



Ecology of the bromeligenous frog *Phyllodytes luteolus* (Anura, Hylidae) from three restinga remnants across Brazil's coast

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ABSTRACT

In this study, we analyzed diet, sexual dimorphism and bromeliad use in three populations of the hylid frog *Phyllodytes luteolus* from restinga habitats along the Brazilian coast. We found 13 arthropods categories in 161 stomachs. Ants and termites were the dominant prey items. The similar trophic niche across populations suggests this species has a conservative diet. We found sexual dimorphism regarding body size and jaw width. We recorded *P. luteolus* in five bromeliad species, but predominantly in *Aechmea blanchetiana* (35.6% of individuals recorded). We recorded solitary individuals in 44% of occupied bromeliads, and never found two males sharing the same bromeliad. The data is suggestive that populations of *P. luteolus* has a conservative diet independent of area, with ants and termites the being most relevant prey items. The sexual dimorphism in jaw and the solitary males may suggest that this species have territorial behavior.

Key words: Atlantic forest, bromeliad, diet, sexual dimorphism, territorial behavior.

INTRODUCTION

Anurans commonly consume arthropods as a primary food resource (Duellman and Trueb 1986, Lima and Moreira 1993, Ferreira et al. 2012), and kinds and sizes of prey consumed may differ (Sabagh et al. 2012, Maia-Carneiro et al. 2013, Coco et al. 2014) between populations. This may be due to prey availability, which can

be different among areas, differences in periods of collection, altitudes, and/or phylogeny (Sabagh et al. 2012). Anurans can also use different types of microhabitat, such as leaf-litter on the forest floor, rocks, streams, ponds, lakes, trees, and bromeliads (Eterovick 1999, Almeida-Gomes et al. 2008, Duré et al. 2009, Martins et al. 2010, Ferreira et al. 2012). Bromeligenous frogs reproduce, forage and complete their entire life cycle inside bromeliads (*sensu* Peixoto 1995). Such dependence of bromeliads is in direct relation with species natural

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history, influencing different aspects of its ecology (Giaretta 1996, Ferreira et al. 2012, Lantyer-Silva et al. 2014).

Phyllodytes luteolus is a bromeligenous anuran species predominantly found in restinga habitats, where they inhabit tank bromeliads (Peixoto 1995, Ferreira et al. 2012). Restingas are sandy, usually open coastal habitats interspersed within the Atlantic forest biome of Brazil. *Phyllodytes luteolus* occurs along the Brazilian coast from the state of Paraíba southwards to the north portion of the state of Rio de Janeiro (Vrcibradic et al. 2006, Frost 2013), with the most inland record being from the state of Minas Gerais, where it occurs in some forest remnants (Feio and Caramaschi 2002). In addition, an introduced population has been recorded for the municipality of Rio de Janeiro (Salles and Silva-Soares 2010). This species is common inside bromeliads from open areas, and avoids bromeliad axils containing less than 100 ml of water (Teixeira et al. 1997). *Phyllodytes luteolus* lay up to three eggs in bromeliad axils, where the larvae develop and feed on debris (Peixoto 1995, Giaretta 1996). Papp and Papp (2000) showed a drastic population reduction of *P. luteolus* after a fire in the Linhares municipality, in the state of Espírito Santo. This fire destroyed more than 99.9% of the bromeliad *Urisea neoglutinosa* (Rocha et al. 1996), supporting the species strong dependence on bromeliads.

Inter-population studies regarding trophic and spatial ecology are important to explain species niche breadth, position in local trophic webs, foraging behavior, and metabolic necessities (Duellman and Trueb 1986, Toft 1980, 1981, Wells 2007). Furthermore, it enables the elucidation of whether these parameters are conservative or variable among localities. In addition, an inter-population study about ecology and behavior of *P. luteolus* may help to elucidate how individuals correlate with each other in a limited space (the bromeliads) inside a limited habitat (the restinga remnants). The goal of this study was to investigate the diet of three populations of *P. luteolus* from

restinga remnants, and to evaluate the relationship of frogs with the bromeliads. We specifically aimed to assess i) the differences in array of prey types consumed and trophic niche among populations, and among adult males, adult females and juveniles, ii) sexual dimorphism in body and head size in the species, and iii) the bromeliad species used by the individuals.

