Brito Filho, M. A., Albuquerque, R. L., Gainsburry, A. M., Colli, G. R., & Mesquita, D. O. (n.d.). Reproduction, Diet, and Sexual Dimorphism in *Micrablepharus Atticolus* (Squamata, Gymnophthalmidae) in Cerrado Enclaves Within Brazilian Amazon Forest. *Journal of Herpetology*, *58*(4), 389–400. https://doi.org/10.1670/2313360

REPRODUCTION, DIET, AND SEXUAL DIMORPHISM IN *MICRABLEPHARUS ATTICOLUS* (SQUAMATA, GYMNOPHTHALMIDAE) IN CERRADO ENCLAVES WITHIN BRAZILIAN AMAZON FOREST

MARCELO A BRITO FILHO, M.S.[1A], RALPH L ALBUQUERQUE, PH.D.[1], ALISSON M GAINSBURRY, PH.D.[2], GUARINO R COLLI, PH.D.[3],
DANIEL O MESQUITA, PH.D.[1]

[1] DEPARTAMENTO DE SISTEMÁTICA E ECOLOGIA, UNIVERSIDADE FEDERAL DA PARAÍBA,
[2] DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF SOUTH FLORIDA ST. PETERSBURG,
[3] DEPARTAMENTO DE ZOOLOGIA, UNIVERSIDADE DE BRASÍLIA

https://doi.org/10.1670/2313360

ABSTRACT

Autecology studies provide essential information on species' life history and natural history, improving our knowledge of evolutionary processes vital for effective biodiversity conservation. Herein, we describe the autecology of *Micrablepharus atticolus* with emphasis on morphometry, diet, and reproduction. We collected specimens from two municipalities (186 km apart) within the state of Rondônia, Brazil, during the dry season (between July and September). *M. atticolus* showed sexual dimorphism in body size and shape. As observed in other gymnophthalmids, females were larger (size dimorphism) and longer, whereas males had larger heads (shape dimorphism). Additionally, males from our study sites had relatively long hind limbs when compared to females. The most important (average of percent numeric, volumetric, and frequency) prey categories were Araneae, Blattodea, and Orthoptera, corresponding to more than 80% of the total prey number. Females had a fixed clutch size of two with more than one clutch per reproductive season. Egg volume was positively correlated to snout-vent length, which might contribute to the sexual dimorphism observed where relatively large females produce relatively large eggs and, therefore, larger offspring. All adult individuals were reproductively active, suggesting high reproductive activity during the dry season. Reproduction in the dry season can be related to the species' dependence on solar incidence to court and copulate. It can also be related to higher availability of oviposition sites, which are limited during extended periods of rain, especially for egg-burrowing species.

Autecology studies aid in the understanding of species' ecology and evolutionary history, providing crucial information for decision-making aimed at conserving species and the environment where they live (Bury, 2006). Autecological studies also provide baseline data to formulate and test ecological and evolutionary hypotheses (Vitt, 2013). In addition, knowledge about species' life history, such as morphology, diet, and reproduction, is critical to support action plans for conservation and elaborate general models that can be useful in studying other groups.

Lizards are an excellent model for ecological studies because they are relatively easy to catch and are generally abundant in the environment (Huey et al., 1983; Vitt & Pianka, 1994). As such, relatively large sample sizes can be attained when compared to other terrestrial vertebrates, leading to outstanding contributions to a breadth of research, such as life history, population and community ecology, evolutionary morphology and ecology traits, and comparative biology (Vitt, 2013; Vitt & Pianka, 2005).

Many lizard species are sexually dimorphic in body size and shape because of sexual selection or differences in environmental pressures experienced by each sex (Cox et al., 2003; Olsson et al., 2002). For example, males of *Aspidoscelis tigris* have larger heads than do females, probably because of intrasexual competition for females (Anderson & Vitt, 1990). Likewise, differences in intrinsic factors related to behavior, physiology, and reproductive effort can also affect sexual dimorphism (Cox et al., 2003). For example, female body size is positively correlated with clutch mass in many species (Doughty, 1997; Pianka & Vitt, 2003; Vitt & Congdon, 1978), implying that larger females can increase reproductive success by accommodating more or larger eggs, as observed in *Kentropyx calcarata* (Franzini et al., 2019).

There is a global tendency for species that live in more seasonal environments to lay fewer and larger clutches compared to species living in habitats with less pronounced seasonality (Mesquita et al., 2016). Clutch size can also be related to foraging habits, body shape, and evolutionary history in lizards (Vitt, 2013). Many sit-and-wait species have robust bodies that allow them to produce more eggs per clutch, whereas active foraging species commonly have elongated bodies and fewer eggs per clutch (Doughty, 1997). Microhabitat use specialization can also influence clutch size in lizards. For example, the saxicolous *Tropidurus semitaeniatus* lives in rock crevices; its flattened body limits space for clutch production and growth (Vitt, 1982).

Food availability in the environment is a critical factor influencing lizards' diets (Siqueira et al., 2013). Foraging mode (Reilly et al., 2007) and environmental factors such as microhabitat use and predator avoidance strategies also influence diet composition (Hawlena & Pérez-Mellado, 2009).

[A] CORRESPONDING AUTHOR: MARCELOA.BIOLOGIA@GMAIL.COM

Food preferences also can reflect phylogenetic conservatism (Mesquita et al., 2006; Mesquita & Colli, 2003). In addition, differences in prey consumption between sexes may be correlated with dimorphism in size and shape of the head (Herrel et al., 2006).

Gymnophthalmidae comprises ca. 296 species distributed in 55 genera (Uetz et al., 2023) and of the total number, 94 species and 33 genera occur in Brazil (Costa et al., 2023). Species of the family Gymnophthalmidae range from Argentina to Mexico, the West Indies, and the continental islands of South and Central America (Vitt & Caldwell, 2013). Gymnophthalmids are relatively small lizards with snout-vent length (SVL) of 40 mm to 150 mm. In general, gymnophthalmid lizards have morphological adaptations for fossoriality, such as reduction or loss of digits and limbs, elongation of the body, and loss of external ear aperture and eyelids (Castoe et al., 2004; Pellegrino et al., 2001; Pianka & Vitt, 2003). Most species have fossorial or semifossorial habits, but terrestrial, semiaquatic, and semiarboreal species may exist.

The genus *Micrablepharus* Boettger, 1885 is comprised of two species: *M. atticolus* Rodrigues, 1996, and *M. maximiliani* Reinhardt and Lütken, 1861. *M. atticolus* is endemic but widely distributed in the Brazilian Cerrado, occurring even in open enclaves in Amazonia (Gainsbury & Colli, 2003; M. G. Santos, 2011). Average SVL for the species is 38 mm, clutch size is two, and they can produce more than one clutch per reproductive season, Sexual dimorphism in body size is lacking (Vieira et al., 2000). They exhibit higher reproductive activity in the dry season and are likely annual, meaning that every year the entire population is replaced, being one of the few species of tetrapod that has a life expectancy of just one year (Sousa et al., 2015).

M. maximiliani has an average SVL of 40 mm and a wider geographical distribution than its sister species, ranging in the Cerrado, Caatinga, and open areas of the Atlantic Forest, Amazonia, and Pantanal. The species also has a fixed clutch size of two and seems to have higher reproductive activity in the dry season, at least in the Cerrado (Sousa et al., 2015). Sexual dimorphism is apparent, with females having larger SVL than males (Dal Vechio et al., 2014).

Both species are commonly associated with sandy soils, termite nests, leaf litter, or rock outcrops and have a diet based mainly on Orthoptera, Araneae, Blattodea, and Hemiptera (Dal Vechio et al., 2014; Mesquita et al., 2006; Moura et al., 2010; Vieira et al., 2000). At sites where *Micrablepharus* are sympatric, *M. maximiliani* are larger than *M. atticolus*, which have smaller body sizes than conspecific nonsympatric populations. Furthermore, the co-occurrence in their overlapped distribution is smaller than expected by chance, suggesting that the species avoid each other and that there is character displacement (body size) when co-occurrence occurs (Campelo, 2017).

