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PSEUDIS LIMELLUM (ANURA: HYLIDAE) DIET DESCRIPTION IN WETLANDS OF PARAGUAY

PSEUDIS LIMELLUM (ANURA: HYLIDAE) DESCRIPCIÓN DE LA DIETA EN HUMEDALES DE PARAGUAY

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Resumen.— Los anfibios anuros cumplen un papel ecológico clave en la regulación de las poblaciones de invertebrados, que constituyen una parte fundamental de su dieta. *Pseudis limellum* es una especie de anuro de pequeño tamaño, ampliamente distribuida en Sudamérica, conocida por sus hábitos acuáticos y su asociación con la vegetación flotante. En este artículo presentamos la dieta de 40 individuos de *P. limellum* mediante la técnica de lavado estomacal en humedales del suroeste de Paraguay. El análisis reveló que la especie consume 14 tipos de presas, incluyendo dos categorías taxonómicas de Araneae y doce de Insecta. Coleoptera, Hymenoptera y Diptera fueron las presas más importantes. Los resultados indican que *P. limellum* es un depredador generalista que emplea un modo de forrajeo pasivo. El tamaño del depredador se relacionó con el volumen medio de las presas consumidas, aunque no con el número total de presas por individuo. Al comparar la dieta de *P. limellum* con otras poblaciones coespecíficas y congéneres, los dípteros fueron presas comunes, mientras que otros ítems alimenticios que son consumidos de manera oportunista, demuestran la plasticidad trófica de esta especie.

Palabras clave.— Amphibia, ecología trófica, Insecta, lavado estomacal, presa-predador.

Abstract.— Anuran amphibians play a key ecological role in regulating invertebrate populations, which constitute a major part of their diet. *Pseudis limellum* is a small anuran species widely distributed across South America, known for its aquatic habits and association with floating vegetation. We studied the diet of 40 *P. limellum* individuals using stomach flushing techniques in the wetlands of southwestern Paraguay. Analysis revealed that the species consumes 14 types of prey, including two taxonomic categories of Araneae and twelve categories of Insecta. Coleoptera, Hymenoptera, and Diptera were the most important prey. The results indicate that *P. limellum* is a generalist predator employing passive foraging. Predator size was related to the mean volume of prey consumed, although not to the total number of preys per individual. When comparing the diet of *P. limellum* with other conspecific and congeneric populations, dipterans were present as common prey, while other food items appeared to be consumed opportunistically, demonstrating the trophic plasticity of this species.

Keywords.— Amphibia, Insecta, predator-prey, stomach flushing, trophic ecology.

INTRODUCTION

Wetlands support high species diversity and provide numerous ecosystem services, including regulating services such as pest control (Millennium Ecosystem Assessment, 2005). Approximately 25 % of the territory of Paraguay comprises humid ecosystems connected to the Paraguay and Paraná rivers (Mereles, 2006). Amphibians are a distinctive group of vertebrates closely associated with these environments, as much of their life cycle depends on aquatic or semi-aquatic conditions (Wells, 2010).

A conspicuous anuran species inhabiting these wetlands is *P. limellum*, whose distribution is associated to both margins of

the Paraguay River (Weiler et al., 2013; Zárate et al., 2019). The *Pseudis limellum* clade includes four species (Caballero-Gini et al., 2024): *P. boliviana* (Gallardo, 1961), *P. caraya* (Gallardo, 1964), *P. laevis* Parker, 1935, and *P. limellum* (Cope, 1862). Of these, only *P. limellum* is present in Paraguay, its distribution also extends to southeastern Bolivia, northwestern Uruguay, northern Argentina, and across the Paraná and Amazon River basins in Brazil (Frost, 2025; Weiler et al., 2013). This frog is aquatic, with adults measuring up to 23 mm in snout-vent length and active both during the day and at night (Garda et al., 2007; Weiler et al., 2013).

