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**Ecological aspects of *Coleodactylus meridionalis* (Squamata: Sphaerodactylidae) in an Atlantic rainforest fragment in Northeastern Brazil**

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1 **Abstract.** Understanding the autecology of cryptic species is fundamental for developing  
2 effective conservation strategies, particularly in threatened biomes such as the Atlantic Forest.  
3 In this study, we investigated ecological aspects of *Coleodactylus meridionalis*, a small  
4 terrestrial lizard with a broad distribution, in an Atlantic Forest fragment. Specifically, we  
5 analyzed the usage of microhabitats, morphological characteristics, reproductive aspects, diet,  
6 and associated endoparasites. We conducted monthly seven-day expeditions from August 2014  
7 to July 2015 in the Campo de Instrução Marechal Newton Cavalcante, Pernambuco, Brazil. We  
8 recorded spatial use by 285 individuals, 271 (95%) of which were found in the forest interior,  
9 predominantly in leaf litter microhabitats (90.5%; N = 258). Females were significantly larger  
10 than males and had proportionally higher head heights. The diet included 22 prey categories,  
11 with Isopoda being the most frequent and voluminous and Psocoptera the most numerous prey  
12 categories found in the stomachs. The population reproduces continuously throughout the year,  
13 with fixed clutches of a single egg. The macro endoparasites found was an acanthocephalan  
14 cystacanth, with a prevalence of 13% and a mean infection intensity of  $1.5 \pm 0.74$ , and a  
15 Brachycoeliidae trematode, with a prevalence of 1.9% and a mean intensity of  $3 \pm 1.9$ . This is  
16 the first record of parasites for *C. meridionalis*, both as a paratenic host for cystacanth and as a  
17 definitive host for Brachycoeliidae.

18 **Keywords.** Diet, Lizard ecology, Microhabitat use, Parasitism, Reproductive strategy, Sexual  
19 dimorphism.

## Introduction

20

21 Autecological studies provide essential baseline data for understanding the ecological  
22 requirements of species and guiding targeted, science-based conservation strategies (Hortal and  
23 Lobo, 2006; Tewksbury et al., 2014). This is particularly relevant for cryptic species or data-  
24 deficient taxa inhabiting historically disturbed biomes, such as the Atlantic Forest, one of the  
25 most threatened biodiversity *hotspots* in the world (Pinto and Voivodic, 2021). In this context,  
26 miniature lizards specialized to live in leaf-litter, such as those of the genus *Coleodactylus*,  
27 present significant knowledge gaps that must be filled to improve our understanding of their  
28 basic ecology.

29 *Coleodactylus* is a genus composed of five species: *Coleodactylus brachystoma*, *C.*  
30 *elizae*, *C. meridionalis*, *C. natalensis*, and *C. septentrionalis*. Among these, *C. meridionalis* is  
31 one of the smallest lizards in Brazil, reaching around 25 mm snout-vent length (Freire, 1999;  
32 Silva et al., 2015). This species is an active forager with a broad distribution, occurring in leaf  
33 litter or piles of woody debris microhabitats within the arboreal Caatinga, highland forest  
34 enclaves in the Caatinga morphoclimatic domain, Atlantic Forest fragments of northeastern  
35 Brazil, and areas of Cerrado vegetation (Feitosa et al., 2022; Uchôa et al., 2022; Roseno et al.,  
36 2024.). Despite its wide range distribution, data on the natural history and ecology of *C.*  
37 *meridionalis* remain limited, with specific data from areas of Caatinga, Cerrado, Restinga and  
38 highland enclaves. These studies have explored the defensive and foraging behavior, diet,  
39 microhabitat usage, sexual dimorphism, hatching, and neonate size of *C. meridionalis* (Colli et  
40 al., 2002; Werneck et al., 2009; Ribeiro et al., 2013; Silva et al., 2015; Feitosa et al., 2022;  
41 Gonçalves-Sousa et al., 2023; Roseno et al., 2024 ).

42 In the present study, we investigated the natural history and ecology of *C. meridionalis*  
43 in an Atlantic Forest fragment within the Aldeia-Beberibe Environmental Protection Area,  
44 Pernambuco, Brazil. Following the Hutchinsonian ecological niche concept, defined as a

45 hypervolume n-dimensional (Hutchinson, 1957), we aimed to estimate key axes for this lizard.  
46 Specifically, we aimed to: (i) explore the spatial (microhabitat use) and trophic (diet)  
47 dimensions of the ecological niche; (ii) estimate the population density; (iii) analyze  
48 morphology (body size and sexual dimorphism); (iv) investigate reproductive aspects; and (v)  
49 identify the macro endoparasites that infect *C. meridionalis*.

50

## 51 **Materials and Methods**

### 52 *Study area*

53 The study was conducted at the Marechal Newton Cavalcante Instruction Camp, a  
54 fragment of Atlantic Forest located between the Metropolitan Region of Recife and Zona da  
55 Mata Norte, Pernambuco state, northeastern Brazil. The area has 7,342 ha of forest and a  
56 constructed area that is part of Aldeia-Beberibe Environmental Protection Area and other forest  
57 fragments. Sampling was conducted in the municipalities of Araçoiaba (07°49'00.8"S;  
58 35°06'08.6"W), Paudalho (07°49'54.3"S; 35°06'53.7"W) and Abreu e Lima (07°50'12.3"S;  
59 35°05'29.8"W). There are two distinct seasons in the region. The dry season lasts from  
60 September to February, and the wet season between March and August. Monthly average  
61 temperature ranges from 21.8°C to 29.1°C, with an average annual rainfall of 2,458 mm (World  
62 Weather Information Service, 2013).

