



ANIMAL SCIENCE

Feeding ecology of endemic frogs of the Atlantic Forest in southern Brazil

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Abstract: Our objective was to describe and compare the diet of endemic anurans of the Atlantic Forest, as well as to evaluate the influence of biotic factors on the trophic ecology of the species. We conducted the study in Mananciais da Serra (Piraquara-PR), a transition region between mixed and dense ombrophilous forest, between January 2019 and February 2020. In this work, we describe the diet of eight species: *Aplastodiscus albosignatus*, *Boana semiguttata*, *Bokermannohyla circumdata*, *Ischnocnema henselii*, *Leptodactylus notoaktites*, *Proceratophrys boiei*, *Rhinella abei* and *Scythrophrys sawayae*. Coleoptera were important prey in the diet of most species, except for *B. circumdata* and *L. notoaktites*. All species showed potential selection for some category of prey. We observed a correlation between the size of the individuals and the volume of consumed prey in *I. henselii*. In general, the niche overlap between species was low, and most species had a broad trophic niche.

Key words: Trophic niche, diet, prey selection, niche breadth.

INTRODUCTION

Trophic ecology is a fundamental part of a species' natural history and provides the necessary information to understand community dynamics and ecosystem functioning (Sih & Christensen 2001, Solé & Rödder 1991). From these studies, we can obtain information on foraging strategies (Toft 1981, Solé et al. 2009), food preferences (Anderson et al. 1999, Rebouças & Solé 2015), generalist or specialist habits and sharing of food resources among species (Anderson et al. 1999, De Oliveira et al. 2019). When we evaluate the food ecology of individuals who share the same habitat, we can generate important information for the development of ecological and evolutionary hypotheses (Menin et al. 2005, Sabagh & Carvalho-e-Silva 2008, De Oliveira et al. 2015).

Amphibians are good models for studies of food ecology in sympatric species, as they have an invertebrate-based diet, similar foraging strategies and small dispersal potential. This facilitates the comparison between individuals and species. In general, sympatric species have access to the same categories of potential prey and, in addition to the fact that most anurans have a generalist diet, it is reasonable to expect them to have similar diets (Sabagh et al. 2010). When we expand the observation scale and consider sympatric species that share morphological, ecological and behavioral characteristics, we can obtain more refined information about resource sharing (Duré & Kehr 2001, 2004).

Many factors can influence the diet of amphibians, such as genus-related differences (De Oliveira & Haddad 2015), seasonality (Maragno & Souza 2011), ontogeny (Luría-Manzano &

Ramírez-Bautista 2019) and body size (Santos-Pereira et al. 2015, Almeida-Santos et al. 2017). The relationship between prey size and body size, such as jaw width, is an expected pattern for frogs since most of these animals swallow their prey whole (Toft 1980, Lima & Magnusson 1998), which limits prey size to the size of the predator's mouth.

Another factor that can have a great influence on the diet of frogs is prey availability in the environment (Rebouças & Solé 2015, De Oliveira & Haddad 2015) since it allows us to assess whether there is a selection of prey in the diet. The assessment of prey selectivity is important information in trophic ecology studies, as it allows us to discuss specialization and food preferences (Isacch & Barg 2002, López et al. 2009). Despite the increase in food ecology studies of neotropical amphibians in recent years (Moser et al. 2017, 2019, De Oliveira et al. 2017a, Da Silva et al. 2018, Farina et al. 2018), few assess the availability of prey in the environment (López et al. 2009, Rebouças & Solé 2015, Solé et al. 2019) and fewer evaluate the trophic relationship of species that share resources (De Oliveira et al. 2018, 2019).

Due to the great richness of anurans that occur in Brazil, there is still a great lack of information about their natural history (Rossa-Feres et al. 2017, Guerra et al. 2018). Thus, this work aims to describe the diet composition of eight amphibians species that are endemic to the Atlantic Forest (*Aplastodiscus albosignatus*, *Boana semiguttata*, *Bokermannohyla circumdata*, *Leptodactylus notoaktites*, *Rhinella abei*, *Scythrophrys sawayae*, *Proceratophrys boiei* and *Ischnocnema henselii*) to contribute with new information about the feeding ecology of these amphibians. In addition, we aim to answer the following questions: (1) Do these species have similar diets? (2) Do they have any food preferences? (3) What is the trophic niche

breadth of these species? (4) Does the body size of the species influence feeding?

MATERIALS AND METHODS

Study site

We conducted the study in subtropical forest environments within the Atlantic Forest biome, in Mananciais da Serra (25°30'28" S 49°1'30" W), municipality of Piraquara, state of Paraná, southern Brazil (Figure 1). The sampled environment is located in a transition zone between the Mixed Ombrophilous Forest, which has the predominance of *Araucaria angustifolia* (Forest with Araucaria) and Dense Ombrophilous Forest (Reginato & Goldenberg 2007). The level of annual precipitation varies from 1400 to 1700, with rains concentrated from October to March (Paraná 1987). The average temperature is 22 °C in the warmer months and 18 °C in the colder months (Ferreira 1996).

