

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

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17

18 **Running title:** Autecology of the gecko *Phyllopezus periosus*

19

20 **Abstract.** *Phyllopezus periosus* is the largest phyllodactilid in Brazil, with a relictual
21 distribution in the Caatinga Domain. Herein, we investigated the autecology of *P. periosus*,
22 describing activity patterns, microhabitat use (spatial niche dimension), foraging mode, body
23 temperature, reproduction, diet (trophic niche dimension), and temperature. Also, we tested the
24 influence of seasonality and ontogeny on these biological aspects. Geckos (n = 116, 54 females,
25 33 males, and 29 juveniles) were sampled from October 2013 to September 2014. *Phyllopezus*

26 *periosus* has an unimodal activity pattern, with peak activity in the early hours of the night.
27 Males are more robust than females, and forelimbs in females are longer than in males. The
28 body temperatures of this thermoconformer gecko are higher in the dry season. The
29 reproductive season begins in the early dry season, with a fixed clutch of two eggs. Although
30 we did not find evidence of more than one clutch per year, the studied population of *P. periosus*
31 reproduces for an extended period throughout the dry season, as highlighted by the presence of
32 juveniles all year. *Phyllopezus periosus* is saxicolous and presents a generalist diet composed
33 mainly of arthropods, also including vertebrates such as frogs and lizards.

34

35 **Keywords.** Caatinga, Daily activity, Diet, Foraging mode, Microhabitat use, Reproduction,
36 Sexual size dimorphism.

37

38

INTRODUCTION

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

48 Studying the various dimensions of the ecological niche of a species is necessary to
49 understand its role within the ecosystem (Pianka, 1973; Pianka et al., 2017). These dimensions
50 can encompass spatial aspects (such as habitat and microhabitat use), trophic interactions

51 (dietary preferences), reproductive behaviors (breeding season, nesting sites, mating rituals, and
52 parental care), behavioral patterns (foraging strategies and territoriality), physiological
53 characteristics (ecological tolerances and requirements regarding physical and chemical
54 factors), as well as temporal factors (diurnal or nocturnal activity, seasonal rhythms, or
55 migrations) (Hutchinson, 1957; Pianka, 1973; Pianka et al., 2017). Understanding the
56 ecological niche breadth of species plays a crucial role in the formulation of conservation
57 strategies, as it allows us to evaluate how environmental changes, such as climate change or
58 natural land conversion, could impact species survival (Pianka et al., 2017).

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

66 *Phyllopezus periosus* is the largest Brazilian phyllodactylid, inhabiting rocky
67 environments in the semiarid region of northeastern Brazil, with a relictual distribution in the
68 Caatinga morphoclimatic domain (Andrade et al., 2013; Franzini et al., 2019; Neta et al., 2014).
69 Recently, *P. periosus* biological data have become available, regarding activity period,
70 demography, foraging, microhabitat use, and morphometry (Freitas et al., 2015; Palmeira et al.,
71 2021; Ragner et al., 2014). Data on communal nests and body temperatures throughout the rainy
72 season is also available (Lima et al., 2011; Passos et al., 2013). However, information about the
73 annual fluctuation or influence of seasonality on the ecology of *P. periosus* is still lacking.

74 Our primary aim was to investigate the autecology of *P. periosus* inhabiting the rocky
75 cliffs of the Missão Velha waterfall canyon, located in the semiarid region of Brazil.

76 Specifically, we investigated activity patterns, microhabitat use, foraging mode, body
77 temperature, reproduction, diet, and temperature and estimated the spatial and trophic niche
78 breadth dimensions. Each of these aspects contributes valuable insights to our understanding of
79 how this species interacts with its habitat and ultimately plays its ecological role.

80

81

MATERIAL AND METHODS

Study site

83 Our study was conducted on the rocky cliffs of the Missão Velha waterfall canyon (7°13'S;
84 39°08'W), Missão Velha municipality, Ceará state, Brazil (Fig. 1A). The waterfall is around 12
85 meters high, and it is accompanied by other river erosion features, such as a canyon (Fig. 1B;
86 Mochiutti et al., 2012). The vegetation is dense, forming a riparian forest contrasting with the
87 vegetation of adjacent shrubby Caatinga, which mainly is characterized by deciduous and
88 hypoxerophytic formations.

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

93

Activity

95 We conducted field expeditions from October 2013 to September 2014, one night per month.
96 Two collectors performed active searches from 18:00 to 23:30, searching for *P. periosus* (Fig.
97 2) in all microhabitats available in the waterfall canyon, including the riparian forest. The total
98 sampling effort was 11 hours per day (5 hours and 30 minutes per collector), totaling 132 hours
99 of sampling. For each individual sighted, we recorded the time of sighting and the microhabitat

100 used. We used a thermo-hygrometer (Instrutherm HT-300; precision $\pm 0.8^{\circ}\text{C}$ temperature and
101 $\pm 3.5\%$ relative humidity) to measure the temperature and humidity every hour (Fig. 3).

102

103 *Microhabitat Use*

104 To evaluate the spatial niche of each species, we recorded the microhabitat used by each gecko
105 according to the following categories: tree canopy and trunk, leaf litter, rock, and open ground.

