Autecology of the gecko *Phyllopezus periosus* (Squamata: Phyllodactylidae) inhabiting rock cliffs of a waterfall canyon from the semi-arid region of northeastern Brazil

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Abstract. *Phyllopezus periosus* is the largest phyllodactilid in Brazil, with a relictual distribution in the Caatinga Domain. Herein, we investigated the autecology of *P. periosus*, describing activity patterns, microhabitat use (spatial niche dimension), foraging mode, body temperature, reproduction, diet (trophic niche dimension), and temperature. Also, we tested the influence of seasonality and ontogeny on these biological aspects. Geckos (n = 116, 54 females, 33 males, and 29 juveniles) were sampled from October 2013 to September 2014. *Phyllopezus periosus* has an unimodal activity pattern, with peak activity in the early hours of the night. Males are more robust than females, and forelimbs in females are longer than in males. The body temperatures of this thermoconformer gecko are higher in the dry season. The reproductive season begins in the early dry season, with a fixed clutch of two eggs. Although we did not find evidence of more than one clutch per year, the studied population of *P. periosus* reproduces for an extended period throughout the dry season, as highlighted by the presence of juveniles all year. *Phyllopezus periosus* is saxicolous and presents a generalist diet composed mainly of arthropods, also including vertebrates such as frogs and lizards.

Keywords. Caatinga, daily activity, diet, foraging mode, microhabitat use, reproduction, sexual size dimorphism.

INTRODUCTION

The life history of lizards has been strongly shaped by the environments occupied during their evolutionary history. The interaction between individuals of a species and habitat dynamics stands as a pivotal subject investigated through autecological investigations (Walter and Hengeveld, 2014). These studies provide valuable insights into adaptations, behaviours, and survival strategies of a species in its ecological context (e.g., Alcantara et al., 2018; Barden and Shine, 1994; Ribeiro et al., 2015; Sousa and Ávila, 2015). Ecological factors such as temperature, food availability, and microhabitat heterogene-ity are some of the main factors that determine the distribution of lizards in a specific place (Gonçalves-Sousa et al., 2023; Gonçalves-Sousa et al., 2022; Sinervo et al., 2010; Wang et al., 2016).

Studying the various dimensions of the ecological niche of a species is necessary to understand its role within the ecosystem (Pianka, 1973; Pianka et al., 2017). These dimensions can encompass spatial aspects (such as habitat and microhabitat use), trophic interactions (dietary preferences), reproductive behaviors (breeding season, nesting sites, mating rituals, and parental care), behavioral patterns (foraging strategies and territoriality), physiological characteristics (ecological tolerances and

requirements regarding physical and chemical factors), as well as temporal factors (diurnal or nocturnal activity, seasonal rhythms, or migrations) (Hutchinson, 1957; Pianka, 1973; Pianka et al., 2017). Understanding the ecological niche breadth of species plays a crucial role in the formulation of conservation strategies, as it allows us to evaluate how environmental changes, such as climate change or natural land conversion, could impact species survival (Pianka et al., 2017).

In the present study, we investigated the autecology of *Phyllopezus periosus*. This gecko is a member of the Phyllodactylidae, a family encompassing 163 species and 10 genera extant in the New World, Northern Africa, Europe, and the Middle East (Gamble et al., 2008; Uetz et al., 2022). The genus *Phyllopezus* comprises eight large-bodied species, crepuscular and nocturnal, oviparous, saxicolous, and arboreal. These species are found in open vegetation in South America (Cacciali et al., 2018; Gamble et al., 2012) and six species are known to occur in Brazil: *P. diamantino, P. lutzae, P. periosus, P. pollicaris, P. przewalskii,* and *P. selmae.*

Phyllopezus periosus is the largest Brazilian phyllodactilid, inhabiting rocky environments in the semiarid region of northeastern Brazil, with a relictual distribution in the Caatinga morphoclimatic domain (Andrade et al., 2013; Franzini et al., 2019; Neta et al., 2014). Recently, *P. periosus* biological data have become available, regarding activity period, demography, foraging, microhabitat use, and morphometry (Freitas et al., 2015; Palmeira et al., 2021; Ragner et al., 2014). Data on communal nests and body temperatures throughout the rainy season is also available (Lima et al., 2011; Passos et al., 2013). However, information about the annual fluctuation or influence of seasonality on the ecology of *P. periosus* is still lacking.

Our primary aim was to investigate the autecology of *P. periosus* inhabiting the rocky cliffs of the Missão Velha waterfall canyon, located in the semiarid region of Brazil. Specifically, we investigated activity patterns, microhabitat use, foraging mode, body temperature, reproduction, diet, and temperature and estimated the spatial and trophic niche breadth dimensions. Each of these aspects contributes valuable insights to our understanding of how this species interacts with its habitat and ultimately plays its ecological role.

MATERIAL AND METHODS

Study site

Our study was conducted on the rocky cliffs of the Missão Velha waterfall canyon (7°13'S; 39°08'W), Missão Velha municipality, Ceará state, Brazil (Fig. 1A). The
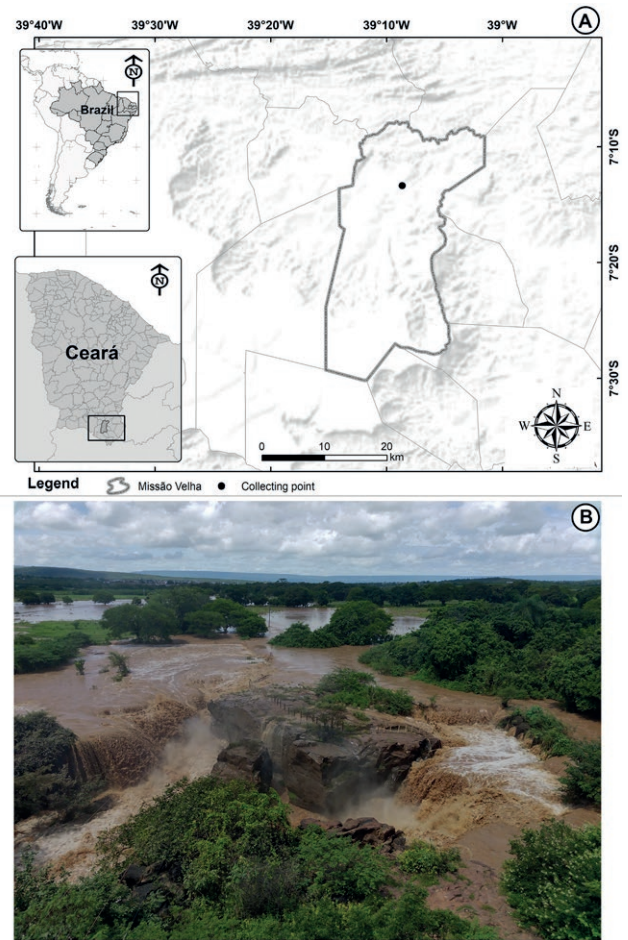