Data collection

We conducted sampling campaigns between January and February 2019, and September 2019 to February 2020. All campaigns had a duration of 5 consecutive nights per month, with samples between 9 pm and 2 am. We located the anurans through active search (Crump & Scott JR 1994) and captured them manually. The collections were carried out with the competent Federal Organ authorization, SISBIO (authorization # - 66853-2) and with authorization of the Ethics Committee for Animal Use from the Biological Sciences Section of the Federal University of Paraná (CEUA/BIO – UFPR, process number 23075.043325/2019-27). Immediately after capture, specimens were packed in a refrigerated styrofoam box to reduce physiological activities (De Oliveira et al. 2015). Stomach content was obtained in two ways: by stomachal flushing and dissection of gastrointestinal organs.

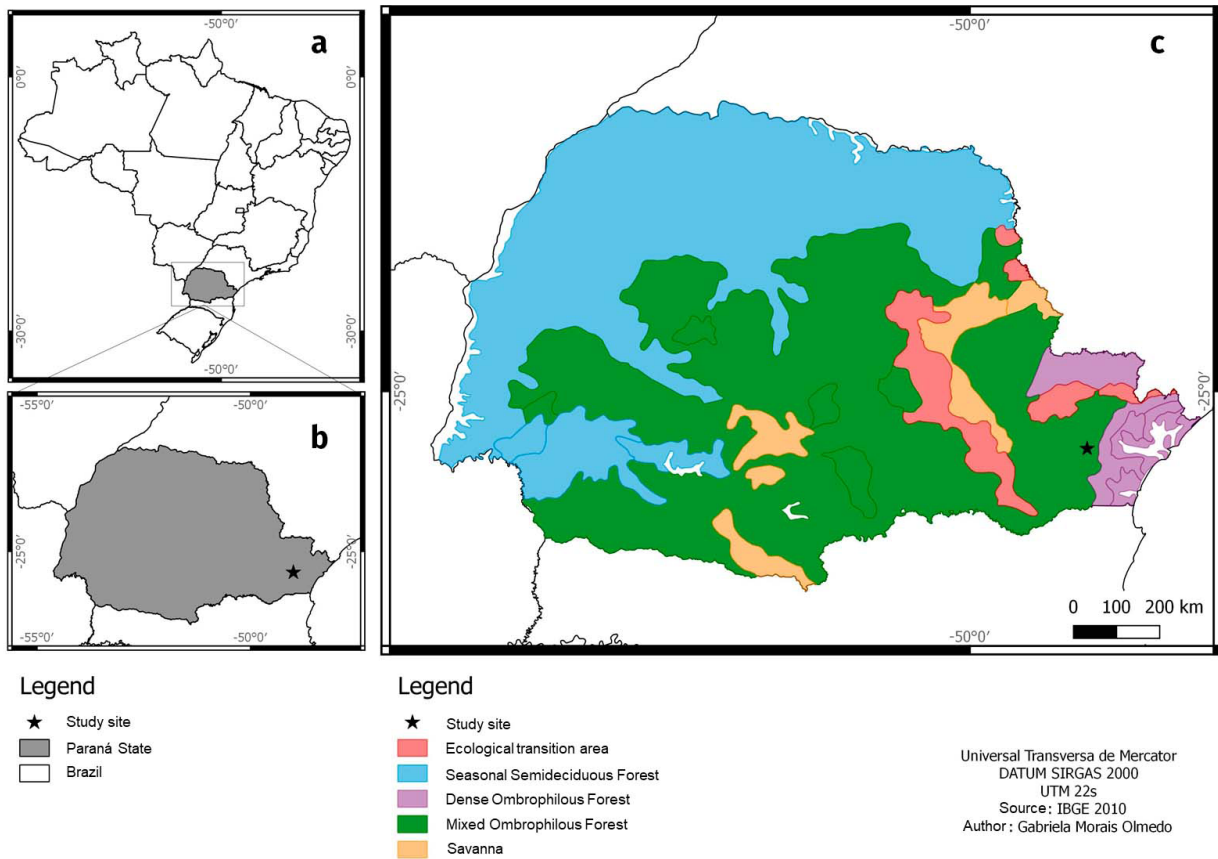


Figure 1. Location of the study area. **a:** Map of Brazil highlighting the state of Paraná; **b:** Map of the state of Paraná highlighting the study area; **c:** Map of the state of Paraná highlighting the physiognomy of vegetation.

Stomach flushing was performed as described by Solé et al. (2005) and was the method used in the species *Proceratophrys boiei* and *Rhinella abei*. Only ten individuals of both species were collected as vouchers and the remaining specimens were released at the same collection site after the stomach flushing process. Further species were collected because they are part of other ongoing studies, which required the collection of individuals. All captured individuals had their mass measured with a digital scale, and the snout-vent length (SVL) and jaw width with a digital caliper. We stored all the extracted food content in vials with 70% ethanol until the screening process with the stereomicroscope. We identified food items at the lowest possible taxonomic level

(Order or Family) using taxonomic guides and identification keys (Ribeiro-Costa & Rocha 2002). After identification and prey quantification, the volume was calculated using the area (mm²) occupied by each item with a graph paper support attached to the bottom of the Petri dish, where we evenly spread each item, maintaining a regular height of 1 mm (Hellawell & Abel 1971, Moser et al. 2020). To calculate the volume (V) of each item, the area value (mm²) was multiplied by its height (1 mm). For each prey category, we calculated the number, volume and frequency of occurrence in absolute terms and percentages.