106 To measure the spatial niche breadth (B_s) of each species, we calculated the inverse of the
107 diversity index of Simpson (1949), which values may range from 1 (exclusive use of a single
108 category of microhabitat) to 5 (equal use of all microhabitat categories recorded). We calculated
109 microhabitat overlap between sexes, and between adults and juveniles in Ecosim software v7.0
110 (Gotelli and Entsminger, 2004) using the overlap index of Pianka (1973), with values of overlap
111 ranging from 0 (without overlap) to 1 (total overlap). We also estimated the height of the
112 microhabitats used. As this population inhabits the walls of the Missão Velha waterfall canyon
113 and the ground of the canyon is very uneven, we assumed the ground (0 m) to be the same as
114 the water level and based our height estimates on this.

115

116 *Foraging*

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

120 We ended observations before 10 minutes when the lizard showed signs of disturbance
121 or vanished from view. Observations shorter than 90 seconds were removed. After registering
122 the foraging behavior, we hand-collected the geckos whenever possible. For each individual
123 observed, we recorded the total time of observation, time spent moving, number of movements,
124 the approximate distance covered, number of prey capture attempts, and number of successful

125 prey captures. We then calculated the proportion of time spent moving (PTM) and the number
126 of moves per minute (MPM) (Cooper Jr et al., 2001).

127

128 *Body Size*

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

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

149

150 *Reproduction*

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

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

171

172 *Trophic niche*

173 We removed the stomach content of all collected geckos and analyzed them under a
174 stereomicroscope to identify prey items to the lowest taxonomic level possible (usually Order,

175 except Formicidae). We measured the length and width of intact prey items with digital calipers
176 (± 0.01 mm). Assuming a roughly equal width and depth of each prey item, we estimated its
177 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 =
178 width. Afterwards, we calculated numeric and volumetric percentages of each prey category.
179 From these percentages, we obtained numeric and volumetric niche breadths using the inverse
180 of the Simpson diversity index. Then, we used the Pianka niche overlap index using the volume
181 of each prey category to evaluate trophic niche overlap between sexes, and between juveniles
182 and adults. We assessed whether there were sexual and/or ontogenetic differences in prey
183 diversity, average abundance, and average volume of items per stomach using the non-
184 parametric Mann-Whitney test U (“wilcox.test” function) in R.

185 To determine the relative contribution of each prey category, we calculated the index of
186 relative importance (IRI) for each species using the formula (Powell et al., 1990): $I =$
187 $\frac{F\%+N\%+V\%}{3}$, where $F\%$, $N\%$, and $V\%$ are the percentages of frequency, number, and volume,
188 respectively.

189 We used the Sorensen similarity index to evaluate similarities in diet between females,
190 males, and juveniles. To test for sexual and ontogenetic differences in the diet, we conducted
191 nonparametric similarity multivariate analyses (ANOSIM), using the Bray-Curtis similarity
192 coefficient and 9999 permutations. Then we performed a discriminant analysis (SIMPER) to
193 determine which prey categories were responsible for sexual and ontogenetic dissimilarities in
194 diets. The ANOSIM and SIMPER analyses were executed in the software PAST 3.0 (Hammer
195 et al., 2001). To assess the seasonal difference in the number or volume found per stomach, we
196 used the Mann-Whitney U test in R. Finally, we used the non-parametric Spearman correlation
197 to verify whether there was a correlation between the gecko cloacal temperature (T_c) and the
198 total number or volume of prey ingested per stomach.

199

200 *Temperature*

201 We measured cloacal temperature (T_c), using a thermal sensor (Instrutherm S-02k, accuracy \pm
202 1°C) coupled to a digital thermo-hygrometer of fast reading (Instrutherm HT-300), in a
203 maximum of 15 seconds after gecko capture. We also assessed the temperature of the substrate
204 (T_{sub}), air (T_{air} ; 2-3 cm above the substrate), and relative humidity close to the substrate (~ 10
205 cm) at the time of capture.

206 We used one-way analysis of variance (ANOVA) to check whether there were
207 significant seasonal differences between T_c , T_{sub} , and T_{air} , and between T_{sub} and T_{air} of the
208 dry and rainy seasons. We performed a multiple linear regression to verify the effects of
209 environmental variables on body temperature. We verified whether there was a relationship
210 between SVL and T_c through a non-parametric Spearman correlation. We used ANOVA to
211 check if there were sexual and ontogenetic differences in T_c .

212

213 RESULTS

214

215 *Activity*

216 We recorded the daily activity of 224 individuals of *P. periosus*. The first active gecko was
217 observed at 18:28, with activity peaking between 19:00 and 20:59, gradually declining until
218 22:59. After 23:00, only four individuals were sighted (Fig. 4B).

219

220 *Microhabitat Use*

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

225 diagonal surfaces (7.1%). We estimated the height of microhabitats occupied by 192
226 individuals: we found 10 individuals on the ground, 11 between 4-5 m, four between 6-7 m,
227 and one at 10 m high (tree canopy). Other 166 individuals were at $1.38 \text{ m} \pm 0.96 \text{ m}$ (Fig. 4D).