Fig. 1. Sampling area of *Phyllopezus periosus*. A: Map showing the location of Missão Velha waterfall, Missão Velha municipality, Northeast Brazil. B: Missão Velha waterfall in the rainy season.

waterfall is around 12 meters high, and it is accompanied by other river erosion features, such as a canyon (Fig. 1B; Mochiutti et al., 2012). The vegetation is dense, forming a riparian forest contrasting with the vegetation of adjacent shrubby Caatinga, which mainly is characterized by deciduous and hypoxerophytic formations.

The studied area is located in the semi-arid region of northeastern Brazil. There are two distinct seasons in this region: one long dry and one short rainy season. The rainy season is condensed from January to April, with annual rainfall of 987 mm and average temperature ranging from 24°C to 26°C (IPECE, 2017).

Activity

We conducted field expeditions from October 2013 to September 2014, one night per month. Two collectors

Fig. 2. *Phyllopezus periosus* of rocky cliffs of the Missão Velha waterfall. A: juvenile; B: adult individual.

Fig. 3. Annual fluctuation of temperature (black bars) and relative humidity (gray line) in the area of the Missão Velha waterfall. Value above gray line represent the highest humidity record.

performed active searches from 18:00 to 23:30, searching for *P. periosus* (Fig. 2) in all microhabitats available in the waterfall canyon, including the riparian forest. The total sampling effort was 11 hours per day (5 hours and 30 minutes per collector), totaling 132 hours of sampling. For each individual sighted, we recorded the time of sighting and the microhabitat used. We used a thermo-hygrometer (Instrutherm HT-300; precision ± 0.8 °C temperature and ± 3.5% relative humidity) to measure the temperature and humidity every hour (Fig. 3).

Microhabitat use

To evaluate the spatial niche of each species, we recorded the microhabitat used by each gecko according to the following categories: tree canopy and trunk, leaf litter, rock, and open ground. To measure the spatial niche breadth (Bs) of each species, we calculated the
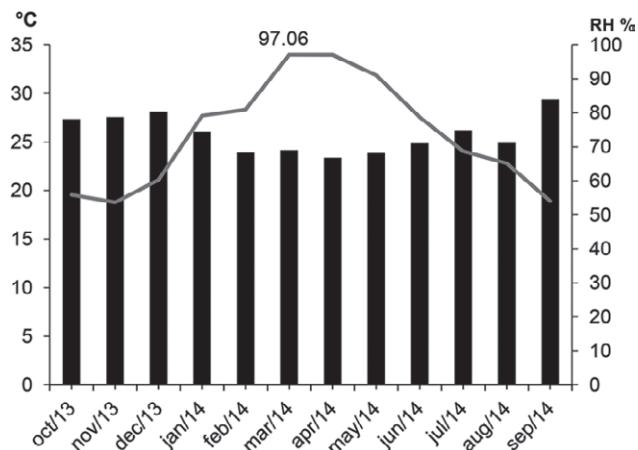
inverse of the diversity index of Simpson (1949), which values may range from 1 (exclusive use of a single category of microhabitat) to 5 (equal use of all microhabitat categories recorded). We calculated microhabitat overlap between sexes, and between adults and juveniles in Ecosim software v7.0 (Gotelli and Entsminger, 2004) using the overlap index of Pianka (1973), with values of overlap ranging from 0 (without overlap) to 1 (total overlap). We also estimated the height of the microhabitats used. As this population inhabits the walls of the Missão Velha waterfall canyon and the ground of the canyon is very uneven, we assumed the ground (0 m) to be the same as the water level and based our height estimates on this.

Foraging

We decreased the brightness of the flashlight after finding each gecko to avoid behavioral disturbances and observed them from a distance of about 5 m (± 1 m). Geckos were observed for up to 12 minutes.

We ended observations before 10 minutes when the lizard showed signs of disturbance or vanished from view. Observations shorter than 90 seconds were removed. After registering the foraging behavior, we hand-collected the geckos whenever possible. For each individual observed, we recorded the total time of observation, time spent moving, number of movements, the approximate distance covered, number of prey capture attempts, and number of successful prey captures. We then calculated the proportion of time spent moving (PTM) and the number of moves per minute (MPM) (Cooper Jr et al., 2001).

Body size

In laboratory conditions, we measured the body mass of each individual using a digital scale (standard deviation ± 0.01), euthanize with a lethal dose of 2% lidocaine hydrochloride (following Resolution #714 of the Conselho Federal de Medicina Veterinária, 2002), and used a digital caliper (± 0.01mm) to measure the following variables: snout-vent length (SVL), tail length (TLE), body width (BWD), body height (BHT), head width (HWD), head height (HHT), head length (HLE), rostrum labial commissure (RLC), forelimb length (FRL), hind limb length (HDL), and original length of the tail (TLO - from the cloaca to the beginning of the regenerated part in individuals who have autotomized the tail at least once in their lifetime). Then, we fixed the euthanized lizards with 10% formalin, preserved them with 70% ethanol, and deposited them at the Coleção Herpetológica of the Universidade Regional do Cariri.

To remove the effect of SVL on the other variables in the morphometric analysis, we used SVL and the residuals of linear regressions between the SVL and each of the other morphometric variables. This method was appropriated because it removes the tendency for individuals with larger body sizes (SVL) to have proportionally larger additional body parts than individuals with smaller bodies. Using the "car" R-package (Fox and Weisberg, 2019), we performed a multivariate analysis of variance (MANOVA) using the "Manova" function to test whether there was sexual or ontogenetic dimorphism in body shape, and a one-way ANOVA with the "Anova" function to assess differences in each variable independently. We also used the "t.test" function from the stats R package (R Core Team, 2019) to conduct t-tests for independent samples, aiming to evaluate sexual differences in body mass.

