

Diet assessment of *Leptodactylus pentadactylus* (Anura, Leptodactylidae) from forest and savanna habitats in the Amazonian domain

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Abstract. The diet of fifty *Leptodactylus pentadactylus* individuals collected through active nocturnal searches at a *terra firme* forest and Amazonian savanna were assessed using stomach flushing. We revealed 129 prey items, where Hemiptera (IRI = 14.63), Orthoptera (13.94), and Araneae (13.06) were the most important prey items in the forest, and Orthoptera (46.66), Araneae (26.58), and Coleoptera (22.06) were the most important prey items in the savanna. The dietary composition of *L. pentadactylus* in the savanna was more diverse (16 prey types, Shannon-Wiener index: $H' = 2.56$) than in the forest (14 prey types, $H' = 2.36$). A significant correlation was found between the SVL and the number of prey from the savanna ($r_s = 0.25$, $p = 0.019$), but there was no relationship in the forest. Overall, the diet of the *L. pentadactylus* follows a generalist and opportunistic pattern resembling other medium- or large-sized *Leptodactylus* species.

Keywords: Amphibia, trophic niche, stomach flushing, natural history.

Introduction

The genus *Leptodactylus* Fitzinger, 1826 is a species-rich clade of Neotropical frogs ranging in size from medium to large (20–250 mm snout-vent length), where some species are active foragers in the leaf-litter, whereas other species are sit-and-wait predators found around ponds or sit outside burrows they occupy permanently (Lima et al. 2012, de Sá et al. 2014). *Leptodactylus* species consume small invertebrate prey (Santana et al. 2019, Baía et al. 2020, Oliveira-Souza et al. 2021). Still, they can also predate on anurans and other small vertebrates (Castro et al. 2011, Sousa et al. 2016, Ceron et al. 2018).

Leptodactylus pentadactylus (Laurenti, 1768) is a large-sized neotropical frog (snout-vent length 133.9–174.2 mm in females and 100.2–195.0 mm in males, de Sá et al. 2014), nocturnal and terrestrial, usually found along forest stream banks (Faria da Costa et al. 2013) that feeds on a variety of invertebrates and occasional vertebrates prey items (do Couto & Menin 2014, do Couto et al. 2018, Santana et al. 2018). Previous studies have examined the diet of adults *L. pentadactylus* in Central Amazonia areas and found them to be generalist and opportunistic predators (do Couto et al. 2018). The species distribution includes the Amazon basin in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela (Barrio-Amorós et al. 2019). In Eastern Amazonia, populations of *L. pentadactylus* occur both in primary forests (Silva e Silva & Costa-Campos 2018) and in the Amazonian savanna (Costa-Campos & Freire 2019).

Considering the lack of natural history information on *L. pentadactylus* from less-explored regions, such as north Brazil, precludes a better understanding of the diet composition of this species in a population from the Amazonian domain. The specific aims of this study were to (i) identify the most important prey items present in *L. pentadactylus* diet; (ii) evaluate whether there are similarities

in prey composition between two habitats (*terra firme* forest and Amazonian savanna).

Material and Methods

The study was conducted in two habitats located in the Amazonian domain. The first area, a *terra firme* forest, was located on the Reserva Extrativista Municipal Beija-Flor Brilho de Fogo (0°47'30.6" N, 51°58'42.1" W; elev. 115 m a.s.l.), municipality of Pedra Branca do Amapari. The second area in the Amazonian savanna was located on the Campo Experimental da Empresa Brasileira de Pesquisa Agropecuária-EMBRAPA (00°23'5" N, 51°02'2" W; elev. 34 m a.s.l.). Both regions are characterized by Am (rainy tropical climates with short dry periods) according to the Köppen-Geiger classification. The mean annual temperature is approximately 27 °C, and the mean annual rainfall is 2850 mm, with the rainy season lasting from January–July and the dry season lasting from August–December (Alvares et al. 2013).

The *terra firme* forest is characterized by a well-drained forest without seasonal flooding, with emergent trees and a closed canopy, and the floodplain areas called *várzea* and *igapó* (Menin et al. 2017), with the Amapari River its main watercourse (Drummond et al. 2008). The Amazonian savanna is characterized by a mosaic of areas with open woody vegetation, areas with a denser woody shrub layer, open grassy areas with sparser shrubs and trees, and seasonally flooded areas in the transition zone with floodplains (Lima et al. 2017, Mustin et al. 2017) including the presence of grassland, scrub grassland, parkland and open woodland savanna (for details see Melém-Júnior et al. 2003, Costa-Campos & Freire 2019).