MATERIALS AND METHODS

STUDY AREAS

Field work was carried out between November 1999 and March 2000, in three restinga sites along the east coast of Brazil: Setiba district (20° 35' S and 39° 13' W) in the municipality of Guarapari, Guriri district, in the municipality of São Mateus (18° 41' S and 39° 45' W), both in the state of Espírito Santo, and one site in the municipality of Prado (17° 18' S and 39° 13' W), in the state of Bahia (Fig. 1). The mean annual temperature on these regions is around 23 °C and the annual rainfall ranges between 1000 and 1350 mm (Nimer 1979). Setiba and Guriri are separated by 210 km, whereas Guriri and Prado are 160 km apart, and Setiba and Prado 380 km apart. The bromeliad species composition varied among localities.

DATA COLLECTION AND STATISTICAL ANALYSES

We conducted diurnal and nocturnal surveys inside bromeliads through visual encounter surveys (Crump and Scott 1994) (total of 80 sampling hours). Moreover, 200 tank bromeliads of different species were randomly sampled in each area (total of 600). All individuals of *P. luteolus* found, were collected (IBAMA collection permit No. 096/99). During the collections in the field amphibians were killed with anesthetic overdose (sodium pentobarbital) as recommended by the protocols of the American Society of Ichthyologists and Herpetologists (ASIH), the Herpetologists' League (HL) (1987), the American Veterinary Medical

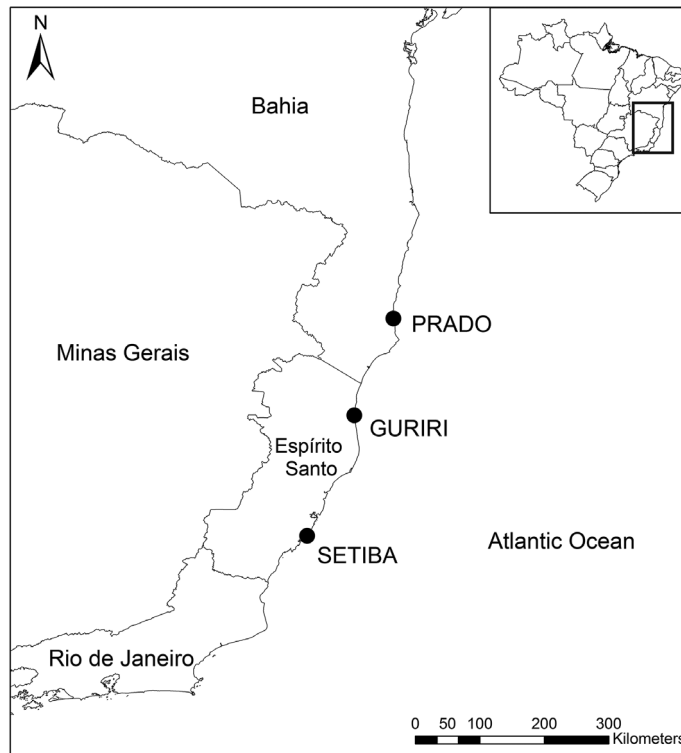


Figure 1 - Map showing restinga habitats where *Phyllodytes luteolus* were collected: Guriri (18°41'S and 39°45'W) and Setiba (20°35'S and 39°13'W), in the state of Espírito Santo, and Prado (17°18'S and 39°13'W), in the state of Bahia.

Association (AVMA) (2000) and the Canadian Council on Animal Care (CCAC) (1993), followed by 10% formalin solution for fixation.

We measured snout-vent length (SVL) and jaw width (JW) of the frogs with calipers to the nearest 0.01 mm. We analyzed gonads to determine sex; those individuals whose gonads were not developed were considered juveniles. We analyzed stomach contents using a stereomicroscope, and characterized the diet in terms of number of individual prey items consumed (N), total volume of prey (V, in mm³), and frequency of occurrence (F) of each prey category. Additionally, for each category of prey we calculated an index of importance value (I_x): I_x = [(n_x/N) + (v_x/V) + (f_x/F)]/3, where n_x, v_x, and f_x are number, volume, and frequency of prey item x, respectively, and N, V, and F are summations of the number, volume, and frequency of all prey items

(Howard et al. 1999). Prey items were identified to the taxonomic level of order (or family, in the case of Formicidae). Unidentified arthropod remains and plant residues were not considered in total volumetric analysis.