Reproduction

The sex of each specimen was determined by dissection and direct examination of gonads. We considered it as reproductively mature when males had enlarged testis and convoluted epididymis, and females had vitellogenic follicles or oviductal eggs. Sexually immature males and females were generically called "juveniles". We estimated the size of sexual maturation by the smallest sexually mature specimen of each sex. For females, we categorize the stage of development of follicles in pre-vitellogenic (small and whitish follicle clusters, when only pre-vitellogenic is present, or intercalated to vitellogenic follicles), vitellogenic (larger and yellow follicles, varying in size for each studied species), and eggs (when it presents the formation of the shell). Then we established the clutch size by counting the eggs present in the oviduct or vitellogenic follicles. When females presented eggs, vitellogenic follicles, or corpus luteum in the ovaries, we considered them to be in reproductive activity.

We recorded the length and width of testis in males, and the length and width of vitellogenic follicles and eggs in females to estimate the volume using the ellipsoid formula. We used SVL and the residuals of testis volumes (as described in the Body Size section) to check whether SVL and testis volume are correlated through the nonparametric Spearman correlation ("cor.test" function, method "spearman") in R. Then, we made a scatter plot with the volume and residual volume of the testis to determine the reproductive season of males, and to verify whether the reproductive season of males corresponds to the reproductive season of females throughout the year. When males presented positive values of volume testis, we considered them to be in reproductive activity.

Trophic niche

We removed the stomach content of all collected geckos and analyzed them under a stereomicroscope to identify prey items to the lowest taxonomic level possible (usually Order, except Formicidae). We measured the length and width of intact prey items with digital calipers (± 0.01 mm). Assuming a roughly equal width and depth of each prey item, we estimated its volume using the ellipsoid formula: $v = \frac{4}{3}\pi\left(\frac{l}{2}\right)\left(\frac{w}{2}\right)^2$, where V = volume, l = length, and w = width. Afterwards, we calculated numeric and volumetric percentages of each prey category. From these percentages, we obtained numeric and volumetric niche breadths using the inverse of the Simpson diversity index. Then, we used the Pianka niche overlap index using the volume of each prey category to evaluate trophic niche overlap between sexes, and between juveniles and adults. We assessed whether there were sexual and/or ontogenetic differences in prey diversity, average abundance, and average volume of items per stomach using the non-parametric Mann-Whitney test U ("wilcox.test" function) in R.

To determine the relative contribution of each prey category, we calculated the index of relative importance (IRI) for each species using the formula (Powell et al., 1990): $I = \frac{F\% + N\% + V\%}{3}$, where F%, N%, and V% are the percentages of frequency, number, and volume, respectively.

We used the Sorensen similarity index to evaluate similarities in diet between females, males, and juveniles. To test for sexual and ontogenetic differences in the diet, we conducted nonparametric similarity multivariate analyses (ANOSIM), using the Bray-Curtis similarity coefficient and 9999 permutations. Then we performed a discriminant analysis (SIMPER) to determine which prey

categories were responsible for sexual and ontogenetic dissimilarities in diets. The ANOSIM and SIMPER analyses were executed in the software PAST 3.0 (Hammer et al., 2001). To assess the seasonal difference in the number or volume found per stomach, we used the Mann-Whitney U test in R. Finally, we used the non-parametric Spearman correlation to verify whether there was a correlation between the gecko cloacal temperature (Tc) and the total number or volume of prey ingested per stomach.

Temperature

We measured cloacal temperature (Tc), using a thermal sensor (Instrutherm S-02k, accuracy ± 1 °C) coupled to a digital thermo-hygrometer of fast reading (Instrutherm HT-300), in a maximum of 15 seconds after gecko capture. We also assessed the temperature of the substrate (Tsub), air (Tair; 2-3 cm above the substrate), and relative humidity close to the substrate (~10 cm) at the time of capture.

We used one-way analysis of variance (ANOVA) to check whether there were significant seasonal differences between Tc, Tsub, and Tair, and between Tsub and Tair of the dry and rainy seasons. We performed a multiple linear regression to verify the effects of environmental variables on body temperature. We verified whether there was a relationship between SVL and Tc through a non-parametric Spearman correlation. We used ANOVA to check if there were sexual and ontogenetic differences in Tc.

RESULTS

Activity

We recorded the daily activity of 224 individuals of *P. periosus*. The first active gecko was observed at 18:28, with activity peaking between 19:00 and 20:59, gradually declining until 22:59. After 23:00, only four individuals were sighted (Fig. 4B).

Microhabitat use

Phyllopezus periosus was found on rocks 194 times out of 224 observations (Fig. 4C), showing that it has specialized preferences for this habitat type (Bs = 1.309). We classified 99 of the 194 individuals found on rocks, categorizing them as follows: 60 individuals were found inhabiting vertical surfaces of rocks (60.6%), 22 in crevices (22.2%), 10 on slabs (10.1%), and 7 on diagonal surfaces (7.1%). We estimated the height of microhabitats occu-

pied by 192 individuals: we found 10 individuals on the ground, 11 between 4-5 m, four between 6-7 m, and one at 10 m high (tree canopy). Other 166 individuals were at 1.38 ± 0.96 m (Fig. 4D).

Foraging

We recorded the foraging behavior of 41 individuals of *P. periosus*: 31 individuals were on rocks, eight on tree trunks, one a on tree canopy, and one on a leaf litter. The total observation time was 347.2 min. There were 154 moves (MPM = 0.444) and the total time the individuals spent moving was 2.19 min (PTM = 0.0063). The average PTM was 0.0084 ± 0.0086 and the average MPM was 0.5855 ± 0.0014. We detected 47 attempts of prey capture (30.52% of total moves), with 26 successful tries (55.32%; Table 1). We were able to collect 20 of the 41 individuals observed (10 females, five males, and five juveniles), with 15 having tails at an advanced stage of regeneration. We did not find *P. periosus* with autotomized and non-regenerated tail in foraging activity or exposed to sighting in their microhabitats.

Body size

We collected 116 specimens of *P. periosus* (54 females, 33 males, and 29 juveniles; Fig. 4A). Males of *P. periosus* are larger than females (Tables 2, 3), but considering the variables individually, females have longer forearms than males, which is the only variable with a significant sexual difference (Table 3). There is no sexual difference in body mass (t = -1.33; P = 0.187).