Frogs were collected manually at night (19:30 to 21:00 h) during weekly field trips in the Amazonian savanna between November 2010 and March 2013 and in the forest during September 2021. We obtained the diet samples by stomach-flushing, following the methodology proposed by Solé et al. (2005), with specimens being released at the capture site on the following day. Stomach contents were fixed in 70% ethanol and later analyzed under a stereomicroscope. We standardized prey identification to order or family level (e.g., Araneae, Coleoptera, Diptera), following the identification key by Rafael et al. (2012).

The volume of each prey item was then calculated using an

ellipsoid formula (Griffiths & Mylotte 1987):

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

with L = prey length and W = prey width. We determined the index of relative importance (IRI), as proposed by Pinkas et al. (1971), for each category using the formula:

$$IRI = F\% (N\% + V\%)$$

where N is the numerical percentage of prey items belonging to a certain category; V is the volumetric percentage of the volume occupied by prey items of that category; and F is the frequency of occurrence percentage of occurrence of each item in relation to the total samples.

To analyze the dimension of the trophic niches breadth, we calculated the Levin's Niche Breadth Index (B) (Krebs 2004), defined as

$$B = 1/\sum pi^2$$

where p is the individual proportion of a given resource i (taxon) found in the diet. To facilitate comparisons between species/area, the Standardized Index of Levins (B_{sta}) was calculated using the following equation:

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

where n represents the number of resources recorded. Values close to zero are attributed to a specialist diet, while values close to one are attributed to a generalist diet.

To analyze if the trophic niche overlaps between the areas/species, with regards to the degree of similarity between their diets, we used the Trophic Niche Overlap Index of Pianka (O_{jk}) (Pianka 1974):

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

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 $O_{jk} > 0.70$ (high), $O_{jk} = 0.4 - 0.7$ (intermediate), and $O_{jk} < 0.40$ (low) when there is overlap complete or no between the

species diets, respectively. We used the niche overlap module from the EcoSim program (version 7.72) (Gotelli & Entsminger 2005) with 1,000 randomizations.

To determine the sampling efficiency, we plotted the prey category accumulation curve in relation to the number of stomachs flushed with the Estimates 9 software (Colwell 2013). In addition, we used the Shannon Diversity Index to quantify diet diversity

$$H' = - \sum pi \ln pi,$$

in which pi is the numeric proportion of prey i in the total number of individuals of n prey types. To determine the relationship between the size (SVL) of frogs with the abundance of prey, we used Spearman's non-parametric correlation coefficient (r_s ; Zar 2010) with $\alpha = 0.05$ using PAST 3.02 software (Hammer et al. 2001).

We performed a permutational multivariate analysis of variance (PERMANOVA) to test if diet composition in terms of prey volume varies between the forest and savanna, using Euclidean distance and 999 permutations (Anderson 2001). Then we executed a Principal Component Analysis (PCA) to check which prey category most contributed to the differentiation. All statistical analyses were conducted in the R software v.4.0.2 (R Development Core Team, 2020) using the vegan package (Oksanen et al. 2015).

Results

We collected 50 individuals of *L. pentadactylus*, 18 in the terra firme forest, and 32 in the Amazonian savanna. Among the analyzed stomachs ($n = 50$), only three stomachs in the savanna were empty. Stomach flushing revealed a total of 129 prey items present in the stomachs (37 items from the forest and 92 from the savanna), whereby a mean of 2.85 (min = 1; max = 8; SD = 2.12) and 6.13 (min = 3; max = 20; SD = 4.45) prey items were found per specimen from the forest and savanna, respectively. The diet of *L. pentadactylus* was mainly composed of arthropods, including 15 categories (Table 1).

Table 1. Comparison of the diet of *Leptodactylus pentadactylus* between forest and savanna in the Amazonian domain, state of Amapá, Brazil. N = number of individuals, F = prey category's frequency of occurrence, V = total volume (in mm³) occupied by prey category, IRI = Index of Relative Importance, (%) = percentage values over the total.