Here, we describe morphometry, diet composition, and reproduction in *M. atticolus* using data from two populations from savanna enclaves in Amazonia of Rondônia state. We ask whether *M. atticolus* conform to the typical features of the Gymnophthalmidae, including: (1) sexually dimorphic body size and shape, with relatively large females having narrower heads relative to males, (2) different diet composition and prey size between sexes that could be related to body size and shape differences, and (3) a positive correlation between body size and clutch volume in females.

Materials and Methods

Data collection.—We used individuals housed in Coleção Herpetológica da Universidade de Brasília (CHUNB) collected in open enclaves of a transitional area between the Amazon Rainforest and the Brazilian savanna (Cerrado) during the dry season. We collected lizards during the dry season in two different municipalities within the state of Rondônia: Vilhena (Z: 20L, 824556.377 E, 8592332.282 N (UTM, Datum WGS 84)) and Pimenta Bueno (Z: 20L, 783883.122 E, 8690202.695 N (UTM, Datum WGS 84)).

Mean monthly temperature of Vilhena is 23.9 °C, and mean annual precipitation is 1,908 mm. The driest month of the year is June, with a mean rainfall of 8 mm, and the wettest is January, with a mean precipitation of 313 mm. Pimenta Bueno has a mean annual temperature of 25.7 °C, with a mean annual rainfall of 1,920 mm. The driest month is July, with mean precipitation of 10 mm, and the wettest is January, with mean precipitation of 299 mm (Merkel, 2024).

We collected specimens from two types of open enclaves found in the region. One location was a latosoil enclave, composed of a stratum of scleromorphic woody plants, and a stratum of herbs growing into an oligotrophic soil with high drainage capacity. The other location was a sandy soil enclave, composed of sparse arborous plants and a ground layer with predomination of sedges (Gainsbury & Colli, 2003).

Morphometrics.—We measured lizards using a digital caliper (precision of 0.1 mm). The following nine morphometric variables were measured: snout-vent length (SVL), tail length (TL), body width (BW), body height (BH), head width (HW), head length (HL), head height (HH), hindlimb length (HLL), and forelimb length (FLL).

We searched for univariate outliers using the boxplot function in R 4.1.2 with a critical value of Z for $P < 0.0001$. We replaced univariate outliers with multiple imputations using the "mice" function in R (Van Buuren & Groothuis-Oudshoorn, 2011), an imputation method for missing data that reduces bias more efficiently than removing the observation or other imputation methods (Penone et al., 2014). We used the same imputation method to estimate TL for individuals with broken tails. In addition, we used Mahalanobis distance to search for multivariate outliers with a critical value of q for $P < 0.01$ and did not find any multivariate outliers.

We calculated body size variable as follows: we $\log_{10}$ transformed all variables post imputation and defined size of individuals as an isometric eigenvector with values of $p^{-0.5}$, where p is the number of variables (Jolicoeur, 1963). We obtained vectors' values by multiplying the $n \times p$ matrix of standardized data, where n is the number of observations, by the isometric vector $p \times 1$ (Rohlf & Bookstein, 1987).

We used the Burnaby method (Burnaby, 1966) to create a matrix containing body shape variables ($\log_{10}$-transformed variables without body size effect), which consists of the multiplication of the $n \times p$ matrix of transformed $\log_{10}$ data by the symmetrical *p x p* matrix, defined as $L = I_p - V(V^TV)^{-1}V^T$, where I_p is the identity *p x p* matrix, *V* is the isometric eigenvector of size defined before, and V^T is the transposed *V* matrix.

We used a one-way ANOVA to test for differences in body size between sexes. To verify existence of dimorphism in body shape, we used logistic regression (Hosmer et al., 2013) with a generalized linear model and binomial error distribution of the body shape variables, comparing it with a constant-only model (null model), and we used a chi-square test of reduction of scaled deviation to verify significance of the model.

We use Guided Regularized Random Forests (GRRF) to estimate importance of each variable. Random Forests is a great tool to estimate importance of variables in a given classification because it has a very high accuracy of classification, is great in detecting nonlinear relationships that might exist between predictive variables and has its own measurements of importance (such as Gini impurity) (Cutler et al., 2012). It can also handle a large number of variables and data with great performance, and use of predictions of several trees returns more accurate predictions and significantly reduces variability and overfitting (Breiman, 2001). Furthermore, the method is also great when dealing with missing data and outliers (Liaw & Wiener, 2002).

The Random Forests method creates a defined number of decision trees (we used 5,000 trees) with individuals as tips, each based on a random subgroup of observations in the database. Each binary partitioning of every tree is created from a random subset of available variables (generally the square root of the total number of predictor variables). The random subgroup is chosen from the binary partitioning of the database based on maximum decrease of Gini impurity (the quantification of the probability of classifying an observation out of its observed class) (Ceriani & Verme, 2012; Grömping, 2009). Thus, each sample chosen does not use every observation. Observations that are not used are called "Out-Of-Bag" and are used to estimate the generalization error and importance of the variables (about 37% of all original observations are left out of each produced sample) (Cutler et al., 2012). The prediction of the analysis is the mean of the predictions of the generated trees. The predicted class (males or females in this study) for each observation is obtained by vote of the majority of "Out-of-Bag" predictions for that observation (Cutler et al., 2012; Strobl et al., 2008). In making the decision trees of a Regularized Random Forest (RRF), regularization penalizes selection of new features for the division when the gain is similar to features utilized in previous divisions. A Guided Regularized Random Forest is an RRF where values of the importance of a Random Forest are used to direct the selection process of RRF features.

We measured importance of variables by the mean decrease of Gini impurity. A binary partitioning in a tree with a high impurity decrease (with few misclassifications of observations) is considered important, so variables considered for this binary partitioning are also crucial for the classification. From the binary partitioning, the importance of the variables is computed as the sum of all decreases of impurity measured for every node in the analysis where the same variable participated in the binary partitioning, normalized by the number of Random Forests (Nembrini et al., 2018).

Finally, we built a Random Forest Model and analyzed effects of sequential removal of predictors, in descending order of importance, in accuracy of the prediction, with 100 repetitions of 10 cross-validations. We used a modified version of the function *rfcv* of the randomForest package for R (Liaw & Wiener, 2002), which uses fixed predictors during all iterations of a defined number of predictors. We measured accuracy of the observed prediction using the Correct Classification Rate (CCR) and Kappa.

Diet.—We analyzed stomach contents of each lizard, classifying each food item to the lowest possible taxonomic level (usually order) using a stereoscopic microscope. We measured the length and width of entire prey items using a digital caliper. Then, we estimated volume of whole prey as an ellipsoid using the following formula:

$$Volume = \frac{4}{3}[\pi\left(\frac{1}{2}Prey\ length\right)\left(\frac{1}{2}Prey\ width\right)^2]$$

We calculated numeric and volumetric proportions for each stomach and pooled stomachs. Then, we calculated numeric and volumetric niche breadth of prey categories for individual and pooled stomachs using the inverse of Simpson's diversity index (Simpson, 1949):

$$S = \frac{1}{\sum_{i=l}^{n} Pi^2}$$

where "*n*" is the number of categories of prey, and "*P*" is the numeric or volumetric proportion of prey category "*i*." We calculated relative importance of every category with the following formula:

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

where F% is the percentage of occurrence of the prey, N% is the numeric percentage, and V% is the volumetric percentage.

To quantify potential differences in diet of males and females, we calculated Pianka's niche overlap index (Pianka, 1973) for number and volume of prey items:

$$O_{kl} = \frac{\sum_i^n p_{il}p_{ik}}{\sum_i^n p_{il}^2 \sum_i^n p_{ik}^2}$$

where O_{kl} is niche overlap between the groups *l* and *k* to the resource *i* (in this case, the groups are males and females). This index varies from 0 (no overlap) to 1 (complete overlap).

To verify if there were differences in number or volume of prey consumed by males and females, we performed ANOVA between total number of prey items for each sex and total volume, mean volume, and maximum volume of prey consumed. We then conducted an ANCOVA with the previous variables, but with the most important variables of body shape in differentiation of sexes as a covariate to verify if there were differences in number or volume of prey consumed by males and females related to differences in body shape between sexes.

