



Eat on the beach: diet composition of an endemic miniature frog from sandy coastal environments of southeastern Brazil

Luiz Fernando Carmo , André Almeida Alves , Manoela Voitovicz-Cardoso & Leandro Talione Sabagh

To cite this article: Luiz Fernando Carmo , André Almeida Alves , Manoela Voitovicz-Cardoso & Leandro Talione Sabagh (2021): Eat on the beach: diet composition of an endemic miniature frog from sandy coastal environments of southeastern Brazil, Studies on Neotropical Fauna and Environment

To link to this article: <https://doi.org/10.1080/01650521.2021.1877414>



Published online: 02 Feb 2021.



Submit your article to this journal [↗](#)







View related articles [↗](#)



View Crossmark data [↗](#)

Eat on the beach: diet composition of an endemic miniature frog from sandy coastal environments of southeastern Brazil

Luiz Fernando Carmo ^a, André Almeida Alves ^b, Manoela Woitovicz-Cardoso ^a
and Leandro Talione Sabagh ^c

^aDepartamento de Vertebrados, Museu Nacional, Quinta da Boa Vista, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil;

^bDepartamento de Zoologia, Instituto de Biologia, Laboratório de Entomologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; ^cDepartamento de Ecologia, Instituto de Biologia, Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

ABSTRACT

Diet is one of the most important dimensions of the ecological niche. *Pseudopaludicola* genus comprises 25 species of which four have their diet studied. In this study, we quantify the diet of the recently described *Pseudopaludicola restinga*, which is found in sandy coastal environments of southeastern Brazil. We obtained a sample of 137 individuals from Parque Nacional da Restinga de Jurubatiba from which 97 were used in analyses of diet composition. We registered 136 prey items distributed in 10 prey categories. Only arthropods were consumed. Insects were the most common food items. Hymenoptera was the most important item in terms of prey frequency, number, and index of relative importance. The variety of prey categories suggests that *P. restinga* is an opportunistic predator. In comparison with dietary information available for other four *Pseudopaludicola* species, *P. restinga* has intermediate values of the number of prey items, niche breadth, and importance index. This study is the first to document aspects of the natural history of *P. restinga* and to compare it with data available for congeners. Data brought here provide a better understanding of life history aspects of *P. restinga*. These information hence could guide development of effective conservation strategies for this poorly known species.

ARTICLE HISTORY

Received 11 July 2020

Accepted 12 January 2021

KEYWORDS

Anura; *Pseudopaludicola restinga*; size relationships; natural history; trophic ecology

Introduction

Amphibians represent an important portion of the biodiverse Brazilian fauna (Jetz & Pyron 2018; Segalla et al. 2019). In many ecosystems, they are important organisms within the trophic webs of aquatic and terrestrial environments (Huckembeck et al. 2014). Their diets consist mostly of invertebrates, with only occasional consumption of vertebrates (Toft 1980, 1981; Toledo et al. 2007; Carmo & Woitovicz-Cardoso 2018). Even with some species exhibiting frugivorous habits, these consumption activities are unusual for amphibians (Silva et al. 1989; Das 1996).

The genus *Pseudopaludicola* currently comprises 25 nominal species of small-sized Neotropical frogs (Andrade et al. 2020; Frost 2020), which are widely distributed in open environments from southern Mexico to Argentina (Lavilla et al. 2016). Data concerning the ecological aspects of this genus still are scarce (Duré et al. 2004; Pereira & Nascimento 2004; Silva et al. 2018). However, it is known that species of this genus prey on small invertebrates (Van Sluys &

Rocha 1998) and are, in turn, preyed upon by snakes and spiders (Corrêa et al. 2016; Kacevas et al. 2019).

Pseudopaludicola restinga Cardozo et al. 2018 was recently described and, as the specific epithet denotes, it was discovered in a sandy coastal environment (called *restinga* habitat) in southeastern Brazil. This species is known from the northern part of the state of Rio de Janeiro (municipality of Carapebus) to the southern part of the state of Espírito Santo (type locality, municipality of Serra), on a coastal range of approximately 275 km. *Pseudopaludicola restinga* is endemic to the restingas, where these frogs inhabit temporary and permanent ponds (Cardozo et al. 2018; Carmo et al. 2019). Restingas are coastal ecosystems endemic to the Atlantic Forest biome (Assumpção & Nascimento 2000; Scarano 2002).

Although the ecologies of Atlantic Forest frogs have been extensively studied (e.g. Sabagh et al. 2012; Rebouças & Solé 2015; Oliveira et al. 2019), there are few studies about anuran feeding habits in sandy coastal environments (Oliveira & Rocha 2015). Studies on the anuran natural history in sandy coastal

environments are needed to fill gaps in our knowledge about the ecological aspects of these species. Herein, we present data about the trophic ecology of *P. restinga* from a protected sandy coastal area in southeastern Brazil and make comparisons to trophic information available for other *Pseudopaludicola* species. Additionally, we propose a trophic niche breadth based on the Index of Relative Importance. Specifically, our study addressed the questions: (i) There is sexual dimorphism in body size in *P. restinga*? (ii) What is the dietary composition of *P. restinga*? (iii) Do differences in diet composition exist between the sexes and seasons? (iv) What are the main prey types consumed by *P. restinga*? (v) Do differences in diet parameters exist among *Pseudopaludicola* species? (vi) How can the trophic ecology of the genus *Pseudopaludicola* be characterized based on our results and the information from previously studied congeneric species?

Materials and methods

Study area and field work

This study was carried out in Parque Nacional da Restinga de Jurubatiba (PNRJ), a sandy coastal environment in the municipality of Carapebus (22.2708°S, 41.6469°W), state of Rio de Janeiro, southeastern Brazil (Figure 1). The site comprises a total area of 14,992 hectares and is one of the largest remnants of preserved sandy coastal plains (restingas) in Brazil (Rocha et al. 2007). The restinga ecosystem is characterized by high salinity, low water potential, high exposure to sunlight, and sandy substrate (Assumpção & Nascimento 2000; Scarano 2002). Annual mean temperature ranges from 21.4°C to 24.7°C, with an average annual precipitation of 1,000 mm (ICMBio 2007). Meteorological data obtained from a meteorological station located in the municipality of Macaé indicate that rainfall is concentrated in the period from October to March (INMET 2020). June–September is defined as the dry season while November–April is considered the rainy season (INMET 2020).