63 The vegetation is classified as Ombrophilous and Seasonal Semideciduous Forest  
64 (Veloso et al., 1991). Before 1944, this area belonged to 11 sugarcane mills; following  
65 expropriation, it began to regenerate (Guimarães et al., 2012). The area is characterized by  
66 herbaceous, shrub and forest canopy strata. It has a conserved forest area as well as various  
67 roads, a weir, several streams and exotic vegetation such as “dendê” (*Elaeis guineensis*), olive  
68 tree (*Syzygium cumini*), mango (*Mangifera indica*), jackfruit (*Artocarpus heterophyllus*) and  
69 bamboo trees.

70

71 *Data collection*

72           Between August 2014 and July 2015, we conducted monthly expeditions of seven days  
73 each to collect the lizards. In the sampled area, we installed 25 sets of Y-shaped pitfall traps,  
74 each containing four 20-liter buckets buried at 120° angles and interconnected by drift fences  
75 and spaced at least 15 meters apart (Cechin and Martins, 2000). We inspected these traps once  
76 a day and kept them open for six consecutive days. The accumulation of leaf litter inside the  
77 buckets simulated the adjacent microhabitats, provided shelter and maintained humidity,  
78 minimizing desiccation and predation risks for captured specimens. We also employed an active  
79 search method, in which three collectors searched in all potential microhabitats used by *C.*  
80 *meridionalis* (Fig. 1). For each active individual found, we recorded the time of activity and the  
81 microhabitat use. The active search was conducted for 6 hours daily over seven days in each  
82 expedition, divided into 3 hours in the day and 3 hours at night (19:00-22:00). To cover different  
83 activity peaks, the diurnal sampling alternated daily between a morning session (08:00-11:00)  
84 and an afternoon session (14:00-17:00). In this way, the total sampling effort of active searches  
85 was 1,512 h (504 per collector), whereas the total time the pitfall traps remained open was  
86 43,200 h (25 pitfall sets x 24 h x 6 days x 12 months).

87           We euthanized the lizards with 2% lidocaine hydrochloride by peritoneal injection and  
88 used a digital caliper (0.01 mm accuracy) to measure the following variables: snout-vent length  
89 (SVL), head length (HeL), head width (HeW), head height (HeH), body width (BoW), and body  
90 height (BoH); forelimb length (FRL), hind limb (HDL), and tail length (TL). Then, we fixed  
91 the collected lizards in 10% formalin, preserved in 70% alcohol and, subsequently, and  
92 deposited them at the Laboratory of Venomous Animals and Toxins of the Federal University  
93 of Pernambuco. All specimens were collected under federal authorization from SISBio /  
94 ICMBio (43750-1 and 43750-2).

95 *Microhabitat use*

96 In the field, we recorded the time of sighting, and the microhabitat used for each  
97 individual at the moment of first sight. These categories correspond to bamboo leaf litter, fallen  
98 trunk, leaf litter, and open ground. We separated the two types of leaf litter because they are  
99 visually and structurally distinct: the bamboo leaf litter is relatively homogeneous with light-  
100 colored, yellowish dry leaves, while the general leaf litter is heterogeneous and frequently dark-  
101 toned. We then used the inverse of the index of Simpson (1949) to calculate the microhabitat  
102 niche breadth and calculated the percentages of microhabitats used according to the occurrence  
103 of lizards.

104 *Population density*

105 To estimate the density of *C. meridionalis* in the studied area, we collected abundance  
106 data from 15 quadrants measuring 10 m x 10 m (100 m<sup>2</sup>). The minimum distance between these  
107 quadrants was 130 meters. Inside each quadrant, three collectors conducted an exhaustive  
108 search by systematically raking and removing the entire leaf-litter layer, starting from the edges,  
109 until the entire 100 m<sup>2</sup> area was cleared to the soil to maximize detection.

110 The average density was calculated by dividing the total number of individuals by the  
111 15 quadrants. This value was then multiplied by 100 to standardize the density per hectare  
112 (ind/ha). We then used the 95% confidence interval to assess the spatial variability in the  
113 abundance of the studied lizard. This interval was calculated based on the sample mean,  
114 standard deviation, and standard error of the mean, considering the Student's t-distribution in  
115 the stats R-package (R Core Team, 2024).

116

117 *Sexual dimorphism*

118 Dimorphism analyses followed the model used by Mesquita et al. (2015), who tested  
119 dimorphism in *Anolis brasiliensis*. We log-transformed (base 10) the morphometric variables

120 and selected the data for multivariate outliers with the mvoutlier R-package (Filzmoser et al.,  
121 2018). No males were considered outliers, but six females were considered outliers using a  
122 maximum limit for outlier detection of 0.001 and were not used in further analyses.