Reproduction

We found 17 females in breeding activity: five females had eggs in their ovaries about to be laid (two eggs per female), five had vitellogenic follicles (always two), and seven had corpus luteum in the ovary. One female had only one egg in its ovary, but there was evidence of recent oviposition. Although we did not find evidence of more than one clutch per year, such as the presence of eggs and vitellogenic follicles at the same time, the studied population of *P. periosus* reproduces for an extended period throughout the dry season, as highlighted by the presence of juveniles all year (except in October and February). Nevertheless, smaller juvenile lizards (SVL < 60 mm) were only found from November to January (four on average), and in March (one specimen). The reproductive period of females appears to
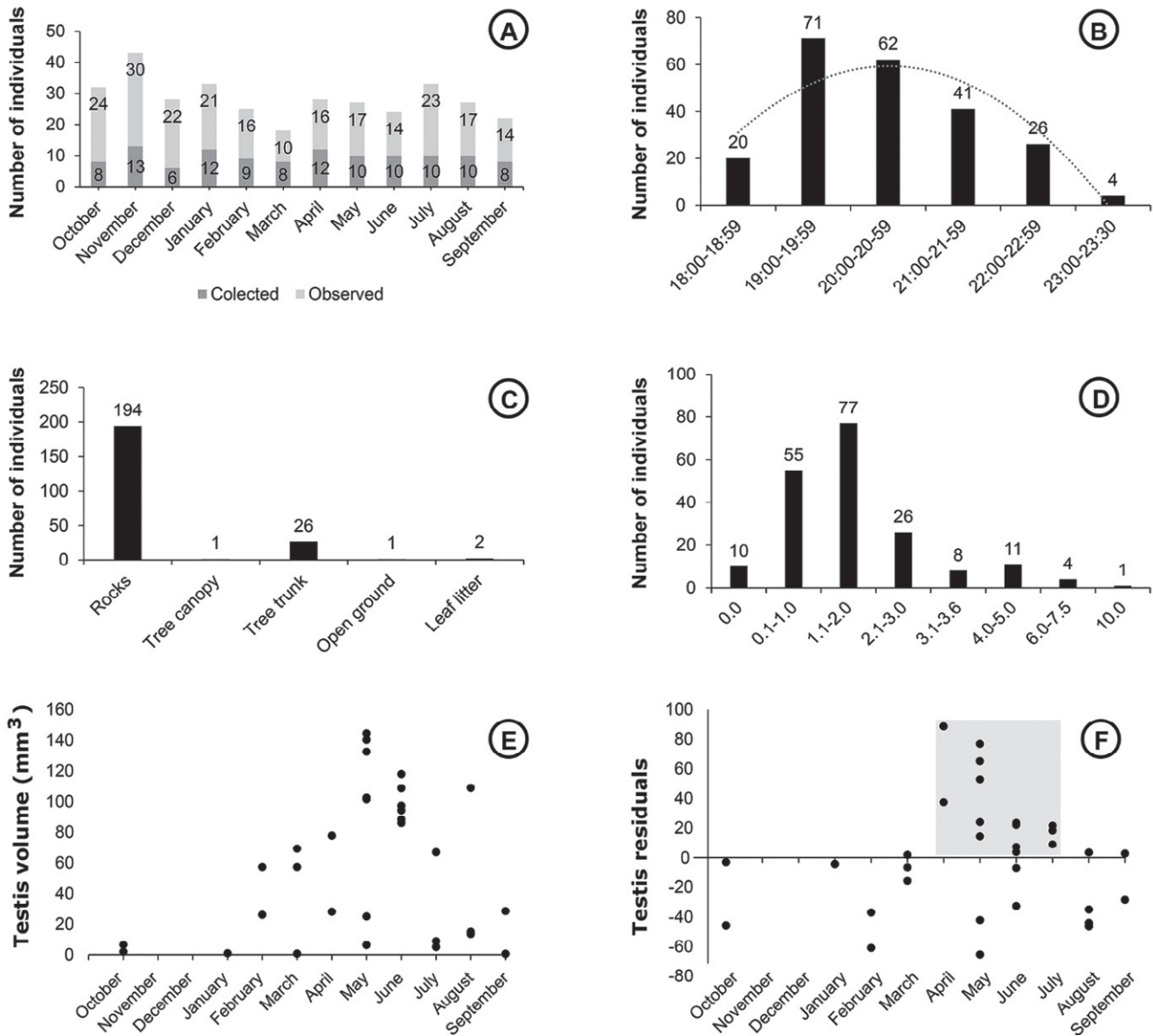
Fig. 4. Ecological data of *P. periosus* from Missão Velha waterfall, Brazilian semiarid region. A: number of individuals observed (light grey bar) and collected (dark grey bar); B: daily activity pattern; C: used microhabitats; D: height categories (in meters) where individuals were first sighted; E: volume (mm³) of testis; F: residuals of linear regressions between the SVL and the volume of testis (gray square highlights individuals with enlarged testis).

have started in May and lasted until November, peaking in July (two females had eggs and two had vitellogenic follicles). The SVL of the smallest sexually mature female was 79.19 mm.

Throughout the year, we collected 17 reproductively active males. The male reproductive period began and ended earlier than that of females, lasting from March to September (Fig. 4–E, F). The volume of the testis is positively correlated with SVL (Spearman = 0.611; P = 0.002). The smallest sexually mature male had an SVL of 84.77 mm.

In November, we found five clutches of *P. periosus*; three of them were in communal nests (Fig. 5). The first and second communal nests had six and four eggs, respectively. They were 15 cm away from each other, one near the edge and the other at the bottom of the same horizontal crevice, which was around 2 cm larger at a height of 180 cm (Fig. 5A). We classified these clutches as separate nests because the eggs of *P. periosus* adhere to each other and to the substrate, establishing a clutch of pooled eggs. The third nest had 10 eggs of *P. periosus* and

Table 1. Foraging of *P. periosus*. Tobs = Observation time in minutes; PTM = Proportion of time moving; MPM = movements per minute; ADT= average distance traveled during the observed time (in cm); PCS = Prey capture success (successful captures/total attempts).