We conducted fieldwork once every 3 months from August 2013 to March 2018. Individuals of *Pseudopaludicola restinga* were collected using pitfall traps and by hand during the night. However, we only used hand-collected frogs for dietary analyses since the opportunistic feeding of individuals captured by pitfall traps could bias the results. We measured the body mass of each live frog with a precision balance (0.01 g precision). Frogs were euthanatized with lidocaine chlorohydrate 2% and fixed in 10% formalin.

Laboratory procedures and data analysis

We measured the snout–vent length (SVL) and jaw width (JW) with digital calipers (0.1 mm precision) of each individual of *P. restinga*, for all specimens collected. Then, we dissected each individual in order to remove and sort out its ingested prey items. This was done to some of the specimens collected. We identified each intact or partially digested item with a stereoscope microscope. The prey items were dried before their length and width dimensions were measured to the nearest millimeter. To quantify the diet of the *P. restinga*, we used the following parameters for each prey category evaluated: abundance (N); frequency (F); volume (V); and index of relative importance (IRI). All of these parameters were converted into percentages (e.g. N%). The volume of each prey item was then calculated using an ellipsoid formula (Griffiths & Mylotte 1987). To infer the importance of each prey category in the diet of *P. restinga*, we calculated the relative importance index (see Pinkas et al. 1971). We calculated the trophic niche breadth (B) (Levins 1968) and trophic niche breadth standardized (B_{st}) (see Hurlbert 1978; Krebs 1999) for prey abundance and volume with Programs for Ecological Methodology (Krebs 2016). The number of prey categories, trophic niche breadth, and IRI% for other *Pseudopaludicola* species were obtained from the available literature. The number of prey categories for these other species was rearranged to be comparable to our results. The trophic niche breadth and the IRI% for other *Pseudopaludicola* species were recalculated, when possible, based on data from the literature. Even so, we calculated the $B_{st}(V)$ according to the prey volume data available in the literature, so these values should be used considering this limitation. Additionally, we calculated the trophic niche breadth to be standardized using the IRI values ($B_{st}(IRI)$) to obtain a niche breadth value that takes into account the number, volume, and frequency of prey categories.

In order to remove possible inaccuracies, we did not consider prey items in advanced stages of digestion and unidentifiable prey. All frog specimens were deposited in the Amphibian Collection of the Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ). The food items were preserved in 70% ethanol and each one was deposited in the same collection, under the same record number as its source.

Sex size differences were tested using the T-test or a Mann–Whitney test when data did not meet the parametric assumptions. Ontogenetic changes in diet were tested using a linear regression with JW as one

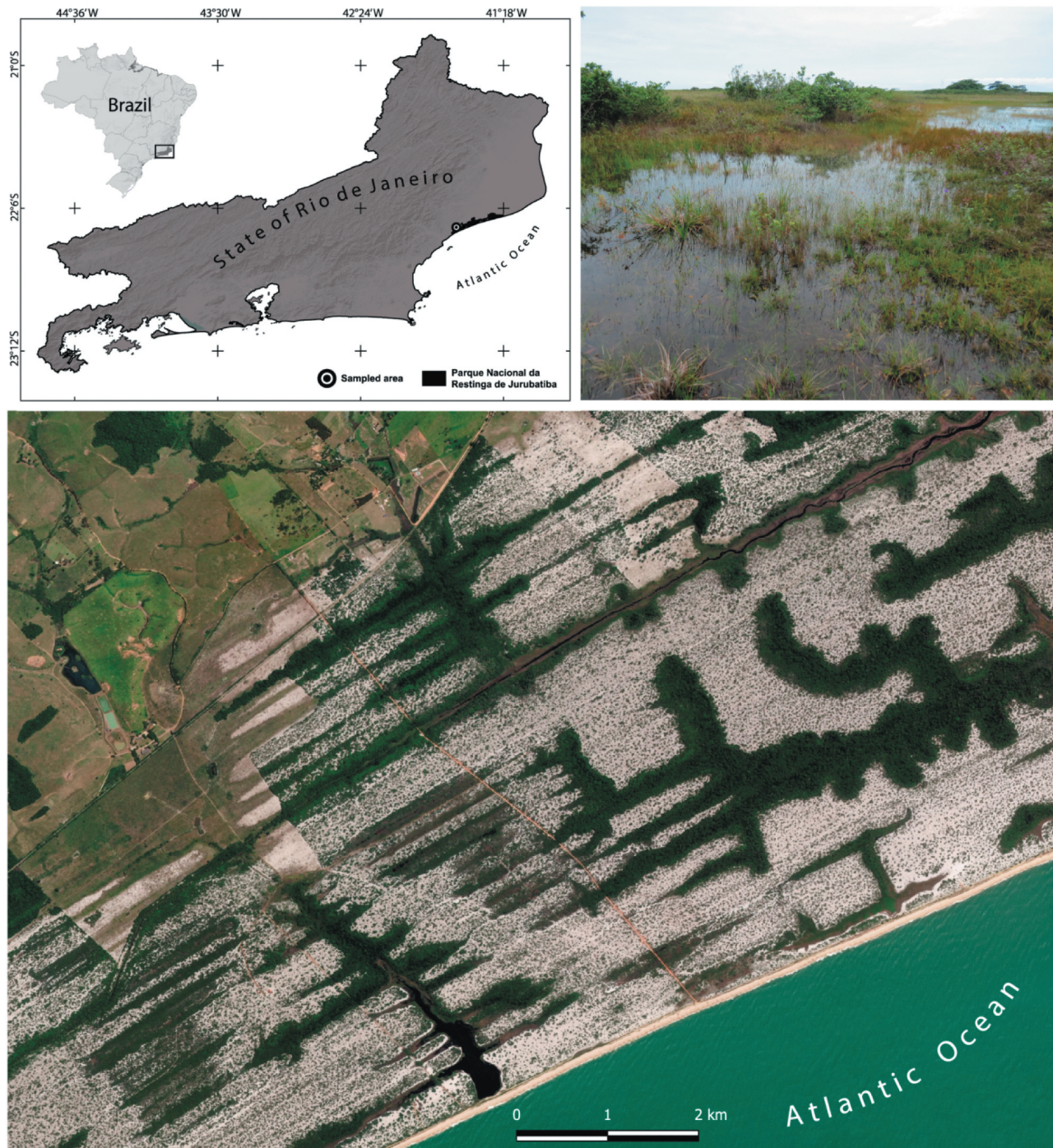


Figure 1. Location of Parque Nacional da Restinga de Jurubatiba, in the state of Rio de Janeiro, southeastern Brazil.