One of the most recognized services provided by amphibians is the regulation of arthropod populations through predation, given that their potential prey includes disease vectors and agricultural pests (Cortés-Gómez et al., 2015; Hocking & Babbitt, 2014; Noor, 1995; Peltzer et al., 2005; Valencia-Aguilar et al., 2013). Additionally, dietary analyses in amphibians are essential for understanding their ecological roles and how they respond to environmental changes (Duellman & Trueb, 1994; Toft, 1980; Wells, 2010). The diet of *P. limellum* has been studied in populations from Provinces of Corrientes (Duré & Kehr, 2001; Macale et al., 2008), Entre Ríos (Peltzer & Lajmanovich, 2002), and Santa Fe (Falico et al., 2012), in Argentina, as well as in the Brazilian Amazon (Garda et al., 2007). Additionally, dietary studies have been conducted on *P. laevis* (Vaz-Silva et al., 2005) and *P. boliviana* (Furtado & Costa-Campos, 2020) in northern Brazil. However, the diet of *P. caraya* remains undescribed. These studies have shown that species within this clade primarily consume dipterans and behave as generalist predators, feeding opportunistically on other prey available in the environment. This trophic pattern is consistent with a passive, sit-and-wait foraging strategy. Parmalee (1999) also demonstrated that among hylid species there are differences in the main prey consumed, with smaller species—such as those in the clade examined here—preferentially preying on dipterans, spiders, beetles, and insect larvae.

For Paraguay, the trophic ecology of anurans remains notably understudied. No dietary information is available for *P. limellum* within the country. Overall, only a few studies exist, including work on anurophagy in Chacoan frogs (Scott & Aquino, 2005), the predation of a leptodactylid species on hylids (Motte et al., 2016), and the diets of two bufonid species: *Melanophryniscus paraguayensis* (Núñez et al., 2021) and *Rhinella diptycha* (Mackenzie & Vladimirova, 2022; Hiscock et al., 2023). This study aims to describe the diet composition and diversity of *P. limellum* in a wetland region of Paraguay, as well as to evaluate the relationship between predator size and prey abundance and size, and to describe possible sex-related differences in diet. By doing so, it contributes to a better understanding of the species' trophic ecology and ecological role in Neotropical wetland ecosystems.

MATERIAL AND METHODS

Fieldwork was conducted in the wetlands of the Ypoá-Ñeembucú Complex, a vast floodplain savanna located in the Ñeembucú Ecoregion of southern Paraguay (Mereles, 2004). This region is characterized by extensive seasonally inundated and waterlogged lowlands, shaped by flat topography and the hydrological influence of the Paraguay and Paraná rivers (Acevedo, 1990). The climate is subtropical, ranging from humid to sub-humid, with a mean annual precipitation of approximately 1500 mm and a mean annual temperature of 22 °C (Fogel, 2000).

We conducted this study at three sampling sites located in the districts of Carapeguá (January, April and November 2018), Quiindy (September 2018) and Tacuaras (February 2020). The Carapeguá site (25.853634° S; 57.41179° W) in the Paraguarí department is characterized by floating plant associations in permanent water. The Quiindy site (25.948583° S; 57.441436° W), also in the Paraguarí department, was located in "tajamares", artificial water reservoirs with aquatic vegetation. The Tacuaras site (26.757305° S; 58.010225° W) in the Ñeembucú department was a flooded grassland.

We captured postmetamorphic individuals during late afternoon and evening hours (17:00-22:00 h) using visual encounter surveys (Crump & Scott, 1994). The temperature ranged from 18°C in September to 31°C in January. Individuals were measured with a digital caliper (precision 0.01 mm), weighed with a digital scale (precision 0.01 g), and stomach contents were extracted using the stomach flushing method (Solé et al., 2005). The regurgitated contents were preserved in 70 % alcohol, and the individuals were released at the capture site in the next hours. Reference specimens from these populations are housed in the Zoological Collection of the FACEN-UNA (Núñez et al., 2022; Tacuaras specimen numbers CZCEN 2366, 2371, 2453, 2458).

