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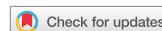
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## Diet composition of *Elachistocleis helianneae* (Anura: Microhylidae) and its (dis)similarities with other Microhylidae from South America

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### ABSTRACT

Knowledge on the trophic ecology of many microhylids is still incipient. Here, we investigated the diet composition of *Elachistocleis helianneae* in an urban forest in the Brazilian eastern Amazon and compared it with other Microhylidae species from South America. Specimens were collected during the rainy season. In total, 63 stomachs were examined, and 38 stomachs (60.3%) contained identifiable items. We identified eight taxonomic categories for males and females. The estimated prey richness indicated that the sampled stomachs were representative. The most important prey category for both males and females was the ant genus *Solenopsis*, based on the Importance Value Index. The analysis of prey-specific abundance indicated that *Solenopsis* was dominant, with more than half of the individuals consuming it. The diet of *E. helianneae* was more similar to that of *E. pearsei* from Colombia, and both species grouped with other microhylids from the Amazon biome, such as *Chiasmocleis hudsoni* and *C. shudikarensis*. The study provides insights into the trophic ecology of *Elachistocleis helianneae*, highlighting its preference for consuming ants.

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## Introduction

Investigating the trophic ecology of anurans is necessary to understand niche relationships, coexistence, sympatry, predation, and trophic web structure (Lima 1998; Parmelee 1998; Caldwell and Vitt 1999; Solé and Rödder 2010). Research on trophic ecology has provided ecologically meaningful insights into Anura assemblages in the neotropics (Toft 1981), focusing primarily on feeding habits in single species. Environmental conditions that determine the availability of food resources coupled with species' morphological and physiological adaptations are now being extensively investigated in these studies, as they define the limits of the fundamental feeding niche of anurans (Toft 1985; Losos 1996; Rosa et al. 2002). Furthermore, intrinsic factors (i.e. sexes) have also been addressed in these studies, as they can generate intrapopulation dietary variation and therefore generate dietary specializations (e.g. Atencia-Gándara et al. 2021).

The foraging habits of anurans as insectivores were labeled into two categories that represent peaks in a dietary spectrum: ant specialists and generalists (Toft 1981). On the one hand, ant specialists consume a variety of small-sized prey from the leaf litter, such as mites and

ants. On the other hand, generalists tend to take a wide variety of prey of different sizes available in the environment. Furthermore, some generalist species can usually be considered opportunists, and some species can also exhibit sit-and-wait behavior, consuming highly mobile prey (e.g. Pedroso-Santos et al. 2024). From that perspective, the dietary composition can be used to establish a species' place in the dietary spectrum, and its relationships with spatial and temporal determinants can represent potential factors in geographic dissimilarities in its dietary composition (Caldas et al. 2019; Atencia-Gándara et al. 2021; Toledo et al. 2021).

Small and fossorial anurans are expected to have a very limited diet regarding prey size and taxa (Simon and Toft 1991). In South America, the fossorial frogs of the family Microhylidae have been the subject of several studies involving diet composition aiming to establish the feeding pattern of different genera such as *Chiasmocleis* (Morales and Vargas 2003; Van Sluys et al. 2006; Lopes et al. 2017; Silva et al. 2019; Díaz et al. 2020; Meurer et al. 2021; Santana et al. 2021), *Dermatonotus* (Carrillo et al. 2020; Machado et al. 2020), *Elachistocleis* (Solé et al. 2002; Berazategui et al. 2007; López et al. 2007; Cossovich et al. 2011; Blanco-Torres et al. 2015; Atencia-Gándara et al. 2017) and *Stereocyclops*

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(Teixeira et al. 2006). Such studies provided vital information on the dietary composition of microhylids, but also revealed that this family has been under-studied in terms of feeding behaviors and geographic variation in feeding habits among species. These frogs are well-known for preying on colonial arthropods, which involves consuming high amounts of ants, termites, and mites.