123 To partition total morphometric variation between size and shape variables, we defined  
124 Body Size as an isometric size variable (Rohlf and Bookstein, 1987). We calculated an isometric  
125 eigenvector defined a priori with values equal to  $p^{-0.5}$ , where  $p$  is the number of variables  
126 (Jolicoeur, 1963). The scores derived from this eigenvector, hereafter referred to as Body Size,  
127 were obtained by post-multiplying the  $n \times p$  matrix of  $\log_{10}$ -transformed data, where  $n$  is the  
128 number of observations, by the  $p \times 1$  isometric eigenvector. To remove the effects of SVL from  
129 the log-transformed variables, we applied the method of Burnaby (1966), multiplying the  $n \times p$   
130 matrix of the  $\log_{10}$ -transformed data by  $p \times p$  of the symmetric matrix  $L$ , defined as:  $L = I_p -$   
131  $V(V^T V)^{-1} V^T$ , where  $I_p$  is the  $p \times p$  matrix,  $V$  is the Body Size eigenvector, and  $V^T$  is the  
132 transposed  $V$  matrix (Rohlf and Bookstein, 1987). The resulting size-adjusted variables were  
133 then considered shape variables. We assessed sexual dimorphism using analysis of variance  
134 (ANOVA) on the Body Size variable and logistic regression on shape variables. To evaluate the  
135 statistical significance of the complete model based on shape variables, we compared it against  
136 a single model constant (null) using a scaled difference chi-square test (Chambers and Hastie,  
137 1992; Faraway, 2016). The importance of each variable was determined through single-term  
138 addition modeling (Chambers and Hastie, 1992).

139

#### 140 *Reproduction*

141 The animals were sexed through direct analysis of the gonads. The presence or absence  
142 of oviductal eggs and/or vitellogenic follicles was verified to determine the status of  
143 reproductive activity of females, considering them sexually mature if they presented either of



144 these two evidence, while those lacking both were considered immature. Sexually mature  
145 females were evaluated for the number, length and width of eggs, as well as the volume,  
146 number, and diameter of the largest vitellogenic follicle. To assess whether body size influences  
147 egg size, we used a parametric correlation of Pearson between SVL and egg volume. The eggs  
148 and vitellogenic follicles found were used to infer the reproductive season, the number of eggs  
149 per clutch, and the frequency of oviposition per season.

150           The assessment of male sexual maturity relied on the presence of convoluted  
151 epididymis, identified under a stereomicroscope. We measured the testes (length and width) to  
152 estimate its volume using the ellipsoid formula. To evaluate the influence of body size on testes  
153 volume, we performed a simple linear regression with SVL as the predictor and testes volume  
154 as the response variable using the stats R-package (R Core Team, 2024).

155

#### 156 *Diet*

157           In the lab, we removed the stomachs of all lizards collected and analyzed them under a  
158 stereomicroscope to identify prey items up to the Order level. Prey items were analyzed for  
159 their frequency, number (abundance), and volume. The length and width of each prey item were  
160 measured using a digital caliper ( $\pm 0.1$  mm accuracy), and its volume (in  $\text{mm}^3$ ) was estimated  
161 using the ellipsoid formula (Dunham, 1983):  $V = 4/3 \pi (w/2)^2 (l/2)$ , where  $w$  is the prey width  
162 and  $l$  is the prey length. The importance index was calculated to determine the relative  
163 importance of each prey category within the total diet, using the formula:  $(F\%+N\%+V\%)/3$ .  
164 Thus, we used the inverse of the index of Simpson (1949) to estimate the food niche breadth,  
165 both numerically and volumetrically.

166           To assess whether the size of the lizard influences the size of the prey it consumes, we  
167 used a multiple linear regression analysis with prey volume as the response variable and SVL,  
168 HeL, HeW, and HeH as predictors. To fit the volume data to a normal distribution, we applied  
169 a base-10 logarithmic transformation. Therefore, the final model was `model_volume = lm`

170 (log\_volume ~ SVL + HeL + HeH + HeW, data = morfo\_volume), which resulted in residuals  
171 with a normal distribution (W = 0.99121, p-value = 0.4901).

172

### 173 *Parasitism*

174 We examined the liver, as well as the digestive, reproductive and respiratory systems in  
175 search of parasites. The parasites found were mounted on temporary slides in Hoyer medium  
176 and subsequently analyzed under light microscopy to be identified based on the specialized  
177 literature (e.g., Yamaguti, 1971; Schmidt, 1986) and by comparison with specimens deposited  
178 in the Parasitological Collection of the Regional University of Cariri.

179 Prevalence and mean intensity of parasite infection were calculated according to Bush  
180 et al. (1997). The index of discrepancy ranges from a minimum value of zero, indicating an  
181 equal distribution of parasites among hosts, to a maximum value of 1 (D = 1), indicating that  
182 all parasites are combined in a single host (Poulin, 1993). These indexes were calculated using  
183 Quantitative Parasitology software 3.0 (Reiczigel et al., 2019).

184

## 185 **Results**

186 In total, 394 *C. meridionalis* specimens were found: 235 by manual capture, 89 by pitfall  
187 traps and 70 by visual identification (sighted but not collected).

### 188 *Microhabitat use*

189 We recorded microhabitat use by 285 individuals of *C. meridionalis*, including 269  
190 adults and 16 juveniles. The distribution across microhabitats was leaf litter (90.52%; n = 258),  
191 bamboo leaf litter (5.96%; n = 17), fallen trunk (1.76%; n = 5) and open ground (1.76%; n = 5).  
192 The niche breadth based on microhabitat use was 1.214, revealing a high degree of  
193 specialization in leaf litter (Table 1).

194 *Population density*

195           The average density of *C. meridionalis* was 2.13 individuals per 100 m<sup>2</sup> quadrant,  
196 which corresponds to 213.33 individuals per hectare. The 95% confidence interval suggests  
197 that the average density per hectare may vary between 78 and 349 individuals. This density  
198 estimate (213 ind/ha) represents the local density within sampled microhabitats, which (based  
199 on our field records) were concentrated in patches of suitable leaf-litter microhabitats.