In the laboratory, the stomach contents were examined under a stereomicroscope to identify the prey, typically to the order level, following Hogue (1993), Gullan & Cranston (2010), and Heckman (2011). In the case of ants, identification was made at the family level (Hymenoptera: Formicidae) because they are highly abundant in the environment and easier to identify at this

taxonomic level (Solé & Rödder, 2010). Prey length and width were measured with AmScope MU900 software and a built-in camera 3.7 to estimate the volume through the ellipsoid formula (Dunham, 1983):

$$V = \frac{4}{3} \Pi (\frac{1}{2} L) (\frac{1}{2} W)^2$$

Using volumetric data (V%), along with prey frequency (F%) and abundance (N%), we calculated the Relative Importance Index (IRI; Pinkas et al., 1971):

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

To assess the relationship between frog size (SVL) and prey abundance or mean prey volume, we applied Spearman's non-parametric correlation coefficient (rs; Zar, 2010) with $\alpha = 0.05$. Differences between males and females in snout–vent length, body mass, number of prey items, and prey volume were tested using Welch's t-tests and Mann–Whitney U tests, depending on data distribution. Both analyses were performed using PAST 3.02 software (Hammer et al., 2001).

Diet diversity and evenness was quantified with the Shannon (H') and Pielou (J') indexes (Shannon & Weaver, 1949):

$$H' = -\Sigma^{s}_{i=1} (p_i \ln p_i)$$

$$J' = H' / \ln s$$

where pi is the proportion of prey type i in the sample, and s is the total number of prey categories.

Niche breadth was estimated using Levins' index (1968):

$$Nb = (\Sigma P_{ij}^2)^{-1}$$

where *Pij* represents the probability of finding the item *i* in the sample *j*. We standardized the Levins' index as described by Krebs (2014), to facilitate comparisons among species or populations:

$$B_A = Nb - 1 / s-1$$

Therefore, species with more specialized diets show values close to 0, whereas generalist species exhibit values approaching 1.

RESULTS

We found that *P. limellum* is active from September to April and vocalizes both day and night. During the study, we captured 88 post-metamorphic individuals, of which 40 (45.4 %) had identifiable stomach content (22 females and 18 males). The mean snout-vent length (SVL) was 17.21 ± 1.88 mm (range, 12.04 – 19.96 mm), and the mean body mass was 0.56 ± 0.16 g (range, 0.19 – 0.90 g). No significant differences in snout–vent length or body mass were found between males and females (Welch's t-tests, p = 0.31 and p = 0.82, respectively). We identified 84 prey items in the 40 analyzed stomachs, with each stomach containing 1 to 6 prey items (2.1 ± 1.6). The volume of ingested prey ranged from 0.10 to 31.22 mm^3 (4 ± 5.74 mm^3). The SVL of *P. limellum* was positively correlated with mean prey volume (rs = 0.32, p = 0.047); however, SVL showed no significant relationship with the number of prey per stomach (rs = 0.12, p = 0.45) (Fig. 2). No significant differences were found in diet metrics: males and females consumed a similar number of prey items (Mann–Whitney U test, U = 91, p = 0.76) and prey volume (U = 85.5, p = 0.58).

We identified 14 types of prey contributing to the diet of this species, with a mean of 1.45 prey types per stomach (maximum = 5). Coleoptera, Hymenoptera, and Diptera were the most significant prey based on their Relative Importance Index (IRI), numerical dominance, and frequency in the stomachs. In terms of volume, Insect larvae, Orthoptera, and Coleoptera were dominant (Fig. 1). Other prey, such as Araneae, Insect larvae and Hemiptera, were of intermediate importance, while Formicidae, Orthoptera, Acari, Lepidoptera, Hemiptera nymphs, Insect pupae, Odonata and Blattodea were considered accidental preys (Fig. 1, Table 1). We also recorded plant material in two stomachs.

The dietary diversity and evenness of *P. limellum* was H' = 2.3 and J' = 0.87. The trophic niche breadth was Nb = 8.2 (standardized BA = 0.55) (Table 1).

