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# Do human-induced habitat changes affect the feeding behaviour of frogs? The case of *Pseudis minuta* Günther, 1858

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**Abstract.** The change of natural environments into agricultural areas is generally accompanied by the control of invertebrate populations, which can alter prey availability for amphibians. The way frogs deal with such changes will determine their survival or extinction from these agricultural landscapes. We compared changes in the diet of the semiaquatic frog *Pseudis minuta* between populations from natural and agricultural environments in the Pampa biome, southern Brazil. We evaluated 34 individuals from agricultural environments and 42 from natural environments, located 1 km from each other, and we also analysed prey availability. In agricultural environments, the diet was composed mostly of beetles, one of the less frequently consumed prey groups in natural environments. This suggests that individuals of *P. minuta* are forced into a narrower trophic niche in agricultural areas, with the availability of food types likely a consequence of the anthropic changes.

**Keywords.** Agroecosystems, diet, human impacts, environmental conversion

## Introduction

Amphibians prey on a great diversity of invertebrates, which makes them important control agents in agricultural areas (Duellman and Trueb, 1994; Attademo et al., 2005). Feeding habits of frogs, and consequently their diet, can be influenced by competition, intraspecific morphological differences, seasonal changes in the environment, and prey availability (Maragno and Souza, 2011; Oliveira and Haddad, 2015; Almeida-Santos et al., 2017; Luría-Manzano and Ramírez-Bautista, 2019; Ceron et al., 2022). Habitat also plays a role in amphibian diet, as frogs tend to feed according to prey availability in the environment (Maneyro and Da Rosa, 2004;

López et al., 2009). Thus, because feeding habits of any organisms can be interpreted differently depending on prey availability (Moroti et al., 2021), information related to prey availability is an important resource for describing and discussing dietary specialization (Isacch and Barg, 2002; López et al., 2009).

In crop agriculture the use of pesticides and herbicides is a common practice that can alter prey availability in the environment and affect anuran communities (Bridges and Semlitsch, 2000; Semlitsch et al., 2000). The conversion of natural habitats into crop monoculture has been shown to reduce species diversity by modifying the composition of the fauna and the relationships between species in communities (Knutson et al., 1999; Altieri et al., 2003; Cushman, 2006). Furthermore, microclimatic conditions and resources available in a modified environment differ from those present in the original environment, which can also lead to a different composition of invertebrates (Gibbs and Stanton, 2001; Dauber and Wolters, 2004).

Trophic relationships are considered one of the main aspects of the life for anurans (Duellman and Trueb, 1994; Vitt and Caldwell, 2009), so studies on feeding ecology can provide relevant information to the understanding of ecosystem dynamics. Most studies on amphibian diets were developed in natural environments within legally protected areas (Sugai et al., 2012; Farina et al., 2018; Moser et al., 2019; Machado et al., 2019; Mendonça et al., 2020), and in fragments of natural landscapes (Silva and Rossa-Feres, 2010; Moser et al.,

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2017; Oliveira et al., 2017), and studies on agricultural lands are still needed to provide comparisons.

*Pseudis minuta*, the Lesser Swimming Frog, is an abundant species in both natural and agricultural lands within the Pampa biome of southern Brazil. It is semiaquatic, living in permanent or temporary ponds with floating vegetation throughout its life cycle, and has a prolonged breeding season (Melchior et al., 2004; Huckembeck et al., 2012). This species is known to feed mainly on hemipterans, spiders, and hymenopterans (Huckembeck et al., 2014). The objective of this study was to compare the diet of *P. minuta* residing in a natural, well-preserved habitat with that in agriculturally modified areas.

## Materials and Methods

**Study area.** We sampled habitats in Fazenda São Miguel, a private property with a total area of 2458.8 hectares located in Tapes Municipality near Porto Alegre, the capital of Rio Grande do Sul State, Brazil. The predominant habitat in this area are native grasslands with a large remnant of the natural Palm Grove Ecosystem (*Butiazal*), which is defined by the palm *Butia odorata*. An adjacent area was converted to crop land in the past 30 years, where rice and soybean crops are planted annually. Both habitats have similar size – about 750 ha of natural palm grove vs. 800 ha of crops. This region is located at sea level and has an average annual temperature of 18.8°C with annual rainfall of around 1213 mm (Maluf, 2000).

