

Trophic niche of *Pseudopaludicola boliviana* (Anura: Leptodactylidae) from northern Brazil

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Abstract. In this work, we studied the diet of *Pseudopaludicola boliviana* from a floodplain area in southern Amapá, Brazil. A total of 141 frogs were collected by hand from March 2017 to March 2018, with 87 individuals collected during the rainy season (January–July) and 54 collected during the dry season (August–December). Of these, 86 stomachs (58 in the rainy season and 28 in the dry season) revealed 284 prey items. Acari (rainy season 35.56%, dry season 20.39%), Coleoptera (23.24%, 49.12%) and Diptera (20.42%, 20.53%) were the most abundant and important prey items. The most frequent items were Coleoptera (65.51%), Diptera (48.27%) and Hymenoptera (37.93%) for the males, and Diptera (57.14%), Acari (42.85%) and Coleoptera (39.28%) for the females. Frog morphometrics (snout-vent length, jaw width, and body weight) did not determine differences in dietary composition. The rarefaction curve did not reach the asymptote and indicated higher taxonomic richness in the diet of males, who also consumed a greater amount of prey than females. Niche breadth varied seasonally, with a wider niche breadth during the rainy season ($Bsta = 0.453$) compared to the dry season ($Bsta = 0.238$). The high trophic niche overlap (rainy season: $Ojk = 0.866$; dry season: $Ojk = 0.708$) between males and females in both seasons indicated similarity in diet during the entire year. During the entire year, *P. boliviana* consumed prey of similar volumetric size but seemed to consume more prey items during the rainy season. We conclude that *P. boliviana* has a generalist diet, marked by high dietary plasticity.

Keywords: Amphibia, Leptodactylidae, diet, niche overlap, prey richness.

Introduction

Studies on the characterization of the trophic ecology aspects are of key importance to understanding the organization in communities and assemblages (Toft 1981, 1985, Schoener 1974, Darst et al. 2005). Anurans play very important functions within the trophic webs of aquatic and terrestrial environments (Sanabria et al. 2005, Huckembeck et al. 2014, Lobos et al. 2016, Watson et al. 2017), acting both as predators and as prey. Thus, several studies have been carried out on Neotropical anurans to investigate the trophic relationships among species (e.g., Sabagh et al. 2010, Oliveira et al. 2015, Moser et al. 2017, Leivas et al. 2018, Furtado & Costa-Campos 2020), focusing on aspects of resource partition by means of the niche breadth and overlapping, and patterns of habitat use among species (e.g., Neckel-Oliveira et al. 2000, Leite-Filho et al. 2017). However, for species of the genus *Pseudopaludicola* Miranda-Ribeiro 1926, few studies have focused on evaluating temporary changes in the diet and between sexes and ontogenetic classes (Atencia-Gándara et al. 2021). Thus, basic data on the natural history of many neotropical anurans are still incipient, and studies of this nature are important for establishing conservation and management policies (Wells 2007).

According to Caldwell (1996), anuran species characterized by having a restricted niche breadth eat more and smaller prey (e.g., ants and mites) than non-specialist or generalist species. However, in the genus *Pseudopaludicola* some species have been described as specialists (Silva et al. 2018a), but not on ants or mites (Toft 1980, 1981), and others as generalists with high consumption of ants or mites

(e.g., Silva et al. 2018b, Carmo et al. 2021). Therefore, the high dietary plasticity of species in this genus has been remarkable regarding the availability and abundance of food items in the environment.

Pseudopaludicola boliviana Parker, 1927 is a small diurnal frog that can be found occupying open environments throughout eastern Colombia, northern Brazil (states of Amapá, Pará, and Roraima), and in Amazonian Venezuela through southern Surinam, Guyana, western non-Andean Bolivia, Argentina, and Paraguay (e.g., Lynch 1989, Lobo 1991, 1994, De la Riva et al. 2000, Andrade et al. 2020). In the state of Amapá, located in the extreme north of Brazil, *P. boliviana* was registered in Amazonian savanna and floodplain areas in the municipality of Macapá and the district of Ariri (see Costa-Campos et al. 2016). However, knowledge on the diet of *P. boliviana* is restricted to only one location on the eastern shore of the Paraná River, Argentina (Duré et al. 2004) and a population from the state of Roraima northern Brazil (Caldwell & Vitt 1999). Nonetheless, these authors did not explore differences in diet composition and the trophic niche aspects of the species according to sex and seasonal variation in the diet.