*Elachistocleis helianneae* Caramaschi (2010) is a small-sized microhylid frog distributed in the Brazilian states of Amazonas, Pará, Rondônia, and Amapá (Caramaschi 2010; Costa-Campos and Freire 2015). This species is poorly known because of its cryptic habits and explosive breeding, which is limited to a few subsequent days (2–3) after heavy rain (rainfall >35 mm) (Sousa and Costa-Campos 2021). Reports on the natural history of this microhylid frog are scarce and limited to the description of the advertisement call (Fonseca et al. 2012; Marinho et al. 2018), tadpole (Dias-Souza et al. 2019) and breeding behavior (Sousa and Costa-Campos 2021).

Recognizing the importance of knowing the aspects of foraging behavior of poorly-known fossorial anurans such as *E. helianneae*, the present study evaluates the dietary composition of *E. helianneae* in an urban forest of eastern Amazon, focusing on the most important prey, trophic niche relationships (i.e. niche breadth and overlap between sexes), and the feeding strategy. In addition, we compare the dissimilarities in the dietary composition of *E. helianneae* in relation to other Microhylidae from South America.

## Material and methods

### Study area and sample collection

This study was conducted in a secondary forest fragment in the surroundings of the Universidade Federal do Amapá (00°00'S, 51°04'W), municipality of Macapá, Amapá state, Brazil. It encompasses a total area of 90 hectares with a landscape characterized by open areas and forest fragments (Figueiredo et al. 2020). The Tropical monsoon climate (Am according to Köppen classification) is characterized by annual rainfall of about 3,300 mm and a mean annual temperature of 27.6°C (Alvares et al. 2013).

Anurans were detected using simultaneous visual and auditory searching (Heyer et al. 1994) and collected by hand during January, February, and March 2021 (the peak of the rainy season) only in forest fragments. Specimens were killed with topical application of 2% Lidocaine shortly after capture, sexed by direct observations of gonads, and their stomachs were dissected and analyzed for collection of stomach contents, according to

the collection license provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio #48102-4).

### Diet analysis

To evaluate the diet, we extracted the stomach contents through an abdominal incision. We used a stereoscope microscope (ZEISS model Stemi 2000-C) to identify and classify the prey items by Order, Suborder or Family following the taxonomic keys of Triplehorn and Johnson (2011) and Rafael et al. (2012). Because the microhylid under study has preferences for ants, we identified the Subfamilies and genera of Formicidae following Baccaro et al. (2015).

We measured prey length and width and estimated prey volume using the ellipsoid formula (Griffiths and Mylott 1987):  $V = (4/3)\pi(L/2)(W/2)^2$  where  $W$  is the width and  $L$  is the length of each prey. We calculated the Importance Value Index (IVI) to determine the importance of each prey category in the diet using the equation of Gadsden and Palacios-Orona (1997):  $IVI = (N\% + F\% + V\%)/3$ , where  $F\%$  is the percentage of frequency of prey occurrence,  $N\%$  is the numerical percentage of prey and  $V\%$  is the volumetric percentage of prey.

To analyze the dimension of the trophic niche breadth for the population and between sexes, we calculated Levin's Niche Breadth Index ( $B$ ) (Pianka 1986). This index is defined by  $B = 1/\sum p_i^2$ , where  $p$  is the individual numerical proportion of a given resource  $i$  (taxon) found in the diet. For a better interpretation of the results, we calculated the Standardized version of Levin's index ( $Bsta$ ) (Hurlbert 1978) using the following equation:  $Bsta = (B - 1)/(n - 1)$ , 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.