Reproduction.—We sexed individuals by direct observation of gonads. We considered reproductively active males with enlarged testes and convoluted epididymis and females with eggs in the oviduct or vitellogenic follicles. We considered simultaneous presence of eggs and follicles as an indicator of production of more than one clutch per re-

TABLE 1. Mean ± SD of the morphometric variables: Snout-vent length (SVL), head length (HL), head width (HW), head height (HH), body width (BW), body height (BH), forelimb length (FLL), hindlimb length (HLL) and tail length (TL), raw (mm) and transformed (with size effect removed), of females and males of *Micrablepharus atticolus*.

	Raw variables (mm)		Transformed variables	
	Females (*n* = 61)	Males (*n* = 96)	Females (*n* = 61)	Males (*n* = 96)
Body size			2.96 ± 0.05	2.89 ± 0.05
SVL	37.27 ± 1.55	34.14 ± 1.40	0.58 ± 0.02	0.57 ± 0.02
HL	6.89 ± 0.34	6.82 ± 0.42	−0.15 ± 0.02	−0.13 ± 0.03
HW	4.90 ± 0.36	4.69 ± 0.37	−0.30 ± 0.02	−0.29 ± 0.03
HH	3.29 ± 0.32	3.22 ± 0.32	−0.47 ± 0.04	−0.46 ± 0.04
BW	6.51 ± 0.64	5.72 ± 0.55	−0.18 ± 0.03	−0.21 ± 0.03
BH	4.78 ± 0.63	4.24 ± 0.55	−0.31 ± 0.05	−0.34 ± 0.05
FLL	8.57 ± 0.69	8.42 ± 0.71	−0.06 ± 0.04	−0.04 ± 0.04
HLL	12.23 ± 0.74	12.32 ± 1.05	0.10 ± 0.03	0.12 ± 0.04
TL	55.39 ± 4.99	55.53 ± 4.88	0.78 ± 0.03	0.78 ± 0.05

productive period. We defined size at reproductive maturity of the population as the size of the smallest reproductively active individual.

We counted number of eggs and follicles and measured length and width of eggs and testes. Then we calculated volume of eggs and testes using the ellipsoid formula mentioned above under "*Diet*." We used a Pearson correlation test to investigate the association between female SVL and egg volume.

RESULTS

Morphometrics.—Female SVL ranged from 33 to 40 mm, while male SVL ranged from 30 to 38 mm. Females (transformed mean ± SD = 2.96 ± 0.05, *n* = 96) were significantly larger ($F_{1,155}$ = 60.05, $P < 0.001$) than were males (mean = 2.89 ± 0.05 mm, *n* = 61) (Table 1). Females had relatively higher values of SVL and BW but lower values of HL, height, and hindlimb length than males (χ^2_9 = 95.27, $P < 0.001$). Predictive accuracy of the Random Forest Model, including all variables, was mean = 81.27 ± 1.31 based on the CCR and mean = 0.59 ± 0.03 based on Kappa (Fig. 1). SVL, HL, and BW were the most important predictors of sex, according to mean decrease in Gini impurity (Fig. 2). In contrast, forelimb length, TL, and HW had little predictive power. When testing the effect of number of variables on predictive accuracy, the model accuracy did not vary significantly with removal of variables (Fig. 3).

Diet.—We analyzed 166 stomachs, 115 of which contained food items. We identified twelve prey categories, with a total of 170 items. We could not measure length and width of 47 partially digested items, so they were not included in volume, importance, and volumetric niche overlap calculations. Based on pooled and individual stomach content data, the most important prey categories were Araneae, Blattodea, and Orthoptera. The Araneae, Blattodea, and Orthoptera categories also had the highest numeric and volumetric proportions (Table 2) and together, they corresponded to 82.35% of all items found (Araneae corresponded to 52.35% of all items, 41.66% of the total volume of prey, and occurred in 51.02% of stomachs).

For pooled stomach data, niche breadth was 3.01 for prey number and 3.15 for prey volume. For individual stomachs, niche breadth averaged mean = 1.26 ± 0.56 for prey number and mean = 1.15 ± 0.33 for prey volume. Trophic niche overlap between males and females was 0.97 for prey number (*n* = 62 males, *n* = 43 females) and 0.99 for prey volume (*n* = 46 males, *n* = 26 females).

We found no difference in number ($F_{1,103}$ = 0.552, P = 0.459) or volume (total volume: $F_{1,70}$ = 0.552, P = 0.459; mean volume: $F_{1,70}$ = 0.198, P = 0.658; maximum volume: $F_{1,70}$ = 0.400, P = 0.529) of prey consumed between males and females. There were also no differences in number ($F_{5,94}$ = 0.060, P = 0.80) or volume (total volume: $F_{5,62}$ = 0.531, P = 0.468; mean volume: $F_{5,62}$ = 0.477, P = 0.492; maximum volume: $F_{5,62}$ = 0.662, P = 0.418) of prey between sexes when considering the most important body shape variables in sexual dimorphism as covariates.

Reproduction.—Of 101 males analyzed, 94 were reproductively active (93.07%). For reproductive males, testis volume averaged 7.44 ± 2.42 (range: 3.02–16.21 mm^3). All adult females were reproductively active (*n* = 63). All females bearing oviductal eggs had two eggs (*n* = 16), and a half (12.6% of all reproductive females) presented eggs and vitellogenic follicles simultaneously. Mean clutch size based on follicle counts was 1.94 ± 0.36 (1–3, *n* = 54) and 1.95 ± 0.33 (1–3, *n* = 63) for follicles and eggs combined.

Mean egg length was 8.94 ± 0.60 mm (7.80–9.94 mm), and mean egg width was 5.66 ± 0.37 mm (3.42–5.12 mm). Mean volume of follicles was 22.83 ± 20.89 mm^3, and mean of egg volume was 127.28 ± 18.80 mm^3 (143.03–255.56 mm^3). We found a positive correlation between egg volume and body size (t_{14} = 2.31, P = 0.036, r = 0.53) and SVL (t_{13} = 3.02, P = 0.009, r = 0.64).

DISCUSSION

Morphometry.—We found sexual dimorphism in body size, with larger females, as opposed to what was found

TABLE 2. Frequency (F), number of prey (n), volume (V) in absolute values and percentages, and importance index of each category for pooled stomachs (PS) and single stomachs (SS) of *Micrablepharus atticolus*; means are followed by ±SD. Bold categories are those with the highest values.

	F	**F(%)**	**n**		**n(%)**		**V**		**V(%)**		**Importance**	
Category			**PS**	**SS**	**PS**	**SS**	**PS**	**SS**	**PS**	**SS**	**PS**	**SS**
Araneae	**75**	**51.02**	**89**	**0.77 ± 0.69**	**52.35**	**55.72 ± 45.07**	**805.21**	**10.19 ± 14.2**	**41.66**	**54.08 ± 46.82**	**48.35**	**55.10**
Blattodea	**34**	**23.13**	**35**	**0.30 ± 0.48**	**20.59**	**22.32 ± 38.34**	**619.10**	**7.84 ± 16.97**	**32.03**	**22.76 ± 39.20**	**25.25**	**21.72**
Orthoptera	**13**	**8.84**	**16**	**0.14 ± 0.44**	**9.41**	**7.90 ± 24.35**	**386.21**	**4.89 ± 13.47**	**19.98**	**12.05 ± 29.82**	**12.75**	**11.30**
Coleoptera	6	4.08	6	0.05 ± 0.22	3.53	4.35 ± 19.38	37.60	0.48 ± 2.26	1.95	4.87 ± 21.26	3.19	4.65
Plant material	6	4.08	6	0.05 ± 0.22	3.53	2.75 ± 14.08	-	-	-	-	2.54	-
Formicidae	5	3.40	9	0.08 ± 0.50	5.29	2.03 ± 11.07	24.37	0.31 ± 1.80	1.26	2.69 ± 15.81	3.32	3.03
Insect larvae	2	1.36	2	0.02 ± 0.13	1.18	1.16 ± 9.80	6.54	0.08 ± 0.60	0.34	1.35 ± 11.27	0.96	1.52
Not identifiable	2	1.36	2	0.01 ± 0.09	1.18	0.43 ± 4.66	-	-	-	-	0.85	-
Hemiptera	1	0.68	1	0.02 ± 0.13	0.59	1.74 ± 13.13	1.56	0.02 ± 0.18	0.08	0.13 ± 1.15	0.45	0.38
Isoptera	1	0.68	2	0.02 ± 0.19	1.18	0.87 ± 9.33	3.21	0.04 ± 0.36	0.17	1.27 ± 11.25	0.67	1.27
Mantodea	1	0.68	1	0.01 ± 0.09	0.59	0.29 ± 3.11	43.95	0.56 ± 4.94	2.27	0.65 ± 5.79	1.18	0.64
Opiliones	1	0.68	1	0.01 ± 0.09	0.59	0.43 ± 4.66	4.92	0.06 ± 0.55	0.25	0.15 ± 1.31	0.51	0.39
Total	147	100	170	-	100	-	-	-	100	-	-	-