We estimated the volume of each prey using the formula for an ovoid spheroid: V = 4/3π (length/2) (width/2)² (Dunham 1983). We used Pianka's overlap index (Pianka 1973) to determine the trophic niche similarity between populations:

$$O_{jk} = \frac{\sum_{i=1}^n p_{ij} \times p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}}$$

where *j* and *k* refer to the populations under comparison and *p_i* is the proportion of prey component

i. We calculated food niche overlap using the proportional values of number and volume of prey consumed. To determine if the frogs from each population statistically differed in terms of prey consumption, we performed a one-way analysis of similarity (ANOSIM) with Bray–Curtis distance measure (Clarke 1993). We also did a nonmetric multidimensional scaling (NMDS) based on a Bray–Curtis dissimilarity matrix to compare prey consumption by each frog from each population. Mean prey volume was estimated as the mean volume of the three largest prey items consumed per frog (or all items when stomach contained less than three). We tested for differences between populations in the number of prey and in the mean prey volume consumed per frog using one-way analysis of variance (ANOVA), followed by Scheffe's post hoc test (Zar 1999) when the results were significant. We used Simple Regression Analysis between prey number and frog SVL and between mean prey volume and frog JW, to evaluate if the number of prey items or the prey volume were associated to body size and JW.

We identified the bromeliad species occupied by *P. luteolus* when the frog was first seen. Additionally, in Setiba and Guriri restingas, we counted the number of frogs per bromeliad, identified the ontogenetic stage (juvenile or adult) and sex, and searched for eggs and/or tadpoles in the bromeliad phytotelmata (i.e. axils and central rosette).

To assess whether there was sexual dimorphism in body size and head width of *P. luteolus*, we used one-way ANOVA for differences in SVL and in JW between males and females of each population. We used analysis of covariance (ANCOVA, with SVL as a covariate; Zar 1999) to test for differences in relative jaw width between sexes.

Descriptive statistics are presented throughout the text as mean \pm one standard deviation. All data were tested for normality and for homogeneity of variances before performing statistical analyses, and were log-transformed when necessary. We performed ANOVA and ANCOVA analysis with

Systat 11 software, and used PAST software for ANOSIM and NMDS analysis.

RESULTS

We analyzed 161 stomach content of *P. luteolus* from three restinga remnants in Brazil, of which 58 were from Setiba (27 males, 23 females, six juveniles and two unknown), 43 from Guriri (20 males, 10 females, 10 juveniles and three unknown) and 60 from Prado (29 males, 26 females, two juveniles and three unknown). A total of 21 stomachs were empty of which: five were from Setiba (8.6%; two males, three females), 14 from Guriri (32.6%; 10 males, two females, two juveniles), and two were from Prado (3.3%; one male, one juvenile). Thirteen different arthropod categories were found in the stomachs (Table I). Formicidae and Isoptera were the most numerous and frequent prey (Table I). These two taxa accounted for more than 90% of prey consumed in each population, and were the most important (Ix) prey items. Isoptera represented the highest proportional volume in the stomachs (55.2% in Setiba, 53.0% in Guriri; 43.0% in Prado), followed by Formicidae (19.3% in Setiba; 16.4% in Guriri; 38.7% in Prado).

There was no difference in the mean number of prey items consumed by males, females and juveniles of *P. luteolus* (ANOVA, $F_{2,118} = 1.350$, $P = 0.263$; Table II). The mean volume of prey ingested differed among males, females and juveniles (ANOVA, $R^2 = 0.091$, $F_{2,117} = 5.890$, $P = 0.004$). Juveniles ingested smaller prey compared to males (Scheffe, $P = 0.019$), and females (Scheffe, $P = 0.004$). There was no difference in the mean volume of prey consumed between adult males and females (Scheffe, $P = 0.639$).