DISCUSSION

The dietary analysis of *P. limellum* populations studied in Paraguay revealed that they feed on 14 types of prey, including two categories from the class Arachnida and 12 from the class Insecta. While Diptera was the primary food source for other species in the *P. limellum* clade (Furtado & Costa-Campos, 2020; Vaz-Silva et al., 2005) and for other populations of *P. limellum* (Duré & Kehr, 2001; Garda et al., 2007; Peltzer & Lajmanovich, 2002), the population examined in this study, relied equally or more on Coleoptera and Hymenoptera, in addition to Diptera (Table 2). Odonata were also significant in the diet of *P. limellum* in northern South America (Garda et al., 2007) and in northeastern Argentina (Falico et al., 2012), though they were of lesser importance in the Paraguayan populations. In the Peruvian Amazon (Cuzco), in a community-level trophic ecology study, Parmalee (1999) found

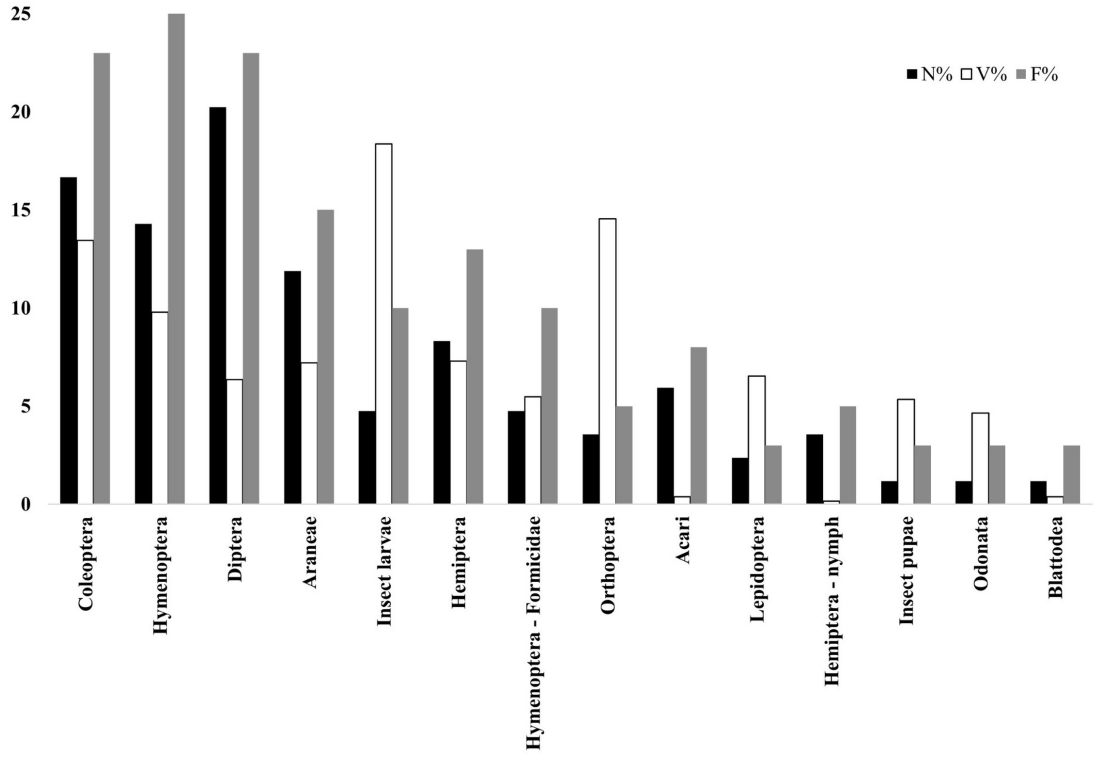

Figura 1. Abundancia, datos volumétricos y frecuencia de presas consumidas por *Pseudis limellum* en humedales de Paraguay. Valores expresados como porcentaje.
Figure 1. Abundance, volumetric data and prey frequency consumed by *Pseudis limellum* frogs in Paraguayan wetlands. Values are expressed as percentages.

Tabla 1. Composición de la dieta de *Pseudis limellum* (n = 40, 22 hembras y 18 machos) en tres sitios en los departamentos Paraguari y Ñeembucú, Paraguay. Abreviaturas: N = abundancia, número de presas; N% = número de presas como porcentaje del total consumido; V = volumen de presas (mm^3); V% = volumen de presas como porcentaje del volumen total; F = frecuencia de ocurrencia de la categoría de presa; F% = frecuencia relativa; IRI = índice de importancia relativa.}

Table 1. Diet composition of *Pseudis limellum* frogs (n = 40, 22 females and 18 males) from three sites in Paraguari and Ñeembucú, Paraguay. Abbreviations are N = abundance, number of preys; N% = number of preys as percentage of total prey consumed; V = prey volume (mm3); V% = volume of prey as percentage of total prey volume; F = frequency of occurrence of prey category; F% = relative frequency; IRI = relative importance index.