In this study, we evaluated the diet composition and trophic overlap between the seasons and sexes of *P. boliviana* in a population from a floodplain area in northern Brazil during the rainy and dry seasons. Also, we tested for differences in the amount of prey consumed between sexes and seasons, as well as the seasonal differences in the volumetric composition of prey, and if the individuals' morphometric characteristics (snout-vent length, jaw width, and body mass) are related to the volume of prey consumed.

Material and Methods

Study site

We carried out this study in a floodplain area along the Matapi River, district of Ariri (00°17'58.0"N, 051°07'48.0"W), approximately 33 km from the municipality of Macapá, Amapá State, Brazil. The climate is Equatorial (Am) according to the Köppen-Geiger classification (Alvares et al. 2013), with an average annual air temperature of 27.6°C. The rainy season in the region begins in January, reaching peak rainfall in March and July, with an annual average of 2,850 mm, and the dry season that goes from August to December, with approximately 160 mm on average (NHMET 2020). Lowland marshes and swamps are the predominant environments in the study area, although it is covered in the savanna.

Data sampling

We collected individuals of *P. boliviana* during the rainy and dry seasons from March 2017 to March 2018, located through active visual search and auditory surveys (Heyer et al. 1994). Frogs were captured by hand late afternoon (17:30 to 19:00 h). After capture, individuals were placed in plastic bags containing air and transported immediately to the laboratory. On the still living individuals, we measured the snout-vent length (SVL) and jaw width of each frog using a digital caliper (0.01 mm precision) and the body weight with a portable scale (0.1 g precision). Frogs were killed using lidocaine and ventrally sectioned to extract gastrointestinal contents, which were stored in 70% ethanol. Thus, frogs' sex was determined by direct observations of gonads, vocal sacs, and nuptial pads. Sexual differences in SVL and body weight were tested using the Student *t*-test (Zar 1996). Posteriorly, the specimens were fixed in 4% formaldehyde and preserved in 70% ethanol (Heyer et al. 1994). Specimens were killed because this work was part of a large research project on the natural history (diet, reproduction, and helminth parasites) of anurans of eastern Amazon, whose methodology requires animal euthanasia. All voucher specimens were housed in the Herpetological Collection of Universidade Federal do Amapá. This research was performed under license number 45990-1 provided by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

Dietary analysis

We analyzed the gastrointestinal content of each frog under a stereomicroscope with graduated oculars. Prey items were identified to the order level according to the identification key by Rafael et al. (2012). We measured the length and width of each prey using a digital caliper (0.01 mm precision) and estimated their volumes using the ellipsoid formula:

$$V = 4/3 \times \pi \times (L/2) \times (W/2)^2,$$

where *L* is the maximum prey length, and *W* is the maximum prey width (Griffiths & Mylotte 1987). To determine the importance of each prey category, we calculated the Index of Relative Importance (*IRI*) (Pinkas et al. 1971), both seasonal (rainy and dry seasons) and annual, using the percentage of occurrence in the stomachs (*FO%*), the numerical percentage (*N%*), and the volumetric percentage (*V%*):

$$IRI = FO\% \times (N\% + V\%).$$

The trophic niche breadth of the species was measured per season using the Levin's index (*B*) described by Pianka (1986):

$$B = 1 / \sum_{i=1}^n p_i^2,$$

where *p* is the numerical or volumetric proportion of prey category *i*, and *n* is the number of prey categories, and we calculated the standardized measure of Levin's index (*B_{sta}*) according to Hurlbert (1978):

$$B_{sta} = (B - 1) / (n - 1),$$

where *B* is the niche breadth value of the Levin's index, and *n* is the total number of prey items consumed by the species. Thus, values close to 0 represent narrow niches, and values close to 1 indicate wide

niches (Krebs 1999).