P. periosus	n	Tobs	PTM	MPM	ADT	PCS
Total	41	347.2	0.0063	0.444	42.39	55.32% (26/47)
Females	10	63.54	0.0105	0.704	59.8	42.86% (3/7)
Males	5	49.45	0.0014	0.121	13.33	100% (1/1)
Juveniles	5	51.00	0.0022	0.569	63	73.33% (11/15)
Not collected	21					

Table 2. Body mass (g) and morphometric variables (mm) of *P. periosus* (mean ± standard deviation) on rocky cliffs of the Missão Velha waterfall, Northeastern Brazil. SVL = Snout-vent length; TLE = tail length; BWD = body width; BHT = body height; HWD = head width; HHT = head height; HLE = head length; RLC = rostrum labial commissure; FRL = forelimb length; HDL = hind limb length.

	Females	Males	Juveniles
Mass	31.74 ± 11.23	36.26 ± 11.61	6.57 ± 4.96
SVL	103.82 ± 10.49	106.43 ± 10.61	61.84 ± 14.31
TLE	98.39 ± 25.49	96.19 ± 28.47	66.67 ± 19.52
BWD	21.85 ± 4.03	22.33 ± 4.06	14.41 ± 15.71
BHT	14.58 ± 2.56	15.43 ± 2.36	7.71 ± 1.95
HWD	20.19 ± 2.04	21.06 ± 2.25	12.84 ± 2.73
HHT	12.48 ± 1.58	13.05 ± 2.03	10.02 ± 12.37
HLE	28.25 ± 2.39	28.9 ± 2.35	18.67 ± 3.35
RLC	17.47 ± 1.65	18.22 ± 2.09	11.47 ± 2.4
FRL	32.57 ± 3.32	32.34 ± 3.00	19.60 ± 4.64
HDL	45.56 ± 4.73	46.40 ± 4.74	27.62 ± 7.03

Table 3. Results of discriminant analysis between *Phyllopezus periosus* males and females and between adults and juveniles on rocky cliffs of the Missão Velha waterfall, Northeastern Brazil. SVL = Snout-vent length; TLE = tail length; BWD = body width; BHT = body height; HWD = head width; HHT = head height; HLE = head length; RLC = rostrum labial commissure; FRL = forelimb length; HDL = hind limb length. F = Fisher; * = p-values < 0.05.

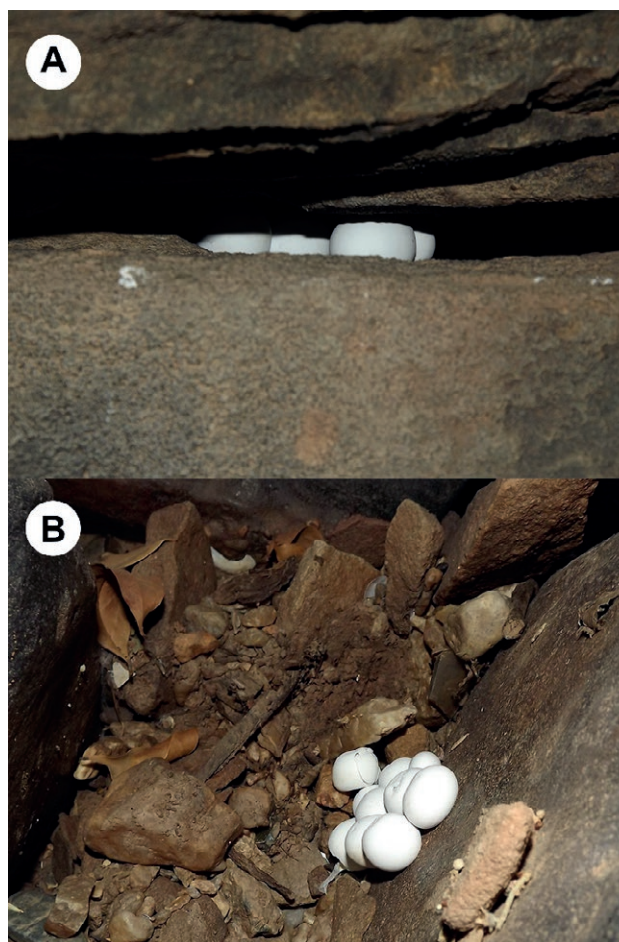|	Males x Females		Adults x Juveniles	
	F	p-value	F	p-value
Body shape	2.867	0.006*	0.426	0.903
SVL	1.260	0.265	-	-
BWD	0.223	0.638	0.107	0.744
BHT	1.140	0.288	0.433	0.512
HWD	3.640	0.060	0.154	0.696
HHT	0.863	0.355	0.052	0.820
HLE	0.279	0.599	0.510	0.477
RLC	2.400	0.125	0.007	0.932
FRL	5.910	0.017*	1.280	0.260
HDL	0.007	0.934	0.784	0.378

Fig. 5. Communal nests of *P. periosus* in horizontal rocky crevice (A), and of both *P. periosus* and *P. pollicaris* in diagonal crevice (B).

two of *P. pollicaris*, found in a vertical crevice of approximately 40 cm in height and 15 cm in width (Fig. 5B). The eggs of *P. pollicaris* have harder shells, do not adhere to each other, and were piled over *P. periosus* eggs. The three *P. periosus* eggs at the bottom of this clutch had many cracks in the shells. We found deteriorated eggshells 30 cm away from that communal nest, revealing that this nest site had previously been used for oviposition.

Diet

Among the 116 geckos collected, 93 had stomach contents (43 females, 23 males, and 27 juveniles), whereas the remaining had empty stomachs (11 females, 10 males, and 2 juveniles). We identified 24 prey categories, with an average diversity of prey per stomach of 1.59 ± 0.74 (1.72

Table 4. Diet composition of *P. periosus* on rocky cliffs of the Missão Velha waterfall, Northeastern Brazil. F = frequency; N = number; V = volume; I = relative importance index.