228

229 *Foraging*

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

239

240 *Body Size*

241 We collected 116 specimens of *P. periosus* (54 females, 33 males, and 29 juveniles; Fig. 4A).
242 Males of *P. periosus* are larger than females (Tables 2, 3), but considering the variables
243 individually, females have longer forearms than males, which is the only variable with a
244 significant sexual difference (Table 3). There is no sexual difference in body mass ($t = -1.33$; p
245 $= 0.187$).

246

247 *Reproduction*

248 We found 17 females in breeding activity: five females had eggs in their ovaries about to be
249 laid (two eggs per female), five had vitellogenic follicles (always two), and seven had corpus

250 luteum in the ovary. One female had only one egg in its ovary, but there was evidence of recent
251 oviposition. Although we did not find evidence of more than one clutch per year, such as the
252 presence of eggs and vitellogenic follicles at the same time, the studied population of *P.*
253 *periosus* reproduces for an extended period throughout the dry season, as highlighted by the
254 presence of juveniles all year (except in October and February). Nevertheless, smaller juvenile
255 lizards (SVL < 60 mm) were only found from November to January (four on average), and in
256 March (one specimen). The reproductive period of females appears to have started in May and
257 lasted until November, peaking in July (two females had eggs and two had vitellogenic
258 follicles). The SVL of the smallest sexually mature female was 79.19 mm.

259 Throughout the year, we collected 17 reproductively active males. The male
260 reproductive period began and ended earlier than that of females, lasting from March to
261 September (Fig. 4–E, F). The volume of the testis is positively correlated with SVL (Spearman
262 $= 0.611$; $p = 0.002$). The smallest sexually mature male had an SVL of 84.77 mm.

263 In November, we found five clutches of *P. periosus*; three of them were in communal
264 nests (Fig. 5). The first and second communal nests had six and four eggs, respectively. They
265 were 15 cm away from each other, one near the edge and the other at the bottom of the same
266 horizontal crevice, which was around 2 cm larger at a height of 180 cm (Fig. 5A). We classified
267 these clutches as separate nests because the eggs of *P. periosus* adhere to each other and to the
268 substrate, establishing a clutch of pooled eggs. The third nest had 10 eggs of *P. periosus* and
269 two of *P. pollicaris*, found in a vertical crevice of approximately 40 cm in height and 15 cm in
270 width (Fig. 5B). The eggs of *P. pollicaris* have harder shells, do not adhere to each other, and
271 were piled over *P. periosus* eggs. The three *P. periosus* eggs at the bottom of this clutch had
272 many cracks in the shells. We found deteriorated eggshells 30 cm away from that communal
273 nest, revealing that this nest site had previously been used for oviposition.

274

275 *Diet*

276 Among the 116 geckos collected, 93 had stomach contents (43 females, 23 males, and 27
277 juveniles), whereas the remaining had empty stomachs (11 females, 10 males, and 2 juveniles).
278 We identified 24 prey categories, with an average diversity of prey per stomach of 1.59 ± 0.74
279 (1.72 ± 0.77 for females, 1.52 ± 0.73 for males, and 1.44 ± 0.70 for juveniles). There was no
280 significant difference in prey diversity per stomach between males and females ($U = 411.5$; p
281 $= 0.267$) or between adults and juveniles ($U = 746.5$; $p = 0.223$).

282 The average number of items per stomach was 2.97 ± 4.11 (3.26 ± 4.40 in females, 3.09
283 ± 5.01 in males, and 2.41 ± 2.59 in juveniles), and the average volume (in mm^3) of prey per
284 stomach was 908.34 ± 1215.48 (985.93 ± 1117.75 in females, 1367.06 ± 1714.94 in males, and
285 394.79 ± 500.20 in juveniles). There were no significant differences in the abundance ($U =$
286 411.5 ; $p = 0.267$) or volume ($U = 438$; $p = 0.451$) of items found in the stomachs for the two
287 sexes. Although there was no ontogenetic difference in the abundance of items found in the
288 stomachs ($U = 838$; $p = 0.657$), adults consumed larger prey than juveniles ($U = 601$; $p =$
289 0.014).

290 The three most important categories in the diet composition of *P. periosus* were the same
291 for both sexes and ontogeny, although they were ranked in reverse order of importance. The
292 categories Isoptera (21.95%), Orthoptera (17.91%), and Coleoptera (15.01%) were the most
293 important items for females; Orthoptera (28.64%), Isoptera (21.44%), and Coleoptera (11.49%)
294 for males; and Coleoptera (22.81%), Orthoptera (15.37%), and Isoptera (12.86%) for juveniles.
295 Coleoptera and Orthoptera were the most frequent categories for females (18.84% and 15.94%,
296 respectively), males (17.65% and 23.53%), and juveniles (28.89% and 13.33%). In number,
297 Isoptera (40.29%), Coleoptera (20.86%), and Orthoptera (9.35%) were the most consumed
298 categories by females; Isoptera (48.61%), Orthoptera (13.89%), and Coleoptera (9.72%) by
299 males; and Coleoptera (32.31%), Isoptera (23.08%), and Orthoptera (9.23%) by juveniles.