In addition, we used the absolute frequency of each prey category (*N*) to evaluate the dietary overlap (*O_{jk}*) between males and females per season using Pianka's index (Pianka 1973):

$$O_{jk} = \sum P_{ij} \times P_{ik} / \sqrt{\sum P_{ij}^2 \times \sum P_{ik}^2},$$

where *j* and *k* refer to the two sexes under comparison, and *P_i* is the proportion of prey category *i*. This index ranges from 0 to 1, with 0 representing total niche separation and 1 indicating total niche overlap.

We tested for differences in the volumetric composition of prey between the rainy and dry seasons using a permutational multivariate analysis of variance (PERMANOVA) through Euclidean distance (Anderson 2001). Additionally, we used Mann-Whitney tests to evaluate whether the number of prey differed between sexes and seasons. We also applied a simple linear regression to verify the possible relationship between SVL, jaw width, and body weight with the mean volume of prey consumed for each individual; only those with prey in their stomachs were considered in this analysis. Lastly, to analyze the sampling size and taxonomic richness of prey consumed by the males and females, we plotted rarefaction curves based on the number of individuals and food items.

All statistical tests were performed with BioEstat 5.3 software (Ayres et al. 2007), with α set at 0.05. All variables were tested for normality of variances (Zar 1996). The niche breadth was analyzed with the software Ecological Methodology (Krebs 1999), and the niche overlap: with the software EcoSim 7.0 (Gotelli & Entsminger 2001). The rarefaction curves were performed with Estimates 9.1 (Gotelli & Colwell 2001).

Results

A total of 141 frogs were captured, of which 77 males and 10 females were collected during the rainy season, and 19 males and 35 females in the dry season. For all males, the body size (SVL) ranged from 9.24 to 15.44 mm (mean = 11.86, SD = 1.29), body weight from 0.1 to 0.5 g (mean = 0.22, SD = 0.08), and jaw width from 3.96 to 5.10 mm (mean = 4.20, SD = 0.26). For all females, the SVL ranged from 10.19 to 15.47 mm (mean = 12.9, SD = 1.05), body weight from 0.1 to 0.4 g (mean = 0.20, SD = 0.08), and jaw width from 4.02 to 5.50 mm (mean = 4.49, SD = 0.32). Females were significantly larger than males in terms of SVL ($t = -4.7083$, $p < 0.0001$; $df = 139$), but the differences in body weight between both sexes was not significant ($t = 1.5168$, $p = 0.1318$; $df = 139$).

A total of 284 prey items were present in the stomachs of 86 specimens, with a mean of 3.30 items per stomach (min = 1, max = 37). The diet of *P. boliviana* was mainly composed of arthropods, including seven prey categories of insects and two for arachnids. The most abundant prey items were Acari (35.56%, $n = 101$), Coleoptera (23.24%, $n = 66$) and Diptera (20.42%, $n = 58$); these prey categories were also the most important in terms of frequency of occurrence. Coleoptera (40.02 mm³ or 50.79% of total), Diptera (11.07 mm³, 14.05%) and Hymenoptera-Formicidae (7.91 mm³, 10.04%) were the prey categories with the highest volumes. According to *IRI*, the most important items in the diet were Coleoptera (*IRI* = 4218.14, 49.12%), Diptera (*IRI* = 1763.71, 20.53%) and Acari (*IRI* = 1751.72, 20.39%). The mean volume of prey consumed per stomach did not increase with SVL ($rs = 0.0441$, $p = 0.6869$, $df = 86$), jaw width ($rs = 0.0694$, $p = 0.5254$, $df = 86$) and body weight ($rs = -0.0714$, $p = 0.8790$, $df = 7$).