independent variable and the bigger volume, and the bigger length item in the stomach. For all hypothesis tests, we used a significance level of $\alpha = 0.05$. To compare the diet composition between sexes and seasons, we used a non-metric multidimensional scaling (NMDS) with Bray–Curtis dis-

tance. These analyses were performed using R version 3.6.3 (R Development Core Team 2019) with package *vegan* (Oksanen et al. 2019) and *ggplot2* (Wickham et al. 2016). We used rarefaction and extrapolation based on Hill's numbers (i.e. the effective number of species – see Hill 1973), which

Table 1. Descriptive statistics of *Pseudopaludicola restinga* biometry from a sandy coastal environment in southeastern Brazil. The data are in mean±SD (min-max). SVL = snout-vent length; JW = jaw width.

	Male (n = 66)	Female (n = 55)	Statistics
SVL (mm)	13.15 ± 1.07 (9.30–14.65)	14.45 ± 1.29 (12.00–17.18)	p < 0.0001 W = 2760
JW (mm)	4.23 ± 0.38 (3.30–5.00)	4.51 ± 0.40 (3.60–5.40)	p < 0.001 T = 3.9143
Mass (g)	0.24 ± 0.07 (0.12–0.36)	0.34 ± 0.13 (0.14–0.66)	p < 0.001 T = 3.8882

Table 2. Diet composition of 54 specimens of *Pseudopaludicola restinga* from a sandy coastal environment in southeastern Brazil. N = abundance; V = volume; F = occurrence frequency; IRI = relative importance index.

Prey item	N	N%	V	V%	F	F%	IRI	IRI%
Insecta								
Blattodea	4	3.70	96.43	20.29	1	1.85	44.43	1.11
Coleoptera (Adult)	15	13.89	75.98	15.98	10	18.52	553.13	13.85
Coleoptera (Larvae)	4	3.70	13.64	2.87	4	7.41	48.69	1.22
Hemiptera	21	19.44	34.81	7.32	14	25.93	693.89	17.38
Hymenoptera (Formicidae)	28	25.93	176.80	37.19	15	27.78	1753.22	43.90
Diptera	17	15.74	40.97	8.62	12	22.22	541.35	13.56
Orthoptera	2	1.85	5.67	1.19	2	3.70	11.27	0.28
Collembola	12	11.11	20.06	4.22	11	20.37	312.30	7.82
Insect remnant	29	-	-	-	20	-	-	-
Arachnida								
Araneae	4	3.70	10.98	2.31	3	5.56	33.41	0.84
Acarina	1	0.93	0.28	0.01	1	1.85	1.73	0.04
Total	137	100	475.38	100			3993.43	100

was proposed by Chao et al. (2014), and assessed the expected richness of prey items to evaluate sample completeness. These analyses were performed in online iNEXT software (Chao et al. 2016).

Results

We collected a total of 137 individuals of *Pseudopaludicola restinga*. These amounted to 66 males, 55 females, and 16 juveniles. Females were bigger than males in all morphometric aspects: 9.0% bigger for SVL ($W = 2760$; $p < 0.0001$), 6.2% for JW ($T = 3.9143$; $p < 0.001$), and 29.4% for mass ($T = 3.8882$; $p < 0.001$). All biometric values are in Table 1.

For the diet study, we euthanized 97 individuals of *P. restinga* (52 females and 45 males) of which 54 (55.7%) individuals had food items in their digestive tracts. From empty stomachs, 57.4% were collected during the rainy seasons and 42.6% in dry seasons. A total of 137 prey items were found in the dissected stomachs of *P. restinga* and categorized into 10 prey categories (all identifiable as arthropods) plus a category identifiable as Insect remnants (Table 2). The number of prey items per stomach varied from 1 to 6 items (mean = 1.5; SD = 1.1). Among the items, Insecta had the highest contribution to the diet, representing 96.35% of the consumed prey items. Arachnida

represented 3.65% of the prey items. Of the Insecta, ants (Hymenoptera: Formicidae) were the most important prey regarding prey frequency, number, and IRI (IRI% = 43.90), followed by Hemiptera (IRI% = 17.38), adult Coleoptera (IRI% = 13.85), and Diptera (IRI% = 13.56) (Table 2). Of the Arachnida, Araneae was the most contribution in diet composition. Although insect remnants represented a significant portion of the prey items, these were not considered in the relative

quantification due to the numeric imprecision and to the advanced stage of fragmentation and decomposition. All prey items categorized as Blattodea were representatives of the family Termitidae. Additionally, we found some plant and mineral remains inside the digestive tracts of the specimens, as well as some fragments of anuran skin. The trophic niche breadth standardized considering the abundance of prey was $B_{st}(N) = 0.35$, and for prey volume was $B_{st}(V) = 0.39$ and for $B_{st}(IRI) = 0.31$ (Table 3).

After a review of available literature, we found six studies about the feeding habits for four of the 25 species of *Pseudopaludicola* currently described. Based on evidence from these four *Pseudopaludicola* species previously studied, and the information about *P. restinga*, the diet of the genus included 20 prey categories (Table 4). The diet of *Pseudopaludicola* species is based primarily on Insecta, but Arachnida was commonly included, though not so important in most of the studied species (Table 4), except for one population of *P. falcipes* from Argentina (López et al. 2005). Annelida and Mollusca Gastropoda were preyed, respectively, only by *P. falcipes* and *P. boliviana* (both populations from Brazil, according to Dias et al. 2018; and Duré et al. 2004).