We calculated trophic niche overlap between sexes using the index of Pianka ( $O_{jk}$ ) (Pianka 1973):  $O_{jk} = \sum P_{ij} P_{ik} / \sqrt{\sum P_{ij}^2 \sum P_{ik}^2}$ , where  $O_{jk}$  is the niche overlap index between the species  $j$  and  $k$ ;  $P_{ij}$  is equivalent to the numerical proportion of the resource type  $i$  relative to the total of resources used by the species  $j$ ;  $P_{ik}$  is the numerical 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 (Gotelli and Entsminger 2001). We evaluated if the observed niche overlap was higher than expected by chance using the software EcoSim, with 1,000 randomizations. For this, the values of resources used in the original matrix were replaced by values between 0 and 1 using the RA2 algorithm, keeping the unused resources as 0 (Gotelli and Entsminger 2005). Therefore, we used the reference of

Gotelli and Entsminger (2001), in which values of  $O_{jk} > 0.70$  are considered high,  $O_{jk} = 0.4–0.7$  are considered intermediate, and  $O_{jk} < 0.40$  are considered low.

The feeding strategy of *E. helianneae* for ants consumed was assessed using a graphical representation plotting the prey-specific abundance ( $P_i$ ) against the frequency of occurrence (F%) of each prey category. We calculated the prey-specific abundance of ants as  $P_i = (\sum S_i / \sum S_{ti}) \times 100$ , where  $S_i$  is the number of prey  $i$  and  $S_{ti}$  is the total number of prey items in those stomachs containing prey  $i$  (Amundsen et al. 1996). This procedure allows for a graphical analysis of prey importance and the feeding strategy of the predator by evaluating the areas of the plot occupied by each prey category (see Figure 2B).

To determine the sampling efficiency, we constructed a rarefaction curve of prey richness based on the number of prey and number of stomachs with 1,000 randomizations using ESTIMATES 9.1 (Gotelli and Colwell 2001). We performed a multiple linear regression to assess a putative relationship of snout-vent length (SVL – measured for each frog using a digital caliper 0.01 mm precision) with volume of stomach content and number of prey as response variables (Zar 1999) using R software (R Core Team 2022). These analyses were performed after assessing a normal distribution of the data. To compare the overall diet composition between sexes (i.e. differences in number and volume of stomach content), we used ANOSIM (Analysis of Similarities) applying Bray-Curtis measure to calculate matrices distances of numerical data and Euclidian distance for volumetric data in the ‘vegan’ package in R software (R Core Team 2022).

Dissimilarities in the diet composition of *E. helianneae* and other microhylids from South America were calculated using abundance data (i.e. considering the family level) from 14 publications. We did not include the studies of Berazategui et al. (2007), Cossovich et al. (2011) and Machado et al. (2020) because their studies provided the abundance data only in relative frequency values. Diet composition follows Morales and Vargas (2003) for *Chiasmocleis antenori*; Van Sluys et al. (2006) for *C. capixaba*; Silva et al. (2019) (‘*C. hudsoni* 2’) and Santana et al. (2021) (‘*C. hudsoni* 1’) for *C. hudsoni*; Lopes et al. (2017) (‘*C. leucosticta* 1’) and Meurer et al. (2021) (‘*C. leucosticta* 2’) for *C. leucosticta*; Díaz et al. (2020) for *C. mehelyi*; Silva et al. (2019) for *C. shudikarensis*; Carrillo et al. (2020) for *Dermatonotus muelleri*; López et al. (2007) for *Elachistocleis bicolor*; our study for *E. helianneae*; Solé et al. (2002) for *E. ovalis*; Blanco-Torres et al. (2015) for *E. panamensis*; Atencia-Gándara et al. (2017) for *E. pearsei*, and Teixeira et al. (2006) for *Stereocyclops incrassatus*. With non-transformed abundance data (i.e. avoiding the effect of removing less abundant genera compared to transformed

data), we calculated Bray-Curtis’ dissimilarity index using the ‘vegan’ package (Oksanen et al. 2019) implemented in R version 4.0.2 (R Core Team 2022).