Prey category	Amazonian savanna				Forest area			
	N%	F%	V%	IRI	N%	F%	V%	IRI
Anura	-	-	-	-	2.38	3.70	2.07	2.72
Lizards	-	-	-	-	2.38	3.70	0.59	2.23
Araneae	7.78	10.39	25.24	26.58	14.29	18.52	6.37	13.06
Blattodea	-	-	-	-	9.52	14.81	6.12	10.15
Chilopoda	-	-	-	-	4.76	7.41	9.32	7.16
Coleoptera	7.78	10.39	11.68	22.06	11.90	11.11	7.74	10.25
Curculionidae	8.73	9.78	4.71	20.08	-	-	-	-
Crustaceae	5.62	5.81	5.55	13.28	-	-	-	-
Pseudothelphusidae	-	-	-	-	-	-	-	-
<i>Fredius reflexifrons</i>	-	-	-	-	2.38	3.70	21.99	9.36
Diplopoda	-	-	-	-	2.38	3.70	4.72	3.60
Diptera	10.76	3.90	0.27	14.75	-	-	-	-
Tabanidae	8.80	6.54	1.48	15.83	-	-	-	-
Hemiptera	3.92	2.60	2.78	7.45	19.05	3.70	21.14	14.63
Coridae	2.76	2.90	1.35	6.11	-	-	-	-
Pentatomidae	2.76	2.90	1.75	6.24	-	-	-	-
Hymenoptera	7.84	4.19	6.24	14.11	9.52	7.41	0.99	5.98
Formicidae	3.48	3.18	5.62	8.53	-	-	-	-
Vespidae	3.48	3.18	5.02	8.33	-	-	-	-
Oligochaeta	0.60	1.40	3.80	3.27	-	-	-	-
Opiliones	3.60	7.98	2.50	12.41	4.76	7.41	1.20	4.46
Orthoptera	18.73	20.68	21.74	46.66	14.29	11.11	16.41	13.94
Nematoda	3.36	4.19	0.27	7.64	-	-	-	-
Scorpiones	-	-	-	-	2.38	3.70	1.32	2.47

Based on the index of relative importance (Fig. 1), individuals from the forest consumed Hemiptera (IRI = 14.63), Orthoptera (IRI = 13.94), and Araneae (IRI = 13.06). In contrast, the diet of savanna individuals was composed of Orthoptera (IRI = 46.66), Araneae (IRI = 26.58), and Coleoptera (IRI = 22.06). One anuran and one lizard were consumed by one of the frogs in the forest, accounting for 2.66% of the overall volume in the diet of the frogs from this area. In the savanna area, the most important categories (Orthoptera, Araneae, and Coleoptera) represent more than 58.66% of the overall volume.

In relation to the use of food resources by the species, *L. pentadactylus* of the savanna area showed the largest trophic breadth ($B_{sta} = 0.66$) relative to that of *L. pentadactylus* of the forest area ($B_{sta} = 0.63$). The analysis of trophic niche overlap in relation to the type of items consumed was 0.51%. Pianka's overlap index between frog diet was medium ($O_{jk} =$

0.51) but statistically higher than expected by chance (mean of simulated indexes: $O_{jk} = 0.43$; $p[\text{observed} \geq \text{expected}] = 0.24$; $p[\text{observed} \leq \text{expected}] = 0.76$).

The prey category accumulation curve, in relation to the number of stomachs flushed, did not reach the asymptote and indicated a higher taxonomic richness in the diet of *L. pentadactylus* (Fig. 2). The dietary composition of *L. pentadactylus* in the savanna was more diverse (16 prey types, Shannon-Wiener index: $H' = 2.56$) than in the forest (14 prey types, $H' = 2.36$). The relationship between the SVL of the frogs and the number of prey was not significant in the forest ($r_s = -0.09$, $p = 0.071$), but it was positive and significant in the savanna ($r_s = 0.25$, $p = 0.019$; Fig. 3). Diet composition differs between the forest and savanna site types ($F = 1.91$; $df = 49$; $p = 0.05$; Fig. 4). Individuals from savanna consumed a larger diversity of prey types (see Table 1) than those from the forest.