**Data collection.** We sampled at four breeding sites, two in palm grove and two in agriculturally modified areas. The distance between the sites was at least 1 km (Fig. 1). For an assessment of the frogs' diet, we located and captured *P. minuta* individuals associated with breeding sites for 15 nights in September–October 2019 (Crump and Scott, 1994). To obtain stomach contents, we performed stomach flushing *in situ* (Solé et al., 2005) and immediately released the frogs at the same point of collection. Stomach contents were preserved in 70% ethanol and screened in the laboratory under a stereomicroscope. Prey categories were identified to the Order level of taxonomy, with the help of taxonomic guides and keys (Ribeiro-Costa and Rocha, 2002). After identifying and quantifying the prey, the area (mm<sup>2</sup>) occupied by each item was calculated using graph paper (Moser et al., 2020). Each prey category was spread evenly over a Petri dish to cover its entire surface and maintain a regular height of 1 mm (Hellowell and Abel, 1971).

**Prey availability.** We installed pitfall traps (500-ml volume cups; Cogalniceanu, 1997) across the areas where the search for frogs was conducted to allow a general characterization of the habitat. We randomly installed four traps 1 m apart at each sampling point. The traps were filled with 100 ml 70% ethanol to euthanize invertebrates and remained open for 24 h. We maintained the collected prey by group (palm grove and agriculture) in containers with 70% ethanol for later identification in the laboratory.

**Data analysis.** For each prey category, we calculated the number, volume, and frequency of occurrence in absolute and percentage terms. To calculate the volume (V), the area occupied by the item was multiplied by 1 mm (e.g., Hyslop, 1980; Moser et al., 2020). To calculate the importance of each prey category, we used the Index of Relative Importance (IRI; Pinkas et al., 1971) as

$$\text{IRI} = (\text{N}\% + \text{V}\%) \cdot \text{FO}\%$$

where N% is the relative abundance of each prey category in the diet, V% is the relative volumetric contribution of the prey category to the diet, and FO% is its relative frequency of occurrence of the prey category in the diet (Pinkas et al., 1971; Krebs, 1999). The higher the IRI value, the greater the importance of a given prey category in the diet.

To facilitate diet comparisons between individuals in the two groups, we calculated the Levins Trophic Niche Amplitude Index (B<sub>sta</sub>), which ranges from 0–1 (Krebs, 1999), using the following equation:

$$\text{B}_{\text{sta}} = (\text{B}-1) / (\text{n}-1)$$

where n represents the number of food categories and

$$\text{B} = 1 / \sum p_i^2$$

where *p* represents the proportion of individuals using a certain category *i* of the analyzed resource. Values closer to zero are considered specialist diets, while those closer to one are considered generalist.

To analyse the food overlap and/or the degree of similarity between the diets of the individuals in the groups, we used the Pianka Trophic Niche Overlap Index ( $O_{jk}$ ) (Pianka, 1973). The index ranges from 0–1, with values closer to 0 indicating low overlap and

$$O_{jk} = \sum_{n=1}^0 p_{ij} \times p_{ik} / \sqrt{\sum_{n=1}^0 p_{ij}^2 \times \sum_{n=1}^0 p_{ik}^2}$$

those closer to 1 higher overlap, which may indicate competition or resource sharing. We used the formula: where  $O_{jk}$  is the niche overlap index between individuals *j* and *k*,  $p_{ij}$  is equivalent to the proportion

of resource type  $i$  in relation to the total resources used by individual  $j$ ,  $p_{ik}$  is the proportion of resources in relation to the total resources used by individual  $k$ ; and  $n$  is the total number of resource categories used by individuals  $j$  and  $k$ . For this analysis, we used the program EcoSim v1.2d.