The number of prey items consumed per frog was not related to frog SVL in any population (Regression Analysis, Setiba: $F_{1,45} = 3.133$, $P = 0.083$, Guriri: $F_{1,45} = 3.133$, $P = 0.956$, and Prado: $F_{1,53} = 0.499$, $P = 0.483$). For Setiba population, the volume of prey was influenced by JW (Regression

TABLE I
Diet of *Phyllodytes luteolus* in three restinga remnants along Brazil's coast (Setiba, Guriri and Prado). N = Number of prey items; F = Frequency of occurrence; V = Volume (in mm³), and Ix = Index of Importance Value. U.A.R = Unidentified arthropod remains.

Prey category	Setiba				Guriri				Prado			
	N (%)	F (%)	V (%)	Ix	N (%)	F (%)	V (%)	Ix	N (%)	F (%)	V (%)	Ix
Arachnida												
Acari	-	-	-	-	3 (1.9)	3 (7.0)	0.2 (<0.1)	3.0	11 (1.6)	5 (8.3)	3.7 (0.1)	3.4
Araneae	3 (0.5)	3 (5.2)	53.6 (2.6)	2.8	-	-	-	-	2 (0.3)	2 (3.3)	35.7 (1.2)	1.2 (1.6)
Chilopoda	1 (0.2)	1 (1.7)	<0.1 (<0.1)	0.6	-	-	-	-	-	-	-	-
Hexapoda												
Blattaria	-	-	-	-	-	-	-	-	1 (0.1)	1 (1.7)	19.6 (0.6)	0.8
Coleoptera												
Adult	24 (4.4)	16 (27.6)	191.7 (9.3)	13.8	6 (3.8)	4 (9.3)	23.3 (2.9)	5.3	22 (3.3)	17 (28.3)	334.2 (11.0)	14.2
Larvae	-	-	-	-	-	-	-	-	1 (0.1)	1 (1.7)	6.7 (0.2)	0.7
Diptera												
Adult	9 (1.6)	5 (8.6)	20.7 (1.0)	3.8	-	-	-	-	-	-	-	-
Pupa	2 (0.4)	1 (1.7)	0.1 (<0.1)	0.7	-	-	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-	-	-	1 (0.1)	1 (1.7)	0.9 (<0.1)	0.6
Hymenoptera												
Formicidae	207 (37.8)	36 (62.1)	395.4 (19.3)	39.7	75 (47.5)	15 (34.9)	133.0 (16.4)	32.9	327 (48.4)	52 (86.7)	1175.4 (38.7)	57.9
Others	3 (0.5)	2 (3.4)	54.0 (2.6)	2.2	-	-	-	-	-	-	-	-
Isoptera	294 (53.7)	24 (41.4)	1132.9 (55.2)	50.1	74 (46.8)	14 (32.6)	429.3 (53.0)	44.1	309 (45.7)	28 (46.7)	1305.9 (43.0)	45.1
Lepidoptera larvae	-	-	-	-	-	-	-	-	1 (0.1)	1 (1.7)	18.7 (0.6)	0.8
Insecta egg	4 (0.7)	1 (1.7)	0.1 (<0.1)	0.8	-	-	-	-	1 (0.1)	1 (1.7)	0.8 (<0.1)	0.6
Plant material												
Mineral	10 (17.2)	10 (17.2)	432.2 (21.1)		8 (18.6)	8 (18.6)	224.3 (27.7)		7 (11.7)	7 (11.7)	63.8 (2.1)	
U.A.R.												
Empty	5 (8.6)		4061.6		14 (32.6)		217.8		2 (3.3)		1956.3	
Total	547 (100)	58 (100)	2052.0 (100)		158 (100)	43 (100)	810.1 (100)		676 (100)	60 (100)	3036.1 (100)	

TABLE II
Number of prey and prey volume (mm³) per stomach for males, females and juveniles of *Phyllodytes luteolus* in three restinga remnants along Brazil's coast.
SD = Standard deviation.

	Number of prey		Prey volume	
	Mean ± SD	Range	Mean ± SD	Range
Males (N=57)	9.8 ± 8.8	1 - 41	5.4 ± 7.1	0.1 - 30.7
Females (N=49)	14.0 ± 15.8	1 - 71	5.9 ± 6.6	0.03 - 30.5
Juveniles (N=15)	6.8 ± 5.1	1 - 16	1.8 ± 2.3	0.04 - 6.8
Total (N=121)	11.1 ± 12.0	1 - 71	5.2 ± 6.6	0.03 - 30.7

Analysis, $F_{1,45} = 19.876$, $R^2 = 0.31$, $P < 0.0001$). In Prado population, the volume of prey had a nearly significant influence by JW ($F_{1,45} = 3.778$, $P = 0.057$), but Guriri's population showed no relationship ($F_{1,20} = 1.781$, $P = 0.197$).