300 Volumetrically, the most important categories were Orthoptera (28.44%), Isoptera (15.40%),
301 and lizards (11.55%) for females; Orthoptera (48.52%), insect larvae (11.51%), and Scorpiones
302 (10.46%) for males; and Orthoptera (23.55%), lizards (20.24%), and Araneae (19.41%) for
303 juveniles.

304 The numerical and volumetric trophic niche breadth of the population was 4.79 and 6.04,
305 respectively (Table 4). Adult males had the smallest numerical ($B_N = 3.630$) and volumetric (B_V
306 $= 3.719$) niche breadths. Juveniles had a greater numerical trophic niche width ($B_N = 5.552$)
307 than females ($B_N = 4.541$). Contrarily, adult females had a greater volumetric niche breadth (B_V
308 $= 7.282$) than juveniles ($B_V = 4.479$).

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

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

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

326

327 *Temperature*

328 Average T_c ($27.85^\circ\text{C} \pm 1.91^\circ\text{C}$; $n = 102$) was higher than T_{sub} ($26.23^\circ\text{C} \pm 2.11^\circ\text{C}$), and T_{air}
329 ($25.49^\circ\text{C} \pm 2.09^\circ\text{C}$). Both T_{sub} and T_{air} have an influence on T_c ($R^2 = 0.618$; $F_{2,99} = 79.99$; p
330 < 0.001), but the β coefficient suggests that T_{sub} ($\beta_{\text{sub}} = 0.88$) exerts more influence than T_{air}
331 ($\beta_{\text{air}} = -0.097$) on T_c .

332 There were seasonal differences in T_c ($F = 27.29$; $p = 0.0001$; Dry season $T_c = 28.54^\circ\text{C}$
333 $\pm 1.78^\circ\text{C}$; Rainy season $T_c = 26.73^\circ\text{C} \pm 1.56^\circ\text{C}$). Both T_{sub} and T_{air} were significantly higher
334 (T_{sub} : $F = 13.85$, $p = 0.0003$; T_{air} : $F = 12.83$; $p = 0.0005$) during the dry season ($T_{\text{sub}} =$
335 $26.81^\circ\text{C} \pm 2.33^\circ\text{C}$; $T_{\text{air}} = 26.04^\circ\text{C} \pm 2.31^\circ\text{C}$) than in the rainy season ($T_{\text{sub}} = 25.36^\circ\text{C} \pm$
336 1.24°C ; $T_{\text{air}} = 24.64^\circ\text{C} \pm 1.27^\circ\text{C}$). In contrast to the dry season ($F = 3.44$; $p = 0.0658$), T_{sub}
337 and T_{air} were significantly different in the rainy season ($F = 6.13$; $p = 0.0155$).

338 There was no significant difference in T_c between males ($T_c = 27.57^\circ\text{C} \pm 1.78^\circ\text{C}$) and
339 females ($28.08^\circ\text{C} \pm 2.07^\circ\text{C}$; $F = 1.15$; $p = 0.287$), or between adults ($27.9^\circ\text{C} \pm 1.98^\circ\text{C}$) and
340 juveniles (27.69 ± 1.72 ; $F = 0.22$; $p = 0.638$).

341 There was no relationship between SVL and T_c (Spearman = -0.0931; $p = 0.352$), nor
342 between T_c of individuals with a tail in the process of regeneration (27.95 ± 1.96 ; $F = 0.34$; p
343 = 0.5599) and those who had never been autotomized (27.72 ± 1.75 ; $F = 0.34$; $p = 0.5599$).

344

345

DISCUSSION

346

347 *Activity*

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

357 *Phyllopezus periosus* coexists with the congener *P. pollicaris* in the canyon of the
358 Missão Velha waterfall, but with a substantially higher population density than *P. pollicaris*
359 (personal observation). *Phyllopezus periosus* preys on *P. pollicaris* and has the advantage of
360 competing for space due to its larger body size. Other potential predators of geckos in the
361 Missão Velha waterfall include the snakes *Oxyhropus trigeminus*, *Micrurus ibiboboca*, and
362 *Pseudoboa nigra*, and the owls *Glaucidium brasilianum* and *Megascops choliba* (personal
363 observation, JGGS and HFO). The competitive and predatory pressure exerted by *P. periosus*
364 and these other predators contributes to the low abundance of *P. pollicaris* in the canyon region.
365 In contrast, we found *P. pollicaris* in Caatinga vegetation around the waterfall canyon, where
366 *P. periosus* was not found.

367

368 *Microhabitat Use*

369 In the present study, *P. periosus* was highly specialized in the use of rocky microhabitats. Rocky
370 substrates favor thermoregulatory activities, which have an impact on all other dimensions of
371 the niche in lizards (Faria and Araujo, 2004; Huey, 1982). A good rocky spot, for example, can

372 reduce the time it takes for the lizard to reach its ideal body temperature, lowering the risk of
373 predation (Vitt et al., 1996). Several studies have reported similar specialized usage of
374 microhabitats (Freitas et al., 2015; Gonçalves-Sousa et al., 2023; Palmeira et al., 2021; Passos
375 et al., 2013; Ragner et al., 2014), except in the type locality, where Rodrigues (1986) found *P.*
376 *periosus* in nine microhabitat categories. However, this author does not present data on the
377 frequency of use in any of them.