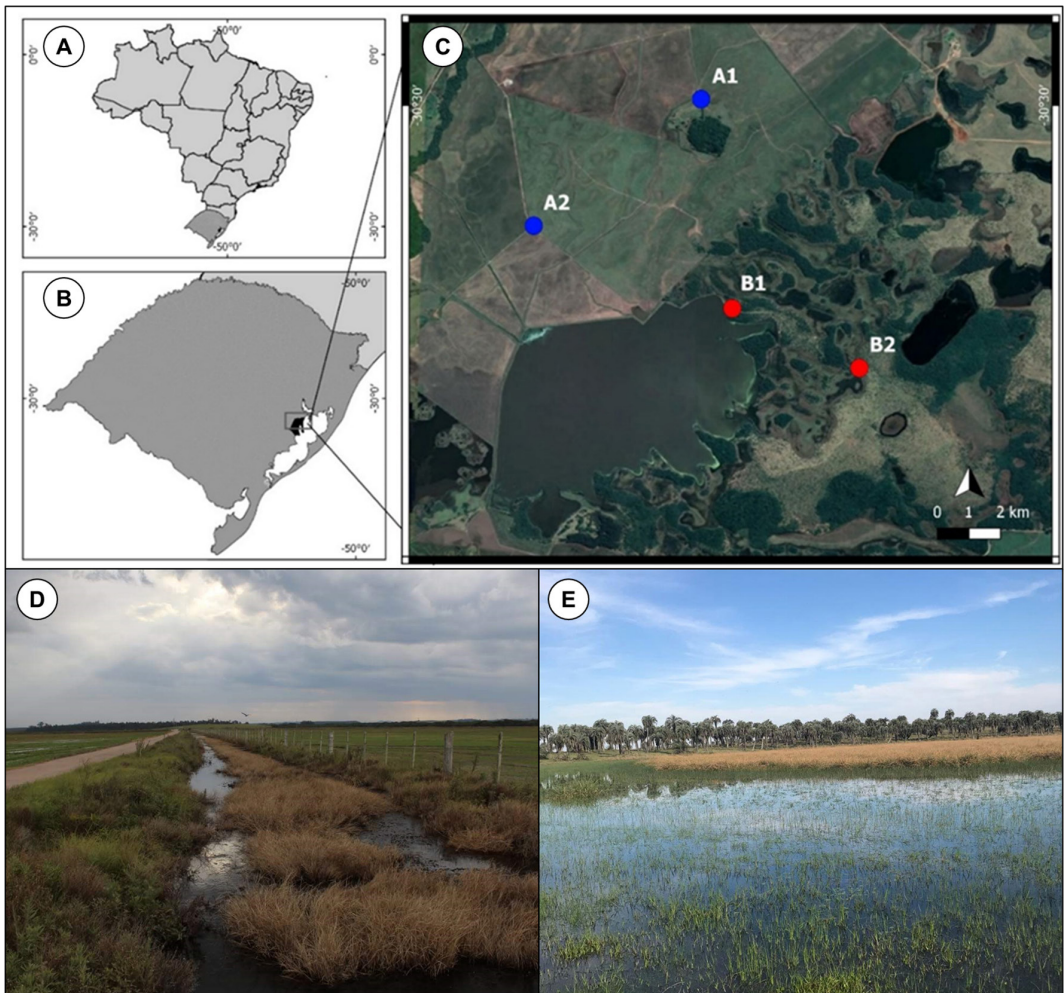
To assess whether prey was actively selected, we calculated the level of selectivity using the Jacobs Electivity Index ( $D$ ). This index evaluates the presence of each prey category found in the diet in relation to its availability in the environment (Jacobs, 1974) through the formula:

$$D = R_k - P_k / (R_k + P_k) - (2R_k 5. P_k)$$

In this formula,  $k$  represents the food category considered and  $R$  and  $P$  represent the proportion of this category in the diet and the environment, respectively. The value of  $D$  varies from -1 to +1, where values closer to +1 indicate a preference for a given prey category (Hayward et al., 2011).

## Results

We sampled 76 individuals of *Pseudis minuta*, with 34 frogs from the Agriculture Group (AG) and 42 from the Palm Grove Group (PG). Of these, 27 had an empty stomach (17 from AG, ten from PG). In AG frogs,