There was no difference in the mean number of prey items per stomach among *P. luteolus* populations (ANOVA, $F_{2,121} = 0.694$, $P = 0.502$). The mean volume of the three largest prey ingested per frog differed among populations (ANOVA, $F_{2,121} = 3.757$, $P = 0.026$). Frogs from Prado consumed larger prey than frogs from Setiba (Scheffe, $P = 0.025$) but not from Guriri (Scheffe, $P = 0.193$; Fig. 2). Prey ingested by frogs from Setiba and Guriri did not differ in mean volume (Scheffe, $P = 0.947$).

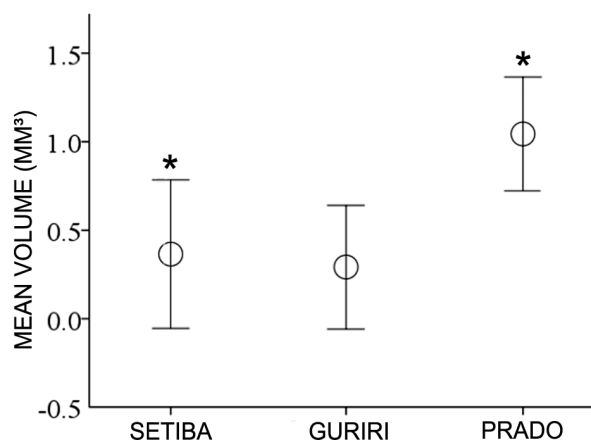


Figure 2 - Mean volume (log-transformed) of the three largest prey items ingested per stomach of *Phyllodytes luteolus* in three remnants restinga along the eastern coast of Brazil (Setiba, Guriri and Prado). The asterisk means that the volume of prey consumed was significantly different between these populations. Sample sizes: Setiba = 47, Guriri = 22 and Prado = 55.

The food niche overlap among populations was high, both in terms of numerical and volumetric proportions of prey items, with values of 0.90 or higher in all cases (Table III). The ANOSIM indicated divergence in prey consumption between populations, but with an R close to zero ($R = 0.0470$, $P = 0.0195$). Prado population had the most divergent prey consumption in comparison with the others (ANOSIM, Prado vs. Setiba: $R = 0.0567$, $P = 0.0118$; Prado vs. Guriri: $R = 0.0895$, $P = 0.0466$). Setiba and Guriri populations had similar prey consumption (ANOSIM, $R = -0.0415$, $P = 0.8687$). The prey consumption between individuals (Fig. 3) can be interpreted as similar, with just a few individuals from Prado standing out (stress = 0.1148).

TABLE III
Diet niche overlap for *Phyllodytes luteolus* in three remnants of restinga along the Brazilian coast based on proportional values of prey items and prey volume.

	Prey items	Prey volume
Setiba x Guriri	0.98	0.99
Guriri x Prado	0.99	0.90
Prado x Setiba	0.98	0.99

Female were larger (SVL) than males in Prado (ANOVA, $R^2 = 0.31$, $F_{1,55} = 24.801$, $P < 0.0001$), but not in Setiba (ANOVA, $F_{1,46} = 0.033$, $P = 0.856$) nor in Guriri (ANOVA, $F_{1,28} = 2.785$, $P = 0.106$) (Table IV). Across the populations, males had comparatively wider jaws than females, irrespective of body size: Setiba – ANCOVA, $R^2 = 0.589$, $F_{1,145} = 47.220$, $P < 0.0001$, Guriri – ANCOVA, $R^2 = 0.710$,