378

379 *Foraging*

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

386 Data on foraging in Gekkota species is limited to only 1% of the species in this order
387 (Palmeira et al., 2021). The great majority of these species are sit-and-wait foragers (e.g., Bauer,
388 2007; Cooper Jr. et al., 2001; Cummings et al., 2021; Palmeira et al., 2021; Whiting et al., 1999)
389 that generally return to their original site after a capture attempt (e.g., Alcantara et al., 2018;
390 Vitt, 1995), while *P. periosus* remains in the exact location where the prey was located,
391 regardless of whether the capture was successful. This strategy divergence could be due to
392 better prey availability in the humid environment around Missão Velha waterfall during most
393 of the year, as suggested by the average PTM found by us (0.0084), which is considerably lower
394 than that found in the population studied by Palmeira et al. (2021) in an area of Caatinga (1.7).
395 On the other hand, because *P. periosus* has a larger body mass than other geckos, this variation
396 may be compensatory, reducing energy expenditure with movements.

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

404

405 *Body Size*

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

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

418

419 *Reproduction*

420 The reproductive period of males begins and ends earlier than that of females in *P. periosus*.
421 This suggests a potential reproductive strategy wherein the females of *P. periosus* can retain

422 sperm from previous mating encounters to fertilize their eggs at a later time, maximizing their
423 reproductive success. This behavior has been observed in a wide range of taxa, from insects to
424 mammals (Cunningham and Birkhead, 1998). The reproductive period of *P. periosus* started at
425 the end of the rainy season, and the smallest specimens were found at the beginning of the rainy
426 season. This strategy ensures that neonates will find enough food to survive in localities where
427 prey availability fluctuates throughout the year, especially in those from arid or semiarid
428 environments (McCluney and Sabo, 2009; Pinheiro et al., 2002; Vasconcellos et al., 2010).

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

447

448 *Diet*

449 The diet of *P. periosus* is mainly composed of arthropods, but it also includes anurans, lizards,
450 vertebrate eggs, and lizards shed skin. Geckos from the semi-arid region of northeastern Brazil
451 usually have an opportunistic feeding habit and exhibit plasticity in response to food availability
452 (Alcantara et al., 2019; Gonçalves-Sousa et al., 2023; Sousa et al., 2017). The most important
453 categories in the diet of the population studied were crickets, termites, and beetles. In other
454 populations of *P. periosus*, spiders (41.5% of total prey consumed) were followed by beetles
455 (25.9%) in Cuité, Paraíba state (Gonçalves-Sousa et al., 2023), and beetles (52.1%) in the
456 Ecological Station of Seridó, Rio Grande do Norte state (Palmeira et al., 2021). Furthermore,
457 because of its abundance, Coleoptera is an essential food item for other geckos from Caatinga,
458 including *Hemidactylus brasilianus* (26.1%), *Lygodactylus klugei* (24.3%), and *P. pollicaris*
459 (24.8%) (Gonçalves-Sousa et al., 2019). Saurophagy reinforces that the diet of *P. periosus* is
460 not only generalist but also opportunistic, with sympatric lizard interactions occasionally
461 leading to predation attempts. *Phyllopezus periosus* feeds on the lizards *P. pollicaris*,
462 *Hemidactylus brasilianus*, and *Tropidurus semitaeniatus* in addition to its own species (Present
463 study; Palmeira et al., 2021).

464 Rodrigues (1986) suggested that when food is scarce due to drought, adult *P. periosus*
465 may diverge from optimal foraging (MacArthur and Pianka, 1966) and feed on small animals
466 only enough to keep themselves alive. Food, on the other hand, is not a scarce resource for this
467 population. The relatively high humidity and presence of water in the lower part of the waterfall
468 most of the year favor a lower seasonal fluctuation of arthropods, which is supported by the
469 presence of both large (mainly crickets) and small (primarily termites and small beetles) prey
470 in the diet of *P. periosus*, as well as the lack of significant food variation between dry and rainy
471 seasons. Moreover, the studied population showed a lower frequency of empty stomachs

472 (19.83%) than other Neotropical geckos (22.4%) or the overall average for nocturnal lizards
473 (24.1%) (Huey and Pianka, 1981). Finally, we found a positive correlation between body
474 temperature and the volume of prey consumed by *P. periosus*. Increased T_c improves digestion
475 by accelerating metabolism and lowering digestion time (Secor, 2009). This mechanism
476 improves the metabolic efficiency of lizards, giving them more time to perform other daily
477 activities or even to feed more in the same night.