The most frequently observed categories in the diet of males were Coleoptera (65.51%, $n = 38$), Diptera (48.27%, $n =$

28), and Hymenoptera-Formicidae and Acari (both 37.93%, $n = 22$) (Fig. 1). For females, the most frequently observed categories in the diet were Diptera (57.14%, $n = 16$), Acari (42.85%, $n = 12$) and Coleoptera (39.28%, $n = 11$). The amount of prey consumed was higher in males than in females (Mann-Whitney test: $U = 6921$, $p < 0.0001$); the average number of

prey items consumed by males was 1.50 (SD = 3.50, range: 1–37), and in the females was 0.50 (SD = 1.30, range: 1–8). The rarefaction curves did not reach an asymptote and indicated the higher taxonomic richness in the diet of males, with nine prey categories vs. the eight categories registered for females (Fig. 2).

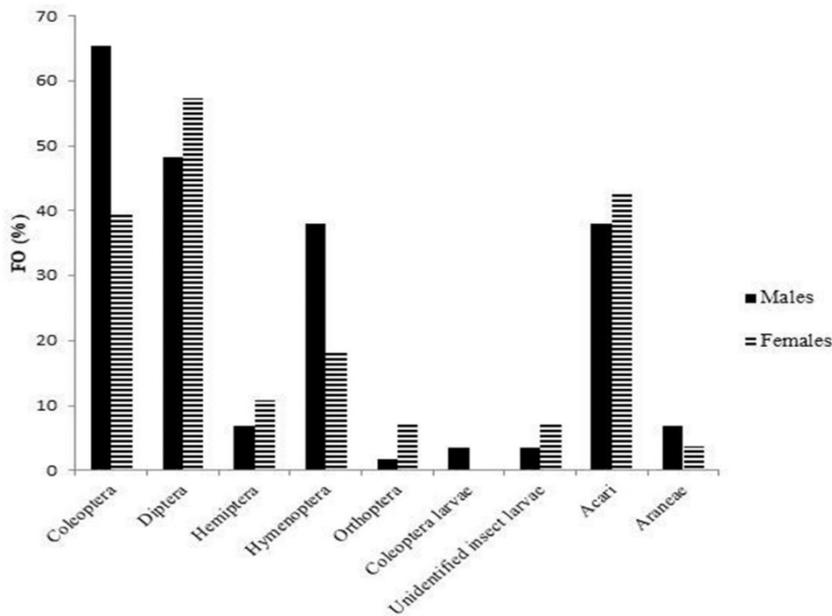


Figure 1. Frequency of occurrence (FO%) of the prey items consumed between males and females of *Pseudopaludicola boliviana* in a floodplain area in southern Amapá, Brazil. Hymenoptera corresponds only to ants.

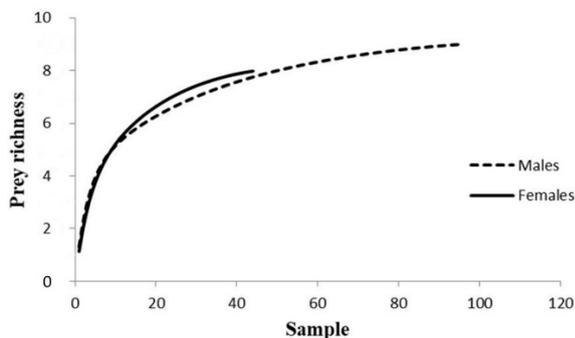


Figure 2. Rarefaction curves based on diet items of males and females of *Pseudopaludicola boliviana*.

Seasonal variation in prey items can be summarized as follow: individuals collected during the rainy season primarily consumed coleopterans ($IRI = 5436.27$, 56.03%), followed by Diptera ($IRI = 1579.51$, 16.28%) and Hymenoptera-Formicidae ($IRI = 1318.78$, 13.59%), whereas Acari ($IRI = 2539.82$, 34.57%), Diptera ($IRI = 2294.60$, 31.23%) and Coleoptera ($IRI = 2114.26$, 28.78%) predominated during the dry season (Table 1, Fig. 3). Hymenoptera-Formicidae was poorly represented in the dry season, and Coleoptera larvae were absent in the dry season, although it was poorly represented in the rainy season. In the rainy season, 58 individuals (50 males and 8 females) had gastrointestinal