Visual analyses of NMDS for *P. restinga* (Figure 2) showed an overlap among diet composition between males and females and also between the dry and rainy

Table 3. Comparison of the number of prey categories and trophic niche breadth of *Pseudopaludicola* species. B_{st} (N) = trophic niche breadth standardized for the abundance of prey; B_{st} (V) = trophic niche breadth standardized for the volume of prey. B_{st} (IRI) = trophic niche breadth standardized for the relative importance index of prey. * The paper that describes *P. falcipes* diet in Brazil does not show the absolute volume values in each prey category, which precludes the B_{st} (V) calculation.

Species	N° prey categories	B_{st} (N)	B_{st} (V)	B_{st} (IRI)	References
<i>P. boliviana</i>	10	0.65	0.32	0.22	Duré et al. 2004
<i>P. canga</i>	6	0.40	0.57	0.22	Van Sluys & Rocha 1998
<i>P. falcipes</i> (AR1)	9	0.19	0.50	0.27	Duré 2002
<i>P. falcipes</i> BR	10	0.48	– *	0.35	Dias et al. 2018
<i>P. pocoto</i>	12	0.24	0.10	0.06	Silva et al. 2018
<i>P. restinga</i>	10	0.35	0.39	0.31	This study

Table 4. Importance Relative Index (*sensu* Pinkas et al. 1971) in percent of the 20 prey categories included in the diet of *Pseudopaludicola*. * We considered Blattodea as Blattodea + Isoptera**We considered Hemiptera as Hemiptera + Homoptera. ***Some previous studies did not specify which Order of Insecta larvae were consumed. '?' and **bold** – For *P. pocoto*, there is not information about Formicidae ingested, only for Hymenoptera as whole.

	<i>P. boliviana</i> AR	<i>P. boliviana</i> BR	<i>P. canga</i>	<i>P. falcipes</i> AR1	<i>P. falcipes</i> BR	<i>P. pocoto</i>	<i>P. restinga</i>
Insecta							
Blattodea*		X				0.06	1.11
Coleoptera (Adult)	11.16	X	2.81	5.40	6.54	77.75	13.85
Coleoptera (Larvae)						3.86	1.22
Collembola	5.90	X		41.28	15.51		7.82
Diptera	53.82	X	27.69	5.69	21.70	3.87	13.56
Diptera (Larvae)			4.29			0.44	
Ephemeroptera						0.10	
Hemiptera**	16.78	X	62.59	10.94	0.23	10.68	17.38
Hymenoptera (Formicidae)	1.13	X		0.62	36.21	?	43.90
Hymenoptera (except ants)	0.61	X		0.20	0.24	1.51	
Lepidoptera (Larvae)						0.01	
Orthoptera	0.56	X	1.58			0.02	0.28
Siphonaptera					0.03		
Trichoptera				0.03			
Insecta Larvae***	0.65	X					
Arachnida							
Araneae	3.74	X	1.04	0.09	1.28	0.28	0.84
Acarina	5.66	X		35.75	18.22	1.41	0.04
Annelida							
Mollusca							
Gastropoda		X					
References	Duré et al. 2004	Caldwell & Vitt 1999	Van Sluys & Rocha 1998	Duré 2002	Dias et al. 2018	Silva et al. 2018	This study

seasons. We found no ontogenetic changes in diet with respect to both JJ and JW ($p > 0.05$). The rarefaction and extrapolation analyses estimated a maximum of 13 prey categories (Figure 3(a)) and the sample completeness curve reached 99.1% of efficiency (Figure 3(b)).

Discussion

According to our results, *Pseudopaludicola restinga* shows sexual size dimorphism with the females being larger than males. This sexual size dimorphism is

expected for anuran species without territorial male combat when male body size is not under selective pressure (Wells 2007). Until now, we have no evidence of territorial male combat in *Pseudopaludicola* species. On the other hand, it is likely that females are under the influence of directional selection to attain bigger body sizes since the clutch size is limited by the mother's size; this can then result in females being larger than males (Wells 2007). As for *P. restinga*, the females are larger than males in *P. boliviana* (Duré et al. 2004), *P. saltica*, *P. mystacalis*, *P. facureae* (as *P. aff. canga*), *P. ternetzi* (Giaretta & Facure 2009), and *P. falcipes* (Ceia 1980). There is no sexual size dimorphism in *Pseudopaludicola pocoto* (Silva et al. 2018), which seems to be the exception in *Pseudopaludicola*.

Our rarefaction analyses showed that this work is representative of the *P. restinga* diet, covering almost 100% of the prey possibilities. The diet of *P. restinga* includes a wide range of prey categories, similar to the diets of *P. boliviana* (Duré et al. 2004) and *P. falcipes* from Brazil (Dias et al. 2018). Despite the same number of categories as *P. boliviana*, *P. restinga* has larger B_{st} (IRI) than *P. boliviana*, which represents to be more generalist food habits. The population of *P. falcipes* from Brazil (Dias et al. 2018) is the only one with a broader trophic niche (B_{st} (IRI) = 0.35) than seen in *P. restinga*, despite its same number of prey categories