Prey item	F	F%	N	N%	V	V%	I
Invertebrates							
Advanced digestion	6	4.11	6	2.182	6313.45	7.475	4.589
Araneae	9	6.16	11	4.000	4872.39	5.769	5.311
Blattodea							
Imago	6	4.11	7	2.545	1500.19	1.776	2.810
Eggs	3	2.05	3	1.091	64.86	0.077	1.074
Coleoptera	32	21.9	57	20.727	5257.46	6.225	16.29
Diplopoda	3	2.05	3	1.091	730.85	0.865	1.337
Diptera	3	2.05	3	1.091	792.36	0.938	1.361
Formicidae	6	4.11	6	2.182	192.43	0.228	2.173
Gastropoda	2	1.37	2	0.727	257.38	0.305	0.801
Hemiptera	8	5.48	9	3.273	5104.69	6.044	4.932
Hymenoptera	4	2.74	5	1.818	307.48	0.364	1.641
Insect larvae	1	0.68	3	1.091	3631.78	4.300	2.025
Isoptera	14	9.59	106	38.545	9414.89	11.147	19.76
Lepidoptera							
Imago	5	3.42	6	2.182	781.01	0.925	2.177
Larvae	1	0.68	1	0.364	882.10	1.044	0.698
Neuroptera	2	1.37	2	0.727	34.70	0.041	0.713
Orthoptera	25	17.1	29	10.545	29874.96	35.371	21.01
Pseudoscorpione	1	0.68	1	0.364	26.85	0.032	0.360
Scolopendomorpha	3	2.05	3	1.091	331.98	0.393	1.180
Scorpione	1	0.68	1	0.364	3300.76	3.908	1.652
Vertebrates							
Anura	2	1.37	2	0.727	1326.38	1.570	1.223
Lizard shed skin	2	1.37	2	0.727	1295.34	1.534	1.210
Lizard	5	3.42	5	1.818	7049.52	8.346	4.530
Vertebrate egg	2	1.37	2	0.727	1118.35	1.324	1.140
Total	146	100	275	100	84462.12	100	100
Niche breadth			4.79		6.03		
Empty stomachs	23	19.82					

± 0.77 for females, 1.52 ± 0.73 for males, and 1.44 ± 0.70 for juveniles). There was no significant difference in prey diversity per stomach between males and females (U = 411.5; P = 0.267) or between adults and juveniles (U = 746.5; P = 0.223).

The average number of items per stomach was 2.97 ± 4.11 (3.26 ± 4.40 in females, 3.09 ± 5.01 in males, and 2.41 ± 2.59 in juveniles), and the average volume (in mm³) of prey per stomach was 908.34 ± 1215.48 (985.93 ± 1117.75 in females, 1367.06 ± 1714.94 in males, and 394.79 ± 500.20 in juveniles). There were no significant differences in the abundance (U = 411.5; P = 0.267) or volume (U = 438; P = 0.451) of items found in the stomachs for the two sexes. Although there was no ontogenetic difference in the abundance of items found in the

stomachs (U = 838; P = 0.657), adults consumed larger prey than juveniles (U = 601; P = 0.014).

The three most important categories in the diet composition of *P. periosus* were the same for both sexes and ontogeny, although they were ranked in reverse order of importance. The categories Isoptera (21.95%), Orthoptera (17.91%), and Coleoptera (15.01%) were the most important items for females; Orthoptera (28.64%), Isoptera (21.44%), and Coleoptera (11.49%) for males; and Coleoptera (22.81%), Orthoptera (15.37%), and Isoptera (12.86%) for juveniles. Coleoptera and Orthoptera were the most frequent categories for females (18.84% and 15.94%, respectively), males (17.65% and 23.53%), and juveniles (28.89% and 13.33%). In number, Isoptera (40.29%), Coleoptera (20.86%), and Orthop-

tera (9.35%) were the most consumed categories by females; Isoptera (48.61%), Orthoptera (13.89%), and Coleoptera (9.72%) by males; and Coleoptera (32.31%), Isoptera (23.08%), and Orthoptera (9.23%) by juveniles. Volumetrically, the most important categories were Orthoptera (28.44%), Isoptera (15.40%), and lizards (11.55%) for females; Orthoptera (48.52%), insect larvae (11.51%), and Scorpiones (10.46%) for males; and Orthoptera (23.55%), lizards (20.24%), and Araneae (19.41%) for juveniles.

The numerical and volumetric trophic niche breadth of the population was 4.79 and 6.04, respectively (Table 4). Adult males had the smallest numerical (B_N = 3.630) and volumetric (B_V = 3.719) niche breadths. Juveniles had a greater numerical trophic niche width (B_N = 5.552) than females (B_N = 4.541). Contrarily, adult females had a greater volumetric niche breadth (B_V = 7.282) than juveniles (B_V = 4.479).

When the proportions of prey categories were compared, there were no sexual (ANOSIM, R = 0.296; P = 0.2035) or ontogenetic differences (ANOSIM, R = 0.259; P = 0.195), although SIMPER revealed a dissimilarity of 48.86% between males and females and 45.34% between adults and juveniles. The categories Isoptera (18.71%), Orthoptera (15.88%), and Coleoptera (7.81%) contributed most to the difference between males and females, while Isoptera (15.05%), Coleoptera (15.21%), and Orthoptera (13%) best explained the difference between adults and juveniles. Furthermore, there was no significant difference in the number (U = 882.00; P = 0.076) or volume (U = 832.00; P = 0.110) of prey items consumed by *P. periosus* during the dry and rainy seasons.

Phyllopezus periosus also ingested frogs and lizards. An adult female specimen ate a frog (Leptodactylidae), and a juvenile ingested an anuran that could not be identified due to the high degree of digestion. One adult female ate the congener *P. pollicaris*, and one juvenile consumed a lizard (Gekkonidae), also not identified due to the degree of digestion. Furthermore, evidence of cannibalism was found, with two adult females and one juvenile that ingested smaller individuals of their own species.

Body temperature was correlated to prey volume (Spearman = -0.228; P = 0.038), but not to prey abundance (Spearman = -0.1192; P = 0.283) found in the stomachs.

Temperature

Average Tc (27.85 ± 1.91 °C; n = 102) was higher than Tsub (26.23 ± 2.11 °C), and Tair (25.49 ± 2.09 °C). Both Tsub and Tair have an influence on Tc (R^2 = 0.618; $F_{2,99}$ = 79.99; P <0.001), but the β coefficient suggests that Tsub ($β_{sub}$ = 0.88) exerts more influence than Tair ($β_{air}$ = -0.097) on Tc.