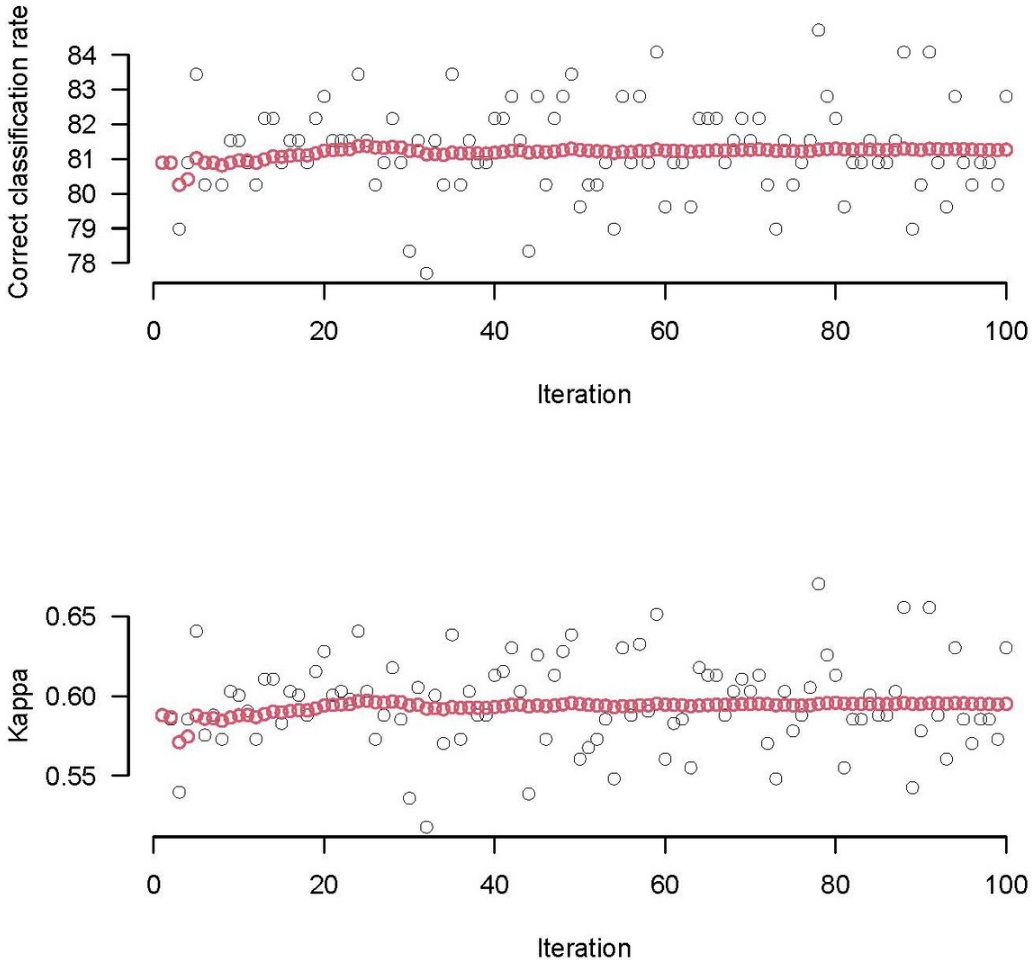

FIG. 1. Accuracy of the Guided Regularized Random Forests (GRRF) model in explaining body shape of males and females of *Micrablepharus atticolus,* based on Correct Classification Rate (CCR; percentage of classification of observations that the model in its observed class classified) and Kappa (values of Kappa between 0.41 and 0.60 are considered with moderate concordance between the model and the actual dataset, between 0.61 and 0.80 are considered substantial concordance, and above 0.80 are almost perfect concordance), for each iteration (number of trees of the forest generated by GRRF).

in Chapada dos Guimarães (Mato Grosso state) and Parque Nacional do Araguaia, Santa Terezinha, Tocantins state (Vieira et al., 2000), but in agreement with the species description (Rodrigues, 1996). Different selective pressures experienced by males and females can lead to sexual dimorphism, such as favoring females with larger body sizes because they have more room for egg production (Anderson & Vitt, 1990; Cox et al., 2003). We found a positive correlation between female SVL and egg volume, indicating that larger females might produce relatively large hatchlings, suggesting the observed dimorphism might have been influenced by differences in reproductive investment.

Considering dimorphism in body shape, we found that males had larger heads and shorter SVL than females, as was observed for *M. maximiliani* (Dal Vechio et al., 2014), and other gymnophthalmids, such as *Anotosaura vanzolinia* (Oliveira et al., 2018), *Anotosaura coralis* (Rodrigues et al., 2013), *Cercosaura schreibersii* (Balestrin et al., 2010), *Dryadosaura nordestina* (Garda et al., 2014), and *Vanzosaura multiscutata* (Vitt, 1982). In all those cases, females had longer SVL and shorter heads (lower HL) than did males, indicating that this dimorphism might be a common trait in the family. The larger heads can result from sexual selection where males with more robust heads have an advantage in male-male territorial disputes (Anderson & Vitt, 1990; Doughty, 1997; Olsson et al., 2002; Vitt, 1982). Larger head size may also be related to niche partitioning, with males and females consuming different prey sizes (Herrel et al., 2006). Some species, like *A. tigris*, have shown an advantage for males with larger heads in male-male combats and no intersexual diet partitioning (Anderson & Vitt, 1990). Some species, such as *Plestiodon laticeps*, show increased head size during the mating season. Because we did not find differences in diet composition between sexes, indicating little to no influence of head shape on diet of each sex, larger heads in males might be related to intrasexual selection. Forced mating can occur in *M. maximiliani* (Gogliath et al., 2010), and if it also occurs in *M. atticolus*, males with robust heads may have a reproductive advantage by having greater biting amplitude and force to hold females during mating.

We found that males have longer hindlimbs than females. In many lizard species, males are more prone to encounter predators because of territory defense, searching for females, and displaying during mating season (Anderson