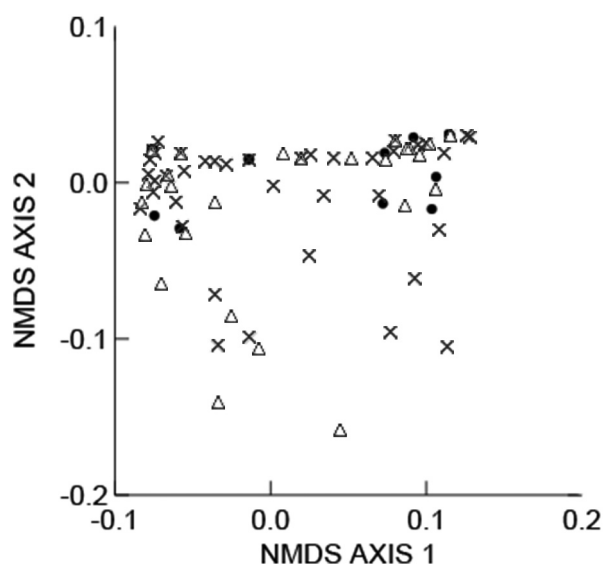


Figure 3 - Multidimensional scaling analyses of the diet composition in individuals of *Phyllodytes luteolus* from Setiba (empty triangles), Guriri (filled dots) and Prado ("X"). Stress = 0.1148.

$F_{1,1,27} = 63.984, P < 0.0001$, Prado – ANCOVA, $R^2 = 0.922, F_{1,1,54} = 480.146, P < 0.0001$.

Phyllodytes luteolus was found in five bromeliad species (Table V), where in 135 bromeliads (22.5%) were occupied by at least one *P. luteolus*. We recorded 102 (25.5%) bromeliads containing individuals of *P. luteolus* in Setiba and Guriri. In 45 of them (44.1%) we found only one individual of *P. luteolus* inside the bromeliad, of which 28 (27.4%) were males and 17 (16.6%) were females. Four individuals (one male, one female and two of unknown sex; each one in a different bromeliad) were found with clutches containing a maximum of six eggs. In 57 of the 102 bromeliads containing *P. luteolus* (55.9%), two to four individuals were found inside the same bromeliad. In none of the cases, males were found sharing a bromeliad, but males co-occurred with females, juveniles and/or tadpoles. In the 14 cases in which tadpoles were present inside bromeliads, there were one to six tadpoles and, in most cases, at least one frog inside the same bromeliad (11 females, four males, one juvenile, and two of unknown sex).

DISCUSSION

The three populations of *P. luteolus* had a diet composed exclusively of arthropods. The diet was composed of a relatively wide variety of prey types, but Formicidae and Isopteras dominated the prey consumed. Similarly, in the restinga of Regência in the state of Espírito Santo, Ferreira et al. (2012) reported on a population of *P. luteolus* that fed on 19 different prey types, with Formicidae and Isoptera being the most important prey. Due to the high proportion of Formicidae and Isoptera consumed, these authors suggested that *P. luteolus* had a specialized diet, predominantly composed of colonial arthropods. Because specialization in diet is a result of evolution, we consider Formicidae and Isoptera as prey preferentially consumed. Apparently, *P. luteolus* has a conservative diet across sites, independently of local peculiarities and differences among sites. It is possible that access to Formicidae and Isoptera might be facilitated in microhabitats that accumulate plant remains, like the interior of some tank bromeliads. Formicidae is commonly associated with bromeliads (Schimid et al. 2010), which may facilitate them being found and subsequent consumption by frogs. Toft (1980, 1981) suggests the use of Jacob's elective index to evaluate if a species has a specialized diet, based on prey abundances in the habitat and in the stomachs. Thus, to better infer if the diet of *P. luteolus* is specialized or generalized, it would be necessary to evaluate whether frogs select prey items or if they consume them according to prey availability inside bromeliads. However, in the absence of specific studies on the arthropod fauna inside bromeliads, at the study sites, we were not able to confirm to what extent *P. luteolus* specializes in colonial insects. The presence of plant remains and sand in the diet of *P. luteolus* was considered accidental ingestion. The difference of empty stomachs between populations may be due to prey availability at the moment of the fieldwork in each locality.

TABLE IV
Number of individuals (N), range, mean and standard deviation (SD) of snout–vent length (SVL, in mm) and jaw width (JW, in mm) of males, females and juveniles of *Phyllodytes luteolus* in three restinga remnants along Brazil’s coast.