The availability of leaf litter and arboreal prey were measured, respectively, with the collection of leaf litter and an entomological umbrella. Six leaf litter samples were collected

per campaign throughout the area where the frogs were collected. The leaf litter was kept in plastic bags and sorted on the same day. The screening process was carried out on white trays with the aid of extra lighting (headlamps). The number of people in the screening process varied but the time was limited to 60 minutes per sample (e.g., 2 people = 30 min each, 4 people = 15 min each). To sample the availability of arboreal prey, we collected eight samples with an entomological umbrella over the same area, with each sample corresponding to a sampled tree. We standardized three strokes on each tree to promote the fall of invertebrates into the entomological umbrella. We stored the invertebrates in Falcon tubes with 70% ethanol for later identification.

Data analysis

The assessment of the importance of each prey category in the diet was calculated by the Index of Relative Importance (IRI) using the following equation: $IRI = (\%N + \%V) \%FO$, where %N is the relative abundance of each prey category in the diet, %V is the relative volumetric contribution of the prey in the diet, and %FO is its relative frequency of occurrence in the diet (Pinkas et al. 1971, Krebs 1999). The higher the IRI value, the greater is the importance of a given prey category in the diet.

To evaluate the level of selectivity in the diet, i.e., whether certain prey was actively selected, the Jacobs Electivity Index (D) was calculated. This index assesses the presence of each prey category found in the diet in relation to its availability in the environment by the following formula: $D = R_k - P_k / (R_k + P_k) - (2 \cdot R_k \cdot P_k)$ (Jacobs 1974). In this formula, "D" is the electivity index, "Rk" represents the proportion of category k in stomach contents and "Pk" is the proportion of prey category k in the environment. The value of D ranges from -1 to +1, with positive values

greater than 0.2 ($D > 0.5$) indicating that a given prey is selected by the anuran (preferred prey).

Trophic niche breadth was calculated using the Levins Trophic Niche Amplitude Index (B) (Krebs 1999), defined by $B = 1 / \sum p_i^2$, where p is the individual proportion of given resource i (taxon) found in the diet. To facilitate comparisons among species, the Standardized Levins Index (Bsta) was calculated, which limits the index to a scale of 0 to 1 according to the following equation: $B_{sta} = (B-1) / (n-1)$, where n represents the number of resources recorded. Values near 0 indicate a specialist diet (narrow niche breadth), while values near 1 indicate a generalist diet (wide niche breadth, Krebs 1999).

To analyze the trophic niche overlap between species, regarding the degree of diet similarity, we used the Pianka's Trophic Niche Overlap Index (O_{jk}) (Pianka 1973), defined by the following equation:

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

, where O_{jk} is the niche overlap index between the species j and k; p_{ij} is equivalent to the proportion of the resource type i relative to the total of resources used by the species j; p_{ik} is the proportion of resource i relative to the total of resources used by the species k; and n is the total number of resource categories used by the species j and k. The index ranges from 0 to 1 when there is no overlap or a complete overlap between the species diets, respectively (Krebs 1999).

To assess whether there is a correlation between diet and species morphometry, we performed a linear regression in the program Past 4.03 (Hammer et al. 2001). We tested the correlation of mass, SVL and jaw width with the volume, number and richness of prey.

RESULTS

Composition of the diet

In total, we assessed the food content of 250 individuals of eight species (48 *Rhinella abei*, 44 *Proceratophrys boiei*, 42 *Aplastodiscus albosignatus*, 42 *Scythrophrys sawayae*, 24 *Bokermannohyla circumdata*, 19 *Leptodactylus notoaktites*, 16 *Boana semiguttata* and 15 *Ischnocnema henselii*). Only one individual from *L. notoaktites*, one from *I. henselii*, four from *B. semiguttata* and three from *A. albosignatus* did not present food content in the gastrointestinal tract. The order Coleoptera was an important category in the diet of several species, being the most important prey item in the diet of *A. albosignatus* (IRI = 85.7%) and *B. semiguttata* (IRI = 71.4%) and the second most important prey in the diet of *P. boiei* (IRI = 26.4%), *I. henselii* (IRI = 21.4%), *S. sawayae* (IRI = 17.7%) and *R. abei* (IRI = 14%), (Table I). Ants were the most important prey in the diet of *R. abei* (IRI = 83%) and *S. sawayae* (55.8%) and the second most important prey category for *L. notoaktites* (35.6%) (Table I). Spiders were important prey only in the diet of *L. notoaktites* (IRI = 57%), amphipods only in the diet of *I. henselii* (IRI = 27.9%) and orthopterans in the diet of *P. boiei* (IRI = 46.8%), configuring the main consumed prey by these species. The order Blattodea was the main prey in the diet of *B. circumdata* (IRI = 61.2%) and the third most important prey for *I. henselii* (IRI = 20.5%). Lepidopteran larvae were the second most consumed prey by *B. semiguttata* (IRI = 22%). Mites were the third most important prey category for *S. sawayae* (IRI = 12%), not being an important prey for other species. Information on the frequency of occurrence, volume and number of consumed prey items for each species is detailed in the Supplementary Material (Tables SI - SVII).