478

479 *Temperature*

480 *Phyllopezus* geckos are thermoconformers, showing a body temperature that fluctuates in
481 accordance with environmental temperature. The body temperature of these geckos appears to
482 be plastic and unrelated to SVL. For example, the average body temperature of *P. periosus* in
483 Missão Velha waterfall ($T_c = 27.5^\circ\text{C}$; maximum SVL = 122.5 mm) seasonally fluctuated, being
484 higher in the dry season ($T_c = 28.54^\circ\text{C}$); yet, T_c was lower than that of another *P. periosus*
485 population in the rainy season ($T_c = 29.4^\circ\text{C}$; Passos et al., 2013). The average T_c of *P. pollicaris*
486 (maximum SVL = 77.9 mm) ranged from 24.4°C in a Cerrado vegetation area to 30.8°C in a
487 Caatinga vegetation area (Ferreira et al., 2014; Recoder et al., 2012). Contrarily, other
488 phyllodactylids, such as *Gymnodactylus geckoides* (maximum SVL = 48 mm) from Brazilian
489 Caatinga, *Phyllodactylus bordai* (69 mm) and *Phyllodactylus tuberculosis* (59.8 mm) from the
490 Mexican semiarid, and *Phyllodactylus xanti* (69 mm) from the Mexican island of San Esteban,
491 were classified as active thermoregulators because their body temperature was around 2°C
492 higher than the temperature of the substrate in which they inhabited (Lara-Resendiz et al.,
493 2013a; Lara-Resendiz et al., 2013b; Vitt, 1995).

494 In summary, *P. periosus* is a typical sit-and-wait forager with an unimodal activity
495 pattern, thermoconformer, sexually dimorphic, highly specialized in microhabitat use, but

496 highly generalist and opportunistic in the use of food resources, and has a long reproductive
497 period, beginning early in the dry season.

498

499

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TABLES

710

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

<i>P. periosus</i>	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					

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715

716 **Table 2.** Body mass (g) and morphometric variables (mm) of *P. periosus* (mean \pm standard
717 deviation) on rocky cliffs of the Missão Velha waterfall, Northeastern Brazil. Bellow: results
718 of discriminant analysis between males and females and between adults and juveniles. SVL
719 = Snout-vent length; TLE = tail length; BWD = body width; BHT = body height; HWD =
720 head width; HHT = head height; HLE = head length; RLC = rostrum labial commissure;
721 FRL = forelimb length; HDL = hind limb length.

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

722

723 **Table 3.** Results of discriminant analysis between *Phyllopezus periosus* males and females and
 724 between adults and juveniles on rocky cliffs of the Missão Velha waterfall, Northeastern Brazil.
 725 SVL = Snout-vent length; TLE = tail length; BWD = body width; BHT = body height; HWD =
 726 head width; HHT = head height; HLE = head length; RLC = rostrum labial commissure; FRL
 727 = 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

728

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

Prey item	F	F%	N	N%	V	V%	I
<i>Invertebrates</i>							
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
<i>Vertebrates</i>							
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					

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FIGURE LEGENDS

Figure 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.

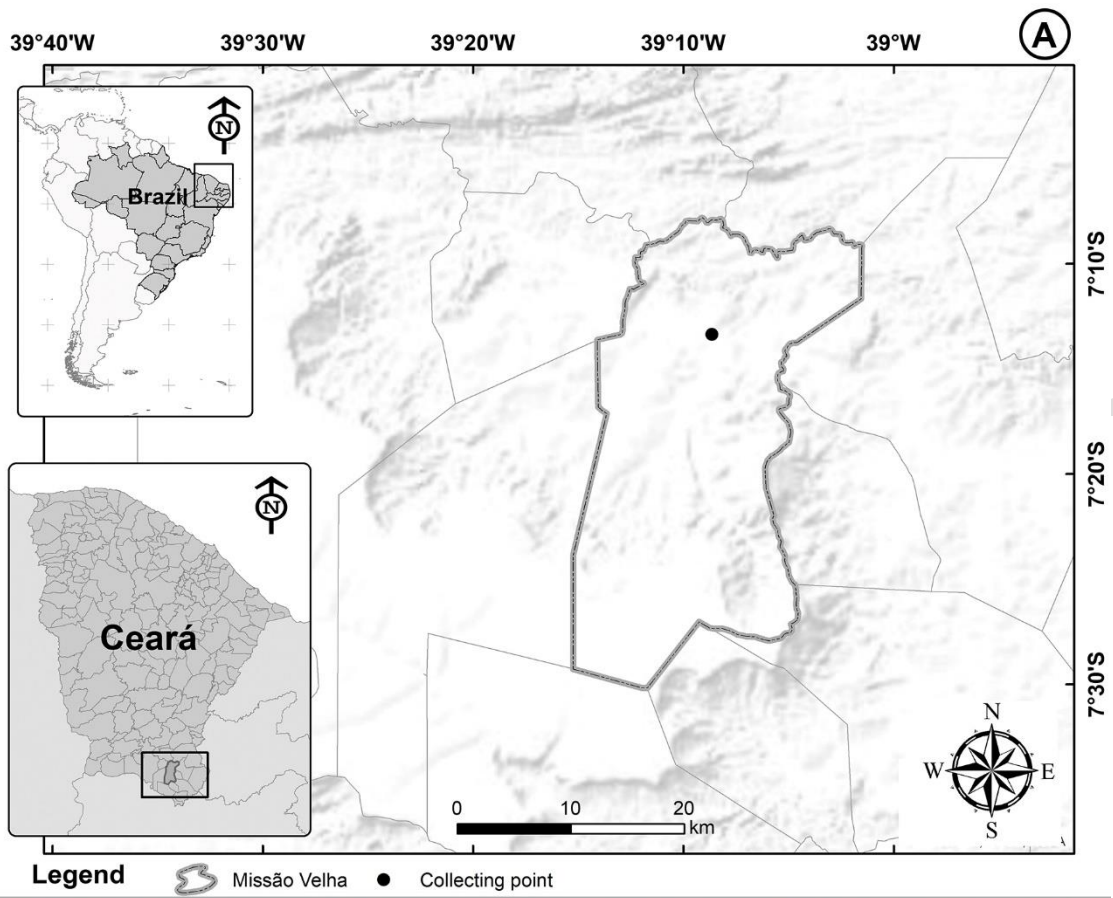
Figure 2. *Phyllopezus periosus* of rocky cliffs of the Missão Velha waterfall. A: juvenile; B: adult individual.