There were seasonal differences in Tc (F = 27.29; P = 0.0001; Dry season Tc = 28.54 ± 1.78 °C; Rainy season Tc = 26.73 ± 1.56 °C). Both Tsub and Tair were significantly higher (Tsub: F = 13.85, P = 0.0003; Tair: F = 12.83; P = 0.0005) during the dry season (Tsub = 26.81 ± 2.33 °C; Tair = 26.04 ± 2.31 °C) than in the rainy season (Tsub = 25.36 ± 1.24 °C; Tair = 24.64 ± 1.27 °C). In contrast to the dry season (F = 3,44; P = 0.0658), Tsub and Tair were significantly different in the rainy season (F = 6.13; P = 0.0155).

There was no significant difference in Tc between males (Tc = 27.57 ± 1.78 °C) and females (28.08 ± 2.07 °C; F = 1.15; P = 0.287), or between adults (27.9 ± 1.98 °C) and juveniles (27.69 ± 1.72 °C; F = 0.22; P = 0.638).

There was no relationship between SVL and Tc (Spearman = -0.0931; P = 0.352), nor between Tc of individuals with a tail in the process of regeneration (27.95 ± 1.96 °C; F = 0.34; P = 0.5599) and those who had never been autotomized (27.72 ± 1.75 °C; F = 0.34; P = 0.5599).

DISCUSSION

Activity

The daily cycle of *P. periosus* is unimodal, peaking between 19:00 and 21:00, and effectively ending around 23:00. Other populations of this gecko showed a time and unimodal activity patterns similar to ours, although a few individuals were also found until close to dawn (Passos et al., 2013; Ragner et al., 2014). *Phyllopezus periosus* had a restricted distribution, occurring almost exclusively on the rocky cliffs of the canyon formed downstream of the Missão Velha waterfall. During the rainy season, the water level rose around 2 m (personal observation, JGGS and HFO), which could cause dispersion out of the canyon. However, although we looked extensively in the Caatinga vegetation adjacent to the canyon in both seasons for *P. periosus*, we were unable to find it there.

Phyllopezus periosus coexists with the congener *P. pollicaris* in the canyon of the Missão Velha waterfall, but with a substantially higher population density than *P. pollicaris* (personal observation). *Phyllopezus periosus* preys on *P. pollicaris* and has the advantage of competing for space due to its larger body size. Other potential predators of geckos in the Missão Velha waterfall include the snakes *Oxyhropus trigeminus*, *Micrurus bonita*, and *Pseudoboa nigra*, and the owls *Glaucidium brasilianum* and *Megascops choliba* (personal observation, JGGS and HFO). The competitive and predatory pressure exerted by *P. periosus* and these other predators contributes to the low abun-

dance of *P. pollicaris* in the canyon region. In contrast, we found *P. pollicaris* in Caatinga vegetation around the waterfall canyon, where *P. periosus* was not found.

Microhabitat use

In the present study, *P. periosus* was highly specialized in the use of rocky microhabitats. Rocky substrates favor thermoregulatory activities, which have an impact on all other dimensions of the niche in lizards (Faria and Araujo, 2004; Huey, 1982). A good rocky spot, for example, can reduce the time it takes for the lizard to reach its ideal body temperature, lowering the risk of predation (Vitt et al., 1996). Several studies have reported similar specialized usage of microhabitats (Freitas et al., 2015; Gonçalves-Sousa et al., 2023; Palmeira et al., 2021; Passos et al., 2013; Ragner et al., 2014), except in the type locality, where Rodrigues (1986) found *P. periosus* in nine microhabitat categories. However, this author does not present data on the frequency of use in any of them.

Foraging

Phyllopezus periosus is a typical sit-and-wait forager (present study; Palmeira et al., 2021). This kind of forager usually has a PTM lower than 0.10 (Perry, 1995), indicating that they spend most of their time waiting for prey to approach. Sit-and-wait foragers generally feed on large active foraging prey that requires little movement to capture (Huey and Pianka, 1981; Perry and Pianka, 1997). The fact that *P. periosus* eats highly mobile prey (crickets, beetles, and termites) confirms its status as a sit-and-wait forager.

Data on foraging in Gekkota species is limited to only 1% of the species in this order (Palmeira et al., 2021). The great majority of these species are sit-and-wait foragers (e.g., Bauer, 2007; Cooper Jr. et al., 2001; Cummings et al., 2021; Palmeira et al., 2021; Whiting et al., 1999) that generally return to their original site after a capture attempt (e.g., Alcantara et al., 2018; Vitt, 1995), while *P. periosus* remains in the exact location where the prey was located, regardless of whether the capture was successful. This strategy divergence could be due to better prey availability in the humid environment around Missão Velha waterfall during most of the year, as suggested by the average PTM found by us (0.0084), which is considerably lower than that found in the population studied by Palmeira et al. (2021) in an area of Caatinga (1.7). On the other hand, because *P. periosus* has a larger body mass than other geckos, this variation may be compensatory, reducing energy expenditure with movements.

We did not find *P. periosus* with an autotomized and non-regenerated tail in foraging activity or exposed to sighting. This finding suggests that after autotomy, *P. periosus* adopts suboptimal foraging behaviors, such as foraging near refugia (mostly rock crevices) or reducing foraging in situations where predation is high risk (see Bels et al., 2019), which occurs as a result of reduced mobility and the loss of the autotomy possibility as a defense strategy. In lizards, tail loss through autotomy has a significant impact on their capacity to flee, jump, and climb, which has a direct impact on their foraging ability (Kuo et al., 2019).

Body size

Although females have longer forelimbs, males of *P. periosus* are larger than females, as in other gecko species (e.g., Johnston and Bouskila, 2007; Massetti et al., 2017; Nieva et al., 2013; Saenz and Conner, 1996). In lizards, sexual dimorphism is usually associated with larger limbs, a larger head, and a longer torso, which can improve locomotor performance and provide benefits in territorial disputes, ensuring the best site for foraging and female selection (Husak and Fox, 2008; Olsson et al., 2002; Van Damme et al., 2008).

The main cost of reproduction in lizards is locomotor performance loss caused by egg formation (Kuo et al., 2019). Females may have evolved this differential allometric growth in the forelimb to aid its support and mobility in vertical microhabitats, such as the rocky cliffs of the Missão Velha waterfall canyon, during the period of egg production, when their body mass greatly increases. Nevertheless, additional research is needed to further understand how this sexual difference in forelimb size affects locomotion and substrate adhesion.