Trophic niche breadth and overlap

The trophic niche breadth of the evaluated species varied from a narrow niche, as in *R. abei* ($B_{sta} = 0.01$) to a broad niche, such as in *I. henselii* ($B_{sta} = 0.62$) (Table I). In ascending order, *L. notoaktites* had a range of 0.26, *S. sawayae* of 0.34, *A. albosignatus* of 0.36, *B. circumdata* of 0.46, *P. boiei* of 0.50 and *B. semiguttata* of 0.59 (Table I). The species with the greatest overlap between their niches were *R. abei* and *S. sawayae* ($O_{jk} = 0.96$), followed by *A. albosignatus* and *B. semiguttata* ($O_{jk} = 0.95$) (Table II). The species *B. circumdata* and *B. semiguttata* had a low niche overlap ($O_{jk} = 0.09$). *Ischnocnema henselii* had an overlap of about 50% with the tree frogs *B. circumdata*, *B. semiguttata* and *A. albosignatus*. *Proceratophrys boiei* had a low niche overlap with *R. abei*, *L. notoaktites*, *S. sawayae* ($O_{jk} = 0.08, 0.11$ and 0.14 , respectively) and a higher overlap with *I. henselii* ($O_{jk} = 0.37$).

Prey selection

According to the Jacobs electivity index, all species selected some prey category ($D > 0.50$) (Tables III and IV). However, these results must be viewed with caution, considering possible problems in the sampling or the availability of the collected individuals, which will be addressed below in the discussion.

Relationship between morphometry and diet

For *I. henselii* and *R. abei*, the volume of consumed prey had a significant correlation with the jaw width ($p = 0.0001$; $R^2 = 0.83$; $p = 0.001$; $R^2 = 0.22$, respectively), SVL ($p = 0.0001$; $R^2 = 0.83$; $p = 0.003$; $R^2 = 0.19$) and mass of individuals ($p = 0.001$; $R^2 = 0.83$; $p = 0.001$; $R^2 = 0.23$). For *P. boiei*, volume was correlated only with SVL ($p = 0.04$; $R^2 = 0.10$) and weight ($p = 0.02$; $R^2 = 0.11$). Prey richness had a positive correlation with the size of the jaw only for *R. abei* ($p = 0.02$; $R^2 = 0.12$). Nevertheless, the R^2 value was high considering only *I. henselii*.

Table I. Prey categories found in the gastrointestinal content of the species evaluated. Legend: Ln = *Leptodactylus notoaktites*, Pb = *Proceratophrys boiei*, Ss = *Scythrophrys sawayae*, Ra = *Rhinella abei*, lh = *Ischnocnema henselii*, Bc = *Bokermannohyla circumdata*, Bs = *Boana semiguttata*, Aa = *Aplastodiscus albosignatus*, IRI% = Index of Relative Importance, Bsta = trophic niche breadth. Red numbers indicate high IRI values. ¹species of terrestrial habit; ²species of tree habit.

	Ln ¹	Pb ¹	Ss ¹	Ra ¹	lh ¹	Bc ²	Bs ²	Aa ²
	IRI%	IRI%	IRI%	IRI%	IRI%	IRI%	IRI%	IRI%
Hymenoptera								
Formicidae	35.58	0.65	55.83	83.33	2.89	4.7	-	5.32
Apidae	-	-	-	0.21	-	-	-	-
Vespidae	-	0.19	-	0.13	1.71	-	-	-
Araneae	57.15	7.69	1.11	0.35	9.8	-	6.49	3.13
Amphipoda	-	1.36	3.72	0.53	27.87	-	-	-
Lepidoptera (larvae)	0.73	0.35	-	0.37	-	-	22.01	-
Coleoptera	0.62	26.39	17.75	14.07	21.38	6.4	71.39	85.68
Orthoptera	-	46.8	-	0.2	2.7	-	-	0.95
Acarina	-	-	12.09	0.01	1.3	1.17	0.12	0.58
Blattodea	1.26	5.5	0.02	0.01	20.5	61.19	-	1.24
Ostracoda	0.31	-	-	-	-	18.75	-	1.73
Gastropoda	0.30	2.57	0.03	0.01	-	-	-	-
Diplopoda	-	0.17	-	0.19	-	1.49	-	-
Hemiptera	3.39	-	-	0.24	1.53	1.83	-	-
Coleoptera (larvae)	-	-	1.41	0.26	1.62	1.17	-	-
Dermaptera	-	-	-	0.01	-	-	-	-
Quilopoda	-	5.6	-	0.01	-	-	-	-
Collembola	-	-	1.91	-	1.37	-	-	-
Pseudoscorpionida	-	-	0.03	0.01	-	-	-	-
Isopoda	-	0.67	5.39	0.04	7.36	-	-	-
Opilionida	-	0.18	-	0.04	-	-	-	-
Diptera	-	0.16	0.65	-	-	-	-	0.76
Lepidoptera	-	1.7	-	-	-	3.29	-	0.62
Ephemeroptera	-	-	-	0.01	-	-	-	-
Mantodea	0.30	-	-	0.01	-	-	-	-
Diptera (larvae)	-	-	0.03	0.01	-	-	-	-
Bsta	0.26	0.50	0.34	0.01	0.62	0.46	0.59	0.36

There was no correlation between morphometry and diet of the other species.