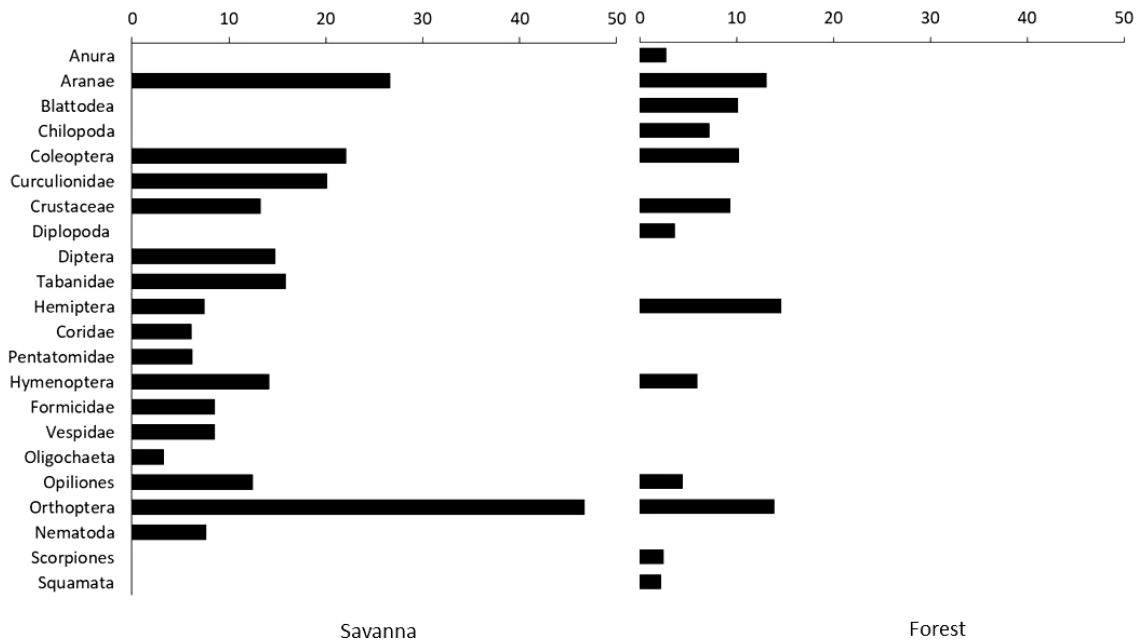


Figure 1. Diet of *Leptodactylus pentadactylus* in the forest and savanna areas in the Amazonian domain, Amapá, Brazil. Bars represent the Index of Relative Importance (IRI).

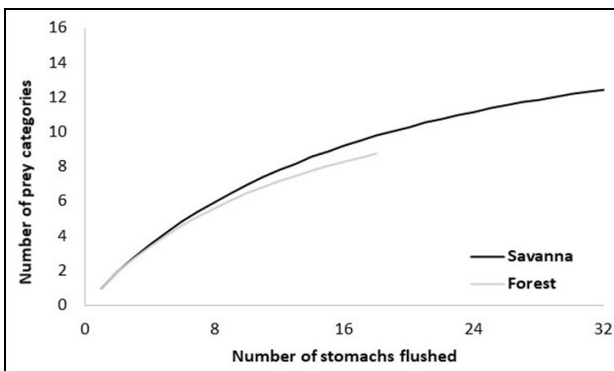


Figure 2. Accumulation curve showing the number of prey categories in relation to the number of stomachs flushed in the forest and savanna areas in the Amazonian domain, state of Amapá, Brazil.

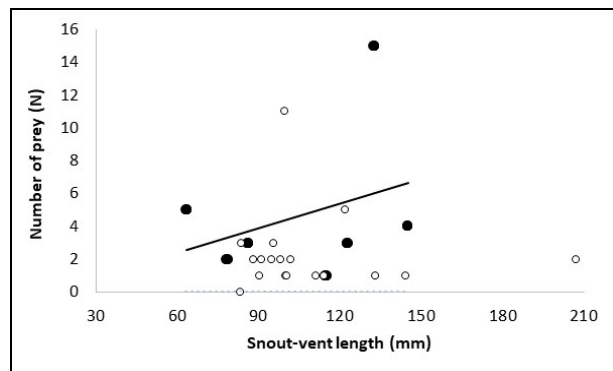


Figure 3. Relationship between snout-vent length (mm) of *L. pentadactylus* in the forest (open circles) and savanna (solid circles) in the Amazonian domain, state of Amapá, Brazil, and the number of preys. Line of tendency in a significant relationship (savanna).