To visualize the results of Bray-Curtis’ distance, we plotted dissimilarity dendrogram based on diet composition. The hierarchical dendrogram was cut by tree function for three clusters ( $k = 3$ ) with the dissimilarity in the ‘stats’ package (version 3.4.2) to define grouping based on dissimilarity. We were also interested in investigating the effect of geographic distance on the compositional dissimilarity of diet between microhylids. Two distance matrices were constructed: (1) a dissimilarity matrix of diet composition using the Bray-Curtis coefficient; and (2) a distance matrix accounting for geographic distance as Haversine distance. We performed the Mantel test using Spearman correlation method and 9999 permutations in the ‘vegan’ package (Oksanen et al. 2013).

The significance level used for all statistics was 0.05, and results are expressed as mean  $\pm$  standard deviation.

## Results

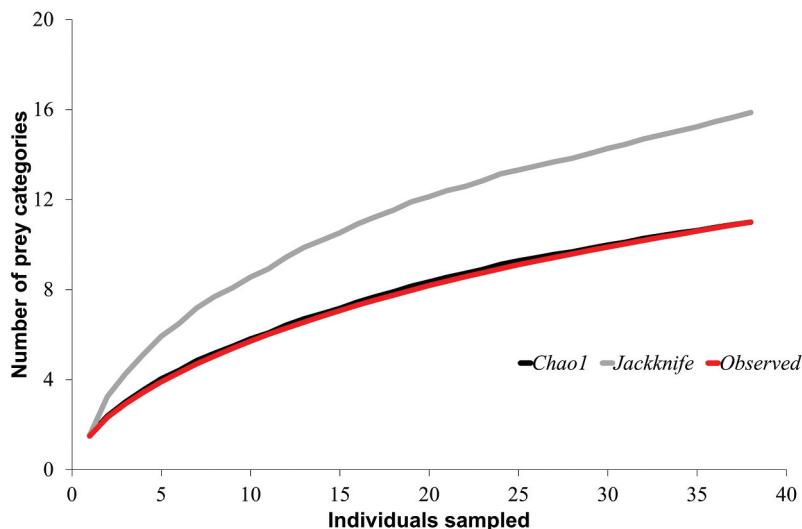
Among the 63 stomachs (43 females and 20 males) of *E. helianneae*, 38 stomachs (60.3%) had food contents (25 females and 13 males). We identified 189 and 399 prey items placed into eight taxonomic categories in males and females, respectively (Table 1). We recorded three prey categories consumed exclusively by females (Acari and the ants *Wasmannia* and *Hypoponera*), and three ant genera recorded only in male samples (*Neivamyrmex*, *Nylanderia* and *Blepharidatta*). The Chao 1 estimator, a nonparametric estimator for species-abundance data, showed 100% representativeness for the number of prey categories found in *E. helianneae*. Jackknife 1 returned an estimated the prey richness of 15.87 compared to the 11 observed (70%) taxa, which also indicates that prey richness found is indeed representative (Figure 1).

The mean number of prey items per stomach was  $23.60 \pm 27.50$  for males, and  $49.90 \pm 125.90$  for females. The mean prey volume per stomach was  $10.50 \pm 15.70 \text{ mm}^3$  for males, and  $35.0 \pm 89.20 \text{ mm}^3$  for females. We identified nine genera of Formicidae in the diet of *E. helianneae*, in addition to two other categories of prey (i.e. Acari and Coleoptera) (see Table 1). The genus *Solenopsis* had the highest IVI values for males (50.04%) and females (87.20%); *Crematogaster* had a greater representation for males than females. The mean number of ants consumed by males was 26.70 (range = 1–67, SD = 28.10) and 66.20 (range = 2–361, SD = 144.70) by females. There were no differences in the composition of dietary taxa between sexes in number of prey ( $R = 0.115$ ,  $p = 0.069$ ) and volume of stomach content ( $R = 0.151$ ,  $p = 0.072$ ).

**Table 1.** Diet composition of males and females of *Elachistocleis helianneae* from an urban forest in eastern Amazon in the municipality of Macapá, state of Amapá, Brazil.