200 *Sexual dimorphism*

201           We analyzed the morphometric measurements of 116 *C. meridionalis* adult specimens,  
202 which 57 were females and 59 were males). We detected sexual dimorphism in the Body Size  
203 isometric variable ( $F_{1,109} = 19.38$ ;  $P < 0.001$ ), with females larger than males (Table 2).  
204 However, model selection analysis showed no significant differences in individual variables  
205 between sexes (all  $P > 0.05$ ).

206 *Reproduction*

207           We analyzed reproductive data of 192 *C. meridionalis* lizards (87 females, 78 males,  
208 and 27 juveniles), of which 153 (75 were females, 72 males and six juveniles) were collected.  
209 The smallest reproductively mature male measured 18.35 mm. Testes volume was significantly  
210 influenced by the SVL ( $F = 13.244$ ; adjusted  $R^2 = 0.1719$ ;  $p = 0.0006$ ), with decreased volume  
211 between July and November (Fig. 2).

212           *Coledactylus meridionalis* presented a fixed clutch size of one egg. Females showed  
213 continuous reproduction throughout the year. However, no reproductively mature females were  
214 found in either April, or from August to October, possibly due to the low number of individuals  
215 collected during this period. The smallest reproductively mature female had an SVL of 17.57  
216 mm. There was no significant correlation between egg volume and female SVL ( $t = -1.549$ ,  $df$   
217  $= 11$ ,  $p = 0.1496$ ).

218 Three eggs of *C. meridionalis* were found at different times under leaf-litter, situated at  
219 the tree base. These eggs were collected with a portion of the substrate and stored at  
220 environmental temperature. One egg (length: 5.15 mm, width: 4.22 mm, weight: 0.051 g),  
221 collected in June, did not hatch. The remaining two eggs (length: 5.20 mm, width: 4.40 mm,  
222 weight: 0.53 g; length: 5.46 mm, width: 4.35 mm, weight: 0.57 g), found together in July,  
223 successfully hatched after 53 days. Post-hatching, the neonates measured: 1) SVL = 11.88 mm,  
224 TL = 8.50 mm, weight = 0.036 g; 2) SVL = 11.16 mm, TL = 9.20 mm, weight = 0.034 g).  
225 Juveniles were found throughout the year, except for April and November, with the highest  
226 numbers recorded in January (N = 5) and June (N = 7).

#### 227 *Diet*

228 We analyzed the diet of all 154 *C. meridionalis* collected. Of these, ten specimens had  
229 empty stomachs and intestines, while seven presented unidentifiable content. We identified a  
230 total of 22 food categories, with an average of two prey categories per stomach (RANGE: 1-5).  
231 The diet of *C. meridionalis* exhibited predominance in frequency with Isopoda (16.8%),  
232 Araneae (14.9%), and Collembola (10.2%); in number with Psocoptera (20.6%), Isoptera  
233 (18.97%), and Collembola (17.53%); and in volume with Isopoda (36.5%). According to the  
234 importance index, the most significant prey category was Isopoda (21.4%), followed by  
235 Psocoptera (12.1%) and Isoptera (11.5%) (Table 3). Among the six juvenile specimens  
236 examined, one had an empty digestive tract, one had unidentifiable content, and four contained  
237 Diptera (n = 1) and Psocoptera (n = 2, n = 2, n = 16).

238 The diet of *C. meridionalis* was generalist, with a numerical food niche breadth of 7.348  
239 and volumetric breadth of 3.641. No significant difference in the diet composition was found  
240 between adult males and females, either in number (ANOSIM, R = 0.0202; p = 0.055) or in  
241 volume (ANOSIM, R = 0.0078; p = 0.265). The multiple linear regression revealed that the size  
242 of the lizards influences the volume of prey ingested (F = 5.001; adjusted R<sup>2</sup> = 0.0982; p =

243 0.001). The two individual variables that showed statistical significance were head width (HeW:  
244  $F = 8.472$ ;  $p = 0.004$ ) and head length (HeL:  $F = 5.411$ ;  $p = 0.021$ ).

245

#### 246 *Parasitism*

247 Out of 154 specimens of *C. meridionalis* (75 females, 73 males and six juveniles, 23  
248 specimens (18 females and five males) were infected by at least one parasite species (total  
249 prevalence of 13.6%). Twenty specimens were infected with cystacanth (Acanthocephala  
250 larvae) ( $N = 30$ ) (Fig. 3A), with a prevalence of 13% and a mean infection intensity of  $1.5 \pm$   
251  $0.74$  (range 1 – 3). These cystacanths were found in eight infection sites: loosely in the body  
252 cavity ( $N = 9$ ), adhered to the body wall ( $N = 7$ ), adhered to the stomach ( $N = 7$ ), adhered to  
253 the liver ( $N = 5$ ), , adhered to the testes ( $N = 2$ ), adhered to follicles ( $N = 4$ ), and subcutaneously  
254 ( $N = 1$ ) (Table 4). Acanthocephala larvae adhered to the liver and stomach caused visible  
255 damage to host tissue due to their extreme adherence.

