. In *The Ecology of Desert Communities*, 249–277. Polis, G. A. (Eds). Tucson: The University of Arizona Press.
- Vitt, L.J. & Blackburn, D.G. (1991). Ecology and life history of the viviparous lizard *Mabuya bistrriata* (Scincidae) in the Brazilian Amazon. *Copeia* 1991, 916–927.
- Vitt, L.J. & Colli, G.R. (1994). Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72, 1986–2008.
- Vitt, L.J. & Carvalho, C.M. (1995). Niche partitioning in a tropical wet season: lizards in the Lavrado area of Northern Brazil. *Copeia* 1995, 305–329.
- Vitt, L.J. & Zani, P.A. (1996). Ecology of the South American lizard *Norops chrysolepis* (Polychrotidae). *Copeia* 1996, 56–68.
- Vitt, L.J. & Pianka, E.R. (2005). Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Science* 102, 7877–7881.
- Vitt, L.J. & Zani, P.A. (2005). Ecology and reproduction of *Anolis capito* in rain forest of southeastern Nicaragua. *Journal of Herpetology* 39, 36–42.
- Vitt, L.J. & Caldwell, J.P. (2014). *Herpetology: An Introductory Biology of Amphibians and Reptiles*. San Diego, California: Academic Press.
- Vitt, L.J., Zani, P.A. & Lima, A.C.M. (1997a). Heliotherms in tropical rain forest: The ecology of *Kentropyx calcarata* (Teiidae) and *Mabuya nigropunctata* (Scincidae) in the Curu a-Una of Brazil. *Journal of Tropical Ecology* 13, 199–220.
- Vitt, L.J., Zani, P.A. &  vila-Pires, T.C.S. (1997b). Ecology of the arboreal tropidurid lizard *Tropidurus* (= *Plica*) *umbra* in the Amazon region. *Canadian Journal of Zoology* 75, 1876–1882.
- Vitt, L.J., Sartorius, S.S., Avila-Pires, T.C.S. & Esposito, E.C. (2001b). Life on the leaf litter: The ecology of *Anolis nitens tandai* in the Brazilian Amazon. *Copeia* 2001, 401–412.
- Vitt, L.J., Avila-Pires, T.C.S., Zani, P.A. & Esposito, M.C. (2002). Life in shade: The ecology of *Anolis trachyderma* (Squamata : Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar anoles. *Copeia* 2002, 275–286.
- Vitt, L.J., Pianka, E.R., Cooper, W.E., Jr. & Schwenk, K. (2003a). History and the global ecology of squamate reptiles. *The American Naturalist* 162, 44–60.
- Vitt, L. J., Avila-Pires, T.C.S., Zani, P.A., Sartorius, S.S. & Esposito, M.C. (2003b). Life above ground: ecology of *Anolis fuscaoratus* in the Amazon rain forest, and comparisons with its nearest relatives. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 81, 142–156.
- Vitt, L.J., Avila-Pires, T.C.S., Esposito, M.C., Sartorius, S.S. & Zani, P. A. (2003c). Sharing amazonian rain-forest trees: Ecology of *Anolis punctatus* and *Anolis transversalis* (Squamata: Polychrotidae). *Journal of Herpetology* 37, 276–285.
- Vitt, L.J., Shepard, D.B., Caldwell, J.P., Vieira, G.H.C., et al. (2007). Living with your food: geckos in the termitaria of Cant ao. *Journal of Zoology* 272, 321–328.
- Vitt, L.J., Shepard, D.B., Vieira, G.H.C., Caldwell, J.P., et al. (2008b). Ecology of *Anolis nitens brasiliensis* in Cerrado woodlands of Cant ao. *Copeia* 144–153.
- Wiederhecker, H.C., Pinto, A.C.S. & Colli, G.R. (2002). Reproductive ecology of *Tropidurus torquatus* (Squamata: Tropicuridae) in the highly seasonal Cerrado biome of central Brazil. *Journal of Herpetology* 36, 82–91.
- Wilson, E.O. (1992). *The Diversity of Life*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press Cambridge, Massachusetts.

Accepted: 4 January 2015