Prey category	Males (n = 13)				Females (n = 25)			
	N (%)	F (%)	V (%)	IVI	N (%)	F (%)	V (%)	IVI
Acari	–	–	–	–	1 (0.25)	1 (4.00)	0.09 (0.03)	1.42
Coleoptera	2 (1.06)	2 (15.38)	14.20 (16.89)	11.11	1 (0.25)	1 (4.00)	4.61 (1.64)	1.96
Formicidae								
Dorylinae								
<i>Neivamyrmex</i>	59 (31.22)	1 (7.69)	4.58 (5.45)	14.78	–	–	–	–
Formicinae								
<i>Nylanderia</i>	5 (2.65)	1 (7.69)	0.28 (0.33)	3.55	–	–	–	–
Myrmicinae								
<i>Blepharidatta</i>	3 (1.59)	1 (7.69)	0.01 (0.01)	3.09	–	–	–	–
<i>Crematogaster</i>	40 (21.16)	4 (30.76)	19.70 (23.43)	25.11	3 (0.75)	2 (8.00)	1.06 (0.38)	3.04
<i>Megalomyrmex</i>	1 (0.53)	1 (7.69)	0.23 (0.28)	2.83	4 (1.00)	2 (8.00)	1.39 (0.49)	3.16
<i>Pheidole</i>	12 (6.35)	2 (15.38)	0.38 (0.45)	7.39	4 (1.00)	1 (4.00)	3.61 (1.29)	2.09
<i>Solenopsis</i>	67 (35.45)	8 (61.53)	44.69 (53.16)	50.04	361 (90.48)	20 (80.00)	255.54 (91.14)	87.20
<i>Wasmannia</i>	–	–	–	–	23 (5.76)	3 (12.00)	13.49 (4.81)	7.52
Ponerinae								
<i>Hypoponera</i>	–	–	–	–	2 (0.50)	2 (8.00)	0.59 (0.21)	2.90

V = volume, N = number, F = frequency, IVI = Importance Value Index.

**Figure 1.** Accumulation curves for prey categories in the diet of *Elachistocleis helianneae*.

We found no significant relationship between the SVL of females and males with the number of prey (Females:  $p = 0.060$ ; Males:  $p = 0.077$ ) and volume of stomach content (Females:  $p = 0.710$ ; Males:  $p = 0.320$ ).

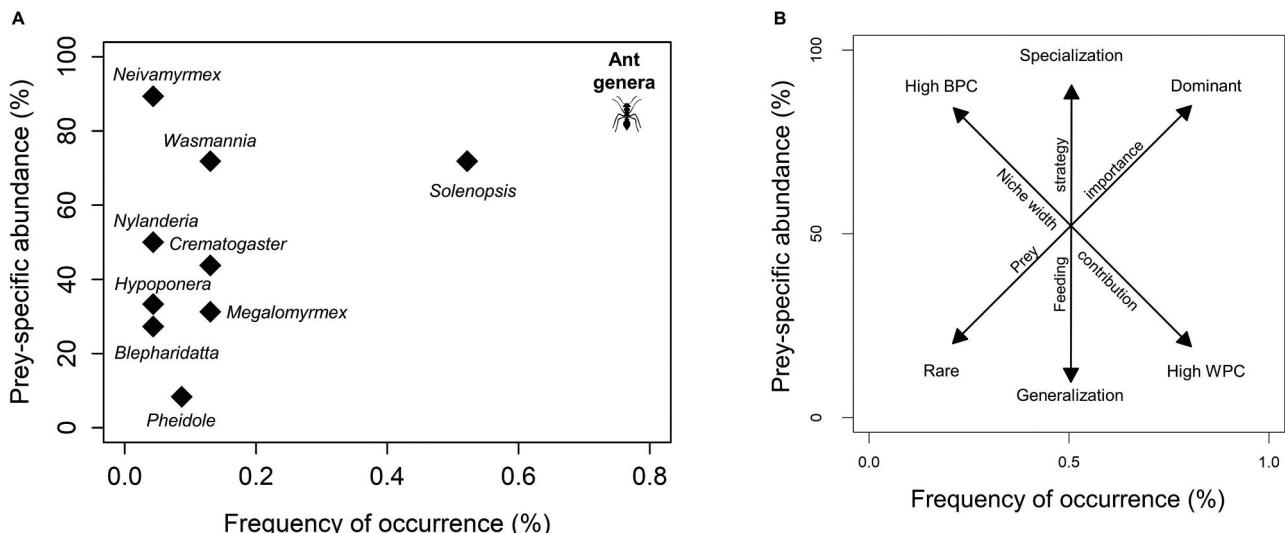
The trophic niche breadth was  $B_{sta} = 0.08$  for the population and males had higher niche breadth than females ( $B_{sta}$  males = 0.38;  $B_{sta}$  females = 0.03). We found an intermediate overlap between sexes ( $O_{jk} = 0.68$ ), which was statistically higher than expected by chance (mean of simulated indexes:  $O_{jk} = 0.12$ ;  $P$  [observed  $\geq$  expected = 0.02;  $P$  [observed  $\leq$  expected = 0.97].