Prey	N	N%	V (mm^3)	V%	F	F%	IRI
ARACHNIDA							
Acari	5	5.95	0.99	0.39	3	7.5	0.48
Araneae	10	11.9	18.29	7.2	6	15	2.87
INSECTA							
Blattodea	1	1.19	1	0.39	1	2.5	0.04
Coleoptera	14	16.67	34.15	13.45	9	22.5	6.78
Diptera	17	20.24	16.15	6.36	9	22.5	5.98
Hemiptera	7	8.33	18.57	7.31	5	12.5	1.96
Hemiptera - nymph	3	3.57	0.43	0.17	2	5	0.19

Tabla 1 (Cont.). Composición de la dieta de *Pseudis limellum* (n = 40, 22 hembras y 18 machos) en tres sitios en los departamentos Paraguari y Ñeembucú, Paraguay. Abreviaturas: N = abundancia, número de presas; N% = número de presas como porcentaje del total consumido; V = volumen de presas (mm^3); V% = volumen de presas como porcentaje del volumen total; F = frecuencia de ocurrencia de la categoría de presa; F% = frecuencia relativa; IRI = índice de importancia relativa.}

Table 1 (Cont.). Diet composition of *Pseudis limellum* frogs (n = 40, 22 females and 18 males) from three sites in Paraguari and Ñeembucú, Paraguay. Abbreviations are N = abundance, number of preys; N% = number of preys as percentage of total prey consumed; V = prey volume (mm3); V% = volume of prey as percentage of total prey volume; F = frequency of occurrence of prey category; F% = relative frequency; IRI = relative importance index.

Prey	N	N%	V (mm^3)	V%	F	F%	IRI
INSECTA (Cont.).							
Hymenoptera	12	14.29	24.89	9.8	10	25	6.02
Hymenoptera - Formicidae	4	4.76	13.89	5.47	4	10	1.02
Lepidoptera	2	2.38	46.63	6.53	1	2.5	0.22
Odonata	1	1.19	16.57	4.65	1	2.5	0.15
Orthoptera	3	3.57	11.82	14.55	2	5	0.91
Insect larvae	4	4.76	36.94	18.36	4	10	2.31
Insect pupae	1	1.19	13.58	5.35	1	2.5	0.16
	84		253.91				

that among hylid species, prey preferences varied according to predator size: smaller hylid frogs preferentially consumed beetles, flies, and wasps. Variation in the dominant prey items across *P. limellum* populations indicates that, while dipterans are a key component of the diet, the species may exploit locally abundant trophic resources opportunistically. This pattern is consistent with previous observations of trophic plasticity, whereby the diet composition shifts in response to fluctuations in prey availability (Falico et al., 2012; López et al. 2015). Prey richness values are very similar across *P. limellum* populations (Table 2). The number of prey items found in the stomachs of *P. limellum* was generally low, often consisting of a single prey type. Consequently, there was no relationship between frog size and the number of prey consumed; however, we observed that larger individuals tended to consume larger prey. We found no differences in the abundance or size of prey consumed by male and female *P. limellum* in Paraguayan wetlands, consistent with the patterns reported by Duré and Kehr (2001) for a population of the same species in Corrientes Province, Argentina, as well as those documented for *Pseudis bolivianus* in the Amazon region of Brazil (Furtado & Costa-Campos, 2020). Other studies (Table 2) addressing the diet of species within the clade did not examine sex-related differences.

Based on the trophic niche breadth, *P. limellum* can be classified as a generalist species that employs a sit-and-wait foraging strategy, as is common among hylids (Parmalee, 1999). This interpretation is supported by the low number of prey items found in the stomachs and by the predominance of highly mobile prey, although sedentary or aggregated prey, such as insect larvae and ants, are occasionally consumed. The species also exhibits cryptic coloration, a trait frequently associated with passive foragers and visually oriented predators (Toft, 1981).