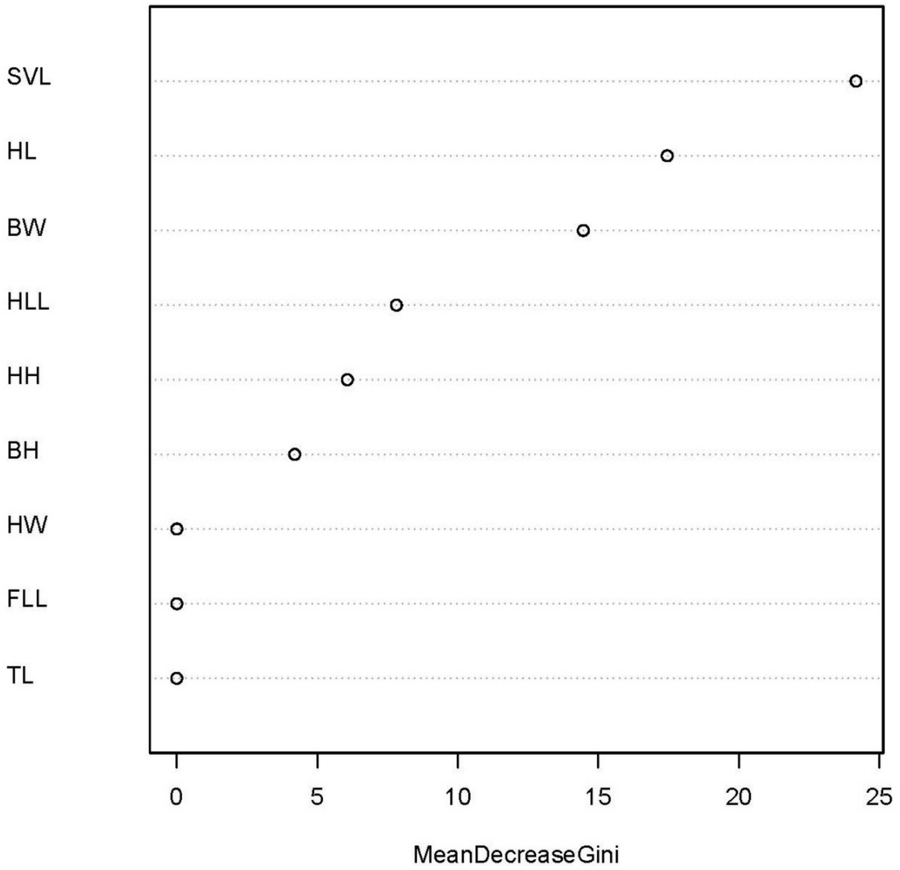

FIG. 2. Importance of body shape variables: Snout-vent length (SVL), head length (HL), body width (BW), hindlimb length (HLL), head height (HH), body height (BH), head width (HW), , forelimb length (FLL), and tail length (TL) in sex morphometrics of *Micrablepharus maximiliani* based on mean decrease in Gini impurity (MeanDecreaseGini). Higher values indicate higher importance in explaining differences between sexes.

& Vitt, 1990). Larger limbs could give them a better chance to flee from these predators (Butler & Losos, 2002; Cruz-Elizalde et al., 2020).

Diet.—The most important prey categories consumed by *M.atticolus* were Araneae, Blattodea, and Orthoptera. Similarly, other populations of *M. atticolus* had Hemiptera, Orthoptera, and Araneae as the most important categories in Cerrado environments of Alto Araguaia (Mato Grosso state) (Vitt, 1991), Chapada dos Guimarães (Mato Grosso state), and Parque Nacional do Araguaia (Tocantins state) (Vieira et al., 2000).

Other species of the family have similar diet composition, with high importance of Araneae and Orthoptera, such as *M. maximiliani* populations from Cerrado environments in Piauí state (Dal Vechio et al., 2014), in Vale do Rio Paranã, Goiás state (De Pinho Werneck et al., 2009), and in Jalapão, Tocantins state (Mesquita et al., 2006), *Vanzosaura* (Lima, 2014), *Potamites* (Vitt & Avila-Pires, 1998), *A. vanzolinia* (de Oliveira & Pessanha, 2013) and *Colobosaura modesta* (Mesquita et al., 2006), and also some teiids, close relatives of Gymnophthalmidae, such as *Ameivula* spp. (Mesquita & Colli, 2003) and *Kentropyx calcarata* (Franzini et al., 2019).

Previously, only five categories of prey were reported as composing the diet of *M. atticolus* (Vieira et al., 2000; Vitt, 1991), Araneae, Insect Larvae, Hemiptera, Lepidoptera, and Orthoptera. Here, we recorded six new categories: Blattodea, Formicidae, Isoptera, Opiliones, Mantodea, and plant material. The high importance of Araneae in the population, corresponding to more than half of total prey volume, suggests that the species prefers this prey type. Because we did not have abundance data for prey categories occurring at the study site, we cannot conclude that there is a preference. Araneae's high prevalence and importance could be just a reflection of prey availability. However, extensive similarity of the diet with other species of the family and with some species of Teiidae suggests that there could be some degree of preference guided by phylogenetic conservatism. This similarity could also be a consequence of foraging habit or food availability.

In general, gymnophthalmid lizards are considered active foragers with high importance of sedentary or gregarious prey to their diet composition, such as termites and insect larvae (de Oliveira & Pessanha, 2013; Garda et al., 2014; Rocha, 1994; M. V. G. Santos et al., 2012; Sousa et al., 2015). However, high consumption of high-mobility prey, such as Orthoptera, is commonly observed in many species of sit-and-wait foragers (Mesquita et al., 2016). Even though we found that *M. atticolus* has high consumption of high-mobility prey, considering only prey mobility is not enough to determine the foraging habit of a species (Ribeiro et al., 2015). The high importance of prey that are considered high energy prey such as Orthoptera, insect larvae, Araneae and Isoptera is commonly observed in scleroglos-

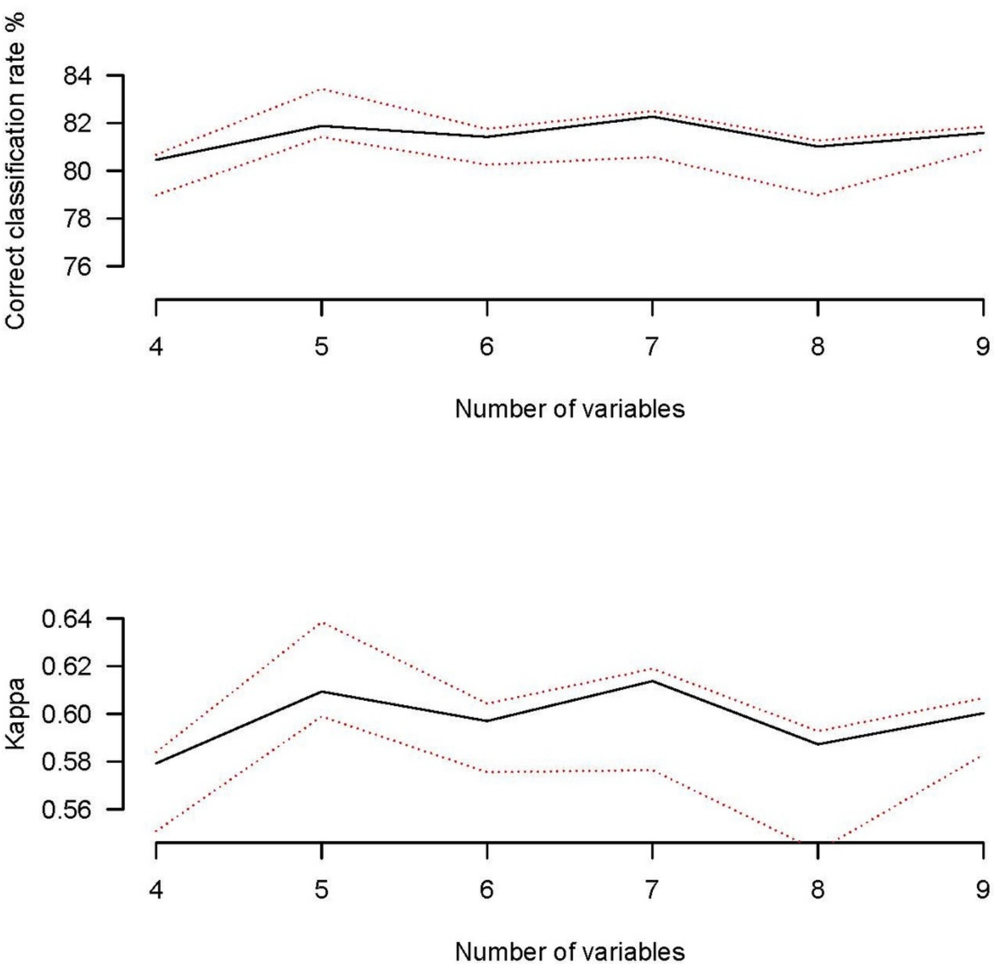

FIG. 3. Accuracy of the Guided Regularized Random Forests (GRRF) model based on Correct Classification Rate (CCR) and Kappa (a measure utilized to observe accuracy of predictive models) according to the number of body shape variables (from 4 to 9) in *Micrablepharus maximiliani* to differentiate body shape between males and females.

san lizards, and it seems to be associated with selection of non-noxious prey, such as ants (Vitt et al., 2003). Despite some gymnophthalmids presenting high importance of ants in their diet, such as *D. nordestina* (Garda et al., 2014) and *A. vanzolinia* (de Oliveira & Pessanha, 2013), consumption of ants is associated with sit-and-wait foragers and seems to be a derived and relatively recent trait within Lacertoidea (Cavalcanti et al., 2024). The diet of *M. atticolus* seems to be a conserved trait, observed in many active foraging lizards, associated with a well-developed vomeronasal system used to discriminate prey.