Figure 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.

Figure 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).

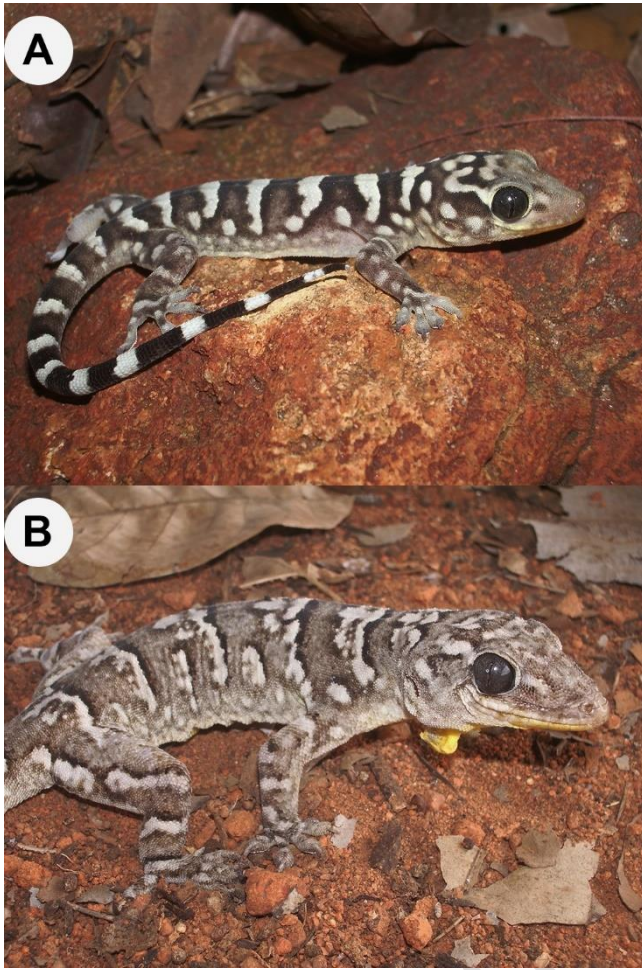
Figure 5. Communal nests of *P. periosus* in horizontal rocky crevice (A), and of both *P. periosus* and *P. pollicaris* in diagonal crevice (B).

754 Fig. 1



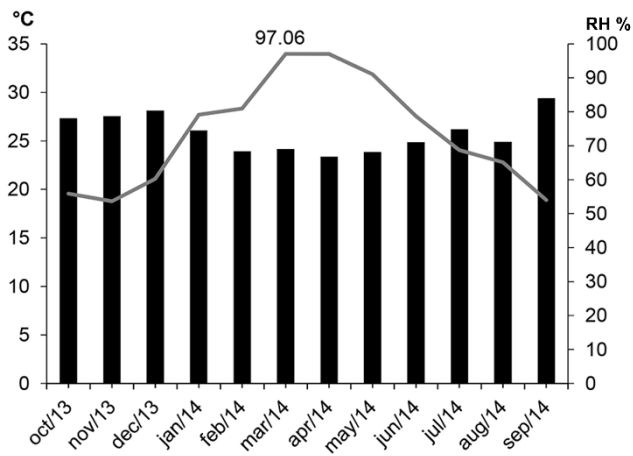
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756 Fig. 2