*Solenopsis* was dominant while most ant types were rare in the diet due to their positioning in the lower left corner of the graph (Figure 2). In general, there is specialization in the consumption of ants of the genera *Solenopsis* at the population level.

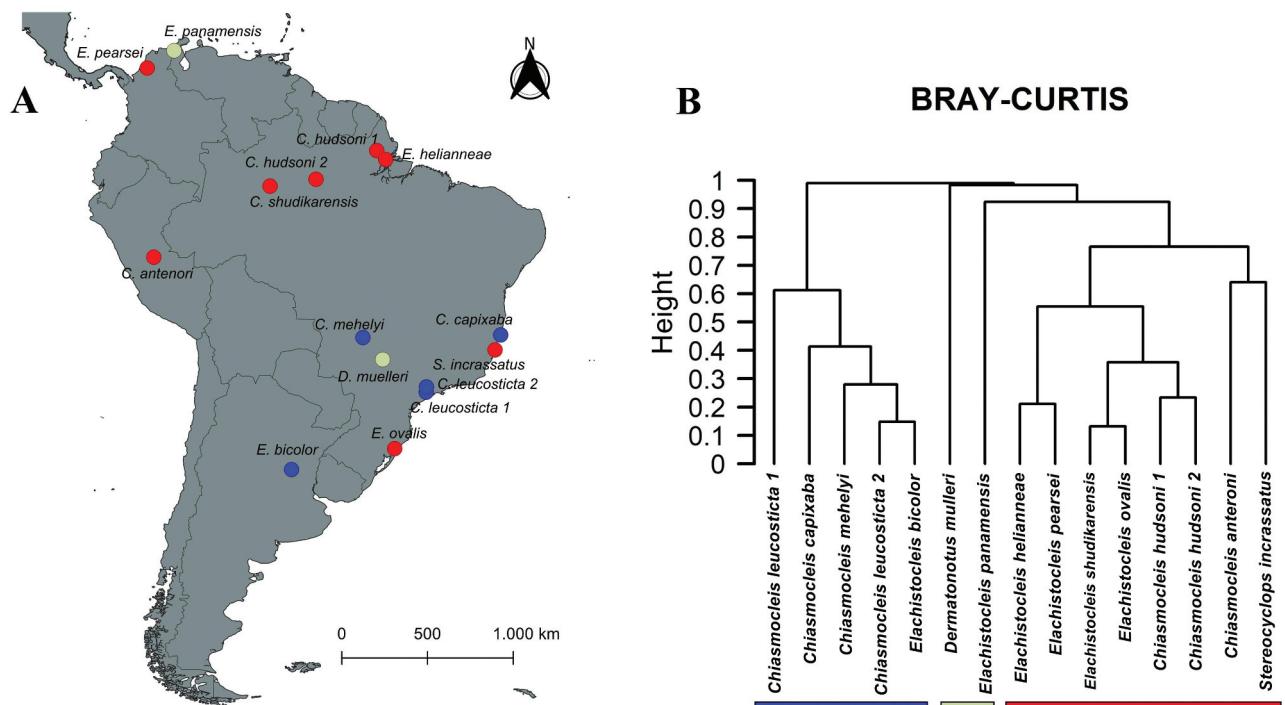
We calculated the dissimilarity between the diet of *E. helianneae* and other microhylids from South America (Figure 3A) and visualized the patterns with a dendrogram (Figure 3B). The diet composition of *Dermatonotus muelleri* and *Elachistocleis panamensis* was highly distinct from all other species included in the analysis. The remaining species were grouped in two clusters with *E. helianneae* grouping together with other microhylids from the Amazon biome, *Chiasmocleis hudsoni* and *Chiasmocleis shudikarensis*. In terms of composition, the diet of *E. helianneae* was more similar to that of *E. pearsei* from Colombia.