Reproduction

The reproductive period of males begins and ends earlier than that of females in *P. periosus*. This suggests a potential reproductive strategy wherein the females of *P. periosus* can retain sperm from previous mating encounters to fertilize their eggs at a later time, maximizing their reproductive success. This behavior has been observed in a wide range of taxa, from insects to mammals (Cunningham and Birkhead, 1998). The reproductive period of *P. periosus* started at the end of the rainy season, and the smallest specimens were found at the beginning of the rainy season. This strategy ensures that neonates will find enough food to survive in localities where prey availability fluctuates throughout the year, especially in those

from arid or semiarid environments (McCluney and Sabo, 2009; Pinheiro et al., 2002; Vasconcellos et al., 2010).

This gecko has fixed two eggs as the clutch size, and communal nests in diagonal and horizontal rock crevices are rather common (Present study; Lima et al., 2011). Lizards from several families, including all seven from the Gekkota infraorder, share a fixed clutch size reproductive method (Meiri et al., 2020; Mesquita et al., 2016). Other geckos from the semiarid Caatinga, such as *Gymnodactylus geckoides, Hemidactylus mabouia, Lygodactylus klugei, and P. pollicaris*, typically reproduce continuously throughout the year (Vitt, 1986; Vitt, 1992). In highly seasonal environments, continuous reproduction throughout the year ensures that the persistence of the population is not jeopardized by unfavorable periods. Seasonality is a strong limiting factor that influences the partial or total halt of the reproductive activity of lizards in climatically atypical years (Castro-Franco and Bustos-Zagal, 2011; Paulissen, 1999; Vitt and Breitenbach, 1993). This is probably what happens to most lizards in the Caatinga in months of greater climatic severity. Temperature and humidity, on the other hand, do not appear to be limiting factors for *P. periosus* in the Missão Velha waterfall because the availability of water and relatively high humidity for most of the year do not result in significant fluctuations in food resources. In fact, the water level of the waterfall appears to be the limiting factor for *P. periosus* activities, as it rises and reduces favorable foraging and oviposition sites after the first rains, which could explain why we did not find females carrying eggs or vitellogenic follicles during the rainy season.

Diet

The diet of *P. periosus* is mainly composed of arthropods, but it also includes anurans, lizards, vertebrate eggs, and lizards shed skin. Geckos from the semi-arid region of northeastern Brazil usually have an opportunistic feeding habit and exhibit plasticity in response to food availability (Alcantara et al., 2019; Gonçalves-Sousa et al., 2023; Sousa et al., 2017). The most important categories in the diet of the population studied were crickets, termites, and beetles. In other populations of *P. periosus*, spiders (41.5% of total prey consumed) were followed by beetles (25.9%) in Cuité, Paraíba state (Gonçalves-Sousa et al., 2023), and beetles (52.1%) in the Ecological Station of Seridó, Rio Grande do Norte state (Palmeira et al., 2021). Furthermore, because of its abundance, Coleoptera is an essential food item for other geckos from Caatinga, including *Hemidactylus brasilianus* (26.1%), *Lygodactylus klugei* (24.3%), and *P. pollicaris* (24.8%) (Gonçalves-Sousa et al., 2019). Saurophagy reinforces that the diet of *P. periosus*

is not only generalist but also opportunistic, with sympatric lizard interactions occasionally leading to predation attempts. *Phyllopezus periosus* feeds on the lizards *P. pollicaris*, *Hemidactylus brasilianus,* and *Tropidurus semitaeniatus* in addition to its own species (Present study; Palmeira et al., 2021).

Rodrigues (1986) suggested that when food is scarce due to drought, adult *P. periosus* may diverge from optimal foraging (MacArthur and Pianka, 1966) and feed on small animals only enough to keep themselves alive. Food, on the other hand, is not a scarce resource for this population. The relatively high humidity and presence of water in the lower part of the waterfall most of the year favor a lower seasonal fluctuation of arthropods, which is supported by the presence of both large (mainly crickets) and small (primarily termites and small beetles) prey in the diet of *P. periosus*, as well as the lack of significant food variation between dry and rainy seasons. Moreover, the studied population showed a lower frequency of empty stomachs (19.83%) than other Neotropical geckos (22.4%) or the overall average for nocturnal lizards (24.1%) (Huey and Pianka, 1981). Finally, we found a positive correlation between body temperature and the volume of prey consumed by *P. periosus*. Increased Tc improves digestion by accelerating metabolism and lowering digestion time (Secor, 2009). This mechanism improves the metabolic efficiency of lizards, giving them more time to perform other daily activities or even to feed more in the same night.

Temperature

Phyllopezus geckos are thermoconformers, showing a body temperature that fluctuates in accordance with environmental temperature. The body temperature of these geckos appears to be plastic and unrelated to SVL. For example, the average body temperature of *P. periosus* in Missão Velha waterfall (Tc = 27.5 °C; maximum SVL = 122.5 mm) seasonally fluctuated, being higher in the dry season (Tc = 28.54 °C); yet, Tc was lower than that of another *P. periosus* population in the rainy season (Tc = 29.4 °C; Passos et al., 2013). The average Tc of *P. pollicaris* (maximum SVL = 77.9 mm) ranged from 24.4 °C in a Cerrado vegetation area to 30.8 °C in a Caatinga vegetation area (Ferreira et al., 2014; Recoder et al., 2012). Contrarily, other phyllodactylids, such as *Gymnodactylus geckoides* (maximum SVL = 48 mm) from Brazilian Caatinga, *Phyllodactylus bordai* (69 mm) and *Phyllodactylus tuberculosis* (59.8 mm) from the Mexican semiarid, and *Phyllodactylus xanti* (69 mm) from the Mexican island of San Esteban, were classified as active thermoregulators because their body temperature was around 2 °C high-

er than the temperature of the substrate in which they inhabited (Lara-Resendiz et al., 2013a; Lara-Resendiz et al., 2013b; Vitt, 1995).

In summary, *P. periosus* is a typical sit-and-wait forager with an unimodal activity pattern, thermoconformer, sexually dimorphic, highly specialized in microhabitat use, but highly generalist and opportunistic in the use of food resources, and has a long reproductive period, beginning early in the dry season.

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