Some lizards present differences in diet composition between sexes, which can be related to morphometric differences (Preest, 1994). Furthermore, trophic differences also influence dimorphism; for example, size or shape of the head may be different between the sexes because of differences in prey consumption (Herrel et al., 2006). The considerable trophic niche overlap between sexes (0.97 for number and 0.99 for volume) indicates no sex differences in diet composition. In addition, we did not find any difference in prey size consumption between sexes using body shape variables as a covariate, indicating that the sexual dimorphism observed likely does not influence the type or size of prey consumed by each sex. Females of the gymnophthalmid *A. vanzolinia* have a larger niche breadth than males, possibly because of differences in energy requirements between sexes (Oliveira et al., 2018). Other species have shown differences in prey consumption between sexes, which could be attributed to differences in microhabitat use or foraging mode (Mesquita et al., 2015). Absence of dietary differences between males and females of *M.atticolus* could indicate lack of intraspecific competition for food (but assessing the prey availability is needed to test this hypothesis), or it could result from absence of differences in microhabitat use or foraging behavior.

Reproduction.—M. atticolus had a fixed clutch size of two eggs, which was expected, because this trait is considered synapomorphic for Gymnophthalmidae (Fitch, 1970). Presence of females with vitellogenic follicles and eggs simultaneously indicates that females can lay at least two clutches per reproductive cycle, in agreement with data reported previously for the species (Vieira et al., 2000), with its sister species *M. maximiliani* (Dal Vechio et al., 2014), and with observations in other species of the family, like *A. vanzolinia* (Oliveira et al., 2018), *D. nordestina* (Garda et al., 2014)*, and V. multiscutata* (Vitt, 1982).

In species with fixed clutch size, females can only increase reproductive investment by increasing egg size or producing additional clutches consecutively (Roff, 1993, 2002). Female body size restricts maximum egg size. Therefore, selection favoring relatively large offspring can result in sexual dimorphism with larger females than males because they can capacitate large relative egg size in their abdomen (Doughty, 1997). We found a positive correlation between SVL and egg volume, suggesting that larger females can produce relatively large eggs, perhaps conferring reproductive success through production of large hatchlings.

M. atticolus also showed high reproductive activity in Chapada dos Guimarães, Mato Grosso state, late in the dry season, and Parque Nacional do Araguaia, Tocantins state, late in the wet season, with only four (out of 40) reproductively inactive individuals (Vieira et al., 2000). In a demographic study conducted over 7 years, *M. atticolus* presented an annual reproductive cycle, with higher reproductive activity in the dry season, and juveniles emerging at the start of the wet season (Sousa et al., 2015). The species' life expectancy is one year, so the entire population is replaced annually. Its sister species, *M. maximiliani*, similarly reproduces during the dry season in Cerrado (Dal Vechio et al., 2014).

Because all individuals used in this study were collected during the dry season, we are unable to describe their reproductive cycle throughout the year. We can only conclude that the population we observed has a high reproductive activity during the dry season because all individuals were reproductively active. However, a demographic study of *M. atticolus* in central Cerrado (Sousa et al., 2015) strongly supported seasonal reproduction, with reproductive activity in the dry season. Thus, although long term studies are needed to confirm this trend, we suggest the possibility of seasonal reproduction in the dry season. Finally, reproductive cycle is a variable trait in many lizard species, with seasonality and precipitation being very important factors that influence reproductive activity (Albuquerque et al., 2018; Mesquita et al., 2016; Mesquita & Colli, 2003). There is a global tendency for species occurring in regions with less pronounced seasonality to present more continuous reproduction throughout the year (Mesquita et al., 2016).

Higher precipitation throughout the year at our study site compared to central Cerrado areas (Sousa et al., 2015) could cause differences in reproductive cycle. For example, if the species depends on dry periods to burrow their eggs, this population may have a shorter period of reproductive activity compared to central Cerrado populations. Flooding in Cerrado soils during the wet season possibly limits laying sites of *Ameivula ocellifera* (Mesquita & Colli, 2003) and *Ameiva plei* in Lesser Antilles (Censky, 1995). If *M. atticolus* also buries their eggs, an increase in rainfall during the rainy season should impact hatching success negatively and influence the reproductive cycle. However, if its reproduction occurs during the dry season because of high abundance of food for juveniles during the wet season, the reproductive period could be extended when compared to populations of central Cerrado.

Seasonal reproduction in the dry season can result from long periods of relatively low solar incidence during the wet season caused by prolonged presence of clouds, making it difficult for heliothermic species to copulate (Mesquita & Colli, 2003). *M. atticolus* from Reserva Ecológica do Roncador (Distrito Federal) are highly dependent on solar incidence, the best predictor of SVL variation throughout the year, as well as survival and recapture rate (Sousa et al., 2015). Thus, reproduction of the species might be constrained or at least have its peak in the dry season, with lowest activity periods occurring during the wet season. More studies are needed to confirm the species' reproductive cycle. We suggest a study of the reproductive cycle with at least one year of duration, and with more detailed data, such as histological analysis of gonads, and using populations of different environments. This could offer great insight about *M. atticolus* reproduction patterns among different environments and expectations relative to other lizard species populations.

In summary, *M. atticolus* is a species that inhabits open areas and presents sexual dimorphism in body size and shape, with females having larger SVL and smaller head dimensions and hindlimbs than males. They feed primarily on spiders, cockroaches, and crickets. They reproduce during the dry season in central Cerrado, but the reproduction cycle of populations of Cerrado enclaves in Amazonia could be different, despite its high reproductive activity in the dry season. Females lay more than one clutch per reproductive cycle, and larger females produce bigger eggs. Even though this study provides essential information about ecology of the species that can be used to assist in its conservation, as well as in understanding evolution within this lizard group, there are still questions about its life history that might be important for understanding their ecology, especially in open enclave populations of Amazonia.

……

ACKNOWLEDGMENTS

We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for a Master's scholarship. DOM and GRC thank CNPq for a research fellowship. RLA thanks CNPq and Fundação de Apoio à Pesquisa do Estado da Paraíba (FAPESQ-PB).

Submitted: January 10, 2024 EST, Accepted: August 03, 2024 EST

REFERENCES

Albuquerque, R. L., dos Santos Protázio, A., Barbosa de Queiroga Cavalcanti, L., Lopez, L. C. S., & Mesquita, D. O. (2018). Geographical Ecology of *Tropidurus hispidus* (Squamata: Tropiduridae) and *Cnemidophorus ocellifer* (Squamata: Teiidae) in a Neotropical Region: A comparison among Atlantic Forest, Caatinga, and Coastal Populations. *Journal of Herpetology*, *52*(2), 145–155. https://doi.org/10.1670/16-018

Anderson, R. A., & Vitt, L. J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia*, *84*(2), 145–157. https://doi.org/10.1007/BF00318265

Balestrin, R. L., Cappellari, L. H., & Outeiral, A. B. (2010). Biologia reprodutiva de *Cercosaura schreibersii* (Squamata, Gymnophthalmidae) e *Cnemidophorus lacertoides* (Squamata, Teiidae) no escudo Sul-Riograndense, Brasil. *Biota Neotropica*, *10*(1), 131–139. https://doi.org/10.1590/S1676-06032010000100013

Breiman, L. (2001). Random forests. *Machine Learning*, *45*(1), 5–32. https://doi.org/10.1023/A:1010933404324

Burnaby, T. P. (1966). Growth-invariant discriminant functions and generalized distances. *Biometrics*, *22*(1), 96. https://doi.org/10.2307/2528217

Bury, R. B. (2006). Natural history, field ecology, conservation biology and wildlife management: Time to connect the dots. *Herpetological Conservation and Biology*, *1*, 56–61.