256 Additionally, three *C. meridionalis* were infected by nine adult Brachycoeliidae worms  
257 (Trematoda: Digenea) (Fig. 3B) found in the esophagus ( $N = 1$ ) and stomach ( $N = 8$ ), with a  
258 prevalence of 1.9% and a mean intensity of infection of  $3 \pm 1.9$  (range 1 – 7) (Table 4). Only  
259 two lizards were infected by both parasites simultaneously. The discrepancy index for  
260 cystacanth was 0.895 and for Brachycoeliidae was 0.983. There was no significant difference  
261 in abundance observed between sexes ( $Z = 0.596$ ;  $P = 0.116$ ), between dry and wet seasons ( $Z$   
262  $= 839$ ;  $P = 0.401$ ) or when considering both sex and season ( $Z = 0.138$ ;  $P = 0.891$ ).

263

264

## 264 **Discussion**

265 *Coleodactylus meridionalis* is a microhabitat specialist, predominantly and almost  
266 exclusively using leaf litter. Similar results have been found in other *C. meridionalis*  
267 populations (Silva et al., 2015; Gonçalves-Sousa et al., 2023) and congenics such as *C.*

268 *septentrionalis*, *C. brachystoma* and *C. natalensis* (Colli et al., 2002; Vitt et al., 2005; Sousa  
269 and Freire, 2011; Lisboa and Freire, 2012), suggesting phylogenetic conservatism in the  
270 microhabitat use. In a Cerrado area, *C. meridionalis* used the same number of microhabitat  
271 categories found by us, but with a more even distribution across two microhabitats (spatial niche  
272 breadth = 2.57).

273 The spatial niche specialization of *C. meridionalis*, with its preference for leaf litter, can  
274 be interpreted through the lens of microevolutionary optimization, particularly regarding fine-  
275 scale crypsis (Hendry and Kinnison, 2001). *Coleodactylus* spp. are known for using a low range  
276 of microhabitats (Present study; Vitt et al., 2005; Lisboa and Freire, 2012; Gonçalves-Sousa et  
277 al., 2023). The cryptic, coppery coloration of *C. meridionalis* (Vanzolini, 1957) favors  
278 camouflage within dark leaf litter, its preferred microhabitat (90.52% of individuals recorded  
279 in this study). However, in bamboo leaf litter, characterized by light-colored, yellowish dry  
280 leaves, *C. meridionalis* was less frequent (5.96%) and displayed intraspecific variation,  
281 exhibiting lighter, orange-toned coloration. This change improves camouflage in this lighter  
282 microhabitat, thereby reducing predation risk. This phenotypic alignment with the substrate  
283 underscores the role of selective pressures on coloration, where this crypsis enhances fitness  
284 and shapes the spatial distribution of the species at local spatial scales.

285 Although no single variable showed a significant difference when tested individually,  
286 the Body Size isometric variable was significant, with females larger than males. In contrast,  
287 Silva et al. (2015) found that males had significantly higher SVL than females in another  
288 population of *C. meridionalis* in a Humid Forest enclave within the Caatinga domain in  
289 northeastern Brazil. These characteristics may vary between different populations, although our  
290 data present a larger sample, which may better explain the morphological pattern of these  
291 lizards. Moreover, in other studies, mean SVL in *Coleodactylus* species was higher in females,  
292 including *C. meridionalis*, *C. elizae* and *C. natalensis* (Freire, 1999; Goncalves et al., 2012).

293 These findings suggest that sexual dimorphism in *C. meridionalis* is a labile functional trait  
294 shaped by different local selective pressures across biomes.

295 Sexual dimorphism in lizards typically results from fecundity or sexual selective  
296 pressures, whose effects appear to geographically change across *C. meridionalis* populations.  
297 The females larger than males found in our study is often linked to fecundity selection (e.g.,  
298 Andersson, 1994; Olsson et al., 2002), but the mechanism for this selection seems multifactorial  
299 in this miniaturized species. *Coleodactylus meridionalis* has a one-egg fixed clutch size, and  
300 our analysis found no significant correlation between egg volume and female SVL. This finding  
301 suggests that the advantage of larger female size is probably not associated with bigger  
302 offspring, but rather to improve energy storage, as in larger fat bodies. Greater energy reserves  
303 would be advantageous for sustaining the continuous reproductive effort observed throughout  
304 the year. On the other hand, *C. meridionalis* males larger than females found by Silva et al.  
305 (2015) suggests that sexual selection (Colli et al., 2003; Mesquita and Colli, 2003) may be  
306 dominant in that Caatinga population.

307 The diet of *C. meridionalis* consisted exclusively of arthropods, exhibiting a generalist  
308 feeding pattern that is best explained by high opportunistic food plasticity. In our study, the  
309 broad food niche dimension is similar to findings from two populations of Atlantic Forest  
310 (Teixeira et al., 2021), Cerrado (Werneck et al., 2009), and a population from Humid Forest  
311 enclave within the Caatinga domain (Silva et al., 2015), but contrasts with the specialist feeding  
312 habits reported in two other Atlantic Forest and Caatinga vegetation areas (Supporting  
313 Information S3 in Gonçalves-Sousa et al., 2023). This shifts across areas in the diet of *C.*  
314 *meridionalis*, even within the same biome or among close areas, reveals strong evidence of  
315 plasticity in prey selection. For example, the Order Isopoda was the main food category ingested  
316 in our study (importance index 21.4%) and in two other populations (35.71% and 34.1%;  
317 Teixeira et al., 2021) of the Atlantic Forest, and in a population from a semideciduous seasonal

318 forest area (48.1% in frequency; Silva et al. 2015). On the other hand, Formicidae (44.1%) and  
319 Insect larvae (35.15%) were the main categories in other populations from the Atlantic Forest  
320 (Teixeira et al., 2021), whereas Isoptera (51%) and Siphonaptera (44.8%) were predominant in  
321 a Caatinga population from Cuité, Paraíba (Gonçalves-Sousa et al., 2023), and Araneae (80.8%)  
322 in another Caatinga population from Palmas de Monte Alto, Bahia (Gonçalves-Sousa et al.,  
323 2023). Additionally, in a Cerrado enclave in São Domingos, Goiás, Isoptera was the most  
324 important prey category (36.87%; Werneck et al., 2009). Therefore, it is plausible to infer that  
325 the diet of *C. meridionalis* is strongly influenced by local ecological factors, such as resource  
326 availability, with the availability of suitable sized food resources for this small lizard in each  
327 area determining the most significant categories in the diet composition.