contents, and 29 individuals (27 males and 2 females) had empty stomachs. In the dry season, 28 individuals (8 males and 20 females) had gastrointestinal contents, and 26 individuals (11 males and 15 females) had empty stomachs. There were no seasonal differences in the volumetric composition of prey (PERMANOVA: $F_{9, 126} = -13.164$, $p = 0.7429$). However, the amount of prey consumed by frogs was higher in the rainy season than in the dry season (Mann-Whitney test: $U = 3146$, $p < 0.0001$); the average number of prey items consumed by frogs in the rainy season was 1.70 (SD = 1.80, range: 1–11) and in the dry season was 0.70 (SD = 3.60, range: 1–37).

Niche breadth varied seasonally, with a wider niche breadth during the rainy season ($Bsta = 0.453$) compared to the dry season ($Bsta = 0.238$). The high trophic niche overlap (Ojk) between males and females in both seasons was 0.866 for the rainy season and 0.708 for the dry season.

Discussion

Our results indicate that *P. boliviana* from a floodplain in northern Brazil has a diet composed mainly of arthropods, corroborating with Caldwell & Vitt (1999) and Duré et al. (2004) in which the main item consumed in terms of volume for both populations were Diptera. However, Coleoptera was the most important prey item in its diet ($IRI = 49.12\%$) and volumetric (50.79%) and occurrence proportions (56.98%), similarly to the results of Silva et al. (2018a), which registered coleopterans (46.16%) as the most important item in the diet of *P. pocoto* from a Caatinga area in northeast Brazil. In fact, the order Coleoptera is considered the most important food

Table 1. Comparison of the diet of *Pseudopaludicola boliviana* between the rainy season (50 males and 8 females) and dry season (8 males and 20 females) in a floodplain area in southern Amapá, Brazil. N = number of prey items, FO = frequency of occurrence, V = volume (mm³), IRI = Index of Relative Importance.

Prey category	Males							Females						
	N	N%	FO	FO%	V	V%	IRI	N	N%	FO	FO%	V	V%	IRI
Rainy season														
Coleoptera	45	28.66	34	68.00	30.87	61.21	6111.57	4	15.38	3	37.50	1.60	31.19	1746.51
Diptera	38	24.20	26	52.00	4.29	8.51	1700.95	4	15.38	3	37.50	0.51	9.94	949.73
Hemiptera	3	1.91	3	6.00	3	5.95	47.16	-	-	-	-	-	-	-
Hymenoptera (Formicidae)	28	17.83	22	44.00	6.11	12.12	1317.81	5	19.23	3	37.50	0.87	16.96	1357.12
Orthoptera	-	-	-	-	-	-	-	2	7.69	1	12.50	0.77	15.01	283.78
Coleoptera larvae	2	1.27	2	4.00	0.74	1.47	10.97	-	-	-	-	-	-	-
Unidentified insect larvae	2	1.27	2	4.00	0.64	1.27	10.17	1	3.85	1	12.50	0.78	15.20	238.14
Acari	34	21.66	19	38.00	2.88	5.71	1039.94	10	38.46	5	62.50	0.60	11.70	3134.84
Araneae	5	3.18	4	8.00	1.90	3.77	55.62	-	-	-	-	-	-	-
Dry season														
Coleoptera	4	8.16	4	50.00	1.67	30.93	1954.46	13	25.00	8	40.00	5.88	32.98	2319.13
Diptera	2	4.08	2	25.00	0.12	2.22	157.60	14	26.92	13	65.00	6.15	34.49	3992.01
Hemiptera	1	2.04	1	12.50	0.02	0.37	30.14	4	7.69	3	15.00	3.54	19.85	413.20
Hymenoptera (Formicidae)	-	-	-	-	-	-	-	2	3.85	2	10.00	0.93	5.22	90.62
Orthoptera	1	2.04	1	12.50	1.04	19.26	266.25	1	1.92	1	5.00	0.27	1.51	17.19
Coleoptera larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified insect larvae	-	-	-	-	-	-	-	1	1.92	1	5.00	0.06	0.34	11.30
Acari	41	83.67	3	37.50	2.55	47.22	4908.59	16	30.77	7	35.00	0.86	4.82	1245.74
Araneae	-	-	-	-	-	-	-	1	1.92	1	5.00	0.14	0.79	13.54