Size metric	Setiba			Guriri			Prado			Total		
	N	Range	Mean ± SD	N	Range	Mean ± SD	N	Range	Mean ± SD	N	Range	Mean ± SD
SVL												
Males	21	18.9 - 25.6	24.2 ± 1.5	20	13.5 - 26.8	23.6 ± 5.4	31	14.0 - 25.8	21.5 ± 3.0	78	13.5 - 26.8	23.1 ± 2.9
Females	27	20.8 - 26.4	24.1 ± 1.5	10	22.8 - 27.2	25.9 ± 1.4	26	20.2 - 27.9	24.9 ± 1.8	57	18.9 - 27.9	24.8 ± 1.7
Juveniles	8	11.4 - 14.8	12.6 ± 1.1	11	9.8 - 25.0	14.5 ± 4.0	5	13.8 - 16.5	15.8 ± 1.1	24	9.8 - 25.0	14.1 ± 3.0
Total	56	11.4 - 26.4	22.5 ± 4.3	42	9.8 - 27.2	22.0 ± 5.5	64	13.8 - 27.9	22.6 ± 3.5	162	9.8 - 27.9	22.4 ± 4.3
JW												
Males	21	7.5 - 9.8	9.1 ± 0.6	20	2.5 - 10.5	9.0 ± 1.7	31	5.5 - 10.3	8.1 ± 1.3	78	5.5 - 25.0	9.1 ± 2.1
Females	27	8.4 - 10.8	9.6 ± 0.6	10	8.0 - 10.0	9.2 ± 0.6	26	8.0 - 10.0	9.2 ± 0.6	57	7.5 - 10.0	9.1 ± 0.6
Juveniles	8	4.0 - 5.4	4.6 ± 0.5	11	2.5 - 9.4	5.0 ± 1.8	5	5.3 - 6.1	5.8 ± 0.3	24	2.5 - 9.4	5.0 ± 1.3
Total	56	4.0 - 10.8	8.7 ± 1.8	42	2.5 - 10.5	7.9 ± 2.4	64	5.3 - 10.3	8.4 ± 1.3	162	2.5 - 25.0	8.5 ± 2.2

TABLE V
Number and percentage of individuals of *Phyllodytes luteolus* found in bromeliads in three restinga remnants along Brazil’s coast.

Bromeliad species	Locality			Total (%)
	Setiba (%)	Guriri (%)	Prado (%)	
<i>Aechmea blanchetiana</i> (Baker) L.B.Sm.	0	31 (88.6)	17 (38.6)	48 (35.6)
<i>Aechmea lingulata</i> (L.) Baker	20 (35.7)	0	0	20 (14.8)
<i>Neoregelia cruenta</i> (R.Graham) L.B.Sm	0	4 (11.4)	5 (11.4)	9 (6.7)
<i>Vriesea neoglutinosa</i> Mez	21 (37.5)	0	0	21 (15.5)
<i>Vriesea procera</i> (Mart. Ex Schult. F.) Whittm.	15 (26.8)	0	22 (50.0)	37 (27.4)
Total	56 (100)	35 (100)	44 (100)	135 (100)

Such as expected, we observed that juveniles of *P. luteolus* tended to consume smaller prey compared to adults. Anurans ingest prey with size proportional to their JW, thus consuming larger prey as their jaw size increases (e.g. Lima and Moreira 1993, Marra et al. 2004, Dietl et al. 2009, Martins et al. 2010). Smaller preys should be less energetically profitable for adults, and the consumption of larger prey should result in a greater amount of energy.

There were some inter-population differences in the mean volume of prey items consumed by *P. luteolus*. The volume of prey consumed may have differed due to variation in prey availability among the studied restingas. The distance between sites might explain the variation in the volume of prey consumed. For instance, a study with *Rhinella ornata* (Spix, 1824) in three different localities (which are at least 27 km distance from each one) revealed that the populations differed with regard to the number and volume of prey consumed by individuals, but with a more similar diet between the areas closest to each other and with similar environments (Maia-Carneiro et al. 2013).