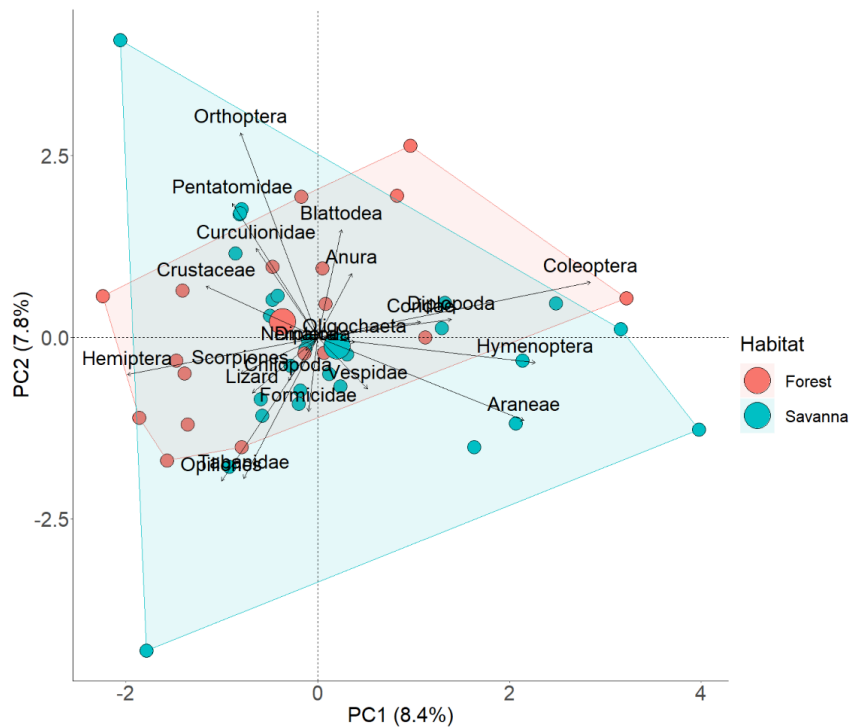


Figure 4. Principal components analysis to evaluate the differences in the diet of *Leptodactylus pentadactylus* sample in the forest and savanna areas in the Amazonian domain, state of Amapá, Brazil.

Discussion

Leptodactylus pentadactylus fed on a wide variety of invertebrates, including arthropods, crustaceans, and vertebrates, but its diet consisted predominantly of insects (e.g., Orthoptera). Similarly to our results, Duellman (1978) in Santa Cecilia (Ecuador), Galatti (1992) in Reserva Adolpho Ducke, a periurban area of Manaus (Brazil), and do Couto et al. (2018) in an urban forest fragment and preserved forest, reported *L. pentadactylus* consuming a variety of invertebrates, mainly arthropods, and occasional vertebrates.

Vertebrates (i.e., anuran and lizard) were found only in the diet of forest species. This record in our study, as well as two small anurans in Ecuador (Duellman 1978), a small lizard (*Alopoglossus angulatus*) in Central Amazonia, Brazil (do Couto et al. 2018), and one toad (*Rhinella* gr. *margaritifera*) in Eastern Amazon, Brazil (Santana et al. 2018) are the only known instances of *L. pentadactylus* preying vertebrates, which suggests that they are not a common part of its diet, and apparently, they result from opportunistic predation. The presence of vertebrates in the diet of *Leptodactylus* species has been previously reported for *L. macrosternum* (Sousa et al. 2016, Esteves-Silva et al. 2018), *L. mystaceus* (Figueiredo et al. 2018, Moreira-Brito et al. 2020) and *L. podicipinus* (Ceron et al. 2018).

Leptodactylus pentadactylus presented a broad trophic niche, composed of large, mobile preys as hemipterans, coleopterans, and spiders, with a tendency towards a sit-and-wait strategy suggested by Toft (1980, 1981) for the family Leptodactylidae. The foraging strategy reported here for *L. pentadactylus* was similar for other species like *L. labyrinthicus* (Ganci et al. 2018), *L. ocellatus* (Sanabria et al. 2005, Solé et al. 2009), *L. podicipinus* (Rodrigues et al. 2004), *L. spixi* (Solé et al. 2019) and *L. natalensis* (Santos et al. 2004).

Regional dietary differences observed in *L. pentadactylus* (e.g., the richness of prey taxa and abundance of each prey taxon) may be related to the climatic and vegetation characteristics of the areas (e.g., Drummond et al. 2008, Costa-Campos & Freire 2019). In the savanna area, *L. pentadactylus* consumed a wide variety of food items indicating a more generalist opportunistic feeding behavior. In this case, it is noteworthy that *L. pentadactylus* presumably experience less competition in the savanna as most congeneric species in this region are restricted to the forest area. Moreover, larger frogs have greater energy uptake demand and consume a higher variety and number of prey categories (Mageski et al. 2018, Le et al. 2020). In addition, there was no significant correlation between SVL and the number of prey items consumed for *L. pentadactylus* in the forest area, and a positive and significant correlation for the savanna area. In this case, changes from forest to savanna provide a gradient in prey composition among different areas; in the forest, there are more habitats for arthropod communities, which can make it difficult for the search by the frogs, while in savanna, prey can be more vulnerable to predators, influencing predator-prey size relationships between populations.

Finally, our study suggests differences in the diet composition of *L. pentadactylus* between forest and savanna areas. Besides having a greater demand for energy uptake, larger frogs can also consume a wide array of prey of different sizes. This may be crucial to settling in contrasting environments, including urbanized landscapes. Further research investigating dietary patterns of anurans in ecological gradients must be encouraged, given that such studies help us to understand how environmental variation alters biological traits of anurans, such as feeding specialization and predator-prey size relationship.

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