328 We found that the size of the lizards, specifically head width and head length,  
329 significantly influenced the volume of prey ingested, with larger lizards consuming larger prey.  
330 This finding aligns with similar results found in some lizard species of the families  
331 Sphaerodactylidae, Teiidae and Tropiduridae (Van Sluys et al., 2004; Vitt et al., 2005; Sales et  
332 al., 2011). In some lizard species, such as the leiosaurid *Enyalius brasiliensis*, both SVL and  
333 head width strongly influence diet, as larger measurements correlate with a greater volume of  
334 prey consumed (Dorigo et al., 2014). In contrast, there are lizards that do not exhibit a  
335 significant correlation between body or head size with prey size. For instance, medium to large-  
336 sized lizards like the tropidurid *Plica plica* and the teiid *Ameivula ocellifera* have a generalist  
337 diet composition, but small prey items, such as ants and termites, plays a significant role in their  
338 diet (Vitt, 1991; Mesquita and Colli, 2003).

339 Lizards are susceptible to several macro endoparasites, such as Acanthocephala,  
340 Cestoda, Nematoda, Pentastomida, and Trematoda (e.g., Ávila and Silva, 2010; Ribeiro et al.,  
341 2012; Sousa et al., 2014). In the present study, we detected infections in *C. meridionalis* caused  
342 by a cystacanth of Acanthocephala and by a trematode from the Brachycoeliidae family.



343 Acanthocephala can use lizards as paratenic or definitive hosts (Nickol et al., 2006; Smales,  
344 2007).

345 Infection by cystacanths can occur through feeding organisms such as termites, which  
346 have been identified as intermediate hosts for Acanthocephala (Amato et al., 2014; Nickol et  
347 al., 2006) and are also part of the diet of *C. meridionalis* in the studied population. In *C.*  
348 *meridionalis*, cystacanth parasites showed low prevalence (14.9%). Nonetheless, this rate is still  
349 higher than those found in another population of *C. meridionalis* (6.2%), as well as in  
350 *Psychosaura macrorhyncha* (7.1%), *Tropidurus hispidus* (3.5% and 0.69%) and *T.*  
351 *semitaeniatus* (0.51%) (Vrcibradic et al., 2002; Brito et al., 2014a; 2014b; Teixeira et al., 2021).  
352 Six out of seven identified infection sites of cystacanth in *C. meridionalis* align with registers  
353 in other host species (Vrcibradic et al., 2002; Nickol et al., 2006; Macedo et al., 2016; Campos  
354 et al., 2021), except for attachment to the testes. The sites with highest infection rates were  
355 those attached to the stomach and to the body wall (both dorsal and ventral), a pattern  
356 commonly observed in other lizards (Vrcibradic et al., 2002; Anjos et al., 2005; Campos et al.,  
357 2021). Subcutaneous infection by Acanthocephala was rare, registered only once in our study  
358 and once for *Anolis cristatellus* (Nickol et al., 2006). Cystacanths were also found parasitizing  
359 *Anolis fuscoauratus* in the same sampled area of this study (Campos et al., 2021). Although we  
360 only encountered the larval stage, this finding highlights the high plasticity of this parasite, as  
361 it can infect lizards adapted to a wide range of microhabitats, including leaf litter and tree  
362 branches.

363 This is the first report of a trematode from the Brachycoeliidae family parasitizing *C.*  
364 *meridionalis*. This finding also represents the third record of parasitism in Sphaerodactylidae  
365 lizards within South America (Ávila and Silva, 2010). In Brazil, the family Brachycoeliidae  
366 (Trematoda) is reported as a Squamata parasite, mostly in lizards living in Caatinga regions and  
367 in the Archipelago of Fernando de Noronha (Ramalho et al., 2009; Ávila and Silva, 2010); in

368 the Amazonia Forest region (Burseley and Goldberg, 2004); and in the southeastern Restinga area  
369 (Rodrigues et al., 1990). The prevalence of Brachycoeliidae infection was low in *C.*  
370 *meridionalis* (1.9%). A low prevalence of trematodes in lizards appears to be a common pattern,  
371 as several studies have found prevalences between 3% and 7% (Goldberg and Bursey, 2000;  
372 Ramalho et al., 2009; Teixeira et al., 2021). Contrarily, the Central America lizard *Lepidophyma*  
373 *flavimaculatum* showed prevalence of 80% (8/10 individuals), but with low infection intensity  
374 ( $2.4 \pm 1.8$ ; Bursey et al., 2006). Unlike *L. flavimaculatum*, where trematodes were almost  
375 uniformly, the discrepancy index (0.993) indicated that these parasites occur clustered in *C.*  
376 *meridionalis*. This finding is mainly due to the fact that 7 out of the 10 collected trematodes  
377 were found in just one host individual, suggesting that this parasite infection may occur casually  
378 or even accidentally in the studied area.