DISCUSSION

This work brings unprecedented information regarding the feeding ecology of *Rhinella abei*, *Scythrophrys sawayae*, *Leptodactylus notoaktites*, *Bokermannohyla circumdata*, *Boana*

semiguttata and *Aplastodiscus albosignatus*, in addition to new information about the diet of populations of *Ischnocnema henselii* and *Proceratophrys boiei* from Mananciais da Serra, state of Paraná.

In general, beetles were important prey in most evaluated species, except for *L. notoaktites* and *B. circumdata*. Despite this, Coleoptera has been recorded as a frequent prey in the diet of

Table II. Prey electivity index of litter species *Leptodactylus notoaktites* (Ln), *Proceratophrys boiei* (Pb), *Scythrophrys sawayae* (Ss), *Rhinella abei* (Ra), *Ischnocnema henselii* (Ih). Legend: PA = Prey availability of leaf litter, n% = number of prey, D = Jacobs electivity index. Red values indicate prey selection.

Prey categories	PA	Ln		Ss		Ih		Ra		Pb	
		n%	D	n%	D	n%	D	n%	D	n%	D
Hymenoptera											
Formicidae	0.31	0.46	0.30	0.35	0.09	0.08	-0.67	0.84	0.84	0.04	-0.85
Apidae	0	0	-	0	-	0	-	0.01	1.00	0	-
Vespidae	0.01	0	-1	0	-1	0.04	0.85	0.01	0.42	0.02	0.67
Araneae	0.17	0.27	0.30	0.03	-0.69	0.08	-0.37	0.01	-0.91	0.11	-0.25
Amphipoda	0.10	0	-1	0.05	-0.32	0.25	0.51	0.01	-0.76	0.07	-0.16
Isopoda	0.10	0	-1	0.08	-0.13	0.08	-0.11	0.00	-0.94	0.04	-0.51
Coleoptera	0.09	0.03	-0.55	0.16	0.32	0.17	0.35	0.07	-0.09	0.18	0.39
Quilopoda	0.02	0.03	0.10	0	-1	0	-1	0.00	-0.94	0.09	0.62
Acarina	0.02	0	-1	0.17	0.80	0.04	0.31	0.00	-0.94	0	-1
Collembola	0.04	0	-1	0.07	0.36	0.04	0.07	0	-1	0	-1
Gastropoda	0.01	0.03	0.29	0.01	-0.45	0	-1	0.00	-0.84	0.07	0.67
Diplopoda	0.02	0	-1	0	-1	0	-1	0.00	-0.60	0.02	0.06
Hemiptera	0.02	0.08	0.70	0	-1	0.04	0.47	0.01	-0.44	0	-1
Coleoptera (larvae)	0.01	0	-1	0.04	0.63	0.04	0.64	0.01	-0.04	0	-1
Orthoptera	0.01	0	-1	0	-1	0.04	0.69	0.00	-0.33	0.23	0.95
Blatodea	0.02	0.03	0.09	0.01	-0.60	0.08	0.59	0.00	-0.89	0.07	0.54
Dermaptera	0.00	0	-1	0	-1	0	-1	0.00	-0.56	0	-1
Pseudoscorpionida	0.01	0	-1	0.01	-0.27	0	-1	0.00	-0.87	0	-1
Lepidoptera (larvae)	0.001	0.03	0.94	0	-1	0	-1	0.00	-0.82	0.02	0.92
Opilionida	0.001	0	-1	0	-1	0	-1	0.00	-0.19	0.02	0.64
Diptera	0.01	0	-1	0.02	0.35	0	-1	0	-1	0.02	0.37
Ephemeroptera	0	0	-	0	-	0	-	0.001	1.00	0.02	-0.07
Lepidoptera	0.002	0	-1	0.002	-1	0.002	-1	0	-	0.02	0.84
Mantodea	0	0.03	0.03	0	-	0	-	0.001	1.00	0	-1
Diptera (larvae)	0.001	0	-1	0.01	0.76	0	-1	0.001	0.44	0	-1
Ostracoda	0	0.03	1	0	-	0	-	0	-	0	-

several leptodactylids (Carvalho et al. 2008, Piatti & Souza 2011, Sugai et al. 2012, Camera et al. 2014, Solé et al. 2019) and as the most important prey in the diet of *Bokermannohyla pseudopseudis* (De Magalhães et al. 2016). The order Coleoptera is often reported as an important prey also in the diet of hylids (Muñoz-Guerrero et al. 2007, Barbosa et al. 2014, Pacheco et al. 2017, Moser et al. 2019) and bufonids (Batista et al. 2011, De Oliveira et al. 2017a, Sabagh et al. 2012). Due to the high species richness of this group, as well as its abundance in the environment, beetles are easy to be found and consumed by several species (Baretta 2007). In the present study, the order Coleoptera was the second most abundant prey item in the arboreal stratum and the fifth most abundant in leaf litter. In addition, according to the Jacobs index, we recorded a food preference of *A. albosignatus* and *B. semiguttata* for Coleoptera. However, it is necessary to have a greater sampling effort to better understand this possible preference.