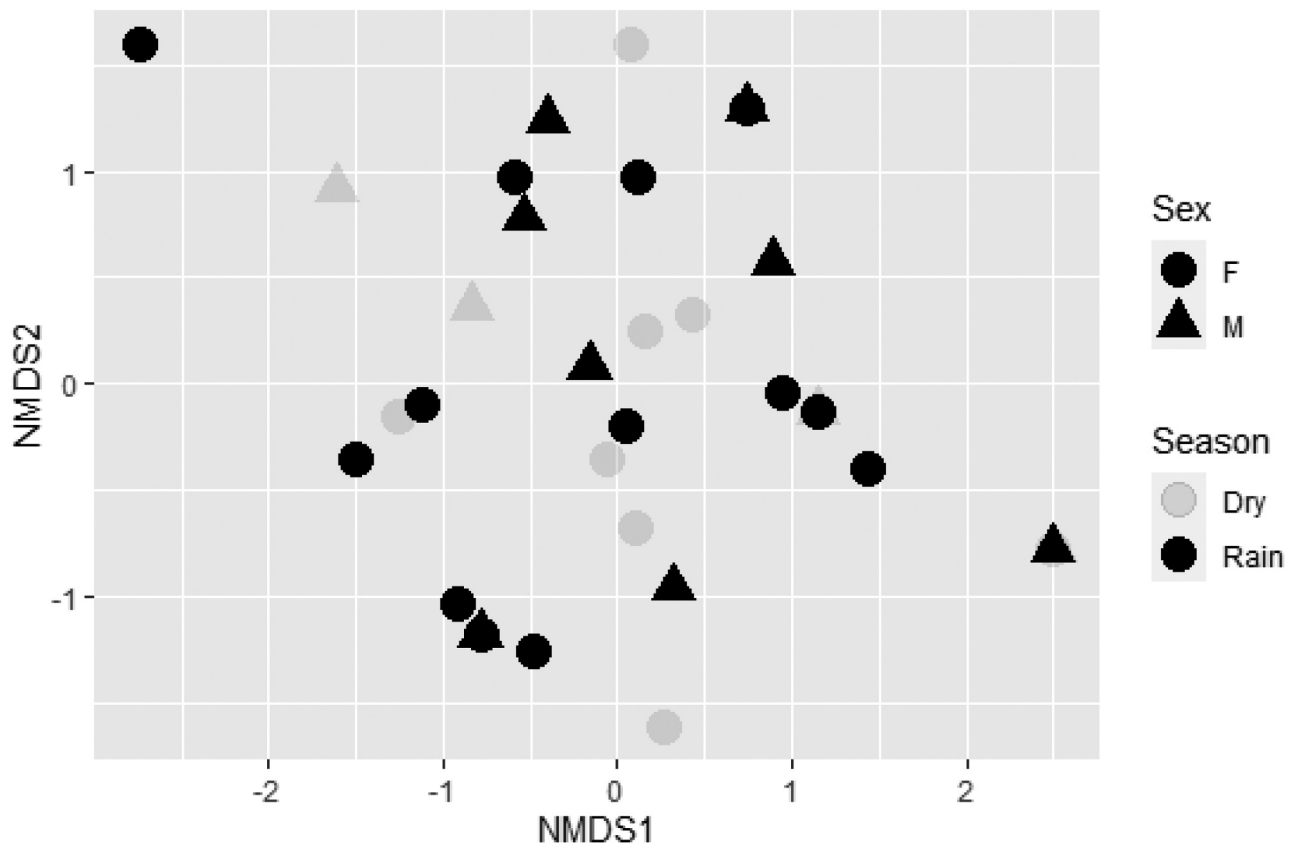


Figure 2. Non-metric multidimensional scaling of *Pseudopaludicola restinga* diet from a sandy coastal environment in southeastern Brazil grouped by sex (geometric forms) and season (color). Stress = 0.05408.

(Table 4). *Pseudopaludicola canga* is the species with fewest prey categories, there only being six (Van Sluys & Rocha 1998).

Considering the dietary evidence for the genus, *Pseudopaludicola* species seem to have a plastic interspecific diet composition, consisting of a range of 20 prey categories considered together. Dietary plasticity among *Pseudopaludicola* species is also evident by the exclusive prey categories ingested as Ephemeroptera (*P. pocoto*, Silva et al. 2018); Trichoptera and Siphonaptera (*P. falcipes*, Duré 2002 and Dias et al. 2018, respectively); and two non-arthropod prey items: Annelida ingested by *P. falcipes* (Dias et al. 2018) and Gastropoda preyed upon by *P. boliviana* (Caldwell & Vitt 1999). Such interspecific plasticity is present as well at the intraspecific level, as is now known for three populations of *P. falcipes* (Table 3). Only for the population from Brazil (Dias et al. 2018), Formicidae was the most important prey item, and ants are not in the first most important items in the diet of the two other populations already studied (Duré 2002; López et al. 2005). Besides the wide range of prey items, *Pseudopaludicola* species have a main category that differs between species (Table

3). *Pseudopaludicola pocoto* ingested mainly Coleoptera (IRI% = 77.75); *P. boliviana* seems to prefer Diptera (IRI%: 53.82); and Collembola is the most important item in two populations of *P. falcipes* (Duré 2002; López et al. 2005). For the third population of *P. falcipes* already studied, Formicidae represents IRI = 36.21%. The same level of importance of Formicidae in the diet was observed for *P. restinga*, whose ants IRI% = 43.90 (Table 3).

Despite the dominant contribution of ants in its dietary composition, *P. restinga* is probably a generalist predator, as indicated by its large trophic niche breadth, the second highest for the genus (Table 3). The variety of prey categories suggests that *P. restinga* is an opportunistic predator similar to their known congeners, which have also been examined in previous studies (Van Sluys & Rocha 1998; Duré 2002; Duré et al. 2004; Dias et al. 2018; Silva et al. 2018). According to Toft (1981), the number of consumed prey items by an opportunistic predator is relatively large and the prey items are frequently small. We have evidence of this for the *P. restinga* dietary composition. Only