Butler, M. A., & Losos, J. B. (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in greater Antillean *Anolis* lizards. *Ecological Monographs*, *72*(4), 541–559. https://doi.org/10.1890/0012-9615(2002)072%5B0541:MSDSSA%5D2.0.CO;2

Campelo, P. H. (2017). *Os padrões de coocorrência de Micrablepharus atticolus e M. maximiliani (Squamata, Gymnophthalmidae) variam com a escala geográfica* [Unpublished MS thesis]. Universidade Federal do Tocantins.

Castoe, T. A., Doan, T. M., & Parkinson, C. L. (2004). Data partitions and complex models in Bayesian analysis: The phylogeny of gymnophthalmid lizards. *Systematic Biology*, *53*(3), 448–469. https://doi.org/10.1080/10635150490445797

Cavalcanti, L. B. Q., Costa, G. C., Colli, G. R., Pianka, E. R., Vitt, L. J., & Mesquita, D. O. (2024). Myrmecophagy in lizards: Evolutionary and ecological implications. *Zoological Journal of the Linnean Society*, *202*(1), Article zlad175. https://doi.org/10.1093/zoolinnean/zlad175

Censky, E. J. (1995). Reproduction in two Lesser Antillean populations of *Ameiva plei* (Teiidae). *Journal of Herpetology*, *29*(4), 553–560. https://doi.org/10.2307/1564738

Ceriani, L., & Verme, P. (2012). The origins of the Gini index: Extracts from Variabilità e Mutabilità (1912) by Corrado Gini. *The Journal of Economic Inequality*, *10*(3), 421–443. https://doi.org/10.1007/s10888-011-9188-x

Costa, H. C., Guedes, T. B., & Bérnils, R. S. (2023). Lista de répteis do Brasil: Padrões e tendências. *Herpetologica Brasileira*, *12*, 56–161.

Cox, R. M., Skelly, S. L., & John-Alder, H. B. (2003). A comparative test of adaptative hypotheses for sexual size dimorphism in lizards. *Evolution*, *57*(7), 1653–1669. https://doi.org/10.1111/j.0014-3820.2003.tb00371.x

Cruz-Elizalde, R., Ramírez-Bautista, A., Rosas Pacheco, L. F., Lozano, A., & Rodríguez-Romero, F. J. (2020). Sexual dimorphism in size and shape among populations of the lizard *Sceloporus variabilis* (Squamata: Phrynosomatidae). *Zoology*, *140*, Article 125781. https://doi.org/10.1016/j.zool.2020.125781

Cutler, A., Cutler, D. R., & Stevens, J. R. (2012). Random forests. In C. Zhang & Y. Ma (Eds.), *Ensemble machine learning* (pp. 157–175). Springer. https://doi.org/10.1007/978-1-4419-9326-7_5

Dal Vechio, F., Recoder, R., Zaher, H., & Rodrigues, M. T. (2014). Natural history of *Micrablepharus maximiliani* (Squamata: Gymnophthalmidae) in a Cerrado region of northeastern Brazil. *Zoologia*, *31*(2), 114–118. https://doi.org/10.1590/S1984-46702014000200002

de Oliveira, B. H. S., & Pessanha, A. L. M. (2013). Microhabitat use and diet of *Anotosaura vanzolinia* (Squamata: Gymnophthalmidae) in a Caatinga area, Brazil. *Biota Neotropica*, *13*(3), 193–198. https://doi.org/10.1590/S1676-06032013000300022

De Pinho Werneck, F., Colli, G. R., & Vitt, L. J. (2009). Determinants of assemblage structure in Neotropical dry forest lizards. *Austral Ecology*, *34*(1), 97–115. https://doi.org/10.1111/j.1442-9993.2008.01915.x

Doughty, P. (1997). The effects of "fixed" clutch sizes on lizard life-histories: Reproduction in the Australian velvet gecko, *Oedura lesueurii*. *Journal of Herpetology*, *31*(2), 266–272. https://doi.org/10.2307/1565395

Fitch, H. S. (1970). *Reproductive cycles in lizards and snakes* (Misc. Pub. No. 52; pp. 1–247). University of Kansas Publications, Museum of Natural History.

Franzini, L. D., Martins Teixeira, A. A. M., Tavares-Bastos, L., Vitt, L. J., & Mesquita, D. O. (2019). Autecology of *Kentropyx calcarata* (Squamata: Teiidae) in a remnant of Atlantic Forest in eastern South America. *Journal of Herpetology*, *53*(3), 209. https://doi.org/10.1670/17-184

Gainsbury, A. M., & Colli, G. R. (2003). Lizard assemblages from natural Cerrado enclaves in southwestern Amazonia: The role of stochastic extinctions and isolation. *Biotropica*, *35*(4), 503–519. https://doi.org/10.1111/j.1744-7429.2003.tb00607.x

Garda, A. A., Medeiros, P. H. S., Lion, M. B., Brito, M. R. M., Vieira, G. H. C., & Mesquita, D. O. (2014). Autecology of *Dryadosaura nordestina* (Squamata: Gymnophthalmidae) from Atlantic Forest fragments in northeastern Brazil. *Zoologia Curitiba*, *31*(5), 418–425. https://doi.org/10.1590/S1984-46702014000500002

Gogliath, M., Ribeiro, L. B., & Freire, E. M. X. (2010). Forced copulation attempt in the blue-tailed lizard, *Micrablepharus maximiliani* (Reinhardt & Luetken, 1862) (Squamata, Gymnophthalmidae) in the Caatinga of northeastern Brazil. *Biota Neotropica*, *10*(4), 347–350. https://doi.org/10.1590/S1676-06032010000400040

Grömping, U. (2009). Variable importance assessment in regression: Linear regression versus random forest. *The American Statistician*, *63*(4), 308–319. https://doi.org/10.1198/tast.2009.08199

Hawlena, D., & Pérez-Mellado, V. (2009). Change your diet or die: Predator-induced shifts in insectivorous lizard feeding ecology. *Oecologia*, *161*(2), 411–419. https://doi.org/10.1007/s00442-009-1375-0

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*(3), 443–454. https://doi.org/10.1111/j.1095-8312.2006.00685.x

Hosmer, D. W., Jr., Lemeshow, S., & Sturdivant, R. X. (2013). *Applied logistic regression*. John Wiley & Sons. https://doi.org/10.1002/9781118548387

Huey, R. B., Pianka, E. R., & Schoener, A. (1983). *Lizard ecology: Studies of a model organism*. Harvard University Press. https://doi.org/10.4159/harvard.9780674183384

Jolicoeur, P. (1963). 193. Note: The multivariate generalization of the allometry equation. *Biometrics*, *19*(3), 497–499. https://doi.org/10.2307/2527939

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, *2*, 18–22. https://doi.org/10.1057/9780230509993

Lima, A. M. C. M. A. (2014). *Ecologia comparativa das espécies do gênero Vanzosaura (Squamata: Gymnophthalmidae) da Caatinga e do Cerrado* [Unpublished MS thesis]. Universidade Federal da Paraíba.

Merkel, A. (2024). *Climate Data for Cities Worldwide – Climate-Data*. http://en.climate-data.org/

Mesquita, D. O., & Colli, G. R. (2003). Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). *Copeia*, *2003*(2), 285–298. https://doi.org/10.1643/0045-8511(2003)003[0285:GVITEO]2.0.CO;2

Mesquita, D. O., Colli, G. R., França, F. G. R., & Vitt, L. J. (2006). Ecology of a Cerrado lizard assemblage in the Jalapão region of Brazil. *Copeia*, *2006*(3), 460–471. https://doi.org/10.1643/0045-8511(2006)2006[460:EOACLA]2.0.CO;2

Mesquita, D. O., Costa, G. C. A. S., Figueredo, F. G. F., Garda, A. A., Bello Soares, A. H., Tavares-Bastos, L., Vasconcellos, M. M., Vieira, G. H., & Vitt, L. J. (2015). The autecology of *Anolis brasiliensis* (Squamata, Dactyloidae) in a Neotropical savanna. *Herpetological Journal*, *25*, 233–244.