379 According to our revision, the most frequent Brachycoeliidae infection site is the  
380 intestine, aligning with preferred infection sites reported for other families of the Digenea  
381 subclass parasitizing lizards (Ávila and Silva, 2010). However, it is noteworthy that within this  
382 subclass, parasites from the same family can infect different sites, such as gallbladder, liver and  
383 intestines, with stomach as a potential infection site (Ávila and Silva, 2010). Considering that  
384 Brachycoeliidae was found inside the stomach and esophagus of *C. meridionalis*, the potential  
385 parasitic sites for this family extend beyond the intestine.

We concluded that *C. meridionalis* is a sexually dimorphic lizard that typically inhabit forested environments, mainly using leaf litter as its microhabitat. This microhabitat preference indicates phylogenetic conservatism. Contrarily, this lizard showed a generalist and opportunistic feeding habit, suggesting high food plasticity and adaptability according to the food resource availability in each area. Lastly, *C. meridionalis* is a paratenic host for cystacanth and a definitive host Brachycoeliidae species.

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565 Table 1. Microhabitats used by  
566 *Coleodactylus meridionalis* in a fragment of  
567 the Atlantic Forest within the Aldeia-  
568 Beberibe Environmental Protection Area,  
569 northeastern Brazil. *n* = number of  
570 microhabitat use records (percentages).

571

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<b>Microhabitat</b>	<b>n (%)</b>
Bamboo leaf litter	17 (5.96)
Leaf litter	258 (90.52)
Fallen trunk	5 (1.76)
Open ground	5 (1.76)
<b>Total</b>	<b>285</b>
<b>Niche breadth</b>	<b>1.214</b>

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573 Table 2. Morphometric measurements (in mm) of adult *Coleodactylus meridionalis* from an  
 574 Atlantic Forest fragment, Pernambuco, northeastern Brazil. SVL (snout-vent length), TL (tail  
 575 length), HeL (head length), HeW (head width), HeH (head height), BoW (body width), BoH  
 576 (body height), FRL (forelimb length), and HDL (hind limb length).

Characters	RANGE (average $\pm$ standard deviation)	
	Females (N = 57)	Males (N = 59)
SVL	17.57 – 25.16 (22.62 $\pm$ 1.66)	18.35 – 23.73 (21.06 $\pm$ 1.14)
TL	12.23 – 21.00 (17.65 $\pm$ 2.4; N= 28)	10.29 – 20.70 (17.20 $\pm$ 2.7; N= 33)
HeL	3.11 – 6.16 (5.28 $\pm$ 0.51)	4.08 – 5.70 (4.99 $\pm$ 0.40)
HeW	2.17 – 3.99 (3.37 $\pm$ 0.36)	2.74 – 3.98 (3.25 $\pm$ 0.27)
HeH	1.06 – 3.27 (2.16 $\pm$ 0.36)	1.57 – 2.84 (2.16 $\pm$ 0.27)
BoW	2.57 – 6.21 (4.36 $\pm$ 0.74)	3.48 – 4.96 (4.05 $\pm$ 0.35)
BoH	1.79 – 4.19 (2.82 $\pm$ 0.52)	1.76 – 3.86 (2.64 $\pm$ 0.45)
FRL	4.42 – 7.59 (5.86 $\pm$ 0.64)	4.12 – 6.48 (5.45 $\pm$ 0.57)
HDL	5.38 – 9.14 (7.23 $\pm$ 0.80)	4.98 – 8.43 (6.99 $\pm$ 0.74)

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579 Table 3. Diet composition of *Coleodactylus meridionalis* in an Atlantic Forest fragment within the  
 580 Aldeia-Beberibe Environmental Protection Area, Pernambuco, northeastern Brazil. F = Frequency;  
 581 N = number; V = Volume (in mm<sup>3</sup>), with their respective percentages; I = importance index of prey  
 582 categories.

<b>Prey category</b>	<b>F</b>	<b>F%</b>	<b>N</b>	<b>N%</b>	<b>V</b>	<b>V%</b>	<b>I</b>
Acari	6	2.80	7	1.42	0.56	0.09	1.44
Araneae	32	14.9	45	9.18	41.2	6.67	10.2
Blattodea							
Blattaria	4	1.80	4	0.81	64.4	10.4	4.37
Isoptera	18	8.40	93	18.97	45.4	7.35	11.5
Coleoptera	3	1.40	10	2.04	2.90	0.46	1.30
Collembola	22	10.2	86	17.5	15.2	2.46	10.0
Dermaptera	2	0.93	2	0.40	11.0	1.78	1.04
Diptera	7	3.27	10	2.04	9.66	1.56	2.29
Lizard shed skin	4	1.86	4	0.81	-	-	0.89
Gastropoda	2	0.93	2	0.40	18.8	3.05	1.46
Hemiptera							
Auchenorrhyncha	3	1.40	3	0.61	1.87	0.30	0.77
Heteroptera	1	0.46	1	0.20	0.25	0.04	0.23
Others	1	0.46	1	0.20	1.32	0.21	0.29
Hymenoptera							
Formicidae	6	2.80	10	2.04	5.16	0.83	1.89
Others	3	1.40	3	0.61	17.7	2.87	1.63
Isopoda	36	16.8	54	11.0	225.9	36.5	21.4
Insect eggs	4	1.80	5	1.02	1.22	0.19	1.02
Insect larvae	21	9.80	30	6.12	42.9	6.94	7.62
Insect pupa	2	0.93	2	0.40	33.1	5.36	2.23
Orthoptera	10	4.60	10	2.04	39.0	6.31	4.34
Pseudoscorpiones	6	2.80	7	1.42	2.45	0.39	1.54
Psocoptera	21	9.80	101	20.6	37.3	6.04	12.1
<b>Trophic niche breadth</b>			<b>7.34</b>		<b>5.78</b>		