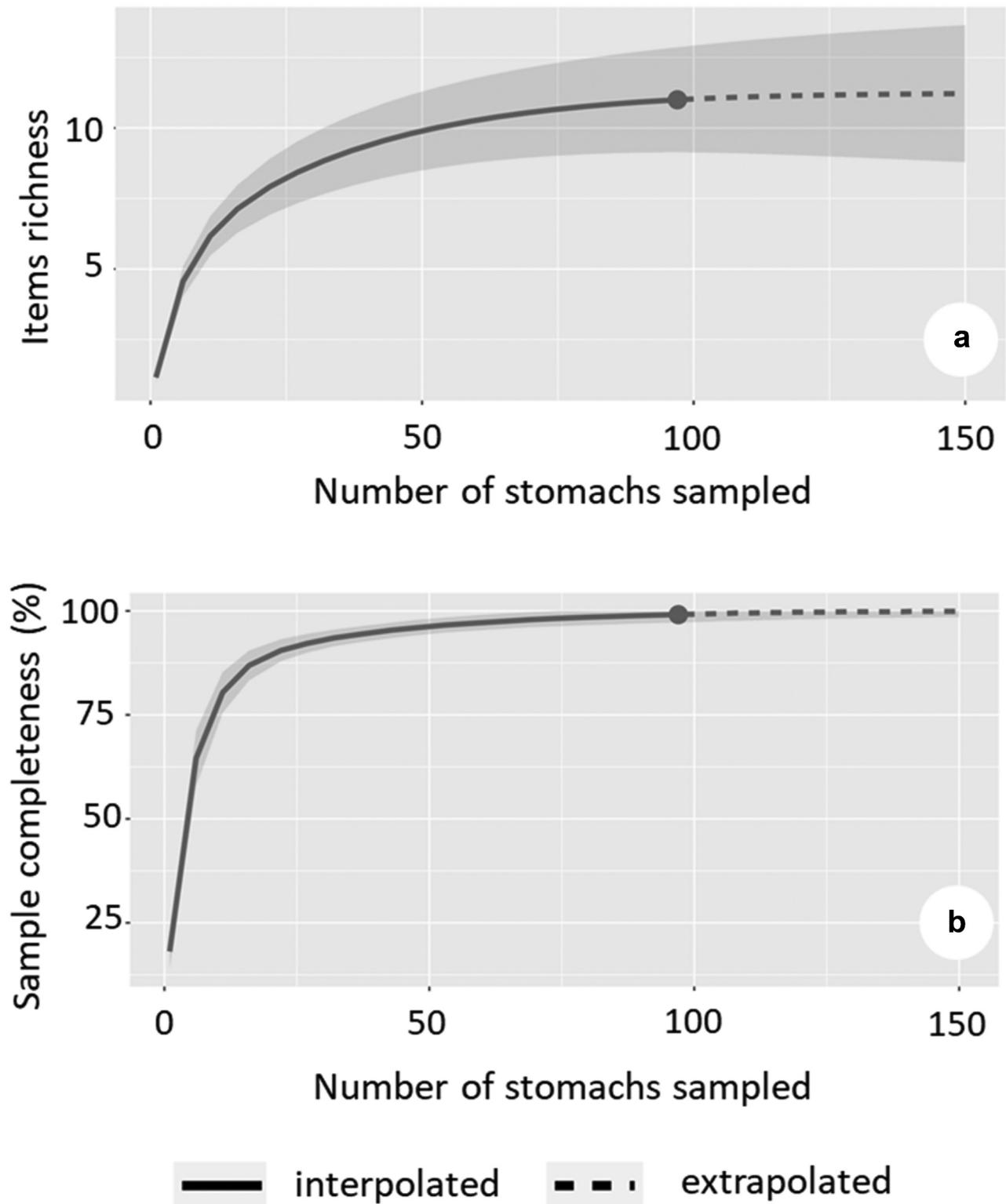


Figure 3. Sample-size based of *Pseudopaludicola restinga* from a sandy coastal environment in southeastern Brazil. (a) rarefaction and extrapolation sampling curve and (b) sample completeness. Both with 95% confidence intervals (shaded areas) obtained by a bootstrap method based on 100 replications. The number of analyzed stomachs is denoted by solid dots.

surveying prey abundance in the *P. restinga* habitat would it be possible to verify if individuals are generalists that eat prey items at the same frequency

as they are present in the habitat – not choosing prey items. But the evidence of high IRI% of Formicidae supports a less generalist dietary

composition in *P. restinga*, an opportunistic predator that engages in active search while foraging for prey.

Pseudopaludicola restinga is the third Leiuperinae to ingest its own skin shed, as dermatophagy has been reported in *Pleurodema bufonina* (Pincheira-Donoso 2002) and *Edalorhina perezii* (Weldon et al. 1993). Dermatophagy (or keratophagy) is the ingestion of skin sheds by amphibians and reptiles (Weldon et al. 1993). There exists a hypothesis about the function of this ingestion of skin sheds. The ingestion of skin could be a way to recycle skin proteins, control ectoparasites, and eliminate olfactory cues that could attract potential predators (Mitchell et al. 2006). The presence of plant remains and small minerals in the digestive tract of *P. restinga* likely represent accidental ingestions during predation events, as reported for several other anurans (e.g. López et al. 2005; Sabagh et al. 2012).

The absence of seasonality on diet composition was unexpected since *Pseudopaludicola restinga* occupies mainly temporary ponds that disappear in the dry season (pers. obs.). It could indicate that *P. restinga* did not feed in the same microhabitat that they occupied during their reproductive activities. These results indicate a temporal consistency in diet and a no resource-limited habitat for the species. There is evidence that mean arthropod abundance decreases only slightly in the dry season in one Peruvian Amazon area (Toft 1980). However, the dry season is much more marked in the Restinga than in Amazonian Forest and it is surprising that arthropods preyed upon by *P. restinga* do not seem to change their abundance in response to this seasonality.

Considering the prey types consumed by *Pseudopaludicola restinga*, which were mainly small and slow prey items but also some small and fast items, it was expected that their gape was not an important morphological trait (Emerson 1985). The diet composed mainly by ants, which are small prey, is not constrained by the size of the gape and then the absence of a relationship between the JW and the size of ingested prey is not unexpected. It is consistent with the predictions proposed by Emerson (1985). In the same way, the similarity in the size of prey ingested by females and males reinforces that *P. restinga* did not prey upon items as large as possible. Instead of it, *P. restinga* seems to be an active searching with a foraging strategy predator (as suggested for *P. falcipes* by López et al. 2005), consuming several small prey items, and, although it is a generalist, it tends to be at the ant-specialist end of the continuum proposed by Toft (1980).

In conclusion, we emphasize that data brought here provide a better understanding of ecology and life history aspects of *Pseudopaludicola restinga*. These information hence guide the development of effective conservation strategies for this poorly known species. Since the habitats of many of the *Pseudopaludicola* species, especially in the morphoclimatic domain of the Atlantic Forest, increasingly becoming fragmented and degraded at a rapid rate, the development of such studies provides essential information to fill gaps in knowledge about the most diverse ecological aspects of dwarf swamp frogs.

Geolocation Information

This study was carried out in Parque Nacional da Restinga de Jurubatiba (PNRJ), a sandy coastal environment in the municipality of Carapebus (22.2708°S, 41.6469°W), state of Rio de Janeiro, southeastern Brazil.