Despite considerable distances between populations (> 150 km), trophic niches of *P. luteolus* were very similar (at least 90% overlap in all cases). The probability of significance in the ANOSIM demonstrates a significant difference between populations, but the R close to 0 indicates similar prey consumption. The similarity between populations is reinforced by observation of the NMDS outcomes in Figure 3. These ANOSIM results can be due to the divergence of Prado from others sites, or the analyzed factor (prey consumption) was a weak factor. Two explanations of extensive diet overlap between the populations are: i) similar arthropod faunas inhabiting bromeliads in the studied restingas, or ii) an inherent preference for Formicidae and Isoptera is characteristic of *P. luteolus*. Evaluation of our

data together with those available in the literature (Ferreira et al. 2012) suggests that *P. luteolus* has some degree of conservatism regarding its trophic niche, feeding on similar prey types (mainly Formicidae and Isoptera) independent of local patterns of prey supply in different sites.

Females were larger than males in the Prado population, which is consistent with observations for congeneric species (e.g. *P. wuchereri*, Caramaschi et al. 2004; *P. maculosus*, Cruz et al. 2006). A possibility for the absence of dimorphism in body size in the other two populations may be due to sample size. Overall, females tend to be larger than males in most anuran species (Shine 1979). This difference in body size occurs due to intra-sexual selection that favors larger relative body size of females, which is linked to a capacity to produce larger clutch sizes or larger eggs (Duellman and Trueb 1986, Martins et al. 2010).

Because no more than one adult male was found in the same bromeliad and male *P. luteolus* have larger proportional jaw widths than females, we propose that males of this species may have territorial behavior. Eterovick (1999) did not record territorial behavior in *P. luteolus*, contrary to Weygoldt (1981), who observed agonistic interactions among males under laboratory conditions. Teixeira et al. (1997) suggested that intra-specific competition among males (e.g. for females, preys, shelters and/or reproductive sites) occurs in *P. luteolus*, and Weygoldt (1981) proposed that the low density of adults per bromeliad suggests that males of this species exhibit intra-specific territorial behavior. In the Brazilian restinga of Regência, two studies also found a high percentage of solitary *P. luteolus* inside bromeliads (individuals were not categorized by sex) – Schneider and Teixeira (2001) observed that up to 80% of individuals were found alone within a bromeliad depending on the bromeliad species, and Ferreira et al. (2012) found that 65% of examined bromeliads had only one *P. luteolus*.

Sexual dimorphism in JW (males having relatively larger jaws than females) also suggests territorial behavior. Males of *P. luteolus* use mandibular odontoids during fights (Weygoldt 1981, Duellman and Trueb 1986), and males with larger jaws are presumably more successful during territorial struggles.

Despite the consumption of a relatively wide array of prey, particular food items, such as colonial insects (ants and termites) for *Phyllodytes luteolus*, might predominantly compose the diet of species. Although may occur intra- and inter-population differences in types and sizes of preys consumed by *P. luteolus*, in some cases these parameters might be conservative. Sexual dimorphism in size jaw width and body size, with males having proportionally larger jaws than females and with females larger-sized than males, might confer an advantages during territorial interactions in males and favor greater fecundity in females.

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RESUMO

Neste estudo, analisamos a dieta, dimorfismo sexual e uso de bromélias em três populações do hilídeo *Phyllodytes luteolus* de habitats de restinga ao longo da costa brasileira. Encontramos 13 categorias de artrópodes em 161 estômagos. Formigas e cupins foram as presas dominantes. O nicho trófico semelhante registrado entre as populações sugere que essa espécie possui uma dieta conservativa. Encontramos dimorfismo sexual referentes ao tamanho do corpo e largura da mandíbula. Observamos *P. luteolus* em cinco espécies de bromélias, mas predominantemente em *Aechmea blanchetiana* (35.6% dos indivíduos encontrados). Encontramos indivíduos solitários em 44% das bromélias ocupadas, e nunca dois machos dividindo a mesma bromélia. Os dados sugerem que as populações de *P. luteolus* possuem uma dieta conservadora independente da localidade, com formigas e cupins como as presas mais relevantes. O dimorfismo sexual no tamanho das mandíbulas e os machos solitários podem sugerir que esta espécie possui comportamento territorial.

Palavras-chave: Mata Atlântica, bromélia, dieta, dimorfismo sexual, comportamento territorial.

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