**Figure 1.** Sampling locality of *Pseudis minuta* in agricultural areas (A1, A2) and a natural area (Palm Grove; B1, B2) in Tapes Municipality, Rio Grande do Sul State, Brazil. (A) Map of Brazil showing the position of Rio Grande do Sul State. (B) Map of Rio Grande do Sul showing the location of Tapes Municipality. (C) Satellite map of the specific sampling areas. (D) Photo of one of the sampled agricultural localities (A2). (E) Photo of one of the sampled Palm Grove localities (B2). Map prepared by Gabriela Morais Olmedo. Photos by Renata K. Farina

we identified 62 prey items in ten prey categories. The most important categories were members of the Coleoptera (IRI = 71.3%) and Araneae (IRI = 12.7%) (Table 1). For PG frogs, we recorded 73 prey items in eight prey categories, where members of Diptera (IRI = 38.6%), Hemiptera (IRI = 19.5%), Hymenoptera (IRI = 17.6%), and Araneae (IRI = 15.4%) were the categories with greatest relative importance (Table 1). Niche breadth was 0.57 for PG individuals and 0.31 for AG individuals (Table 1, Fig. 2). Niche overlap between individuals from the two areas was 51%.

In the pitfall traps, we collected 197 potential prey items in ten prey categories in agricultural areas and 354 in eight prey categories in the undisturbed areas (Table 2). Members of Archaeognatha, Isopoda, and Thysanoptera were exclusive to agricultural areas, while Acari were only found in undisturbed areas. Even though our prey availability analysis was skewed towards terrestrial invertebrates, our result regarding coleopterans stands out (Table 2): we found no selection for this prey category in undisturbed areas ( $D = 0$ ) but in agriculture areas this prey item appeared to be favoured ( $D = 0.71$ ).

## Discussion

Our results showed differences in the diet pattern of *Pseudis minuta* between natural and agricultural areas. While dipterans were the most important prey (IRI = 38.6%) in PG frogs, these insects were not as relevant in AG individuals, even though they were available in the environment. Huckembeck et al. (2014) reported that *P. minuta* in natural habitat did not consume dipterans frequently, but it has been documented that these insects are important in the diets of *P. bolbodactyla* Lutz, 1925, *P. cardosoi* Kwet, 2000, and *P. paradoxa* (Linnaeus, 1758) (Teixeira et al., 2004; Miranda et al., 2006; Downie et al., 2010; Rocha, 2016). We found that hemipterans (IRI = 19.5%), hymenopterans (IRI = 17.6%), and spiders (IRI = 15.4%) were important in the diet of PG frogs, confirming the results of Huckembeck et al. (2014). In general, the most important prey categories for *P. minuta* in our study were hemipterans, coleopterans, dipterans, and spiders. While the importance of these prey types for the species had already been reported by Huckembeck et al. (2014), their findings did not include the order Diptera. *Pseudis minuta* uses a sit-and-wait strategy for foraging, and individuals are found floating on the surface of the water body among aquatic plants,

**Table 1.** Prey categories found in the stomach contents of *Pseudis minuta* in the Agriculture and Palm Grove groups, Tapes Municipality, Rio Grande do Sul State, Brazil. Abbreviations include N% (percentage of the number of prey consumed), V% (percentage of the volume of prey consumed), FO% (percentage of the frequency of occurrence of each prey category), IRI% (percentage of the Index of Relative Importance) and Bsta (Levins Trophic Niche Amplitude Index). Values for important prey categories are printed in bold.

Prey Category	Agriculture				Palm Grove			
	N%	V%	FO%	IRI%	N%	V%	FO%	IRI%
Araneae	12.9	16.04	25	<b>12.17</b>	10.96	24.62	20	<b>15.4</b>
Blattodea	1.61	5.3	4.17	0.48	0	0	0	0
Coleoptera	46.77	45.71	45.83	<b>71.31</b>	8.22	10.42	20	8.06
Diptera	12.9	1.84	16.67	4.13	24.7	25.9	19	<b>38.6</b>
Diptera larvae	1.61	0.28	4.17	0.13	0	0	0	0
Hymenoptera	6.45	1.31	16.67	2.17	28.77	5.21	24	<b>17.64</b>
Gastropoda	0	0	0	0	1.37	0.04	4	0.12
Hemiptera	6.45	16.92	16.67	6.55	17.81	19.67	24	<b>19.46</b>
Odonata	4.84	5.19	8.33	1.41	1.37	8.33	4	0.84
Odonata larvae	1.61	2.82	4.17	0.31	0	0	0	0
Orthoptera	4.84	4.59	8.33	1.32	6.85	5.42	12	3.18
Bsta	0.31				0.57			



**Table 2.** Jacobs Electivity Index for *Pseudis minuta* prey in the Agriculture and Palm Grove groups, Tapes Municipality, Rio Grande do Sul State, Brazil. Abbreviations include N% (percentage of the number of prey consumed), PA% (percentage of the prey availability), and D (Jacobs Electivity Index).