Across the *P. limellum* clade, most populations are generalist feeders and, except for the population from Corrientes, adopt a passive foraging mode (Table 2). However, the trophic niche breadth (B_A) varies noticeably among species and populations, indicating that although the clade shares general feeding characteristics, local diets differ—likely reflecting variation in prey availability related to habitat type and seasonality.

Populations with low B_A values, such as *P. boliviana* from the Amazon (B_A = 0.08) and *P. limellum* from Corrientes (B_A = 0.11), consume multiple prey categories but show strong numerical dominance of dipterans. In contrast, populations with higher B_A values, such as *P. laevis* (B_A = 0.62) and *P. limellum* from Paraguay (B_A = 0.55), display broader, more generalist diets. This pattern suggests a more flexible feeding strategy in environments where invertebrate diversity or abundance is higher or more variable. Overall, these findings highlight trophic plasticity as a common trait in the genus, with its expression shaped by geographic and environmental differences, local prey availability, and characteristics intrinsic to each population.

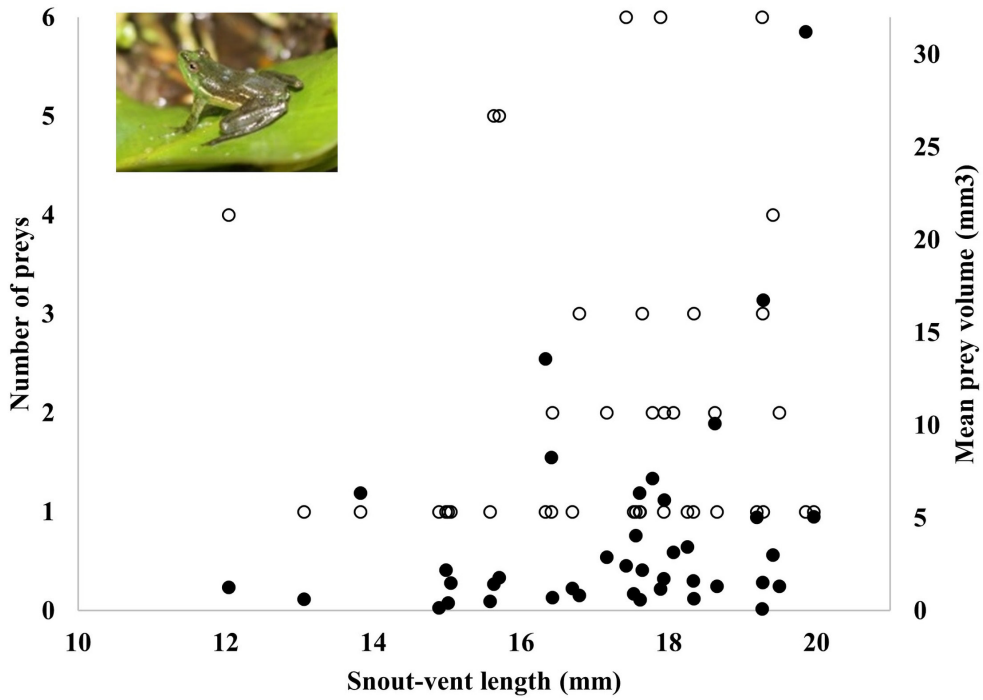

Figura 2. Relación entre la longitud hocico-cloaca (mm) de individuos postmetamórficos de *Pseudis limellum* en Paraguay con el número (círculos abiertos) y el volumen promedio (círculos sólidos) de presas consumidas. Foto: Fátima Ortiz.

Figure 2. Relationship between snout-vent length (mm) of postmetamorphic *Pseudis limellum* in Paraguay to the number (open circles) and mean volume (solid circles) of prey consumed. Photo: Fátima Ortiz.

Tabla 2. Descripción de la dieta e índices de diversidad trófica y amplitud del nicho de especies del clado *Pseudis limellum* con datos de bibliografía. El tamaño de muestra es indicado en paréntesis. Las categorías de las presas están al nivel de Orden. Índices; H' = diversidad de Shannon, J' = equidad de Pielou, Nb = Amplitud del nicho de Levins, BA = Amplitud del nicho de Levins estandarizado. El símbolo (—) indica valores no reportados. El asterisco (*) indica que fue calculado a partir de los valores provistos en el artículo.