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585 Table 4. Lizard species parasitized by cystacanths (*Acanthocephala* larvae) and Brachycoeliidae  
 586 (Trematoda), with data on prevalence (P), mean intensity of infection (MII)  $\pm$  standard error (SE),  
 587 and infection sites. Cystacanth infection sites: (1) free in the body cavity, (2) subcutaneous, (3)  
 588 attached to the stomach, (4) attached to the liver, (5) attached to the peritoneous, (6) attached to the  
 589 testes, (7) attached to reproductive follicles, (8) attached to the intestine, (9) attached to the lung.  
 590 Trematoda infection sites: inside the (A) esophagus, (B) stomach, (C) intestine. (-) no data available.

	Host species	P (in %)	MI I $\pm$ SE	Infection site	Source
Cystacanth ( <i>Acanthocephala</i> larvae)	<i>Ameiva ameiva</i>	35.70	1	-	Smales, 2007
	<i>Ameiva ameiva</i>	60	-	1	Macedo et al., 20016
	<i>Anolis cristatellus</i>	67	-	2	Nickol et al., 2006
	<i>Coleodactylus meridionalis</i>	13	1.5 $\pm$ 0.74	1:7	Present study
	<i>Hemidactylus agrius</i>	-	-	1	Anjos et al., 2011
	<i>Hemidactylus mabouia</i>	33.70	4.2 $\pm$ 7	3, 5, 8	Anjos et al., 2005
	<i>Brasiliscincus agilis</i>	90.90	15 $\pm$ 10.7	1, 3:5, 8-9	Vrcibradic et al., 2002
	<i>Brasiliscincus agilis</i>	57.10	6.3 $\pm$ 10.7	1, 3:5, 8-9	Vrcibradic et al., 2002
	<i>Psychosaura macrorhyncha</i>	90.90	35.5 $\pm$ 45.8	1, 3:5, 8-9	Vrcibradic et al., 2002
	<i>Psychosaura macrorhyncha</i>	7.10	3	-	Vrcibradic et al., 2002
	<i>Anolis fuscoauratus</i>	37.50	2.15 $\pm$ 2.2	1, 3:5, 7-8	Campos et al., 2016
	<i>Tropidurus hispidus</i>	3.50	-	-	Brito et al., 2014a
	<i>Tropidurus hispidus</i>	0.69	3.5	-	Brito et al., 2014b
	<i>Tropidurus semitaeniatus</i>	0.51	1	-	Brito et al., 2014b
<i>Tupinambis teguixin</i>	14.30	1	-	Smales, 2007	
Brachycoeliidae (Trematoda: Digenea)	<i>Anolis sagrei</i>	3	1	C	Goldberg & Bursey, 2000
	<i>Cercosaura eigenmanni</i>	7	1	C	Bursey & Goldberg, 2004
	<i>Coleodactylus meridionalis</i>	1.90	3 $\pm$ 1.9	A, B	Present study
	<i>Diploglossus lessonae</i>	-	-	C	Ávila & Silva, 2010
	<i>Lepidophyma flavimaculatum</i>	80	2.4 $\pm$ 1.8	-	Bursey et al., 2006
	<i>Trachylepis atlantica</i>	4	3	C	Ramalho et al., 2009
	<i>Tropidurus torquatus</i>	33.30	-	C	Rodrigues et al., 1990

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592

593 Fig. 1. *Coleodactylus meridionalis* from a bamboo litter microhabitat, displaying characteristic  
594 orange markings, within an Atlantic Forest fragment in the Aldeia-Beberibe Environmental  
595 Protection Area, northeastern Brazil. Photo: José Vieira de Araújo-Neto.

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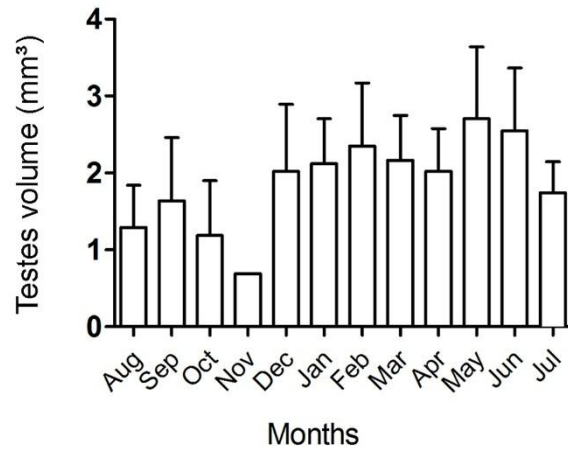
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607 **Fig. 2.** Monthly variation in testes volume (mm<sup>3</sup>) of adult male *Coleodactylus meridionalis* of  
608 an Atlantic Forest fragment within the Aldeia-Beberibe Environmental Protection Area,  
609 northeastern Brazil.

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611 Fig. 3. Parasites found in *Coleodactylus meridionalis* of an Atlantic Forest fragment within the  
612 Aldeia-Beberibe Environmental Protection Area, northeastern Brazil. (A) Cystacanth  
613 (Acanthocephala); (B) Ventral view of Brachycoeliidae (Trematoda: Digenea).

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