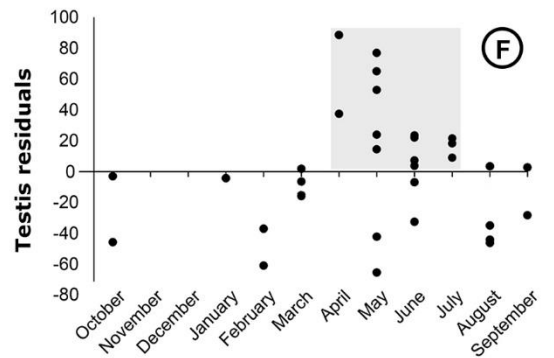
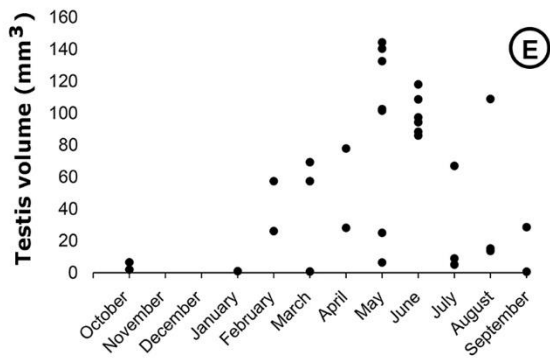
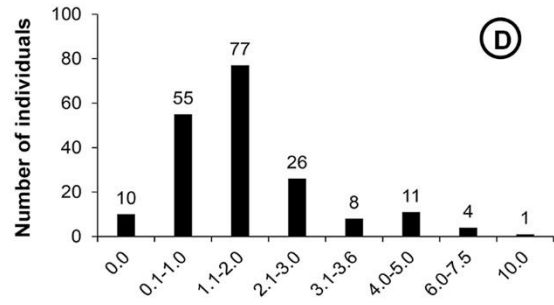
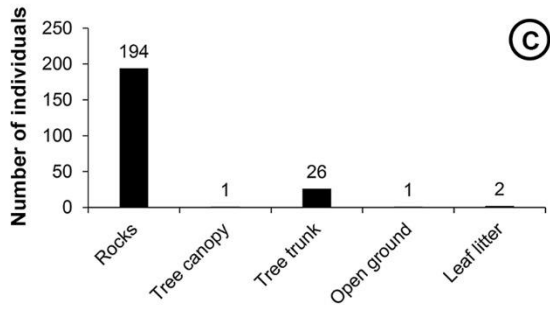
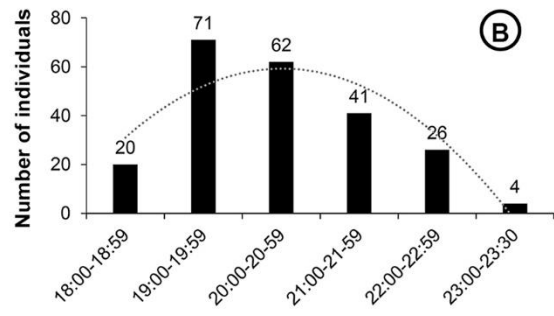
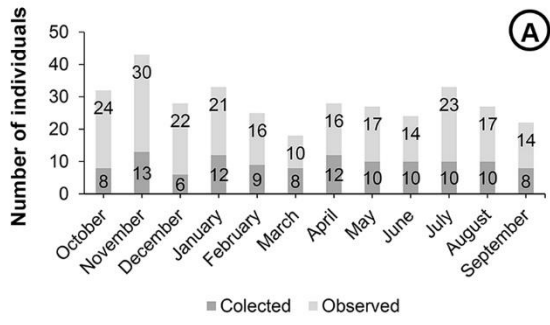
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758 Fig. 3



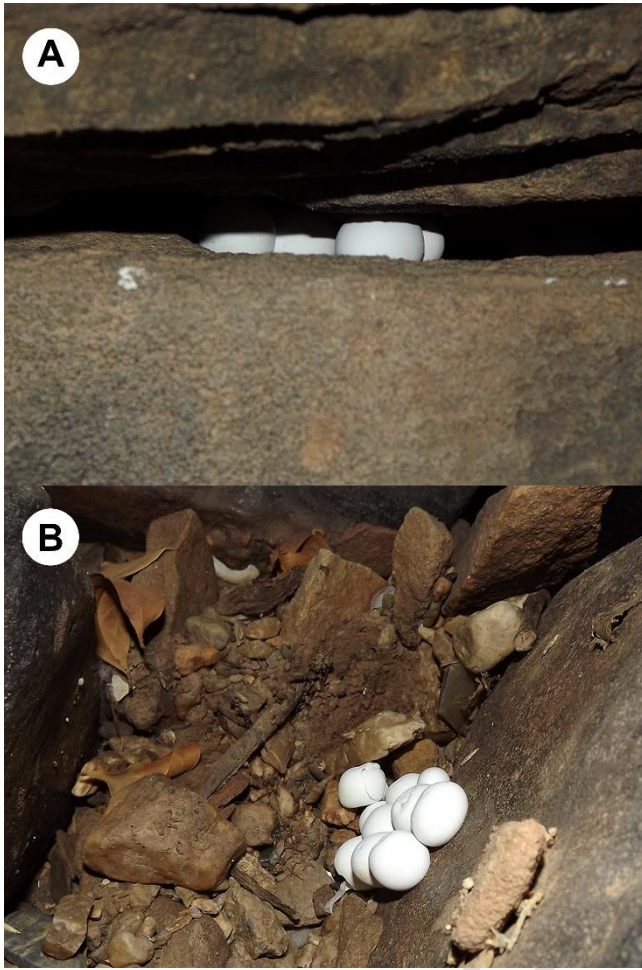
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762 Fig. 5



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