Prey Categories	Agriculture			Palm Grove		
	N%	PA%	D	N%	PA%	D
Acari	0	0	-	0	0.02	-1
Araneae	0.13	0.03	0.66	0.11	0.06	0.32
Archaeognatha	0	0.01	-1.00	0	0	-
Blattodea	0.02	0	1.00	0	0	-
Coleoptera	0.47	0.13	0.71	0.08	0.08	0
Collembola	0	0.2	-1.00	0	0.3	-1
Diptera	0.13	0.43	-0.67	0.25	0.35	-0.24
Diptera larvae	0.02	0	1.00	0	0	-
Gastropoda	0	0	-	0.01	0	1
Hemiptera	0.06	0.01	0.73	0.18	0.01	0.91
Hymenoptera	0.06	0.17	-0.52	0.29	0.15	0.40
Isopoda	0	0.02	-1.00	0	0	-
Odonata	0.05	0	1.00	0.01	0	1
Odonata larvae	0.02	0	1.00	0	0	-
Orthoptera	0.05	0.01	0.68	0.07	0.04	0.29
Thysanoptera	0	0.01	-1.00	0	0	-

an environment where they can find many terrestrial invertebrates (Huckembeck et al., 2012, 2014). Thus, although its diet consists mainly of terrestrial prey, this species seems to feed in the water, where they can also find various terrestrial prey, in addition to flying invertebrates. This pattern was also reported for this genus by Duré and Kehr (2001).

AG individuals showed some selectivity for coleopterans ( $D=0.71$ ), which were the most important category in their diet. This result should be viewed with caution because our sampling of prey availability was conducted for terrestrial invertebrates only, and this may not reflect the real invertebrate diversity in the sampled environments. However, we believe that the comparison of these results between the sampled areas is valid, since we standardized our sampling. Other studies in agroecosystems have shown coleopterans to be the most frequent prey category in the diet of some frog species, such as in coffee plantations in Colombia (Hoyos-Hoyos et al., 2012) and in rice plantations in the Pantanal region of Mato Grosso do Sul, where they were documented to be the most important prey category for *Leptodactylus macrosternum* Miranda-Ribeiro, 1926, *L. podicipinus* (Cope, 1863), and *Rhinella granulosa* (Spix, 1824) (Piatti, 2009). This pattern may be related to the lower diversity of prey generally available in agroecosystems in relation to natural environments (Altieri et al., 2003). As in Palm

Grove, hemipterans (IRI = 19.5%) and spiders (IRI = 15.4%) were also very important prey items for AG individuals. In response to anthropic changes in drastically homogenized environments, the scarcity of resources, together with physical and chemical changes, can lead to a decrease in diversity in a community (Piatti, 2009). We hypothesize that feeding on coleopterans and avoiding dipterans in the agriculture environment may be advantageous to acquiring greater biomass and, consequently, energy gain (MacArthur and Pianka, 1966). Although beetles have elytra that can make digestion difficult, their generally large size and slow movements can lead amphibians to feed on this invertebrate in environments with low variety and abundance of prey (Hirai and Matsui, 2001).

Three prey categories were consumed by AG frogs but not by PG frogs, Blattodeans, and Odonata larvae. Gastropoda (snails) was the only prey category consumed by PG individuals that was not consumed by AG frogs. Niche breadth was greater in the PG group ( $Bsta = 0.57$ ), which apparently is showing a more generalist feeding behaviour by consuming three prey categories in similar proportion (spiders, hemipterans, and dipterans). AG individuals had a narrower niche by almost half ( $Bsta = 0.31$ ), likely due to the high consumption of beetles, and therefore appear to be more specialized. Similarly, Falico et al. (2012) proposed that *P. paradoxa* is a generalist predator

that tends to feed opportunistically according to the abundance of temporary prey. Miranda et al. (2006) suggested that the feeding habits of *P. cardosoi* varied seasonally according to the availability of prey in the environment. Considering that *P. minuta* is a generalist species, the decrease in its trophic niche observed in agricultural areas may indicate that this population is suffering pressure from environmental conditions that impact this important aspect of its natural history.

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