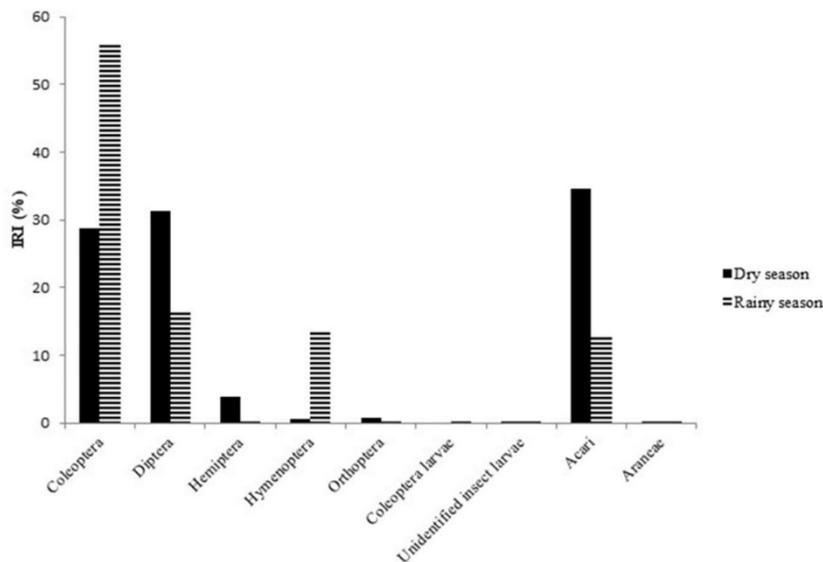


Figure 3. Diet of *Pseudopaludicola boliviana* during rainy and dry seasons in a floodplain area in southern Amapá, Brazil. Bars represent the Index of Relative Importance (IRI%). Hymenoptera corresponds only to ants. Note the distinction of the diet composition of the species during the year.

item for neotropical leptodactylid species (Maneyro et al. 2004, Oliveira et al. 2015, Moser et al. 2017), supporting the data obtained in the present study and other investigations on food aspects carried out in anuran assemblages in the Neotropical region (e.g., Leite-Filho et al. 2015, 2017).

In addition, *P. boliviana* did not present an exclusive prey category in our study, having a diet composition similar to the population of Corrientes, Argentina (Duré et al. 2004) and the population of Roraima, Brazil (Caldwell & Vitt 1999). However, Caldwell & Vitt (1999) registered Gastropoda and

Gryllidae as prey categories for the population from northern Brazil. Our study corroborates the findings by Van Sluys & Rocha (1998) and Duré (2002), in which the orders Acari, Collembola, Coleoptera, and Diptera were the most consumed prey items in the diet of *Pseudopaludicola* sp. (cited as *P. gr. falcipes*) and *P. falcipes* in populations from north Brazil and northeastern Argentina, respectively. However, Silva et al. (2018b) recorded Formicidae as the prey category for a population in southern Brazil for this latter species, being the most representative of the diet. But the population

analyzed in our study showed a more restricted food spectrum than the *P. boliviana* population of Corrientes, Argentina, which had a standardized niche breadth of 0.61 (Duré et al. 2004). Although small leptodactylids are characterized by a more specialized diet with a narrower niche breadth (Maneyro & Carreira 2012, Oliveira et al. 2015, Moser et al. 2017, Sanches et al. 2019), we reinforce that *P. boliviana* has a generalist diet. Our data may indicate that this species is marked by a high dietary plasticity, which may be related to prey availability in the environment during the entire year. Such food plasticity has been noted for species of *Pseudopaludicola*, in which *P. falcipes* was the species that showed high food plasticity, with trophic niche breadths of 0.17 for a population from Argentina (Duré 2002) and 0.47 for populations from southern Brazil (Silva et al. 2018b).