Ants were important prey categories only in the diet of *R. abei*, *S. sawayae* and *L. notoaktites*. Apparently, *P. boiei* avoids the consumption of ants, as this pattern has also been recorded for other populations in the states of São Paulo (Giaretta et al. 1998), Espírito Santo (Teixeira et al. 2002) and Rio de Janeiro (Klaion et al. 2011). The low importance of ants in the diet of other *Proceratophrys* species indicates that this pattern may extend to the genus in general (Moreira & Barreto 1996, Boquimpani-Freitas et al. 2002, Almeida-Santos et al. 2017). Regarding hylids, represented here by the species *Bokermannohyla circumdata*, *Boana semiguttata* and *Aplastodiscus albosignatus*, the consumption of ants also appears to be avoided in several other species (Muñoz-Guerrero et al. 2007, De Magalhães et al. 2016, De Oliveira et al. 2017b, Moser et al. 2019). Unlike the results found in this study, *I. henselii* had already been characterized as an ant predator (Dietl et al. 2009), with ants being previously recorded as the second most important category in the

Table III. Index of electivity of prey of tree species *Aplastodiscus albosignatus* (Aa), *Boana semiguttata* (Bs) and *Bokermannohyla circumdata* (Bc). Legend: PA = Availability of tree prey, n% = number of prey, D = Jacobs electivity index. Red values indicate prey selection.

Prey categories	Aa			Bs		Bc	
	PA	N%	D	N%	D	N%	D
Formicidae	0.082	0.125	0.23	0	-1	0.095	0.08
Araneae	0.254	0.083	-0.58	0.2	-0.15	0	-1
Coleoptera	0.123	0.458	0.71	0.533	0.78	0.095	-0.14
Acarina	0.079	0.042	-0.33	0.133	0.28	0.048	-0.26
Diplopoda	0.009	0	-1	0	-1	0.048	0.69
Hemiptera	0.044	0	-1	0	-1	0.048	0.04
Coleoptera (larvae)	0.003	0	-1	0	-1	0.048	0.88
Orthoptera	0.006	0.042	0.75	0	-1	0	-1
Blatodea	0.026	0.042	0.24	0	-1	0.190	0.80
Lepidoptera (larvae)	0.059	0	-1	0.133	0.42	0	-1
Diptera	0.059	0.042	-0.18	0	-1	0	-1
Lepidoptera	0.002	0.042	0.93	0	-1	0.048	0.94
Ostracoda	0	0.125	1	0	-	0.381	1

diet of this species (Santos-Pereira et al. 2015). Although they are usually very abundant in the environment, some amphibian species avoid the consumption of this prey type due to their rigid exoskeleton, formic acid and quinones (Hirai & Matsui 2002). However, it is plausible to consider that this does not apply to several species, such as *R. abei*, *S. sawayae* and *L. notoaktites*, which have frequently consumed ants and demonstrate efficient physiological conditions to digest and metabolize them. It is interesting to note that mites were relevant prey only in the diet of *S. sawayae*, and it is also possible to observe a food preference for this prey type ($D = 0.80$). Mites may be important items in the diet of small species that forage in the leaf litter (Lima & Magnusson 1998, Van Sluys et al. 2001, Martins et al. 2010, Almeida-Santos et al. 2011, Santos-Pereira et al. 2015).

Although spiders are often recorded as important prey in the diet of hylids (De Magalhães et al. 2016, De Oliveira et al. 2017b, Pacheco et al. 2017, Moser et al. 2019), this pattern was not found in the present study, even though spiders were the most abundant prey category available in the evaluated arboreal stratum. The order Araneae was important only for *L. notoaktites*,

being the main category of consumed prey (57%). There is no available information about the diet of this species but spiders were not prey of great relevance for *L. spixi* (Solé et al. 2019), *L. elenae* (Piatti & Souza 2011) and *L. mystaceus* (Camera et al. 2014), species that belong to the same group as *L. notoaktites*. The high consumption of spiders by *L. notoaktites* may be related to their abundance in the environment, since they were the second most recorded prey category in the leaf litter.