## Discussion

The diet of *Elachistocleis helianneae* is predominantly composed of ants and the richness estimators indicated



**Figure 2.** Feeding strategy of *Elachistocleis helianneae*, according to ant-specific abundance (%) and frequency of occurrence (F%) of each ant category (A), and the diagram for feeding strategy interpretation considering the prey importance (rare to dominant), the niche width contribution (BPC = between-phenotype component; WPC = within-phenotype component) and the feeding strategy (B; based on Amundsen et al. 1996).



**Figure 3.** Map showing the distribution of Microhylidae species studied in terms of diet composition in South America (A) and a hierarchical clustering dendrogram of diet composition similarity based on Bray-Curtis' dissimilarity (B). Color bars in (B) represent clusters delimited in dendrogram and colors in map (A) display geographic distribution, with the corresponding group color.

a sufficient sample to determine prey diversity. However, increasing the number of samples would likely yield trophic novelties which probably would represent occasional consumption. This question needs to be addressed when it comes to data sampling of microhylids. The fossorial habits and explosive breeding of microhylids make their

capture difficult, which is limited to a short period during breeding events in the rainy season (Wells 1977; Elgue and Maneyro 2017). Nonetheless, the dietary composition assembled in most studies with microhylids quite well represents the main prey categories consumed by a small sample, because they are specialist species. Unlike

generalist species, which require larger samples to better characterize the sampling efficiency (e.g. Pedroso-Santos et al. 2022).

Morphological adaptations to fossoriality are expected to exert some influence on the type of prey consumed by fossorial frogs (De Sá et al. 2012). According to Simon and Toft (1991) both mites and ants are low-search-cost prey and thus become highly profitable to small-sized anurans. As previous studies demonstrate, ants and mites constitute the majority of dietary intake by microhylids (e.g. Van Sluys et al. 2006; Lopes et al. 2017). *Elachistocleis helianneae* corroborates this pattern exhibiting a diversity of ant taxa in its diet. Overall, Microhylidae frogs may be regarded as ant specialists on the perspective that ants (mites and termites in some cases) become a profitable source of nutrition even though they are costly to digest due to the high proportion of chitin in their exoskeleton (Toft 1981; Lima and Moreira 1993).

Preying on colonial insects, which host large populations above and underneath the soil, allows for an increase in number of prey consumed per unit of time (Hölldobler and Wilson 1990). Microhylids frogs in the genus *Elachistocleis* exhibit explosive reproduction, forming mating aggregations that sometimes involve groups of individuals in temporary ponds during a very short period (Rodrigues et al. 2003; Thomé and Brasileiro 2007; Elgue and Maneyro 2017; Sousa and Costa-Campos 2021). Thus, active foraging may be the best way to capture small, slow-moving and locally abundant or gregarious prey and may be a more efficient way to obtain and allocate energy for reproduction when the reproductive period is short (Toft 1985; López et al. 2017).