Although the richness of prey items recorded in this study for *P. boliviana* appears to be low with nine prey categories, it is in accordance with what is recognized for species of *Pseudopaludicola*: 11 prey categories were found in a population from Argentina, and 10 prey categories from a tropical lowland forest, northern Brazil (Caldwell & Vitt 1999, Duré et al. 2004), 12 prey categories found in *P. pusilla* from the Colombian Caribbean region (Atencia-Gándara et al. 2021), 13 prey categories in *P. pocoto* from northeast Brazil (Silva et al. 2018a), 11 categories in *P. restinga* from southeastern Brazil (Carmo et al. 2021), 7 categories of registered prey and 10 categories of prey recognized in *Pseudopaludicola* sp. (cited as *P. gr. falcipes*) and *P. falcipes* for populations from northern and southern Brazil, respectively (Van Sluys & Rocha 1998, Silva et al. 2018b), and 10 prey categories from northeastern Argentina (Duré 2002). Such similarity in the richness of prey categories has also been noted for other small leptodactylids (e.g., Leite-Filho et al. 2015, Sanches et al. 2019), which may be related to the preference for foraging on relatively small prey found in leaf litter, mainly representing prey categories with considerable mobility (e.g., Araneae, Coleoptera, Hymenoptera, Hemiptera, and Orthoptera) (Toft 1981). On the one hand, the predator's body size is a stronger predictor of determining the low volumetric proportions in the diet composition in species restricted to leaf litter (Caldwell & Vitt 1999). On the other hand, the larger variety of small-sized prey consumed by leaf litter species reflects their physiological needs – eating as many preys as possible to fulfill their energetic requirements. This is because specialized species consume their prey to optimize the uptake of chemicals necessary for defense, whereas generalist species do not consume their prey to optimize digestion (Simon & Toft 1991, Caldwell & Vitt 1999). This is supported in our study by the fact that *P. boliviana* consumed prey of low volume found on the leaf litter and evidenced by the dietary overlap regarding a high amount of prey considered highly chitinous (i.g., Acari and Coleoptera) and soft-bodied prey (i.g., Diptera), which can be regarded as prey requiring short and long digestion (Donnelly 1991).

Although Toft (1980, 1981) argued that the high consumption of mites and ants is restricted to leaf litter species considered ant specialists, our study may suggest that the high consumption of mites in *P. boliviana* reflects the availability and abundance of this prey in the study area, a parameter that we did not evaluate. This is because mites are among the most abundant arthropods in soil ecosystems all

over the world (Schatz 2004, Manu et al. 2016), and have been reported, partially or primarily, in the diet of other generalist leptodactylids (e.g., Silva et al. 2018b, Baia et al. 2020). Moreover, ants were also part of the diet of *P. boliviana*, representing a frequency of 31.40% in the analyzed stomachs, but it was not the prey with the highest IRI; similar results were observed by Caldwell & Vitt (1999), where ants formed the second largest numerical and volumetric proportion on the diet of *P. boliviana*. Ants are frequently reported in the diet of generalist species (e.g., Almeida et al. 2019). Their consumption may also be related to the availability of this prey in the environment (e.g., Menin et al. 2005, Oliveira et al. 2018).

Intrinsic factors, such as sex (Shine 1989), and external environmental factors, such as seasonality (da Rosa et al. 2011), can generate intrapopulation diet variation and can alter the degree of individual dietary specialization (e.g., Svanbäck & Persson 2004). Therefore, these conditions can diminish intraspecific competition (Schoener 1967, Bolnick et al. 2003) by altering the individual niche breadth when the population niche also changes seasonally (Araújo et al. 2007). These conditions are supported in the present study by the fact that the differences in the amount of prey consumed by the frogs between the seasons may explain the wider niche breadth during the rainy season, with the highest consumption of prey and niche overlap. Thus, our results support the hypothesis that *P. boliviana* might adjust its diet according to the seasonal changes in resource availability and abundance. Similar results about the amount of prey consumed between seasons were registered for *P. pusilla* from an anthropic savanna of the Colombian Caribbean region (Atencia-Gándara et al. 2021). Indeed, in tropical environments, seasonality influences invertebrate prey diversity (Vasconcellos et al. 2010), and dietary plasticity in these environments can be an ecological advantage for anuran populations (Maneyro & da Rosa 2004).