Table 2. Diet description and indices for trophic diversity and niche breadth of species in the *Pseudis limellum* clade with literature data. Sample sizes are indicated in parentheses. Prey categories were at the Order level. Terms are H' = Shannon Diversity Index, J' = Pielou's Eveness Index, Nb = Levins Niche Breadth, BA = Levins Standardized Niche Breadth. The symbol (—) indicates unreported values. The asterisk (*) denotes values calculated from the information provided in the respective publications.

Species	Prey categories	Most important preys	Type of diet and foraging mode	H'	J'	Nb	BA	Source
Pseudis boliviana (n = 60) Amazonas, Brazil	18	Diptera	generalist, passive forager	—	—	2.42 - 2.48	0.08*	Furtado & Costa-Campos (2020)
Pseudis laevis (n = 53) Pará, Brazil	9	Diptera	generalist, passive forager	—	—	5.97	0.62*	Vaz-Silva et al. (2005)
Pseudis limellum (n = 46) Corrientes, Argentina	13	Diptera	generalist, active forager	0.94	—	2.31	0.11*	Duré & Kehr (2001)

Tabla 2 (Cont.). Descripción de la dieta e índices de diversidad trófica y amplitud del nicho de especies del clado *Pseudis limellum* con datos de bibliografía. El tamaño de muestra es indicado en paréntesis. Las categorías de las presas están al nivel de Orden. Índices; H' = diversidad de Shannon, J' = equidad de Shannon-Wiener, Nb = Amplitud del nicho de Levins, BA = Amplitud del nicho de Levins estandarizado. El símbolo (—) indica valores no reportados. El asterisco (*) indica que fue calculado a partir de los valores provistos en el artículo.

Table 2 (Cont.). Diet description and indices for trophic diversity and niche breadth of species in the *Pseudis limellum* clade with literature data. Sample sizes are indicated in parentheses. Prey categories were at the Order level. Terms are H' = Shannon Diversity Index, J' = Evenness measure of the Shannon-Wiener, Nb = Levins Niche Breadth, BA = Levins Standardized Niche Breadth. The symbol (—) indicates unreported values. The asterisk (*) denotes values calculated from the information provided in the respective publications.

Species	Prey categories	Most important preys	Type of diet and foraging mode	H'	J'	Nb	BA	Source
Pseudis limellum (n = 31) Entre Ríos, Argentina	8	Diptera	generalist, passive forager	0.14	—	3	0.29*	Peltzer & Lajmanovich (2002)
Pseudis limellum (n = 91) Amazonas and Pará, Brazil	12	Diptera	generalist	—	—	—	—	Garda et al. (2007)
Pseudis limellum (n = 15) Esteros del Iberá, Corrientes, Argentina	12	Diptera	generalist, passive forager	—	—	—	0.29	Macale et al. (2008)
Pseudis limellum (n = 11) San Javier, Santa Fé, Argentina	11	Odonata	generalist	—	—	—	—	Falico et al. (2012)
Pseudis limellum (n = 40) Paraguarí and Ñeembucú, Paraguay	14	Coleoptera, Hymenoptera and Diptera	generalist, passive forager	2.3	0.87	8.2	0.55	This study

CONCLUSIONS

Based on the data presented in this study, as well as dietary information from other conspecific and congeneric populations, *P. limellum* consumes a wide range of invertebrate groups—primarily insects—by opportunistically preying on those that are seasonally abundant. These patterns confirm its status as a generalist predator with a sit-and-wait foraging strategy.

Although Diptera has consistently been reported as the dominant prey in other populations and closely related species, Paraguayan populations exhibited a more balanced consumption pattern, including notable proportions of Coleoptera and Hymenoptera. The low number of prey items per individual, the absence of correlation between body size and prey number, and the occasional presence of sedentary prey such as insect larvae and ants further support a predominantly passive foraging behavior. Understanding the trophic interactions of amphibians such as *P. limellum* is essential for clarifying their ecological role and supporting biodiversity conservation. As key components of wetland ecosystems, amphibians contribute to nutrient cycling and the regulation of invertebrate populations. Thus, trophic ecology studies provide valuable insights for assessing ecosystem health and for the conservation of the essential services that wetlands offer.

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