We observed a predominance of Myrmicinae ants in the diet of males and females of *E. helianneae* (see Table 1). Myrmicinae is the largest ant subfamily and the most diversified group due to their abundance and distribution in different habitats, including arboreal, soil-inhabiting, and leaf-litter species (Fernández 2003; Baccaro et al. 2015). Ant genera consumed by *E. helianneae* were similar to that found in *E. bicolor* (López et al. 2007) and *E. ovalis* in south Brazil (Solé et al. 2002), *Chiasmocleis mehelyi* in south-west Brazil (Díaz et al. 2020), and *C. shudikarensis* (Silva et al. 2019) and *Chiasmocleis hudsoni* (Santana et al. 2021) in Brazilian Amazon. Ant diversity, revealed by a genus-level classification, reinforces an active myrmecophagous behavior in different types of ants displayed by microhylids such as *E. helianneae*.

In terms of diet composition, *E. helianneae* was nested with *E. pearsei*, *E. ovalis* and *Chiasmocleis* in Amazonia. The diet of *E. helianneae* was more similar to that of *E. pearsei* because of the elevated proportion of ants (up to 90% of abundance) and the low consumption or lack of termites (Atencia-Gándara et al. 2017). The prey composition of

microhylids in Amazonia (Morales and Vargas 2003; Silva et al. 2019; Santana et al. 2021) plus *E. ovalis* (Solé et al. 2002) and *Stereocyclops incrassatus* (Teixeira et al. 2006) can be characterized by a lack of 'occasional' prey such as spiders, collembolans and hemipterans. An intriguing finding is that mites are not a significant prey for *Elachistocleis* species compared to *Chiasmocleis* (Morales and Vargas 2003; Van Sluys et al. 2006; Lopes et al. 2017; Silva et al. 2019; Santana et al. 2021). This may be relevant if we consider that the Bray-Curtis index is sensitive to differences in abundance between prey categories, and that abundant prey are weighted more than rare prey in a dissimilarity matrix (Ricotta and Podani 2017). Overall, microhylids are myrmecophagous. However, the importance of mites varies among regions and species. In this sense, *Elachistocleis* species may not be considered important mite predators as *Chiasmocleis*.

As expected, our results showed a lack of relationship between SVL and dietary variables (i.e. number of prey and volume of stomach contents). Indeed, these relationships are more common in generalist species that feed in small proportions and on larger prey, than specialist species that feed in higher proportions but on small-sized prey (Lima and Magnusson 2000). From this perspective, we did not observe differences between the diets of males and females. Intrapopulation diet variations are more recognized in generalist than specialist species (Lima and Moreira 1993). However, this may also be related to sexual size dimorphism (e.g. Pedroso-Santos et al. 2024), and different energy demands between sexes (Wells 2007); both factors were not analyzed in our study. Therefore, on the one hand, ant-specialist species that do not exhibit sexual size dimorphism may not exhibit intrapopulation dietary variation (e.g. McElroy and Donoso 2019; Figueiredo et al. 2022). On the other hand, ant-specialist species that exhibit sexual size dimorphism may exhibit intrapopulation dietary variation, such as the microhylid *Chiasmocleis mehelyi* (Díaz et al. 2020).

Our study is the first to describe the trophic ecology of *Elachistocleis helianneae*, as well as to compare the diets of South American microhylids, an approach poorly explored in studies of trophic ecology in anurans. Therefore, this study helps to fill an important knowledge gap within the genus *Elachistocleis*. However, we reinforce the importance of integrating feeding ecology with data on sexual dimorphism and other aspects that investigate intrapopulation variations in microhylids, such as the energetic demands between males and females, factors that are still poorly studied for ant-specialist species.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Data availability statement

The dataset that supports our results is publicly available on Figshare: <https://doi.org/10.6084/m9.figshare.26069260>

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