Concerning the hylids, several individuals of the three analyzed species had their stomach and intestine empty or only with highly digested food content, making identification unviable (indicated as “others” in the supplementary material tables). This pattern was also found for other hylids (Da Silva & De Britto-Pereira 2006, Duré & Kehr 2004, Menin et al. 2005, Solé & Pelz 2007). In addition, considering individuals who had identifiable gastrointestinal content, the vast majority had only one or two items in the stomach and/or intestine. Parmelee (1999) observed that species belonging to the family Hylidae tend to have a higher percentage of empty stomachs and consume a smaller number of prey items when compared to amphibians

Table IV. Overlap of trophic niche among the species evaluated (O_{ijk}). Legend: *Ln* = *Leptodactylus notoaktites*, *Pb* = *Proceratophrys boiei*, *Ss* = *Scythrophrys sawayae*, *Ra* = *Rhinella abei*, *Ih* = *Ischnocnema henselii*, *Bc* = *Bokermannohyla circumdata*, *Bs* = *Boana semiguttata*, *Aa* = *Aplastodiscus albosignatus*. ¹species of terrestrial habit; ²species of tree habit.

	Ln¹	Pb¹	Ss¹	Ra¹	Ih¹	Bc²	Bs²	Aa²
Ln	-	0.11	0.45	0.46	0.22	0.04	0.07	0.05
Pb	-	-	0.14	0.08	0.37	0.13	0.47	0.48
Ss	-	-	-	0.96	0.25	0.09	0.27	0.34
Ra	-	-	-	-	0.13	0.08	0.16	0.22
Ih	-	-	-	-	-	0.51	0.50	0.52
Bc	-	-	-	-	-	-	0.09	0.11
Bs	-	-	-	-	-	-	-	0.95
Aa	-	-	-	-	-	-	-	-

from other families. There is less information available about the diet of arboreal amphibians compared to litter amphibians (Lima et al. 2010). This happens due to the difficulty in collecting these species and because they are mostly found during reproductive activity, a period in which hylids eat less and prioritize reproduction (Solé & Pelz 2007).

The niche breadth of the evaluated species varied from a narrow niche ($B_{sta} = 0.01$), in the case of *R. abei*, to a broad niche ($B_{sta} = 0.62$) in *I. henselii*. This narrow niche breadth found for *R. abei* has also been recorded for other species of the genus (Isacch & Barg 2002, Sabagh & Carvalho-e-Silva 2008, Ferreira & Teixeira 2009). Bufonids are characterized by having a generalist and similar diet (Duellman & Trueb 1994, Parmelee 1999, Sabagh et al. 2012) although they often have a narrow niche (characteristic of specialist species). However, due to the narrow niche, some species of this genus have already been considered specialists in ants, such as *R. arenarum*, *R. dorbignyi* (Isacch & Barg 2002) and *R. granulosa* (Damasceno 2005). Besides, Ferreira & Teixeira (2009) and Da Rosa et al. (2002) characterized *R. crucifer* and *R. gr. granulosa* as ant specialists, even though they did not evaluate the availability of prey in the environment. In the present study, even consuming 22 categories of prey, *R. abei* presented a strong selection for ants, which made up more than 80% of the species' diet. This discrepancy in relation to the other categories of consumed prey resulted in a narrow niche breadth. According to Pianka (2017), a narrow trophic niche is favored by a large number of available resources. In other words, with a large abundance of available prey, species can choose to feed on the prey of their choice.

Leptodactylus notoaktites presented a slightly broader trophic niche ($B_{sta} = 0.26$). Species of the family Leptodactylidae, in

general, are considered generalists concerning food due to their sit-and-wait foraging strategy (Solé et al. 2019, Sugai et al. 2012, Toft 1981). In the literature, the genus *Leptodactylus* shows a variety of trophic niche breadths, both narrow and broad (França et al. 2004, Araújo et al. 2007, Solé et al. 2009, Schaefer et al. 2015, De Oliveira et al. 2019). This variation in the amplitude of these species may be related to the abundance of prey available in the environment. De Oliveira et al. (2019) recorded that *L. latrans* decreased its niche breadth during the warmer months, a period in which there are usually more prey items available in the environment (Yom-Tov & Geffen 2006), demonstrating an opportunistic behavior by the species.

The species *S. sawayae*, *A. albosignatus*, *B. circumdata*, *P. boiei*, *B. semiguttata* and *I. henselii* had broader niches ($B_{sta} = 0.34, 0.36, 0.46, 0.50, 0.59, 0.62$, respectively), demonstrating a generalist diet. The same generalist pattern was also found for other populations of *P. boiei* and *I. henselii* (Teixeira et al. 2002, Dietl et al. 2009, Santos-Pereira et al. 2015) and other hylid species (Barbosa et al. 2014, De Oliveira et al. 2019, Moser et al. 2019, Sabagh et al. 2010). The trophic niche breadth recorded for another species of *Aplastodiscus*, *A. perviridis* ($B_{sta} = 0.27$), was narrower than for the congener species in this study ($B_{sta} = 0.36$). The authors considered that *A. perviridis* had a more specialized diet than most hylids in the studied period (De Oliveira et al. 2017b).