Mesquita, D. O., Costa, G. C., Colli, G. R., Costa, T. B., Shepard, D. B., Vitt, L. J., & Pianka, E. R. (2016). Life-history patterns of lizards of the world. *The American Naturalist*, *187*(6), 689–705. https://doi.org/10.1086/686055

Moura, M. R., Dayrell, J. S., & São-Pedro, V. D. A. (2010). Reptilia, Gymnophthalmidae, *Micrablepharus maximiliani* (Reinhardt and Lutken, 1861): Distribution extension, new state record and geographic distribution map. *Check List*, *6*(3), 419–426. https://doi.org/10.15560/6.3.419

Nembrini, S., König, I. R., & Wright, M. N. (2018). The revival of the Gini importance? *Bioinformatics*, *34*(21), 3711–3718. https://doi.org/10.1093/bioinformatics/bty373

Oliveira, B. H. S., de Queiroz, R. N. M., de Queiroga Cavalcanti, L. B., & Mesquita, D. O. (2018). Autecology of Neotropical lizard species *Anotosaura vanzolinia* (Squamata, Gymnophthalmidae) in a Caatinga region, north-eastern Brazilian. *Herpetological Journal*, *28*, 19–26.

Olsson, M. R., Shine, R., Wapstra, E., Uivari, B., & Madsen, T. (2002). Sexual dimorphism in lizard body shape: The roles of sexual selection and fecundity selection. *Evolution*, *56*(7), 1538–1542. https://doi.org/10.1111/j.0014-3820.2002.tb01464.x

Pellegrino, K., Rodrigues, M., Yonenaga-Yassuda, Y., & Sites, J. (2001). A molecular perspective on the evolution of microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. *Biological Journal of the Linnean Society*, *74*(3), 315–338. https://doi.org/10.1006/bijl.2001.0580

Penone, C., Davidson, A. D., Shoemaker, K. T., Di Marco, M., Rondinini, C., Brooks, T. M., Young, B. E., Graham, C. H., & Costa, G. C. (2014). Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution*, *5*(9), 961–970. https://doi.org/10.1111/2041-210X.12232

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, *4*(1), 53–74. https://doi.org/10.1146/annurev.es.04.110173.000413

Pianka, E. R., & Vitt, L. J. (2003). *Lizards: Windows to the evolution of diversity*. University of California Press.

Preest, M. R. (1994). Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: Why do females take smaller prey than males? *Journal of Herpetology*, *28*(3), 292–298. https://doi.org/10.2307/1564527

Reilly, S. M., McBrayer, L. D., & Miles, D. B. (Eds.). (2007). *Lizard Ecology: The evolutionary consequences of foraging mode*. Cambridge University Press.

Ribeiro, S. C., Teles, D. A., Mesquita, D. O., Almeida, W. O., dos Anjos, L. A., & Guarnieri, M. C. (2015). Ecology of the skink, *Mabuya arajara* Rebouças-Spieker, 1981, in the Araripe Plateau, northeastern Brazil. *Journal of Herpetology*, *49*(2), 237–244. https://doi.org/10.1670/13-018

Rocha, C. (1994). A ecologia de Lagartos no Brasil: Status e perspectivas. In A. T. Bernardes & G. A. Cotta (Eds.), *Herpetologia no Brasil I. Belo Horizonte. L.B. Nascimentio* (pp. 35–57). Fundação Biodiversitas e Fundação Ezequiel Dias, Universidade Católica de Minas Gerais.

Rodrigues, M. T. (1996). A new species of lizard, genus *Micrablepharus* (Squamata: Gymnophthalmidae), from Brazil. *Herpetologica*, *52*, 535–541.

Rodrigues, M. T., Teixeira, M., Dal Vechio, F. D., Amaro, R. C., Nisa, C., Guerrero, A. C., Damasceno, R., Roscito, J. G., Nunes, P. M. S., & Recoder, R. S. (2013). Rediscovery of the earless microteiid lizard *Anotosaura collaris* Amaral, 1933 (Squamata: Gymnophthalmidae): A redescription complemented by osteological, hemipenial, molecular, karyological, physiological and ecological data. *Zootaxa*, *3731*, 345–370. https://doi.org/10.11646/zootaxa.3731.3.5

Roff, D. (1993). *Evolution of life histories: Theory and naalysis*. Chapman & Hall.

Roff, D. (2002). *Life history evolution*. Sinauer Associates.

Rohlf, F. J., & Bookstein, F. L. (1987). A comment on shearing as a method for "size correction." *Systematic Zoology*, *36*(4), 356–367. https://doi.org/10.2307/2413400

Santos, M. G. (2011). *Filogeografia de* Micrablepharus atticolus *(Squamata, Gymnophthalmidae) no Cerrado brasileiro* [Unpublished MS thesis]. Universidade de Brasília.

Santos, M. V. G., Macedo, I. G. S., Sousa, R. S., Gogliath, M., & Ribeiro, L. B. (2012). Diet of *Nothobachia ablephara* (Squamata: Gymnophthalmidae) in a Caatinga area of the San Francisco Valley in northeastern Brazil. *Herpetology Notes*, *5*, 305–307.

Simpson, E. H. (1949). Measurement of diversity. *Nature*, *163*(4148), 688–688. https://doi.org/10.1038/163688a0

Siqueira, C. C., Kiefer, M. C., Sluys, M. V., & Rocha, C. F. D. (2013). Variation in the diet of the lizard *Tropidurus torquatus* along its coastal range in Brazil. *Biota Neotropica*, *13*(3), 93–101. https://doi.org/10.1590/S1676-06032013000300012

Sousa, H. C., Soares, A. H. S. B., Costa, B. M., Pantoja, D. L., Caetano, G. H., Queiroz, T. A., & Colli, G. R. (2015). Fire regimes and the demography of the lizard *Micrablepharus atticolus* (Squamata, Gymnophthalmidae) in a Biodiversity Hotspot. *South American Journal of Herpetology*, *10*(3), 143–156. https://doi.org/10.2994/SAJH-D-15-00011.1

Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., & Zeileis, A. (2008). Conditional variable importance for random forests. *BMC Bioinformatics*, *9*, 307. https://doi.org/10.1186/1471-2105-9-307

Uetz, P., Freed, P., Aguilar, R., Reyes, F., Kudera, J., & Hosek, J. (2023). *The Reptile Database*. http://www.reptile-database.org/

Van Buuren, S., & Groothuis-Oudshoorn, K. (2011). Mice: Multivariate imputation by chained equations in R. *Journal of Statistical Software*, *45*, 1–67. https://doi.org/10.18637/jss.v045.i03

Vieira, G. H. C., Mesquita, D. O., Péres, A. K., Jr., Kitayama, K., & Colli, G. R. (2000). Natural history: *Micrablepharus atticolus*. *Herpetological Review*, *31*, 241–242.

Vitt, L. J. (1982). Sexual dimorphism and reproduction in the microteiid lizard, *Gymnophthalmus multiscutatus*. *Journal of Herpetology*, *16*(3), 325–329. https://doi.org/10.2307/1563730

Vitt, L. J. (1991). An introduction to the ecology of Cerrado lizards. *Journal of Herpetology*, *25*(1), 79–90. https://doi.org/10.2307/1564798

Vitt, L. J. (2013). Walking the natural-history trail. *Herpetologica*, *69*(2), 105–117. https://doi.org/10.1655/HERPETOLOGICA-D-13-00027

Vitt, L. J., & Avila-Pires, T. C. S. (1998). Ecology of two sympatric species of *Neusticurus* (Sauria: Gymnophthalmidae) in the western Amazon of Brazil. *Copeia*, *1998*(3), 570–582. https://doi.org/10.2307/1447787

Vitt, L. J., & Caldwell, J. P. (2013). *Herpetology: An introductory biology of amphibians and reptiles*. Academic Press.

Vitt, L. J., & Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards: Resolution of a paradox. *American Naturalist*, *112*(985), 595–608. https://doi.org/10.1086/283300

Vitt, L. J., & Pianka, E. R. (1994). *Lizard ecology: Historical and experimental perspectives*. Princeton University Press. https://doi.org/10.1515/9781400863945

Vitt, L. J., & Pianka, E. R. (2005). Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(22), 7877–7881. https://doi.org/10.1073/pnas.0501104102

Vitt, L. J., Pianka, E. R., Cooper, W. E., & Schwenk, K. (2003). History and the global ecology of squamate reptiles. *The American Naturalist*, *162*(1), 44–60. https://doi.org/10.1086/375172