Acknowledgments

We thank B. Jennings for English revision and for valuable suggestions in the manuscript. We thank four anonymous reviewers for their valuable suggestions in the manuscript. We are indebted to J. P. Pombal Jr. for allowing access to the specimens under his care. We are grateful to S.O. Guimarães, I. R. Miguel, P. Pinna and D. Fernandes for co-working at field expeditions. We are grateful to M. Cezar and M.B. Pessanha for the permits to access the National Park. In addition, it also integrates the program: Levantamento e Aspectos Biológicos da Herpetofauna do Parque Nacional da Restinga de Jurubatiba, RJ, Brasil, subsidized by Fundação de Amparo a Pesquisa do Estado do Rio de Janeiro (FAPERJ). We also thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial supports of L.F. Carmo 132763/2020-6, and A. A Alves 134269/2019-5. M. Woitowicz-Cardoso is grateful for the fellowship E-26/200.111/2019 subsidized by FAPERJ. Both promoting institutions were extremely important for the development of this research. We are grateful to all staff of the Instituto de Biodiversidade e Sustentabilidade (NUPEM/UFRJ) and Museu Nacional, Universidade Federal do Rio de Janeiro for logistical support and incentive during the campaigns. The specimens were collected under permit #38378-11, granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This project is part of the program Pesquisas Ecológicas de Longa Duração (PELD): Mudanças Climáticas Globais e o Funcionamento dos Ecossistemas Costeiros da Bacia de Campos: uma perspectiva espaço-temporal (Brazilian Long

Term Ecological Research - PELD: Global Climate Change and the Functioning of Coastal Ecosystems in the Bacia de Campos: A Space-time Perspective), initiated in August 2013 and subsidized by Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq 403841/2012-007 and 441610/2016-1). This project also received funding from Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ E-26/111.217/2014, and E-26/200.111/2019).

ORCID

Luiz Fernando Carmo  <http://orcid.org/0000-0002-9873-3186>

André Almeida Alves  <http://orcid.org/0000-0001-9613-6874>

Manoela Woitoviz-Cardoso  <http://orcid.org/0000-0003-1011-9075>

Leandro Talione Sabagh  <http://orcid.org/0000-0003-4437-9529>

References

- Andrade FS, Haga IA, Lyra ML, de Carvalho TR, Haddad CFB, Giaretta AA, Toledo LF. 2020. Reassessment of the taxonomic status of *Pseudopaludicola parnaiba* (Anura, Leptodactylidae, Leiuperinae), with the description of a new cryptic species from the Brazilian Cerrado. *Eur J Taxon.* 679:1–36. doi:10.5852/ejt.2020.679.
- Assumpção J, Nascimento MT. 2000. Estrutura e composição florística de quatro formações vegetais de restinga no complexo lagunar Grussaí/ Iquipari, São João da Barra, RJ, Brasil. *Acta Bot Bras.* 14(3):301–315.
- Caldwell JP, Vitt LJ. 1999. Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian Rain Forest. *Oikos.* 84(3):383–397.
- Cardozo DE, Baldo D, Pupin N, Gasparini JL, Haddad CFB. 2018. A new species of *Pseudopaludicola* (Anura, Leiuperinae) from Espírito Santo, Brazil. *PeerJ.* 6:e4766. doi:10.7717/peerj.4766.
- Carmo LF, Miguel IR, Pinna PH, Fernandes DS, Woitoviz-Cardoso M. 2019. Amphibians of the Parque Nacional da Restinga de Jurubatiba, a sandy coastal environment in southeastern Brazil. *Biota Neotrop.* 19(2):e20190727.
- Carmo LF, Woitoviz-Cardoso M. 2018. Spoiling friendship: first report on predation of anuran by *Aparasphenodon brunoi* Miranda-Ribeiro, 1920 (Anura: Hylidae). *Herpetol Notes.* 11:375–377.
- Cei JM. 1980. Amphibians of Argentina. *Monitor Zool Italiano N S Monogr.* 2:1–609.
- Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr.* 84(1):45–67.
- Chao A, Ma KH, Hsieh TC. 2016. iNEXT (iNterpolation and EXTrapolation) Online: software for interpolation and extrapolation of species diversity. Program and User's Guide. Available from: http://chao.stat.nthu.edu.tw/wordpress/software_download/
- Corrêa DN, Quintela FM, Loebmann D. 2016. Feeding ecology of *Erythrolamprus jaegeri jaegeri* (Günther, 1858) and *Erythrolamprus poecilogyrus sublineatus* (Cope, 1860) in the coastal zone of Subtropical Brazil (Serpentes, Dipsadidae). *An Acad Bras Ciênc.* 88(1):293–308.
- Das I. 1996. Folivory and seasonal changes in diet in *Rana hexadactyla* (Anura, Ranidae). *J Zool.* 238:785–794.
- Dias J, Moser CF, Dutra-Araújo D, Oro N, Tozetti AM. 2018. Diet of *Pseudopaludicola falcipes* (Anura: Leptodactylidae) in southern Brazil. *Herpetol Notes.* 11:911–913.
- Duré MI. 2002. *Pseudopaludicola falcipes* (CNC): diet. *Herpetol Rev.* 33(2):128.
- Duré MI, Schaefer EF, Hamann MI, Kehr AI. 2004. Consideraciones ecológicas sobre la dieta, la reproducción y el parasitismo de *Pseudopaludicola boliviana* (Anura, Leptodactylidae) de Corrientes, Argentina. *Phyllomedusa.* 3:121–131.
- Emerson SB. 1985. Skull shape in frogs-Correlations with diet. *Herpetologica.* 41:177–188.
- Frost DR. 2020. Amphibian species of the world: an Online Reference. Version 6.0. New York (USA): American Museum of Natural History; [cited 2020 Jan 7]. Available from: <http://research.amnh.org/vz/herpetology/amphibia/>
- Giaretta AA, Facure KG. 2009. Habitat, egg-laying behaviour, eggs and tadpoles of four sympatric species of *Pseudopaludicola* (Anura, Leiuperidae). *J Nat Hist.* 43(15):995–1009.
- Griffiths RA, Mylotte VJ. 1987. Microhabitat selection and feeding relations of smooth and warty newts, *Triturus vulgaris* and *Triturus cristatus*, at an upland pond in Mid-Wales. *Holarctic Ecol.* 10:1–7.
- Hill M. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology.* 54:427–432.
- Huckembeck S, Loebmann D, Albertoni EF, Hefler SM, Oliveira MC, Garcia AM. 2014. Feeding ecology and basal food sources that sustain the Paradoxal frog *Pseudis minuta*: a multiple approach combining stomach content, prey availability, and stable isotopes. *Hydrobiologia.* 740:253–264.
- Hurlbert SH. 1978. The measure of niche overlap and some relatives. *Ecology.* 59(1):67–77.
- ICMBio. 2007. Instituto Chico Mendes de Conservação da Biodiversidade. Plano de Manejo do Parque Nacional da Restinga de Jurubatiba. Brasília; p. 670.
- Instituto Nacional de Meteorologia – INMET. 2020. [Online]. [cited Apr 3 2020]. Available from: <http://www.inmet.gov.br>
- Jetz W, Pyron RA. 2018. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat Ecol Evol.* 2:850–858. doi:10.1038/s41559-018-0515-5
- Kacevas N, Gobel N, Laborda Á, Laufer G. 2019. Predation on *Pseudopaludicola falcipes* (Hensel, 1867) (Anura: Leptodactylidae) by *Lycosa thorelli* (Keyserling, 1877) (Araneae: Lycosidae). *Herpetol Notes.* 12:999–1000.
- Krebs CJ. 1999. *Ecological methodology.* 2nd ed. California: Benjamin Cummings. p. 624.
- Krebs CJ. 2016. *Programs for ecological methodology Version 7.3.* 2nd ed. Vancouver (B.C. Canada): Department of Zoology, University of British Columbia.