Jacobs' electivity index indicated that all species select at least one category of prey. Despite the great sampling effort invested to gather data about the prey availability, we cannot rule out the possibility that the sampling was insufficient for some prey categories. For example, the species *P. boiei*, *A. albosignatus* and *B. circumdata* showed selection for Lepidoptera, a prey type that is difficult to sample in both

arboreal stratum and leaf litter. Likewise, the prey categories Blattodea, Chilopoda, Opilionida and Coleoptera larvae were not very representative in the leaf litter (less than 2%). This may have happened because they are very common under logs or in the bark, places that have not been sampled. Thus, the selection of these prey categories by species such as *P. boiei* (Blattodea, Chilopoda and Opilionida), *L. notoaktites* (Coleoptera larvae) and *I. henselii* (Blattodea and Coleoptera larvae) must be viewed with caution. However, if we consider that a species is moving to the places where these invertebrates are located (e.g., under trunks) to feed on them, this would constitute a selection. Taking this into account, it is interesting to highlight the selection of *P. boiei* for Orthoptera and *I. henselii* for Amphipoda, both prey types that were important in the diet of these species. Concerning *P. boiei*, other studies have already recorded the importance of this prey item in the diet of other populations (Giaretta et al. 1998, Klaion et al. 2011), as well as of other species of the same genus (Moreira & Barreto 1996, Boquimpani-Freitas et al. 2002, Almeida-Santos et al. 2017). Thus, it is feasible to consider that *P. boiei* is selecting this prey type. Regarding *I. henselii*, other studies on the diet of this species did not record Amphipoda as an important prey (Dietl et al. 2009, Santos-Pereira et al. 2015). Despite this, we believe that this species is indeed selecting amphipods in the environment since these invertebrates were well sampled in the leaf litter.

In general, the niche overlap between species was low, except for *S. sawayae* and *R. abei*, as well as *A. albosignatus* and *B. semiguttata*, which had a trophic niche overlap of 96% and 95%, respectively. The high niche overlap between *S. sawayae* and *R. abei* may be related to the large size difference between both species. Thus, despite consuming prey belonging

to the same order, *S. sawayae* is conditioned to prey only on small prey due to its small size, while *R. abei* manages to prey on larger ants and beetles. This occurs because body size, such as the jaw width, is a limiting factor in the consumption of prey in small species (Menzies & Parker 2018, Menin et al. 2005). The high niche overlap recorded between *A. albosignatus* and *B. semiguttata* is mainly due to the high importance of the order Coleoptera, which was also one of the most abundant prey items in the arboreal stratum.

It is interesting to note that *P. boiei* and *I. henselii*, litter species, had a median niche overlap with tree species (*Bokermannohyla circumdata*, *Boana semiguttata* and *Aplastodiscus albosignatus*). This overlap is mainly due to the frequent consumption of the order Coleoptera by these species. However, as Coleoptera is a very diverse insect order, the overlap may be smaller between litter and arboreal species if prey items are identified at the family or genus level.

The relationship between consumed prey volume and predator size is a pattern already recorded for several amphibians (Klaion et al. 2011, Santos-Pereira et al. 2015, Almeida-Santos et al. 2017). Since amphibians are animals that swallow the prey as a whole, jaw width (and, consequently, the SVL) is a limiting factor in relation to the size of the consumed prey (Toft 1980). In the present study, this pattern was found only for the leaf litter species *S. sawayae*, *R. abei* and *I. henselii*. In addition, we recorded that for *R. abei* richness of consumed prey increases with the size of the amphibians. Larger amphibians, with wider jaws, can consume prey of varying sizes, both small and large prey. This increases the number of prey categories that these individuals can feed on compared to smaller individuals, which can consume only small-prey categories (Batista et al. 2011, Sales et

al. 2011). Although we found these patterns, the coefficient of determination (R^2) was high only for *I. henselli*. This pattern may not have been recorded for other species due to the number of sampled individuals, as well as the low amount of food consumed, mainly by arboreal species.

The present work contributes with new information about the trophic ecology of the evaluated species. The low trophic niche overlap observed between the species suggests that the availability of prey in the environment is high, facilitating the food and spatial resource partition and being able to avoid competitive interactions. In general, the species showed generalist feeding behavior. Although *R. abei* demonstrated a specialized ant diet in the sampled period, the high richness of consumed prey reveals a generalist behavior with opportunistic habits.

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SUPPLEMENTARY MATERIAL

Table S1. Categories of prey consumed by *Aplastodiscus albosignatus* in the Araucaria forest, Paraná, southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total

volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SII. Categories of prey consumed by *Leptodactylus notoaktites* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SIII. Categories of prey consumed by *Proceratophrys boiei* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SIV. Categories of prey consumed by *Ischnocnema henselii* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SV. Categories of prey consumed by por *Bokermannohyla circumdata* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SVI. Categories of prey consumed by por *Boana semiguttata* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SVII. Categories of prey consumed by por *Rhinella abei* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

Table SVIII. Categories of prey consumed by *Scythrophrys sawayae* in the Araucaria forest, Paran , southern Brazil. FO = frequency of occurrence of each category of prey; IRI = Index of Relative Importance; N = number of individuals; V = total volume of prey (mm^3); (%) = percentage related to the total; Bsta = trophic niche breadth.

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