On the other hand, intrapopulation diet variation is commonly related to sexual size differences (Lima & Moreira 1993). Although there were differences in size between males and females in the study population, our results indicated that the mean volume of prey consumed did not increase with the SVL. Therefore, the difference in the amount of prey consumed between males and females of *P. boliviana* indicates that it is the main intrapopulation dietary variation in our study, which may diminish intraspecific competition. Unlike the observations by Atencia-Gándara et al. (2021), the intrapopulation diet variation described for *P. pusilla* referred to the larger size of prey consumed by females.

The absence of food items in almost half of the stomachs in our sample is a result similar to those commonly reported in other studies on the trophic ecology of anurans (e.g., Menin et al. 2005, Solé & Pelz 2007, Solé et al. 2009, Oliveira et al. 2017, Silva et al. 2021). For instance, the absence of food items in male stomachs may be related to alternating nights of vocalization and feeding activity during the breeding period (Menin et al. 2005). In contrast, for females, the high consumption of food items prior to the breeding period prioritizes the storage of energy reserves, which explains the absence of food items in their stomachs after this period (Anderson et al. 1999, Hirai & Matsui 2000). Although we recorded the most empty stomachs for males during the

breeding period (n = 27) and for females after the breeding period (n = 15), we cannot hypothesize whether these conditions influenced the occurrence of empty stomachs in the present study due to the small sample of females in the breeding period (n = 10). Therefore, additional robust data on the influence of reproductive activity on empty stomachs in *Pseudopaludicola* species are needed.

For leptodactylid species, several studies have shown a relationship between the morphological aspects of the frog with the largest or mean volume of prey consumed (e.g., Maneyro et al. 2004, Ferreira et al. 2007, Sanches et al. 2019, Baia et al. 2020), suggesting that these relationships may benefit resource sharing among species (Toft 1995, Lima & Moreira 1993, Vitt & Caldwell 1994, Caldwell 1996). However, these relationships have been widely described for species of the genus *Leptodactylus* Fitzinger, 1826, which consume fewer but larger prey. According to Lima & Magnusson (2000), these correlations are significantly positive in species that feed on small proportions but on larger prey than those that eat a larger variety of small-sized prey. This latter condition occurs in *Pseudopaludicola*, which feeds on various small leaf litter prey, as observed for other leptodactylids that forage on the ground with no such correlations (e.g., Rebouças & Solé 2015, Sanches et al. 2019). Therefore, our data corroborate other studies that have cited the lack of these correlations for *Pseudopaludicola* (Caldwell & Vitt 1999, Van Sluys & Rocha 1998, Carmo et al. 2018, Silva et al. 2018a).

We conclude that *P. boliviana* from northern Brazil has a generalist diet and a restricted food spectrum, foraging on small leaf litter prey as expected for *Pseudopaludicola* species. Our data demonstrate that this species is marked by high food plasticity related to the availability of prey in the environment. In addition, the high diet overlap between males and females indicated a strong similarity in the sharing of resources during the entire year. The lack of significant differences between the volume of prey consumed by the species, as well as relationships of morphometric variables with the mean volume of prey ingested, further reinforce the hypothesis that *P. boliviana* can establish strong competitive interactions in the environment. The higher taxonomic richness in males' diet may be related to our sample size, and more individuals sampled may reveal additional categories. In conclusion, our results represent the third study on the feeding habits of this species, thus contributing to the knowledge of the ecology of leptodactylids. Lastly, we reinforce that future studies evaluating the availability of prey in the environment are important to better characterize the feeding aspects of *Pseudopaludicola* species.

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