- Lavilla EO, Caballero-Gini A, Bueno-Villafaña D, Cardozo D. 2016. Notes on the distribution of the genus *Pseudopaludicola* Miranda-Ribeiro, 1926 (Anura: Leptodactylidae) in Paraguay. *Check List*. 12(6):1–9.
- Levins R. 1968. *Evolution in changing environments*. Princeton (NJ): Princeton University Press.
- López JA, Peltzer PM, Lajmanovich RC. 2005. Dieta y solapamiento del subnicho trófico de nueve especies de leptodactílicos en el Parque General San Martín (Argentina). *Rev Esp Herp*. 19:19–31.
- Mitchell JC, Groves JD, Walls SC. 2006. Keratophagy in Reptiles: review, hypothesis, and recommendations. *S Am J Herpetol*. 1(1):42–53.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin RP, O'hara RB, Simpson GL, Solymos P, et al. 2019. *Vegan: community ecology package*. R package version 2.5-6. Available from: <https://CRAN.R-project.org/package=vegan>
- Oliveira JC, Rocha CFD. 2015. Journal of coastal conservation: a review on the anurofauna of Brazil's sandy coastal plains. How much do we know about it? *J Coast Conserv*. 19(1):35–49.
- Oliveira RM, Schilling AC, Solé M. 2019. Trophic ecology of two *Pithecopus* species (Anura: Phyllomedusidae) living in syntopy in southern Bahia, Brazil. *Stud Neotrop Fauna E*. 54(1):10–21.
- Pereira EG, Nascimento LB. 2004. Descrição da vocalização e do girino de *Pseudopaludicola mineira* Lobo, 1994, com notas sobre a morfologia de adultos (Amphibia, Anura, Leptodactylidae). *Arquivos Do Museu Nacional*. 62(3):233–240.
- Pincheira-Donoso D. 2002. Note of the diet of *Pleurodema bufonina* Bell, 1843 (Anura-Leptodactylidae). *Gayana*. 66(1):77–80.
- Pinkas LM, Oliphant S, Iverson ILK. 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. *Calif Fish Game*. 152:1–105.
- R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org/>
- Rebouças R, Solé M. 2015. Diet of *Adenomera thomei* (Almeida and Angulo, 2006)(Anura: Leptodactylidae) from a rubber tree plantation in southern Bahia, Brazil. *Stud Neotrop Fauna E*. 50(2):73–79.
- Rocha CFD, Bergallo HG, Van Sluys M, Alvez MAS, Jamel CE. 2007. The remnants of restinga habitats in the Brazilian Atlantic Forest of Rio de Janeiro state, Brazil: habitat loss and risk of disappearance. *Braz J Biol*. 67(2):263–273.
- Sabagh LT, Carvalho-e-Silva AMPT, Rocha CFD. 2012. Diet of the toad *Rhinella icterica* (Anura: Bufonidae) from Atlantic Forest Highlands of southeastern Brazil. *Biota Neotrop*. 12(4):258–262. ISSN 1676-0603. Available from: <https://www.biotaneotropica.org.br/v12n4/en/abstract?short-communication+bn01612042012>
- Scarano FR. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic Rainforest. *Ann Bot*. 90:517–524.
- Segalla MV, Caramaschi U, Cruz CAG, Garcia PCA, Grant T, Haddad CFB, Santana DJ, Toledo LF, Langone JA. 2019. Brazilian Amphibians: list of Species. *Herpetologia Brasileira*. 8:65–96.
- Silva CS, Sousa JGG, Lima YF, Ávila RW, Morais HM. 2018. Diet and morphological aspects of a population of *Pseudopaludicola pocoto* (Anura: Leptodactylidae) from Northeast Brazil. *Neotrop Biol Conserv*. 13(4):313–320.
- Silva HR, Britto-Pereira MC, Caramaschi U. 1989. Frugivory and seed dispersal by *Hyla truncata*, a Neotropical tree-frog. *Copeia*. 1989:785–794.
- Toft CA. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia*. 45:131–141.
- Toft CA. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *J Herpetol*. 15:130–144.
- Toledo LF, Ribeiro R, Haddad CF. 2007. Anurans as prey: an exploratory analysis and size relationships between predators and their prey. *J Zool*. 271:170–177.
- Van Sluys M, Rocha CD. 1998. Feeding habits and microhabitat utilization by two syntopic Brazilian Amazonian frogs (*Hyla minuta* and *Pseudopaludicola* sp. (gr. *falcipes*)). *Braz J Biol*. 58:559–562.
- Weldon PJ, Demeter BJ, Rosscoe R. 1993. A survey of shed skin-eating (dermatophagy) in amphibians and reptiles. *J Herpetol*. 27:219–228.
- Wells KD. 2007. *The ecology and behavior of amphibians*. Chicago: The University of Chicago Press.
- Wickham H, Chang W, Wickham MH. 2016. Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics. Version. 2(1):1–189.